



Rufous hummingbirds' memory for flower location

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We used an open-field analogue of the eight-arm radial maze to investigate the role of memory during foraging by rufous hummingbirds, *Selasphorus rufus*. In experiment 1 we attempted to determine whether birds were able to differentiate between flowers of the same type that they had emptied, flowers they had seen but not visited and new flowers. They were tested with three trial types, all of which involved birds visiting four rewarded flowers in the first phase of a trial. In 'free' trials, the bird was allowed to choose four from eight flowers. In 'forced' trials there were only four flowers available in phase 1 and in 'mixed' trials the bird could choose four from six available flowers. In all trial types eight flowers (including all those in the same locations as in phase 1) were presented to the bird on its return in phase 2. The four rewarded flowers were those not visited in phase 1. In free and mixed trials, birds were better than chance at avoiding the flowers they had emptied in phase 1. In mixed trials, birds were more likely to visit the new flowers that were unique to phase 2. In experiment 2 we tested whether flower height was a floral feature remembered by birds. Birds were given forced and free trials in which the flowers in the radial maze were presented at two heights. As performance in both trial types was better than chance we suggest that hummingbirds use flower height to remember the locations of flowers.

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Evidence from laboratory and field studies shows that hummingbirds can both remember and subsequently avoid flowers they have visited recently (Cole et al. 1982; Brown & Gass 1993; Brown 1994). They can also be trained to return to consistently rewarded flowers (Hurly & Healy 1996; Healy & Hurly 1998). We, and others, have been exploring the roles that different kinds of information that the birds learn about these flowers play in subsequent flower choices. The birds learn about a flower's nectar quality and content, its colour and its spatial location in a horizontal plane (e.g. Collias & Collias 1968; Miller & Miller 1971; Gass & Sutherland 1985; Miller et al. 1985; Wolf & Hainsworth 1991; Healy & Hurly 1995, 1998; Hurly 1996; Hurly & Healy 1996). They also pay attention to the spatial scale of flower distribution, using visual or spatial arrangements of other flowers to remember outcomes of previous visits when those flowers are close to the flower in question. When flowers are further apart, the birds appear to use other, more global, landmarks (Brown & Gass 1993; Healy & Hurly 1998).

Hummingbirds, then, appear to use a variety of information to make choices about which flowers to visit.

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However, there is yet more information relating to a flower's location and contents that birds might also learn and use in flower choice. In the experiments described here, we investigated two of these: flowers that have been seen on previous foraging bouts and flower height. We chose these two features based on results from two previous sets of experiments investigating flower choice in rufous hummingbirds, *Selasphorus rufus*. The first of these results comes from an experiment by Hurly (1996) in which he presented birds with an array of four visually identical flowers, only one of which contained sucrose. As the flower contained more sucrose than the bird could finish in a single visit, a return to that flower when the bird next visited the array was deemed to be 'correct'. Birds also correctly avoided flowers they had previously found to be empty. On the occasions that birds made errors (i.e. did not visit only the single rewarded flower upon return to the array), they chose flowers they had seen but not probed on the previous visit to the array. Hurly interpreted this behaviour as sampling rather than making an error (see also Wilkie et al. 1999) because birds checked these previously unvisited flowers more often than would be expected by chance. Possibly then, while foraging at one flower or a group of flowers, a bird might register the fact that there are other flowers nearby worth visiting on a subsequent foraging bout. The bird may even use these other flowers to help encode the location of the flower(s) from which it is currently feeding. What,

then, if on later visits to the general area of these flowers, the bird finds that there are entirely new flowers also present? The hummingbird may treat the two types of flowers differently. For example, older, unvisited flowers may be visited before new flowers because in some species they may contain more accumulated nectar. In other conditions, new flowers may be more valuable because older flowers could have lost nectar to absorption, spoilage or theft by other pollinators.

