

Memory for flowers in rufous hummingbirds: location or local visual cues?

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Abstract. Rufous hummingbirds, *Selasphorus rufus*, remember locations of flowers. They avoid flowers they have emptied recently and those they have found to be empty. In contrast, after one brief experience they return to flowers they have left with food remaining. To determine whether hummingbirds primarily use spatial or colour/pattern cues to return to previously visited flowers, two field experiments were performed. In the first, subjects fed from a reward flower and on their subsequent return had to choose between visual cues that were dissociated from spatial cues. The birds showed a marked preference for returning to the correct location of the previously visited flower and not to the flower bearing the appropriate colour/pattern. The second experiment involved a delayed-matching-to-location task in which the subjects fed from, but did not deplete, a focal flower and on return had to choose between the focal flower and a new distractive flower. The latter was presented at three different distances from the focal flower and was either the same or different in colour to the focal flower. Subjects most often chose the focal flower when the distractive flower was of a different colour, whereas performance was poor when it resembled the focal flower. However, a significant interaction between the colour and distance of the distractive flower suggests that the hummingbirds were able to discriminate between focal and distractive flowers under both conditions, but that they employed different foraging tactics according to the colour of the distractive flower in the choice phase.

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Unpredictability in food location is both spatially and temporally reduced for animals that feed on renewable food compared with animals that feed on non-renewable food. The ability to remember food locations and to detect the rate of renewal would allow such animals to exploit renewable food resources more efficiently.

There is abundant evidence that various species of hummingbird, and other nectar-feeding birds, employ some sort of memory while foraging. Foraging patterns are often non-random, suggesting efficient use of nectar crops (Gill & Wolf 1977; Kamil 1978; Wolf & Hainsworth 1990). Hummingbirds return preferentially to patches of flowers that have been enriched artificially (Gass & Sutherland 1985) and they learn the position of

rewards in an array of feeders (Miller et al. 1985). Recent evidence from field experiments strongly suggests the effective use of spatial memory in at least one species of hummingbird. The rufous hummingbird, *Selasphorus rufus*, feeds on flowers that replace their nectar loads within 24 h of being emptied (Armstrong et al. 1987). They avoid visiting flowers they have emptied recently (Healy & Hurly 1995) and they remember, and respond appropriately to, the locations of rewarded and non-rewarded flowers after a single brief visit (Hurly 1996). In addition, laboratory experiments have shown that hummingbirds can learn both spatial locations and spatial patterns (Brown & Gass 1993; Sutherland & Gass 1995).

Whilst hummingbirds clearly employ some sort of spatial memory, it is not clear what they are remembering or how they use this memory during foraging. When a hummingbird visits a flower it might remember this flower by attending to at least two types of cue. First, it may remember specific visual cues closely associated with the

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flower (e.g. the flower colour or shape) and return by using these cues as a beacon. Alternatively, the bird may attend to several more distal cues and return by remembering the position of the site with respect to these more global landmarks. Whilst hummingbirds may be capable of learning various types of cues on various spatial scales, we wished to examine which cues they attended to while engaged in natural foraging behaviour.

In this study we employed two different methods to investigate the cues rufous hummingbirds used to return to a flower that they did not empty on their first visit. The first method was based on a design developed by Brodbeck (1994) to dissociate memory for object-specific cues and global cues in food-storing birds (see also Clayton & Krebs 1994; Brodbeck & Shettleworth 1995). An animal locates the single rewarded site within an array of four visually distinct feeders. It is allowed to feed from the rewarded site but leaves the site without having fully depleted it. The rewarded feeder is then switched with one of the non-rewarded feeders and when the animal returns we observe which feeder it visits first. One feeder is at the correct location, another feeder bears the correct local visual cues and two irrelevant feeders are distractive. This method, whilst not testing memory capabilities for the two different types of cue, can tell us which of the cue types the birds prefer to remember, or attend to, when foraging at flowers.

The second method of exploring cue use by hummingbirds is a delayed-matching-to-location task (e.g. Wilkie 1989; Olson 1991; Healy & Krebs 1992). In our experiment birds were presented with a single rewarded 'flower' which was only partially emptied on the first visit. Upon return, a bird had to choose to return to the original location or to an alternative (distractive) flower. We manipulated spatial cues by presenting a visually similar distractive flower at three different distances (3, 40 and 80 cm) from the original rewarded location. We predicted that ability to return to the reward would increase with distance between distractive flower and reward. On some trials we presented a distractive flower that differed in colour from that of the rewarded flower. We predicted that performance (return to the original flower) would be better when the distractive flower was of a different colour to the reward. Distance, however, should make little difference to performance on these trials.

