



Spatial memory in rufous hummingbirds: memory for rewarded and non-rewarded sites

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Abstract. The foraging ecology of rufous hummingbirds, *Selasphorus rufus*, suggests that this species may have good spatial memory capabilities. Six adult male hummingbirds were tested in a one-trial learning experiment in the field. Subjects searched for a single sucrose reward among four identical artificial flowers (Search Phase). Following a retention interval, subjects returned to locate the reward again (Return Phase). Performance during the Search Phase was no better than expected by chance, indicating that the hummingbirds could not detect the sucrose through intrinsic cues (e.g. odour). During the Return Phase, subjects performed significantly better than chance and could have done so only by remembering the spatial location of rewarded flowers. In addition, subjects avoided revisiting non-rewarded flowers, suggesting memory for these locations as well. Finally, information about rewarded and non-rewarded locations was combined to direct sampling behaviour towards flowers the birds had not yet encountered.

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Studies of spatial memory have focused mostly on rats, often requiring a subject to remember the locations of food rewards as in the radial-arm maze (Olton & Samuelson 1976; Brown & Cook 1986). Pigeons, another traditional laboratory animal, initially performed poorly in the radial-arm maze (Bond et al. 1981), but performance was greatly enhanced when the maze was modified into an open-field design (Spetch & Edwards 1986). This new design was likely to be more compatible with the natural foraging behaviour of pigeons than were the traditional tunnel mazes designed for rats.

Additional work on spatial memory has focused on species that are not traditional laboratory animals, but that may possess special memory abilities because of their foraging ecology (Kamil & Balda 1990; Healy & Krebs 1992a). For example, many parids and corvids hoard and recover thousands of food items per year (Gibb 1960). Spatial memory abilities have been tested in these taxa using analogues of the radial-arm maze (Hilton & Krebs 1990; Olson et al. 1993) and other paradigms in which the subjects had to

recall the locations of rewards in laboratory settings (Krebs et al. 1990; Shettleworth et al. 1990; Brodbeck et al. 1992; Healy & Krebs 1992a, b).

Hummingbirds too, might be expected to demonstrate adaptive specializations in their spatial abilities because of their foraging ecology. They visit hundreds of flowers each day and would benefit by avoiding revisits to flowers they have already emptied. Hummingbirds should also remember the locations of high nectar reward and re-visit them after replenishment has occurred. The visual similarity of flowers of the same species suggests that memory for spatial location, rather than visual cues, will be employed. Indeed, hummingbirds and other nectar-feeding species forage non-randomly among patches of flowers, suggesting some remembrance of both spatial and temporal information (Gill & Wolf 1977; Kamil 1978). Simple experiments have clearly demonstrated memory for patches of flowers (Gass & Sutherland 1985; Sutherland & Gass 1995) and for position within a patch (Miller et al. 1985). Finally, there is good evidence that hummingbirds remember specific point locations (Cole et al. 1982; Healy & Hurly 1995) and that they learn both spatial locations and spatial associations (Brown & Gass 1993).

Here I present the results of a field study that examines the ability of rufous hummingbirds,

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Selasphorus rufus, to recall the location of a reward after a single learning experience; an example of one-trial associative learning (Brodbeck et al. 1992). That is, the subjects searched for a single reward amongst four artificial flowers and then fed from, but did not deplete, that flower. Upon return, the subjects might use spatial memory to relocate the reward and to avoid non-rewarded flowers.

Despite the fact that most individual flowers contain only a few microlitres of nectar (Gass & Roberts 1993), hummingbirds should remember these point locations and return to them when sufficient time has elapsed for nectar replenishment to have occurred. Additionally, foraging bouts may be terminated within a high-quality inflorescence or some other localized patch of flowers such that the birds should return to that patch but avoid specific flowers they have emptied recently. In general, the defence of breeding or feeding territories should select for the ability to track the spatial and temporal distribution of nectar within and between days.

METHODS

Study Site and Study Animals

We conducted the study during June and July 1993 in a valley of the Eastern Range of the Rocky Mountains (elevation 1400 m) 20 km southwest of Beaver Mines, Alberta, Canada (49°29'N, 114°25'W). Subjects were six male rufous hummingbirds that had defended breeding territories around feeders since early May. To minimize stress, hummingbirds were not captured but were uniquely marked by spraying the upper breast with a spot of coloured ink while they visited a feeder.