In experiment 1, we presented male rufous hummingbirds with an array of flowers that they were allowed to visit twice. We used three trial types that differed during the original visit to the array. In 'free' trials, the bird was allowed to check and empty only four of eight flowers containing sucrose, thus he saw the remaining four flowers but knew nothing of their contents; in 'forced' trials, the bird was given only four flowers to check (all containing sucrose); and in 'mixed' trials the bird was presented with six flowers containing sucrose but allowed to check only four. On his subsequent visit to the array in all three treatments the bird was faced with eight flowers, the four previously visited and emptied flowers and the other four containing sucrose (Healy & Hurly (1995) showed that these birds do not use cues emanating from the sucrose itself to make flower choices). We predicted that the hummingbird would avoid the flowers he had recently emptied in all three trial types. In the mixed trials the bird might show a preference for either the two new flowers or the two flowers he had seen but not visited in phase 1 of the trial.

The rationale for the second experiment was derived from the fact that although there is ample evidence that rufous hummingbirds can remember the spatial locations of a number of flowers in a horizontal plane, flowers also differ in their height from the ground. Indeed, Blem et al. (1997) found that rufous hummingbirds preferred the highest sucrose sources when these artificial sources were presented at a number of heights, ranging from 0.25 to 3.0 m above the ground (see also Wolf & Hainsworth 1990). Whereas Blem et al. (1997) interpreted this preference as a predation avoidance response, it is also possible that the higher flowers were more conspicuous as they were further from the undergrowth. Not only might flower height affect conspicuousness, it should also contribute to discrimination between flowers by adding vertical information to the horizontal planar information. A bird feeding from a plant bearing inflorescences with a number of flowers might remember the approximate heights of emptied flowers in order to avoid them on subsequent visits. In experiment 2, we presented hummingbirds with a simple array of flowers at either 40 or 110 cm from the ground. In phase 1 of 'free' trials, eight flowers containing sucrose, two each on four 'plant stalks', were presented and the bird was allowed to empty four of them. In phase 1 of 'forced' trials, four plant stalks but only four flowers (two high and two low) were presented. In both trial types, the bird was faced with eight flowers on his return to the array (phase 2) and we noted whether he avoided those four flowers he had recently emptied (which were still empty). If high flowers were preferred, then birds would be expected to visit the

high flowers in both phases of free trials and thus performance in phase 2 would be significantly worse than random and in phase 2 of forced trials performance would be no different from random for the same reason.

EXPERIMENT 1

Methods

Subjects

The experiment was conducted 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), Canada. We used nine experimentally naïve, male rufous hummingbirds which had set up feeding territories in this valley. They were all identifiable by a small amount of coloured ink which we applied on to their breast feathers when they were sitting at their feeder. Birds remain at their feeders or return within a few minutes after application of this ink. In 8 years of study, no birds have disappeared or lost their territory as a result of this marking technique. Trials were run between 0800 and 2000 hours Mountain Standard Time in June and July 1998.

Initial training

We placed artificial feeders containing 14% sucrose solution in potential territories during mid-May and by late May the majority were defended by males. A bird could then be ink marked, his feeder removed, and trained to feed from small artificial 'flowers'. We returned the feeder after training and between experimental trials. A flower consisted of a cardboard disk (5.8 cm diameter), the centre of which was pierced by a syringe tip forming a well capable of holding 120 µl of sucrose solution. The flowers were mounted on 60-cm wooden stakes. The bird learned to feed from a single flower filled with 20% sucrose which was moved a short distance (ca. 1 m) after each visit. When the bird had fed three times, he was presented with four flowers each containing 15 µl of 20% sucrose solution. Once the bird was consistently moving between and probing these four flowers training was complete. Training usually took no longer than 2 h to complete.

Experimental trials

Prior to a trial we removed the bird's feeder and set up the array. Birds were presented with three types of trial (free, forced and mixed) each with two phases. In phase 1 of 'free' trials the bird was presented with eight flowers (configuration below) all containing a 15-µl sucrose reward. Either the bird left or we chased him away after he had fed from four flowers. On the bird's return to the array in phase 2, only the flowers he had seen, but not visited in phase 1, contained sucrose. In phase 1 of 'forced' trials we presented four flowers and four empty stakes on the bird's first visit to the array. All four flowers contained 15 µl of sucrose and the locations of the reward flowers in phase 1 were determined in a pseudorandom fashion with the constraint that there were no more than two adjacent rewarded flowers. On the bird's return to the

array (phase 2) he was presented with eight flowers, four new flowers having been placed on the empty stakes. These new flowers contained 15 μ l of sucrose and the previously emptied flowers remained empty. In 'mixed' trials the bird was presented in phase 1 with six rewarded flowers but allowed to visit only four of them. As in the other trial types, when the bird returned to the array in phase 2 he was presented with eight flowers. Only the two previously unvisited flowers and the two new flowers contained sucrose. Flower colour pattern was unique to each trial. Patterns were typically geometric features such as straight and wavy lines, circles, squares and triangles.