EXPERIMENT 1

Methods

Subjects and experimental site

We conducted the experiments along the length of a valley (1400 m elevation) in the Eastern Rocky Mountains 20 km southwest of Beaver Mines, Alberta (49°29'N; 114°25'W) where male hummingbirds defend breeding territories from May to August. These birds migrate to Canada from Mexico in the spring and return in late summer. The subjects used in this experiment were nine adult male rufous hummingbirds. Each was marked on the breast with a distinctive coloured ink mark. Trials were run between 0800 and 1900 hours Mountain Standard Time during May 1994.

Initial training

Artificial feeders containing 14% sucrose solution were placed in 17 sites during late April. By mid-May most feeders were defended by males. We then trained birds to feed from small artificial flowers. These flowers consisted of a cardboard disk (5.8 cm diameter) pierced by a syringe tip forming a well capable of holding 120 μ l of sucrose solution. We painted the cardboard disks with unique patterns using 13 distinctive colours (two colours per disc) and thus provided visual cues based upon both colour and pattern. The flowers were mounted on 60-cm wooden stakes. During training, the birds learned to feed from a single flower containing 20% sucrose solution which was moved a short distance (ca 60 cm) until the bird would search a wide area for it. Birds would not empty a flower during a single visit. When the bird had fed from the training flower 6–10 times (1–2 h), the experiment began.

Experimental procedure

Upon completion of training, we set out four unique flowers roughly in a square 80 cm to a side. These flowers were chosen to be different from the training flower and to have base colours and patterns as different from each other as possible. One of these flowers was chosen as the reward and was the only one containing sucrose. The other flowers were empty. The bird searched the flowers

until it discovered the reward site, drank some of the sucrose, then left the array (phase 1). For the next 5 min the experimenter stood in the centre of the array to prevent the bird from returning. The reward flower was then emptied, rinsed with water, dried and switched with another flower, to test whether the bird returned to the location at which it had most recently fed or to the flower with the appropriate colour pattern. On return to the array, the bird's visits were recorded (phase 2). Throughout the experiment a visit is defined as a probe into a flower by the bird. The mean (\pm SE) retention interval was 16.8 ± 2.7 min. As none of the flowers contained food in phase 2 the birds tended to search several flowers before leaving, although on only two trials did birds visit all four sites. On completion of the first trial, we removed the flowers and returned the feeder for at least 30 min. Following this inter-trial interval, we removed the feeder and a second trial began. This trial employed four flowers as different from the previous four and the training flower as possible. In addition, we presented the second array in a location that was at least 2 m from the first site. As we wanted to test the birds' initial preference for cue type without them learning to respond to a particular cue we (1) attempted to minimize the training required and (2) gave each of the nine birds only two trials.

Results

We used chi-squared tests to determine whether the birds appeared to use memory of any cue for a return visit to the array and whether the return visit was more likely to be made to the reward flower's original location or to its local colour/pattern.

To ascertain whether the birds used memory at all, we assessed only first return visits to the array. When the data for each bird from both trials were combined there was a highly significant effect: first choices in phase 2 were made significantly more often to the location, or to the flower bearing the visual cues associated with the original reward flower, than to other flowers in the array ($\chi^2=10.89$, $df=1$, $P<0.001$). In only two of the 18 trials did a bird make its first return visit to one of the two irrelevant flowers. Thus it does appear that the birds remembered something about the flower visited during the sampling phase and preferentially returned to that flower.