Training

We performed experiments within a subject's territory between 0630 and 2100 hours Mountain Standard Time. We temporarily removed the feeder containing 16% (by weight) sucrose solution and replaced it with an artificial flower. The flower consisted of a cork (3 cm high, tapered from 2.5 to 3.5 cm diameter) glued to a dowel (80 cm) which was set in the ground. A syringe tip cover containing 600 µl of 20% sucrose projected vertically from the top of the cork.

Once the bird fed from the flower, the nectar well was refilled to capacity and moved a few metres to a different location and the bird was again permitted to feed. After six such training trials within 60–100 min a subject tended to locate the flower quickly, and at this stage we began experimental trials.

Experiments

A grid measuring 3 × 3 m with nine sites was established with no particular orientation to compass direction at a new location within the territory. A random number generator was used to select four flower sites from the nine possible sites within this grid, and all grid markers were removed. Visually, the four flowers seemed identical. One site was randomly designated 'Reward' and that flower was filled with 600 µl of 20% sucrose. The other flowers were filled with water, and one was randomly designated 'Switch'. For the initial Search Phase, the bird searched the flowers until it found the reward and drank a mean of 229 µl of solution (unpublished data). The observer stood within the grid to keep the subject away for a minimum retention interval of 5 min, but the subject determined the maximum interval. To ensure that the subject was returning to the actual spatial location of the reward rather than remembering some subtle visual cues of the flower, we exchanged the Reward flower with the Switch flower. We adjusted the contents such that the flower now at the Reward site again contained 600 µl of sucrose, whereas the flower at the Switch site contained water. For the Return Phase, the bird again visited the flowers and probed them with its bill until it discovered and fed from the Reward flower. We removed the flowers for a minimum inter-trial interval of 10 min, then the next trial occurred at a new location at least 5 m distant. Each bird completed 16 trials at unique locations over the course of 2 or 3 days. Each subject experienced identical flowers of only one colour, but colours (red, yellow, orange) differed between subjects.

Analysis

We assessed performance in both the Search and Return Phases as the number of individual flowers visited to locate the Reward site (no revisits within a phase ever occurred). If subjects

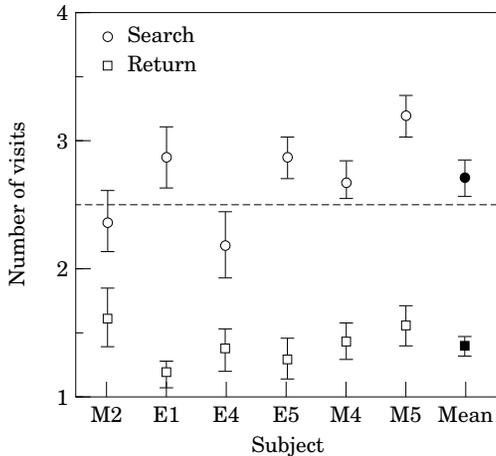


Figure 1. Performance of individual rufous hummingbirds searching for a single reward among four flowers. Each open symbol represents the mean (\pm SE) number of flowers visited across 16 trials for either the initial Search Phase or the subsequent Return Phase. The closed symbols represent the mean performance across the six subjects. The dashed line refers to chance level of performance; perfect performance is one visit.

searched for the reward with no memory or cue to guide them, one, two, three or four visits might be needed to discover the Reward. Thus, under both random and systematic searching, the expected number of visits due to chance is 2.5 (i.e. arithmetic mean of 1, 2, 3 and 4). Deviations from this expected value were assessed using one-sample *t*-tests. The tests were two-tailed because there are two alternative hypotheses. The subjects may remember spatial locations and hence find the Reward with fewer than 2.5 visits; alternatively, they may remember visual cues and thus be drawn to the Switch location. On average, birds searching with visual cues would make more than 2.5 visits.