All trial types involved variations on the same general array configuration. Arrays comprised eight wooden stakes (height 60 cm), arranged in a circle and spaced 70 cm from each other (radius of the circle 90 cm). A flower was mounted on the top of either four or eight of the stakes. Birds had unrestricted access to all the flowers. A minimum retention interval (RI) of 5 min was imposed by the observer who chased the bird away if he returned within this time. The intertrial interval (ITI) was a minimum of twice the length of the RI in the preceding trial. During this period we returned the bird's feeder to its original location.

To constitute a valid trial the bird had to visit four flowers in phase 1. If fewer than four flowers were visited the trial was aborted. Similarly, the trial was aborted if fewer than four flowers were visited in phase 2. In the event of a trial being aborted another trial of the same type was carried out on completion of all the other trials. The same set of flowers was used in the later trial as in the original trial but the array was presented in a new location. Consecutive trials were conducted at a minimum distance of 3 m from the preceding trial.

We determined the order in which trial types were presented by randomly drawing the three trial types and repeating this process until a bird had completed a minimum of five trials of each type.

Results

Repeated visits to the same flower within phase 2 of trials were rare (6.9% of all phase 2 visits across all trial types) and were omitted from the analysis. This finding is consistent with the 6% revisit rate found in a similar experiment by Healy & Hurly (1995).

Performance relative to chance

We defined performance in phase 2 of a trial as the number of correct (nonempty) flowers visited on the first four choices in phase 2. To assess the use of memory, we compared performance with the chance performance of 50% (two correct choices in the first four visits). For each trial type, we computed the mean performance for each bird and then compared the mean performance across birds with the chance expectation of two, with a one-sample t test (one-tailed because the alternative to the null hypothesis is performance better than chance). Performance was significantly better than chance in free and mixed trials but not on forced trials (one-sample

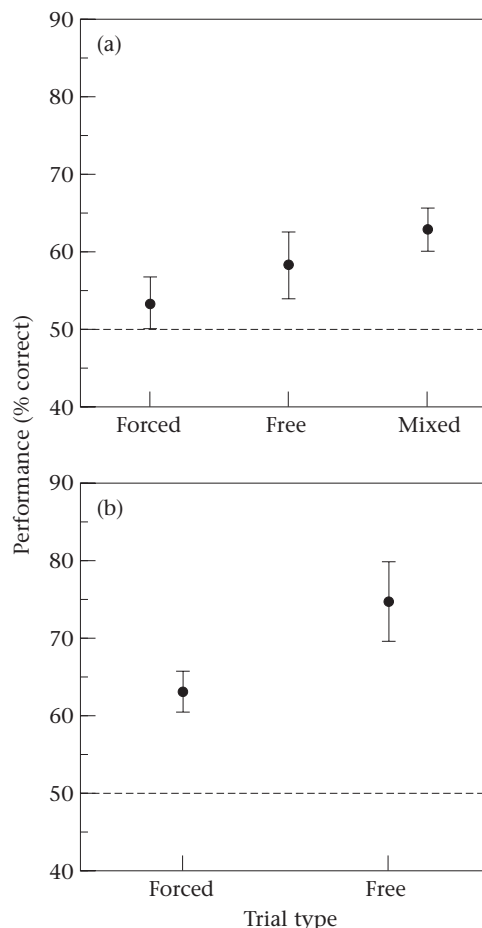


Figure 1. Performance of hummingbirds in terms of the percentage of correct (nonempty) flowers chosen upon returning to the experimental array. Chance performance is denoted by the dotted line at 50%. (a) Mean \pm SE performance of nine birds, for each trial type, forced (only four flowers presented in phase 1), free (bird visited any four of eight flowers in phase 1) and mixed (six flowers presented in phase 1, bird allowed to visit four), in experiment 1. (b) Mean \pm SE performance of six birds for each trial type in experiment 2.

t tests: forced trials: $t_8=0.97$, NS; free trials: $t_8=1.92$, $P<0.05$; mixed trials: $t_8=4.65$, $P<0.001$; see Fig. 1a).