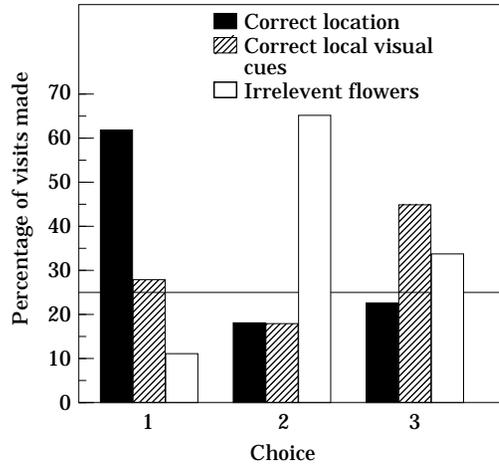


Figure 1. The percentage of visits made by nine rufous hummingbirds to each flower type for the 18 first choices, the 17 second choices and the nine third choices of flowers. The horizontal line at 25% represents the percentage of visits expected if the birds had chosen either the correct location or the site bearing the correct colour pattern at random. Data for the choices to the two irrelevant flowers are combined in this graph. The chance level for choices to irrelevant flowers is thus 50% and not 25%.

To determine whether visual cues or spatial cues were used in the choice of flowers during phase 2, we examined the number of first visits to the correct location, to the flower bearing the correct visual cues and to irrelevant flowers. The distribution of first choices was significantly different from random ($\chi^2=14.89$, $df=2$, $P<0.001$) with the skew towards choice of location (Fig. 1). The birds returned preferentially to the flower in the same location as that from which they had fed in phase 1. As the flowers did not hold sugar solution in phase 2 we could analyse data for the birds' second and third choices. We assumed that the birds could choose the same flower again (sampling with replacement), although in fact they never did this. There was no significant difference between the selection of relevant and irrelevant flowers on the second visit ($\chi^2=1.47$, $df=1$, $P>0.25$) or on the third visit ($\chi^2=1.00$, $df=1$, $P>0.25$). This may have been because the birds remembered only the location, or only the local visual features of the flower, or because upon finding no reward in the first flower visited the birds reverted to a strategy of sampling the nearest flowers.

EXPERIMENT 2

Methods

Subjects

The subjects used in this experiment were six adult male rufous hummingbirds that had been used in the previous experiment.

Initial training

At least 7 days elapsed after the end of experiment 1 before the six birds were trained and tested in experiment 2.

As in experiment 1, we removed the feeder and trained the birds to feed from an artificial flower. The flowers consisted of a cork glued to the top of an 80-cm stake. Inserted into the top of the cork was a syringe cover capable of containing 600 μ l of sucrose solution. Both the cork and the syringe cover were painted either red or yellow. As the birds were familiar with feeding from artificial flowers in general, minimal training was required. Once the bird was feeding from the flower near where the feeder was located, we presented a single flower on four separate occasions at different locations within its territory. Each of these locations was at least 2 m from the previous location. On two of the trials the flower presented was a yellow flower and on two trials it was red. For three of the birds yellow flowers contained sucrose and red flowers contained water and vice versa for the other three birds. The experiment began once the bird had completed these four training trials.

Experimental procedure

Trials in this experiment consisted of two parts. In phase 1 the focal flower was placed in a new location and filled with 20% sucrose solution. When the bird found the flower it drank to satiation and left behind more than half of the original volume. Phase 2 of a trial began after a retention interval of at least 5 min. During the retention interval the original flower (the 'focal' flower) was replaced by a virtually identical focal flower which was filled with sucrose solution. A distractive flower filled with water was also presented. The appearance and location of the distractive flower varied. Its colour with respect to the focal flower was either the same or different

Table I. Mean retention intervals and inter-trial intervals across 60 trials for each of the six hummingbirds tested in experiment 2

Subject	Retention interval (min)	Inter-trial interval (min)
B10	12.0	32.1
B4	13.6	40.9
Pk5	13.7	34.9
Prp2	10.9	36.7
Y3	12.8	33.2
R11	10.7	41.4
Mean	12.3	36.5

and it was positioned either 3, 40 or 80 cm from the focal flower. When the bird returned (phase 2) we recorded its choice of flower. If it chose the distractive flower first it was allowed to move to the focal flower and feed until satiated.

Although the retention interval was set at a minimum of 5 min it could be much longer as determined by the return of the subject. The inter-trial interval was always at least twice the length of the previous retention interval.

Each bird was given 60 trials. Each colour and distance combination of the distractive flower was tested 10 times. We selected the order of presentation of these combinations from a balanced, unbiased schedule with the restriction that a set of all six colour-distance combinations was used before a new set began. The direction of the distractive flower with respect to the reward was also selected from a balanced, unbiased schedule of the eight cardinal compass bearings (N, NE, E, SE, S, SW, W, NW). To ensure that the bird was not responding to some subtle cues associated with individual flowers, the focal flower from phase 1 was replaced in phase 2. Each trial occurred at a location at least 2 m from the previous trial and birds were tested over 4 or 5 days.

