
Cognitive Ecology: Foraging in Hummingbirds as a Model System

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Cognitive abilities, especially learning and memory, are nearly always studied in the laboratory. This is because the laboratory environment allows for strict control over the testing conditions, any one of which may affect performance. These potential extraneous variables range from those emanating from the test environment, for example, lighting (both the level and the light–dark schedule), temperature, presence or absence of conspecifics and availability of cues (such as visual landmarks, directional noises or smells), through the animal’s motivational state (hunger level, sexual arousal), to those from the animal’s previous experience, for example, familiarity with the test procedure (pulling levers, pecking at lights). Investigations of learning and memory performance under such strictly controlled conditions have been useful in demonstrating what animals are capable of learning and remembering. For example, pigeons have been found to remember at least 400 photographic slides for longer than 12 months (Vaughan and Greene, 1984). However, while this memory capacity is impressive, it is still not clear to what use the pigeon puts this ability in its daily life. In other instances, assessments of learning and memory performances of animals in the laboratory vastly underestimate their real abilities. For example, tits tested with touch screen tasks can remember locations of images only for a few seconds or minutes (Biegler *et al.*, 2001; Hampton and Shettleworth, 1996a,b; Healy, 1995), whereas when retrieving food caches in the laboratory or in the field, they can remember locations of caches for hours, days, weeks, even months (Haftorn, 1956; Healy and Suhonen, 1996; Stevens and Krebs, 1986).

One of the fundamental assumptions underlying the validity of testing cognitive abilities under laboratory conditions (and, thus, the almost

universal testing of these abilities in either pigeons or rats) is that there is a commonality of such abilities due to evolutionary descent (see [Macphail and Bolhuis, 2001](#), for an exposition on this). However, there is a different, and not incompatible, view that evolution by natural selection produces diversity in design through local adaptation. Although Macphail and Bolhuis (see also [Bolhuis and Macphail, 2001](#)) argue that natural selection has acted only on perceptual systems such as the sensory processing areas, but not on central, cognitive processing regions (e.g., the hippocampus), this is not the view of others (e.g., [Dwyer and Clayton, 2002](#); [Flombaum et al., 2002](#); [Hampton et al., 2002](#); [MacDougall-Shackleton and Ball, 2002](#)). At the least it would seem sensible to look for evidence that selection has or has not had a hand in shaping cognitive processing.

A more ethological view has driven much of comparative psychology and, more recently, cognitive ecology [such as work on learning and memory in food-storing birds (e.g., [Hilton and Krebs, 1990](#); [Bednekoff et al. 1997](#)), on cue use of sticklebacks living in different environments (e.g., [Girvan and Braithwaite, 1998](#)), and on shore crab prey handling (e.g., [Hughes and O'Brien, 2001](#))]. The cognitive abilities of a wide range of species have been investigated although these tests, too, have all been carried out in the laboratory. It is rare, however, for results gained in the laboratory to be compared with results from the field. And yet, the strict control allowed by laboratory investigations requires that some caution should be exercised in generalizing to evolutionary or ecological contexts. This is, in part, because such control requires many variables to be kept constant, made irrelevant or removed, often without knowing whether they are important to the animal.

There are, potentially, at least two advantages to investigating cognitive abilities in the field environment in which the animal lives. The first is that of gaining an understanding of the ecological or social demands that may act as selective forces on the cognitive abilities of the animal. The other is that tests of animals in the field, under “natural” conditions, offer the potential for insight into what it is that animals actually do rather than what it is they can do. This is important as it is in this situation that natural selection acts. Although we emphasize this second advantage, the rationale underpinning all our experiments is based on the first, as we believe that, to understand fully the workings of the brains of other animals, the mechanistic underpinnings elucidated in the laboratory (and perhaps in the field) will need to be married to the predictions produced from an understanding of the selective pressures under which the behavior of the animal has evolved and is maintained.