Comparison between trial types

We compared the birds' ability to avoid those flowers they had visited in phase 1 on their return to the array in phase 2 across the three trial types with a repeated measures ANOVA. We looked at performance on both the birds' first choice of flower in phase 2 and their first four choices in phase 2. These data were arcsine square-root transformed before analysis. There was no significant difference between the trial types in performance for either the first choice made in phase 2 ($F_{2,16}=0.11$, NS) or for the first four choices ($F_{2,16}=1.60$, NS).

Mixed trials

We also looked at which flowers the birds chose in phase 2 of mixed trials to determine whether they tended to visit new or previously seen but unvisited flowers. In

43 trials for which we could determine whether the subject first visited a new or previously seen flower, the subjects visited a new flower 31 times (72%; cumulative binomial probability=0.003).

Effect of retention interval

Although we enforced a minimum RI of 5 min, the maximum length of RI could not be controlled. Retention intervals thus ranged from 5 to 44 min ($\bar{X} \pm \text{SE} = 7.4 \pm 0.32$ min). To determine whether performance declined with increased RI, we divided the data into the three treatment types and then correlated performance and RI for every trial (ignoring possible non-independence within birds). None of the correlations was significant (forced trials: $r_{43} = -0.064$, NS; free trials: $r_{43} = -0.118$, NS; mixed trials: $r_{43} = -0.088$, NS). We also investigated correlations between performance and RI across all trials for each separate bird. Again, no correlations were significant ($|r_{13}| < 0.37$, NS); nor was the mean of the correlation coefficients for the nine subjects different from zero (one-sample t test: $t_8 = 2.12$, NS). Therefore, there is no evidence for an effect of RI on performance.

Discussion

In this experiment birds performed significantly better than chance in free and mixed trials but not in forced trials. Their general performance was rather poor in comparison with the birds tested by Healy & Hurly (1995) and it is not clear why this is so. Although Healy & Hurly tested both males and females, there were no substantial sex differences so it seems unlikely that the sex of the subjects explains the poorer performances in the current experiment. Possibly, the size of the reward we used (15 μl per flower whereas Healy & Hurly used 40 μl per flower) meant birds visited flowers for such short periods of time that they learned which flowers were emptied less accurately.

In the mixed trials hummingbirds were faced with four flowers that they had emptied and four flowers that contained sucrose. Of these latter four, two had been seen, but not visited, during phase 1 of the trial and two had not been seen before. The hummingbirds were more than twice as likely to select a new flower first than a previously seen flower, suggesting that they were easily able to distinguish between these two flower types.

EXPERIMENT 2

In experiment 2 we investigated whether hummingbirds remember the height of the flowers they have visited. We carried out forced and free trials as described in experiment 1 using eight-flower arrays in which the flowers were presented to the birds at two heights.

Methods

Subjects

Six hummingbirds from experiment 1 were used in this experiment which was run immediately after experiment

1 was completed. The birds in this experiment were tested as soon as they had finished experiment 1 and were not chosen on the basis of their earlier performance. Only six birds could be tested before the birds' territorial defence deteriorated in preparation for migration.

Procedure

The subjects did not require training because they were accustomed to visiting experimental flowers. We presented flowers in a cubic array consisting of four vertical wooden sticks mounted 70 cm apart. On each stick two cardboard flowers (diameter 5.8 cm) were mounted at heights of 40 and 110 cm, such that the eight flowers were at the corners of a cube, 70 cm per side.

Birds were presented with both forced and free trials as described in the previous experiment. The flower colour patterns used were the same within a trial but unique to each trial. They had not been used in experiment 1. All other procedures remained the same, with the presentation of flowers on forced trials constrained such that two flowers were placed at the upper and two at the lower height in phase 1. Ten trials of each type were carried out on each bird with the trial types alternating.