Table I shows the average retention and inter-trial intervals.

Results

As birds were provided with an excess of sucrose solution in phase 1 they did not drain the focal flower. We therefore expected them to return to that location in phase 2 and performance was assessed as the number of times the bird chose the focal flower in phase 2.

To begin, we needed to determine whether the birds remembered the location of the focal flower. A one-sample *t*-test (two-tailed) was used to compare choice of the focal flower against chance performance, in this case 30 of 60 trials. The focal flower was chosen significantly more often than expected ($\bar{X} \pm SE = 41.5 \pm 1.06$; $t = 10.88$, $df = 5$, $P < 0.0001$). These data can be divided into 30 trials in which the distractive flower was a different colour from the focal flower and 30 trials in which it was the same colour. In both cases chance performance was 15 trials. When the distractive flower was a different colour from the focal flower performance was very good ($\bar{X} \pm SE = 25.83 \pm 0.60$; $t = 18.03$, $df = 5$, $P < 0.0001$). Performance was not significantly different from chance, however, when the distractive flower was the same colour as the focal flower ($\bar{X} \pm SE = 15.67 \pm 0.62$; $t = 1.09$, $df = 5$, $P = 0.328$).

Colour pattern versus global cues

It seems from the above analyses that the birds relied heavily on the difference in colour between the focal and distractive flowers to choose the focal flower in phase 2 and thus the birds were unable to remember the location of the focal flower without this additional cue. However, further examination of the data suggests an alternative interpretation. Repeated-measures ANOVA allowed us to test simultaneously the effects of distance and colour of the distractive flower on performance. Significant heterogeneity can be attributed to colour ($F_{1,5} = 286.23$, $P = 0.0001$), but not to distance ($F_{2,10} = 0.65$, $P = 0.54$). There was, however, a significant interaction between the effects of colour and distance ($F_{1,5} = 286.23$, $P = 0.0001$): response to the distance of the distractive flower depended on its colour (Fig. 2).

A distractive flower of a different colour should facilitate discrimination between focal and distractive flowers. In addition, discrimination could improve as distance increases because the greater separation between the two flowers should reduce confusion. When the distractive flower was a different colour, performance tended to increase with distance, but this increase was not significant (linear contrast: $F_{1,10} = 2.27$, $P = 0.163$; Fig. 2). This may be because performance was well above chance even at a distance of 3 cm (chance = 5; $\bar{X} \pm SE = 8.00 \pm 0.37$; $t = 8.21$, $df = 5$, $P = 0.0004$). When the distractive flower was the same colour

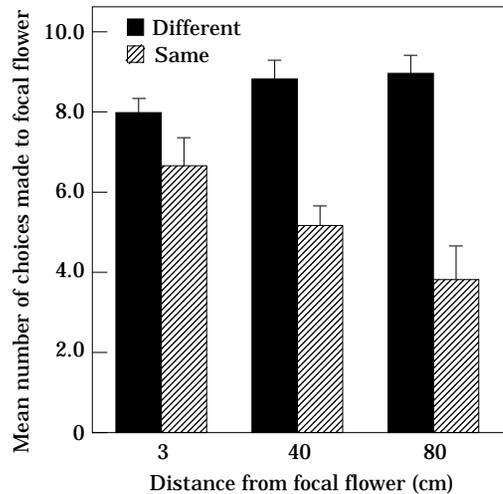


Figure 2. The number of choices (out of 10) made by six rufous hummingbirds of the focal flower when the distractive flower was either the same or a different colour, and was placed 3, 40 or 80 cm from the focal flower. Values are means and standard errors.

as the focal flower the task would appear to be much more difficult and we would expect poorer performance levels, but that performance would improve with distance. In fact, when the distractive flower was the same colour, distance had a significant negative effect on performance (linear contrast: $F_{1,10} = 5.84$, $P = 0.036$; Fig. 2). The flower chosen in phase 2 seemed to depend on the similarity of the two flowers: when the distractive flower was different the birds chose the focal flower, but when it was the same colour as the focal flower they often chose the distractive flower.