RESULTS

Accuracy of Performance

The consistently small number of visits during the Return Phase of a trial indicates that the hummingbirds learned something about the location of the reward during the Search Phase and used this information to relocate the Reward (Fig. 1). Performance averaged across all six birds was

significantly better than chance ($t=16.10$, $df=5$, $P<0.0001$), as were the individual performances on the 16 trials for each subject ($t_s>3.90$, $df=15$, $P_s<0.002$). It is likely that the subjects remembered the actual spatial location of the Reward because all other alternative interpretations can be eliminated.

First, no predictable spatial pattern was likely to exist in the location of the Reward, because each trial grid was established in a different location and the specific Reward site was randomized within this grid. Second, the birds did not use visual or olfactory cues intrinsic to the sucrose solution to lead them to the Reward flower. Such cues would allow the subjects to locate the Reward readily during the Search Phase. Searching relied upon probing flowers directly, and average performance across the six subjects did not differ significantly from chance ($t=1.47$, $df=5$, $P=0.2027$; Fig. 1), nor did any individuals perform better than chance. Two of the six individuals (E5 and M5) performed significantly worse than chance, however ($t_s>2.40$, $df=15$, $P_s<0.03$). This poor performance may be the result of birds attempting to use a subtle visual cue or a rule across trials when they had no spatial information about the flowers in the new trial location, but I have no data with which to test this possibility.

Third, there is no evidence that the birds attempted to use subtle visual cues to relocate the Reward flower. Such a tactic would lead them to the Switch location during the Return Phase. The probability of returning by chance to the Switch location on a first Return visit is 0.25. Over 16 trials, an average of four first Return visits to Switch might be expected if a bird searched randomly, and significantly more if it was drawn to the features of the former Reward flower now in the Switch location. The actual mean (\pm SE) number of first Return visits to the Switch location was 2.17 ± 0.48 significantly fewer than expected by chance ($t=3.841$, $df=5$, $P=0.0121$).

Errors

Although performance during the Return Phase far exceeded that expected by chance, it was not perfect (Fig. 1). To determine whether imperfect performance was due exclusively to failure of memory, I examined the 33 instances in which the first visit in the Return Phase was not to the Reward site. Given this first error, and excluding

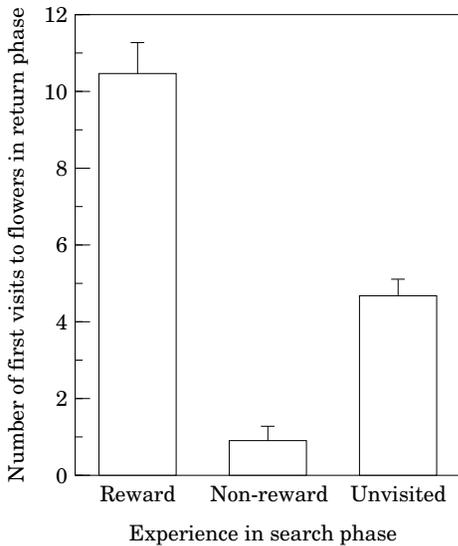


Figure 2. Mean (\pm SE) number of first visits by six hummingbirds to flowers during the Return Phase. Each subject completed 16 trials and the location of the first Return visit within each trial was classified according to how the subject experienced that flower during the previous Search Phase. During the Search Phase, the flower may have contained sucrose (Reward) or water (Non-reward), or it may not have been visited at all (Unencountered).

revisits (which never occurred), the subjects are expected by chance to make an average of two (i.e. 1, 2 or 3) visits to locate the Reward out of the remaining three sites (see Analysis in Methods). Although data are too few to analyse on an individual basis, the average number of visits for each of the six subjects was less than two (range 1–1.5). Mean performance across the six subjects was significantly better than chance ($\bar{X} \pm$ SE probes = 1.18 ± 0.08 ; $t = 10.74$, $df = 5$, $P < 0.0001$). Thus, despite an initial error, the subjects seemed to retain at least some memory for the Reward site.

To examine these 'errors' further, it is useful to adopt an alternative measure of performance, namely 'site of first visit' during the Return Phase. This first site can be classified according to how a subject experienced it during the Search Phase. The flower may have contained sucrose (Reward), it may have contained water (Non-reward), or the subject may not have visited it during the Search Phase (Unencountered) and thus would not know what it contained. During the Return Phase, birds

distinctly favoured Reward sites and avoided Non-reward sites (repeated-measures ANOVA: $F_{2,10} = 51.386$, $P < 0.0001$; Fig. 2; all three categories differed from each other according to contrasts, $F_{s,1,10} > 15.0$, $P_s < 0.003$). Three implications can be drawn from this analysis.