Results

Flower height

We examined preference for flower height by recording the heights of the first choice and the first two choices made in phase 1 of trials. We calculated the number of times each subject chose upper flowers and compared the mean performance of the six subjects with chance (50%, no preference). In free trials hummingbirds weakly preferred higher flowers in that a mean \pm SE of $67 \pm 6\%$ of the first choices were to an upper flower (one-sample t test: $t_5 = 2.988$, $P = 0.031$). Across the first two choices of phase 1, birds chose upper flowers $61 \pm 5\%$ of the time ($t_5 = 2.445$, $P = 0.053$). In forced trials no clear preference was seen (first choice: $63 \pm 6\%$; $t_5 = 2.169$, $P = 0.08$; first 2 choices: $53 \pm 7\%$; $t_5 = 0.674$, $P = 0.50$).

Performance relative to chance

We used one-sample t tests to compare the birds' performance in phase 2 with chance (50%) levels (Fig. 1b). The tests were two tailed because a strong preference for upper flowers could conceivably cause the birds to perform worse than expected by chance. Performance in both forced and free trials was significantly better than chance (one-sample t tests: forced trials: $t_5 = 5.01$, $P < 0.01$; free trials: $t_5 = 4.85$, $P < 0.01$).

Comparison between trial types

We used repeated measures ANOVAs (data were arcsine square-root transformed prior to analysis) to investigate whether performance in phase 2 differed between the free and forced trial types. Trial type did not have a significant effect on performance measured on the first choice ($F_{1,5} = 3.73$, NS) or on the first four choices ($F_{1,5} = 3.87$, NS). Performance on forced trials in which we determined the flowers visited in phase 1 was no worse than in free trials in which the bird determined which flowers to visit.

Effect of retention interval

We investigated whether the time the birds spent away from the array was correlated with performance as measured on the first four choices of phase 2. Retention intervals ranged from 5 to 32 min ($\bar{X} \pm \text{SE} = 8.82 \pm 0.21$). Examining data by subject, one bird showed a significant positive correlation between performance and RI ($r_{18} = 0.55$, $P = 0.01$). For all other birds, however, there was no apparent effect of RI on performance, as revealed by nonsignificant correlations ($|r_{18}| < 0.31$, $P_s > 0.18$). Furthermore, the mean correlation coefficient was not significantly different from zero ($t_5 = 0.65$, NS). Similarly, examining data by trial type, there was no significant correlation between performance and RI (forced trials: $r_{58} = -0.068$, NS; free trials: $r_{58} = -0.047$, NS). Longer retention intervals, therefore, did not appear to impair birds' performances.

Comparison of performance across experiments

The subjects had all been tested in experiment 1. A repeated measures ANOVA shows that their performance in experiment 2 was significantly better than in experiment 1 ($F_{1,5} = 8.636$; $P = 0.032$; Fig. 1). There was no overall effect of trial type ($F_{1,5} = 4.021$; $P = 0.101$), nor was there an interaction between experiment and trial type ($F_{1,5} = 0.186$, $P = 0.684$). This difference in performance cannot be attributed to retention interval because the RI for experiment 2 was slightly longer than in experiment 1.

Discussion

Birds performed significantly better than chance both in free and forced trials with flowers at two different heights. This suggests that birds can remember flower height over and above any preference they might have for higher flowers. Superior performance in experiment 2 may be due to the presence of the vertical dimension in this experiment. We cannot, however, rule out the possibility that hummingbirds performed better in experiment 2 merely because of their experience with similar memory tasks in experiment 1.

GENERAL DISCUSSION

The results from experiment 1 reveal several properties of the memory of hummingbirds foraging under relatively natural conditions. First, while foraging on a number of flowers, the hummingbirds remembered which flowers they had emptied recently and preferentially visited others when they returned to the patch. Similar results have been reported by Healy & Hurly (1995) and by Cole et al. (1982). Second, the hummingbirds noticed and remembered the locations of other nearby flowers even when they had not yet visited them (see also Hurly 1996). Third, returning to an array of flowers, the hummingbirds identified new flowers that were not present 5–44 min earlier. Fourth, the hummingbirds distinguished between new flowers and flowers they had seen but not yet visited. Thus, we know that rufous, and other, hummingbirds