If the above interpretation is correct and the birds behaved differently towards same and different distractive flowers as distance varied, then this difference may be learned and thus develop throughout the experiment. We examined the number of times a subject chose the focal flower during the first two cycles of the experiment (each cycle contained three presentations of same and three presentations of different) and compared it with the results from the last two cycles. Colour of the distractive flower significantly influenced choice of focal flower ($F_{1,5} = 63.95$, $P < 0.001$), and while there was no overall effect of time ($F_{1,5} = 2.17$, $P > 0.2$), there was a significant interaction between time and colour ($F_{1,5} = 7.48$,

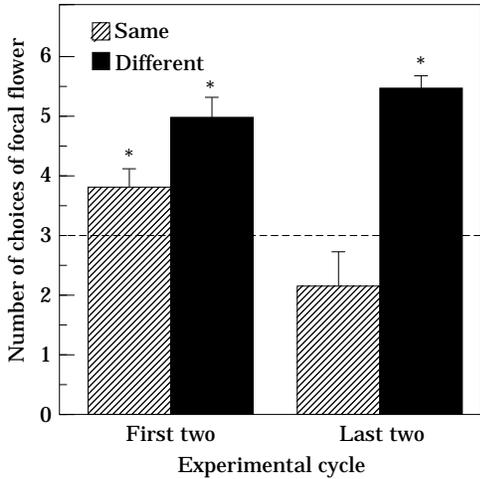


Figure 3. The number of choices made by six rufous hummingbirds of the focal flower when the distractive flower was either the same or a different colour on the first two experimental cycles compared with the number of choices made on the last two cycles. The values are calculated from six visits for each of the six birds and represent means and standard errors. The asterisk denotes a value that is significantly different from the chance level of three choices (dotted line; two-tailed, one-sample t -tests: $df=5$, $P_s<0.05$).

$P<0.05$; Fig. 3). When the distractive flower was a different colour from the focal flower, performance was significantly above chance at both the beginning and end of the experiment, and showed minor, but not significant, improvement (linear contrast: $F_{1,5}=0.80$, $P>0.40$; Fig. 3). However, when the distractive flower was the same colour as the focal flower, performance was initially better than chance, but declined significantly by the end of the experiment (linear contrast: $F_{1,5}=8.85$, $P<0.05$; Fig. 3) such that final performance averaged less than chance, but not significantly so. Thus the hummingbirds returned to the previously rewarded location early in the experiment even when the distractive flower was the same colour as the focal flower. The apparent decline in performance with time was not likely to be due to errors, but was perhaps due to a shift in foraging or sampling tactics.

Finally, we can compare these sampling tactics across experiments. In the first experiment, birds tended to return to the previous location rather than to a colour on both test occasions. In

experiment 2 they tended to behave in the same way, although analyses may be limited by the small sample size ($N=5$). The first two times the birds experienced a distractive flower that was the same colour as the focal flower they chose the focal flower more often than expected by chance (one-sample t -test comparing 1.67 ± 0.21 versus 1; $t=3.162$, $df=5$, $P=0.025$). When the distractive flower differed in colour from the focal flower the subjects again favoured the focal location, but this preference was not quite statistically significant (one-sample t -test comparing 1.50 ± 0.22 versus 1; $t=3.162$, $df=5$, $P=0.076$).

DISCUSSION

The results from the two experiments were: (1) rufous hummingbirds preferred to return to the flower designated by the correct spatial cues rather than to the flower bearing the correct colour/pattern cues; (2) in a delayed-matching-to-location task the birds' tendency to choose the focal flower when the distractive flower was a different colour increased with increasing distance between the two flowers; (3) when the distractive flower was the same colour as the focal flower the birds' tendency to choose the focal flower decreased with increasing distance between the two flowers.

Rufous hummingbirds were tested for their preference to respond to global (spatial) or local (colour/pattern) cues in a task that dissociated the two cue types. There was a general preference for returning in phase 2 to the flower in the same location as that of the flower fed from in phase 1. Because both training and testing were minimal, this preference for responding to spatial over colour/pattern cues was likely to be an expression of normal cue use during foraging behaviour rather than a response learned within the context of the experiment. Additional insight into cue choice comes from studies of food-storing birds which, like hummingbirds, remember many locations associated with food (e.g. Balda & Kamil 1989; Sherry 1989). Preference for distal cues over local visual cues has been demonstrated in food-storing corvids (Bossema 1979; Vander Wall 1982), although this may have been because the more distal cues were far more prominent. More compelling evidence for dependence on distal cues for hoard recovery comes from

experiments involving rotation and translation of cues (e.g. Bennett 1993; Herz et al. 1994).