First, within a trial, the subjects remembered the location of the Reward. Out of 16 trials, only four visits to Reward are expected if the subjects selected flowers at random. Instead, a mean of 10.5 first visits were made to the Reward flower in the Return Phase (Fig. 2). Second, subjects also remembered the locations of Non-reward flowers and usually avoided these locations (Fig. 2). Third, conventional analysis usually describes visits to sites other than Reward as 'errors'. The present analysis of the 33 first visits to sites other than Reward suggests that the only true errors may be the five visits to Non-reward sites. Specifically, the 28 visits to sites not encountered during the Search Phase may be a form of sampling behaviour that is directed by working memory for the Reward and Non-reward sites.

More compelling evidence that memory directs sampling behaviour is found by examining these 'errors' in detail. During the Search Phase, a bird would have visited an average of 2.5 flowers to find the Reward. Thus, in the Return Phase, there would be an average of 1.5 Unencountered flowers and an average of 1.5 Non-reward (encountered) flowers. Consequently, if no memory were retained to the Return Phase, a bird would have an equal probability of visiting Unencountered and Non-reward flowers. There was a significant bias towards visiting Unencountered flowers ($\chi^2 = 16.03$, $df = 1$, $P < 0.0001$; Table I). The actual availability of Unencountered and Non-reward flowers during the Return Phase was not 1.5 each, but 1.313 and 1.687, respectively. Using these figures to generate expected values, the observed visits were again biased towards Unencountered flowers ($\chi^2 = 22.65$, $df = 1$, $P \ll 0.001$; Table I). Thus, first-visit 'errors' appear to be a form of sampling in which the subjects recalled both Reward and Non-reward sites, but chose first to visit sites about which they had no current information.

Additional evidence that these first visits are directed sampling behaviour comes from an analysis of distance to the true Reward. If these visits were errors, then they might be biased by memory for the Reward site. The 33 visits were

Table I. Distribution of first visits to the array during the Return Phase that were not to the Reward Flower

	Search experience		Row total
	Unencountered	Encountered	
Distance to reward			
Nearest to reward	13	3	16
Not nearest to reward	15	2	17
Column total	28	5	33

These 'errors' are examined for spatial bias (distance to the Reward) and for experience bias (flower encountered or unencountered during previous Search Phase).

equally distributed, however, between flowers that were the closest to the Reward site and flowers that were more distant ($\chi^2=0.03$, $df=1$, $P>0.8$; Table I). There was no interaction between distance and experience ($\chi^2=0.31$, $df=1$, $P>0.5$; Table I).

Temporal Effects

There was no evidence for altered performance with experience. Examination of the 16 trials as four blocks of four trials indicated that, although performance within each block was significantly better than chance ($t_s>5.4$, $df=5$, $P_s<0.003$), there was no significant variation between blocks in the number of visits required to find the Reward during the Return Phase (repeated-measures ANOVA: $F_{3,15}=2.50$, $P=0.0991$). Thus, there is no evidence that performance improved with learning or that interference between trials diminished the ability to recall the Reward location. Such potential interference may have been minimized because the interval between trials ($\bar{X} \pm SE=39.6 \pm 3.7$ min) was much longer than the retention interval within trials (12.6 ± 0.8 min).

DISCUSSION

After searching a novel array of four identical flowers for a single reward, male rufous hummingbirds usually returned to the reward site following a mean retention interval of 12.6 min. Performance did not depend entirely upon memory for the spatial location of the Reward site. Sometimes memory for the location of the Reward was combined with memory for the locations of

Non-reward sites, resulting in the sampling of Unencountered flowers in 29% of the trials.