We have used foraging in free-living rufous hummingbirds, *Selasphorus rufus*, as a model system in which to assess cognitive abilities, particularly

learning and memory, in animals in the field [see also Gass and Montgomerie (1981) and Gass and Sutherland (1985)]. The value of this system is twofold: first, and possibly most important, are the logistic advantages. These are multiple: the birds (1) will feed from artificial feeders in preference to real flowers; (2) establish and vigorously and successfully defend a territory around the feeder; (3) can be individually marked by application of ink onto breast feathers (rings on the legs would not be visible); (4) can be watched from within a few meters without the use of a hide or other stealth, or binoculars; (5) come to feed regularly throughout the day (approximately every 10 min); and (6) learn rapidly (i.e., within 1–2 h) to feed from a wide variety of “feeders” and “flowers.” Furthermore, (7) once initially trained, the number, color, size, shape, location, and contents of these flowers can be varied without apparently disturbing the bird.

Ironically, the combination of all of these features results in a system that is close to an open-field version of a laboratory system. It is for this reason that we consider the hummingbird system useful and thus perhaps a model system for addressing questions concerning learning and memory in the field. Classic field experiments typically involve manipulating one feature or another in the environment of some animals and comparing the outcome of that manipulation with the behavior of animals that were not manipulated. A major assumption is that all other things are equal aside from the manipulated feature. Such an assumption is different from the approach used to assess learning and memory in the laboratory, in which each variable (sometimes even implausible ones) is kept either constant or, at the least, measured. Venturing into the field to test learning and memory abilities, then, means a compromise between the opposite desires of wanting to test animals under natural conditions and of wanting to be sure that the results are not due to one of many possible extraneous variables. The logistics of testing foraging in territorial rufous hummingbirds are such that this behavior appears to offer a compromise that will irritate both field zoologists and laboratory psychologists but may also continue the integration between the two groups that has been seen in song learning, imprinting, and food storing.

The second advantage to using foraging in hummingbirds for investigating cognition in the field is that the birds feed on flowers that would seem to require learning and memory in at least two ways: (1) because the flowers of different species vary in color, shape, size, location and content, the birds may learn their species-specific features; and (2) some of the flowers refill once emptied, but do so over the course of several hours. Foraging could thus be more efficient if they could avoid flowers emptied recently.

In the heyday of optimal foraging studies, the notion that these birds, or indeed any nectarivore, might use memory of flowers during foraging was not initially entertained. Rather, descriptions of decision making began with attempts to match the behavior of the animal to simple rules in the hope that once one understood how the animal made a single choice then subsequent choices could be accurately predicted. To a considerable degree such simple decision rules have been applied successfully to foraging in the hymenopterans, for example, the upward spiral visiting of flowers on an inflorescence by bees or the downward movement by some other species (Waddington and Heinrich, 1979). Sharing as they do with the hymenopterans many physical and behavioral characteristics, it was, perhaps, surprising that hummingbird foraging could not be described in the same, relatively simple ways (Hainsworth *et al.*, 1983; Pyke, 1981, 1984; Wolf and Hainsworth, 1990; for a possible exception see discussion of traplining by hummingbirds, e.g., Feinsinger, 1976; Gill, 1988; also see below).

However, unlike the hymenopterans, at least some species of hummingbird are territorial (Feinsinger and Chaplin, 1975, Kodric-Brown and Brown, 1978). Territoriality has been correlated with systematic foraging in other bird species [amakihi, *Loxops virens* (Kamil, 1978); pied wagtails, *Motacilla alba* (Davies and Houston, 1981)] and, in the sunbird *Leonotis nepetifolia*, such systematic foraging was estimated to enhance intake by as much as 25% (Gill and Wolf, 1977). One of the ways in which territory owners might use systematic foraging to enhance intake is to feed on the edges of their territories in the morning. As the edges are the most susceptible to conspecific intrusion, this early edge foraging followed by moving to the center of the territory as the day goes on should result in lowered nectar loss to intruders and a smaller area to defend later in the day (Paton and Carpenter, 1984).

This “defense by exploitation” might well be energetically much less costly than suffering the loss of nectar (intruders can be responsible for removing significant amounts; Yeaton and Laughrin, 1976) or of chasing intruders from within their territory (Gass and Montgomerie, 1981). Rufous hummingbirds en route to overwintering grounds appear to carry out such defense by exploitation, with foraging bouts during the early morning at one or a few plants near to the territory edge (Gass and Montgomerie, 1981; see also Sutherland *et al.*, 1982). Both this behavior and that of returning to feed at plants from which they have just chased off intruders (see Paton and Carpenter, 1984) would seem to require a far more flexible foraging technique than those typically described for the hymenopterans. Combining this foraging behavior with the observation that a territorial male spends the majority of his day sitting high up in a tall

tree from which he can survey all, or most, of his territory, led us to propose that foraging efficiency might be increased if the male could remember which flowers he has recently emptied in order to avoid revisiting them too soon. It is perhaps pertinent to point out here that defense by exploitation would not be successful if territorial hummingbirds chose which flowers to visit solely on the basis of their color, as has sometimes been suggested (see below).