Experiments involving dissociation of local object cues and spatial cues show interesting differences between food-storing and non-storing bird species: food-storing species prefer to return to food sites specified by spatial cues whereas non-storers tend to return as often to sites bearing the correct local object cues as to those sites in the correct location. The hummingbirds' preference for spatial cues in experiment 1 far exceeds those shown by non-storing species (Clayton & Krebs 1994; Brodbeck & Shettleworth 1995), matches those shown by black-capped chickadees, *Parus atricapillus* (Brodbeck 1994; Brodbeck & Shettleworth 1995), but was somewhat lower than preferences shown by marsh tits, *P. palustris*, and jays, *Garrulus glandarius* (Clayton & Krebs 1994). This preference for attending to, or remembering, the location of flowers rather than the colour of them does not seem surprising as a hummingbird's territory contains many flowers of the same species. It would be advantageous for a bird to remember which flowers of that species it had emptied recently and avoid them until they were replenished. Perhaps the selection pressure on hummingbirds to remember the locations of many flowers is similar to the selection pressure on food-storers to remember storage sites.

The demonstration that hummingbirds in this experiment attended more to spatial cues than to colour/pattern cues indicates a preference for cue type, not necessarily that they were better at remembering spatial information than the colour and pattern features of a flower. In a laboratory task, Brown & Gass (1993) also found a strong tendency for rufous hummingbirds to return to a previously rewarded location in an array. They also showed that spatial memory performance in hummingbirds was enhanced when prominent visual cues were added to an experimental array. However, these data do not address differences in memory capacity for the two types of cue. Nor does the fact that these birds can remember feeding locations when prominent colour/pattern cues are absent (Gass & Sutherland 1985; Miller et al. 1985). Memory for the two types of cues is most clearly distinguished when the cues are presented separately in the same experimental set-up. Presenting a bird with tests of memory for one or the other cue only is problematic in a field situation. To investigate this possibility further it may be

necessary to adopt experimental techniques similar to those used by Healy (1995), in which birds were tested in the laboratory with two-dimensional images presented on touch screen monitors. This was done in an attempt to minimize the many confounding contextual variables associated with more naturalistic settings in which the birds may move around large three-dimensional spaces. As removed as this technique may appear to be from the spatial information processing performed by a hummingbird in the field, it has been shown, in pigeons, *Columba livia*, at least, that landmark use in a touch screen task is similar to landmark use in open-field spatial tasks (Spetch et al. 1992).

In experiment 1 we found that the birds returned to the location of a previously non-depleted site despite the changes in the visual features of that flower. The most obvious cue to that location was the flower's position in the array. In experiment 2, we attempted to test a bird's ability to remember the location of a flower without the aid of either unique local visual cues or position cues relative to other artificial flowers in an array. To our knowledge, all other tests of hummingbird memory (including experiment 1) have used arrays of 'flowers' (Miller & Miller 1971; Miller et al. 1985; Brown & Gass 1993; Brown 1994; Healy & Hurly 1995; Hurly 1996). Furthermore, most other tests have allowed birds to make repeated visits to the flowers, whereas experiments 1 and 2 allowed only a single visit (<10 s exposure; see also Healy & Hurly 1995; Hurly 1996). A single flower was presented in phase 1, and in phase 2 the bird had to choose between a flower in the original location and an alternative, distractive flower. We assumed that the bird would return to the focal flower because it had not depleted the available sucrose in phase 1. The good performance on the trials in which the flowers were different colours is not surprising. The colours of the focal and distractive flowers did not change within subjects for the entire experiment and the birds learnt the colour discrimination within the first few trials (see Fig. 3). Thus, a bird may not have remembered the exact spatial location of the focal flower, but rather may have developed a generalized rule such as 'red is usually rewarded, yellow is never rewarded'. The birds rarely sampled, or made mistakes, by choosing the distractive flower of a different colour (Fig. 2). Such sampling, or errors, tended to

be made the closer the flowers were together (Wilkie & Summers 1982), suggesting either confusion of spatial location or low costs of sampling nearby flowers.