The ability of hummingbirds to return to Reward sites with significant accuracy is not unique. Food-storing birds of the families Paridae and Corvidae show similar memory abilities when they store and then recover food in the laboratory (see Kamil & Balda 1990; Krebs et al. 1990, and references therein); these species use spatial memory while recovering hoards rather than searching for cues intrinsic to the hoarded food or the hoard sites themselves (Shettleworth & Krebs 1982; Balda & Kamil 1992). Furthermore, there is some evidence that parids can remember the locations of their hoards and also the locations and status of hoards that they have already emptied both within and between bouts of hoarding and recovery (Sherry et al. 1982; Shettleworth & Krebs 1982).

This study of hummingbirds is unique in two aspects. First, trials were performed in the field with direct data on the ability of the hummingbirds to return to reward sites. Field experiments with food-storing marsh tits relied on indirect assessments of return visits (Cowie et al. 1981; Sherry et al. 1982). Gass & Sutherland (1985) also have complete data on return visits for rufous hummingbirds, but they were concerned with repeated rather than single-trial experience. Second, the use of unique locations for each trial virtually eliminated the possibility of proactive interference between trials with respect to location (Roberts & Dale 1981) while preserving tests of spatial memory within trials, and permitted a detailed analysis of apparent 'errors'. While it has often been suggested that lack of accuracy in performance can be partially attributed to factors other than failure of memory (e.g. low sampling

costs or motivation: Kamil & Balda 1990; Brodbeck et al. 1992), it is difficult to provide direct evidence for this claim. Compelling evidence has recently been provided by Brown & Huggins (1993), who demonstrated that the choice accuracy of rats in radial mazes was independently influenced by both working memory and the strength of 'choice-criterion' (see also Wilkie & Spetch 1981; Devenport 1989).

In the present study, analyses of apparent 'errors' indicate that the hummingbirds deliberately sampled flowers they had not yet encountered, while retaining memory for the locations of Reward and Non-reward flowers. Of the 96 trials, 33 first visits during the Return Phase were not to the Reward site. Of these 33 visits, 28 were to flowers not encountered during the Search Phase, and these visits were not influenced by distance to Reward. These results are in marked contrast with the behaviour of parids and corvids performing both hoarding and other spatial memory tasks (e.g. 'window-shopping') using specific artificial sites in the laboratory. In almost all cases they tended to visit Non-reward sites more frequently than Unencountered sites, or revisited old emptied sites more often than expected by chance (Shettleworth & Krebs 1986; Kamil & Balda 1990; Krebs et al. 1990; Shettleworth et al. 1990; Kamil et al. 1993).

The sampling behaviour observed in the rufous hummingbirds appears to be a behavioural mechanism that provides additional information about local resources at some small cost to short-term intake rate (Stephens & Krebs 1986). Whether this exceptional ability to track both rewarded and non-rewarded sites is unique to hummingbirds is not clear. The field conditions and the unique locations of each trial probably provided a rich source of cues for the hummingbirds. The poorer performances of parids and corvids in analogous experiments (see references above) may be due to conducting trials in somewhat barren laboratory conditions. Black-capped chickadees, *Parus atricapillus*, can associate food rewards with both spatial and visual cues (Hampton & Sherry 1994), but their performance is enhanced when visual cues and spatial locations are unique to each trial (Brodbeck et al. 1992). Similar results have been found for pigeons (Zentall et al. 1990). Although hummingbirds are capable of associating food with both spatial location and colour cues in multi-trial tests (Brown & Gass 1993; Miller et al.

1985), the relative importance to one-trial associative learning of these two environmental attributes is as yet unknown. In one experiment designed to dissociate spatial location and local visual cues, rufous hummingbirds preferred to return to the spatial location of a reward they had experienced only once rather than to local visual cues (Hurly & Healy, in press).

Rufous hummingbirds showed excellent spatial memory in an analogue of the radial-arm maze (Healy & Hurly 1995). In both free and forced trials, they readily avoided sites that they had previously emptied. In the present study, rufous hummingbirds easily returned to flowers that they had not emptied, and avoided unprofitable flowers, after only one brief experience at these sites. Because proficient spatial memory appears to be fundamental to natural foraging behaviour in hummingbirds, this ability may resemble the type of adaptive specialization of memory that is expected in food-storing birds (Kamil & Balda 1990; Healy & Krebs 1992a). Regardless of whether these spatial abilities are unique adaptive specializations, hummingbirds prove to be excellent subjects for studies of spatial memory in both the laboratory and the field.

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