I. LEARNING AND MEMORY

Systematic foraging by hummingbirds was first discussed with reference to traplining, a behavior in which the birds revisit frequently renewing flowers or plants apparently in some regular, routelike fashion, as fur trappers and bees do (Feinsinger and Colwell, 1978; Stiles and Wolf, 1979; see also Garrison and Gass, 1999; Gill, 1988). There has been some attempt at differentiating between traplining and territoriality in hummingbirds in terms of the morphological characteristics of birds (e.g., body size; bill length; wing disk loading, which affects hovering energetics; see Feinsinger and Colwell, 1978) and flower availability, as well as the spectrum of potential competitors, but it seems plausible that both foraging techniques would require at least a modicum of memory.

The maintenance of a trapline route may entail visiting a small number of flowers (usually dispersed "rich" flowers containing 70–120 μl of nectar per flower), whereas territorial hummingbirds (those for which there are quantitative data) defend territories containing at least several hundred flowers (Armstrong *et al.*, 1987; Gass, 1979). Nonetheless, unless it is supposed that trapliners can see the next flower to visit, or can remember the appropriate direction in which to fly from the one they are currently feeding on, these birds must remember the locations of flowers and possibly associate those locations with the time at which they were last visited. Unfortunately there are no substantial, quantitative data on traplining in hummingbirds, so we do not know the number of flowers, or the time intervals between visits, that characterize this kind of foraging, which is found particularly in the hermit hummingbirds. Territorial birds, on the other hand, may well be able to see all, or most, of the flowers in their territory from their guard post, although this is not very helpful with respect to foraging systematically. They, too, must remember which flowers or plants they have fed on and how recently.

Some of the first descriptions of learning and memory in hummingbirds come from Bené (1941, 1945), who showed that preferences for the color of a flower could be learned, irrespective of the common anecdotes

associating hummingbirds with an innate preference for red objects. Bené also described the rapid learning by a female black-chinned hummingbird (*Archilochus alexandri*) of an association between a new artificial feeder and its contents of dilute honey. After three successive trips to the feeder, the visual features of the feeder were dramatically changed, and yet on her fourth visit, the bird flew straight to the feeder and probed it. Bené changed the visual characteristics of the feeder several times, seemingly without affecting the foraging of the bird, before moving the feeder to a number of different locations in succession. Bené reported that, for up to four locations, the bird visited the previous locations in the reverse order to that in which they had been learned. Later, when as many as nine locations had been used, the bird no longer visited them in any apparent order but would take shortcuts between these previously rewarded locations. Although not totally compelling, these early data, along with an experiment by Lyerly *et al.* (1950), which tested color and position preferences in a Mexican violet-eared hummingbird (*Colibri thalassinus*), suggest that these birds pay attention to, and learn, the locations of food rewards, irrespective of their visual features.

A. COLOR AND ITS ROLE IN FLOWER CHOICE

More substantial subsequent experiments have shown that the anecdotal reports of hummingbirds visiting red flowers (or red objects of many kinds) are unlikely to be due to an innate preference for red but rather that birds learn an association between reward and the color of the rewarded location. So why is this preference for red still a common assertion? Grant (1966) put forward a hypothesis that seems plausible although it is still untested. Grant noted that the prevalence of red-colored flowers that are exclusively hummingbird pollinated was true for the Californian flora and perhaps, after Pickens (1930), also for the hummingbird-pollinated flora of eastern North America. However, this is not the case for tropical and subtropical America, which have many species of hummingbird apparently feeding from and pollinating flowers of colors other than red. Grant also noted that, of the hummingbird species found in California and eastern North America, six were migratory while the sole resident species (Anna's hummingbird, *Calypte anna*) typically makes postbreeding movements to higher elevations. Thus the flora that these birds are feeding on is frequently exposed to birds that are either simply passing through or making only a temporary stop. Grant supposed that it would be advantageous to both the plants and the birds for the flowers to be highly conspicuous (and most agree that for diurnal birds foraging in a somewhat open environment, red on a green background offers the highest contrast;

e.g., Ridley, 1930; Siitari *et al.*, 1999). Once the birds had learned that the conspicuous red flowers signalled reward, it would be beneficial for them to generalize from one red flower to another. It would also be advantageous for both parties (plants and hummingbirds) for the hummingbird-pollinated Californian flora to converge on the use of red rather than other colors. Support for this idea comes from Thomson *et al.* (2000), who found that the North American flowers that are visited by hummingbirds are more likely to be red or orange than are their close relatives that are visited by bees.