When the distractive and focal flowers were the same colour local visual cues were not available, nor were subtle visual features of an individual flower salient because new flowers were substituted between phases 1 and 2. To make the correct choice the bird had to make use of more global cues. This would seem to be a more difficult task than that in experiment 1 or in the other trials of experiment 2. In order for the birds to return to the correct flower they would have had to take into account either large-scale features of the field in which the flowers were placed (e.g. trees, hills) or fine-scale features such as nearby low-lying clumps of weeds or small ant hills. That they were able to do this task at all is suggested by the data from the first two cycles shown in Fig. 3, but the birds' performance was much poorer. In addition, it appears that, over the course of the experiment, the motivation to make the correct choice changed and it is possible that performance was poor not because of errors, but rather because of sampling. Each focal flower was presented at a trial-unique location. Thus a bird may have generalized a rule such as 'yellow flowers are usually rewarded, therefore investigate new yellow flowers'. Such a rule would explain the increased preference for the distractive flower as the distance between the focal and distractive flowers increased. That is, as the two flowers became easier to discriminate on the basis of spatial location alone, the birds tended to sample the 'new' one. Such sampling behaviour had potentially high benefits as a rewarded flower contained enough sucrose solution for four to six feeding bouts. Sampling costs were low because the distractive flower was never more than 80 cm away and contained only water which, whilst unpalatable to the hummingbirds, was not harmful.

There is good evidence for sampling behaviour in hummingbirds. Even after many visits to a single reward site hummingbirds make frequent exploratory shifts to non-rewarded sites (Miller & Miller 1971; Brown & Gass 1993). Hurly (1996) observed that rufous hummingbirds returned to flowers they had found recently to contain food rather than to identical alternative flowers in an array. If they did not return immediately to the reward flower, they avoided flowers that they had

already found to be empty and preferentially visited flowers that they had not yet investigated. In that experiment (Hurly 1996) and in experiment 2 all flowers were constructed to be virtually identical so that the hummingbirds would have to rely on spatial, rather than colour/pattern, cues. It is interesting to compare the high rates of sampling in these cases with the low rate observed in experiment 1. All flowers in experiment 1 were visually unique, hence in phase 2 birds rarely sampled flowers that had no visual cues similar to the reward flower they had visited in phase 1.

It was not our intention in these experiments to determine whether the birds had a tendency to learn a win-shift or win-stay strategy as Cole et al. (1982) have done previously. Rather, we used a non-depleting focal flower to act as an incentive to return. We wanted to know whether the birds could remember either the colour pattern or the location of this focal flower. In the array test of experiment 1 the birds did seem to remember the location of the focal flower. In experiment 2 the birds very quickly learned the colour discrimination in trials with a distractive flower of a different colour and consequently were able to make the correct choice. When the flowers were the same colour the birds may still have recognized and remembered the location and content of the focal flower, but they tended to sample the distractive flower. Thus they appeared to employ different foraging tactics depending on whether they had generalized colour/pattern information about the reward-containing focal flower.

The results from these experiments suggest first that rufous hummingbirds prefer to attend to, or remember, global spatial cues of flowers rather than colour/pattern cues intrinsic to the flowers. Second, these data support Hurly's (1996) claim that the birds remember not only the location of flowers but also their contents. Finally, the birds can discriminate and generalize the local visual features of flowers and alter their foraging tactics accordingly. Visual cues can be learned rapidly to aid discrimination between flowers that are visually distinguishable or to enable generalization for efficient sampling of similar flowers in new locations.