remember the spatial locations of flowers (Healy & Hurly 1995; Hurly & Healy 1996) and they remember various aspects of the status of these flowers: flowers visited and emptied (this study and Healy & Hurly 1995); flowers found to be empty (Brown & Gass 1993; Sutherland & Gass 1995; Hurly 1996; Healy & Hurly 1998); flowers fed from, but not completely emptied (Miller et al. 1985; Hurly 1996; Hurly & Healy 1996); flowers seen but not yet visited (this study; Hurly 1996); and new flowers (this study). Making decisions about which flowers to visit based on information gained previously requires spatial memory when the flowers, as in these experiments, all look alike. To make correct choices of flowers within arrays such as the ones we used, the birds must be able to use 'global' cues (which may be locational or directional) to locate the array, and then use global and/or within-array cues such as the position of each flower relative to the others to locate the correct flower(s) (see Healy & Hurly 1998). For birds to make decisions as accurately on forced trials when the visual aspect of the array changed quite considerably between the two visits, as they did on free trials, would suggest that in experiment 2 birds were using extra-array cues to relocate individual flowers, rather than within-array cues (see also Healy & Hurly 1995). It is not clear what these extra-array cues were but they might have been visual landmarks such as nearby trees and bushes.

While the hummingbirds in our study were clearly able to discriminate between new flowers and flowers seen but not visited, it is not clear why they did so. Preference for new flowers may indicate that they are more valuable than older flowers, because of nectar spoilage, absorption, or theft (Gill 1988). Despite the highly territorial nature of male rufous hummingbirds, we have frequently observed both intraspecific and interspecific theft of nectar from territories (see also Paton & Carpenter 1994).

In the second experiment, rufous hummingbirds were able to remember the locations of flowers in three dimensions. While they may possess a weak preference for visiting higher flowers, this potential preference was overshadowed by the avoidance of flowers they had emptied recently and thus they performed well on the spatial memory task. These memory abilities are consistent with other studies showing that rufous hummingbirds can remember flower locations that are only a few cm apart (Brown & Gass 1993; Sutherland & Gass, 1995; Hurly & Healy 1996). Height preferences could be adaptive because tall inflorescences may have more flowers (Wolf & Hainsworth 1990) or they may help birds to avoid predators in the underbrush (Blem et al. 1997). Alternatively, tall flowers or inflorescences may merely be more conspicuous or they may be closer to the elevated perches from which the foraging birds have been maintaining a watch for intruders.

Past experiments with hummingbirds seem to have been restricted to reward locations in a two-dimensional plane (e.g. Healy & Hurly 1995, 1998; Sutherland & Gass 1995), probably for logistical simplicity in the experimental manipulations. Given that hummingbirds forage on a variety of flower species, it is not surprising that they are able to use a third dimension to encode spatial location.

Indeed, the superior performance in experiment 2 may be the result of increased salience of flower locations owing to the presence of a vertical dimension in the arrays. Fox squirrels, *Sciurus niger*, show excellent spatial memory in three dimensions when tested in the field (Jacobs & Shiflett 1999), pigeons, *Columba livia*, appear to attend to three-dimensional relationships when shown multiple two-dimensional views of a scene (Spetch et al. 1998) and rats, *Rattus norvegicus*, in a three-dimensional maze appear to give priority to goal heights when learning goal locations (Grobéty & Schenk 1992).

We have explained the results of both experiments in the context of advantages to a territorial hummingbird of being able to remember his foraging experiences in order to make subsequent choices that will optimize the return he gets from his defended flowers. It may be that flowering plants make use of the cognitive abilities of hummingbirds to their own advantage. The effect of mutualistic interactions between hummingbirds and the plants they pollinate on the morphological features of both are well known. The perceptual and cognitive abilities of hummingbirds might also have been shaped by, and helped to shape, floral attributes. For example, it is claimed that much of the Californian flora has red flowers because of the major role that hummingbirds play in the pollination of these plants (Grant & Grant 1967). Although not yet tested, this may be because red is the most conspicuous colour to the hummingbirds in this environment (it is not, as is still popularly believed, due to a fixed preference for red, see e.g. Meléndez-Ackerman et al. 1997). Although hummingbirds can learn colour preferences, flower location appears to be more salient in remembering food sources (e.g. Miller et al. 1985). Thus, while the shaping of the visual characteristics of flowers by the perceptual abilities of their pollinating hummingbirds may seem obvious, it also seems possible that the spatial and temporal distribution of the flowers might usefully exploit a bird's cognitive abilities. Future work on the cognitive abilities of hummingbirds would benefit from a greater understanding of the floral features of the plants on which they feed.

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