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REFERENCES

- Armstrong, D. P., Gass, C. L. & Sutherland, G. D. 1987. Should foragers remember where they've been? Explorations of a simulation model based on the behavior and energetics of territorial hummingbirds. In: *Foraging Behavior* (Ed. by A. C. Kamil, J. R. Krebs & H. R. Pulliam), pp. 563–586. New York: Plenum Press.
- Balda, R. P. & Kamil, A. C. 1989. A comparative study of cache recovery by three corvid species. *Anim. Behav.*, **38**, 486–495.
- Bennett, A. T. D. 1993. Spatial memory in a food storing corvid. I. Near tall landmarks are primarily used. *J. comp. Physiol.*, **173**, 193–207.
- Bossemma, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. *Behaviour*, **70**, 1–117.
- Brodbeck, D. R. 1994. Memory for spatial and local cues: a comparison of a storing and a non-storing species. *Anim. Learn. and Behav.*, **22**, 119–133.
- Brodbeck, D. R. & Shettleworth, S. J. 1995. Matching location and color of a compound stimulus: comparison of a food-storing and a non-storing bird species. *J. exp. Psych.: Anim. Behav. Proc.*, **21**, 64–77.
- Brown, G. S. 1994. Spatial association learning by rufous hummingbirds (*Selasphorus rufus*): effects of relative spacing among stimuli. *J. comp. Psychol.*, **108**, 29–35.
- Brown, G. S. & Gass, C. L. 1993. Spatial association learning by hummingbirds. *Anim. Behav.*, **46**, 487–497.
- Clayton, N. S. & Krebs, J. R. 1994. Memory for spatial and object-specific cues in food-storing and non-storing birds. *J. comp. Physiol.*, **174**, 371–379.
- Cole, S., Hainsworth, F. R., Kamil, A. C., Mercier, T. & Wolf, L. L. 1982. Spatial learning as an adaptation in hummingbirds. *Science*, **217**, 655–657.
- Gass, C. L. & Sutherland, G. D. 1985. Specialization by territorial hummingbirds on experimentally enriched patches of flowers: energetic profitability and learning. *Can. J. Zool.*, **63**, 2125–2133.
- Gill, F. B. & Wolf, L. L. 1977. Nonrandom foraging by sunbirds in a patchy environment. *Ecology*, **58**, 1284–1296.
- Healy, S. D. 1995. Memory for objects and positions: delayed-non-matching-to-sample in tits. *Q. Jl exp. Psychol.*, **48B**, 179–191.
- Healy, S. D. & Hurly, T. A. 1995. Spatial memory in rufous hummingbirds (*Selasphorus rufus*): a field test. *Anim. Learn. Behav.*, **23**, 63–68.
- Healy, S. D. & Krebs, J. R. 1992. Delayed-matching-to-sample by marsh tits and great tits. *Q. Jl exp. Psychol.*, **45B**, 33–47.
- Herz, R. S., Zanette, L. & Sherry, D. F. 1994. Spatial cues for cache retrieval by black-capped chickadees. *Anim. Behav.*, **48**, 343–351.
- Hurly, T. A. 1996. Spatial memory in rufous hummingbirds: memory for rewarded and non-rewarded sites. *Anim. Behav.*, **51**, 177–183.
- Kamil, A. C. 1978. Systematic foraging by a nectar-feeding bird, the amakihi (*Loxops virens*). *J. comp. Physiol. Psychol.*, **3**, 388–396.
- Miller, R. S. & Miller, R. E. 1971. Feeding activity and color preference of rubythroated hummingbirds. *Condor*, **73**, 309–313.
- Miller, R. S., Tamm, S., Sutherland, G. D. & Gass, C. L. 1985. Cues for orientation in hummingbird foraging: color and position. *Can. J. Zool.*, **63**, 18–21.
- Olson, D. 1991. Species differences in spatial memory among Clark's nutcrackers, pigeons and scrub jays. *J. exp. Psychol. Anim. Behav. Proc.*, **17**, 363–376.
- Sherry, D. F. 1989. Food storing in the Paridae. *Wilson Bull.*, **101**, 289–304.
- Spetch, M. L., Cheng, K. & Mondloch, M. V. 1992. Landmark use by pigeons in a touch-screen spatial search task. *Anim. Learn. Behav.*, **20**, 281–292.
- Sutherland, G. D. & Gass, C. L. 1995. Learning and remembering of spatial patterns by hummingbirds. *Anim. Behav.*, **50**, 1273–1286.
- Vander Wall, S. B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. *Anim. Behav.*, **30**, 84–94.
- Wilkie, D. M. 1989. Evidence that pigeons represent Euclidean properties of space. *J. exp. Psychol. Anim. Behav. Proc.*, **15**, 114–123.
- Wilkie, D. M. & Summers, R. J. 1982. Pigeons' spatial memory: factors affecting delayed matching of key location. *J. exp. Analysis Behav.*, **37**, 45–56.
- Wolf, L. L. & Hainsworth, F. R. 1990. Non-random foraging by hummingbirds: patterns of movement between *Ipomopsis aggregata* (Pursh) V. Grant inflorescences. *Funct. Ecol.*, **4**, 149–157.