An additional possibility is that by using red the plants are also decreasing the detectability of their flowers by bees (Raven, 1972). Chittka *et al.* (2001) found that bumblebees took longer to find red flowers than to find blue or yellow flowers. The morphology of these hummingbird-pollinated flowers is also different from those typically pollinated by insects or bats, with differing flower structure and nectar content (both amount and concentration). Insects and bats are therefore inappropriate for pollinating these flowers, and plants would benefit by dissuading them. In spite of this some bees do rob hummingbird flowers. Other birds, such as songbirds, that are equally able to detect hummingbird flowers, are likely to learn to avoid them as a food source as they are unable to digest sucrose, the major component of the nectar of these flowers (Stiles and Freeman, 1993). However, experimental evidence, of the kind we have for the role of visual information in foraging and on the evolution of color vision in the hymenopterans (e.g., Chittka and Briscoe, 2001; Chittka *et al.*, 2001), is still sadly lacking for hummingbirds.

Because of the ever recurring discussion of the role of red coloration in hummingbird foraging (see also a parallel literature on coloration of fruits; e.g., Willson and Whelan, 1990), the most substantial investigations into learning and memory in these birds have involved presentations of differently colored feeders, often containing the same level of reward. All these studies have found both that hummingbirds will readily learn any given color, if rewarded for doing so, and that they quickly develop preferences for feeders in particular locations. For example, a number of the experiments have involved presenting birds with feeders in a line, and found that the birds always develop preferences for the feeders at the ends, even though they will also readily visit the other, intervening feeders. However, there is a problem with assuming that spatial cues are playing a more substantial role than color when considering the data collected in these experiments. Several articles describe this kind of experiment, and each apparently tested the same individual(s) on a series of occasions (e.g., Bené, 1941, 1945; Collias and Collias, 1968; Grant, 1966; Lyerly *et al.*, 1950; Miller and Miller, 1971). However, it is not possible to determine how

many birds were really involved in these experiments, as they were not individually marked. It was presumed that the birds were making return visits because the feeder visited on one trip was more likely to receive a subsequent visit. Visiting the feeder on the end of a row, however, may also be a result of that feeder being more conspicuous, or nearer to the place the bird(s) approach from.

Although it is likely to be correct that the birds in question were revisiting, one of the prerequisites for carrying out work on learning and memory, whether in field or laboratory, is that it must be possible to identify animals individually. Sometimes in the laboratory, and nearly always in the field, this means that animals must be marked, particularly animals like the hummingbirds, among whom individual differences in morphology are insufficient to discriminate between them. Making a comment at all about the need for individual recognition may seem patronizing, as it is a fundamental feature of most experiments on behavior in the field; however, it is a recurring feature of most of the fieldwork on learning and memory in hummingbirds that it has been carried out on unmarked individuals. Reading this literature might give the impression, inaccurately, that individual marking was not necessary.

The problem of determining whether the same birds visit the test flowers might explain the discrepancy between two studies examining the relative preference of hummingbirds for flower color and morphology (see below for a description). The intention of these studies was to examine the role that flower color plays in “pollination syndromes,” the elements that tie together a specific plant–pollinator coevolutionary relationship. Fixed (usually assumed to be innate) color preferences have long been assumed to be an essential component in this but, more recently, not least because of the consistent finding that pollinators (not just hummingbirds) will rapidly learn color–reward associations, it has been suggested that color merely plays a role in increasing the conspicuousness of the flower.

Morphological features, such as the size and shape of the flower, have been proposed as being more closely associated with the quality of reward offered and thus these elements are more likely to have been selected for in close association with pollinator morphology. [Meléndez-Ackerman *et al.* \(1997\)](#) allowed 6 captive hummingbirds to choose between 66 experimental flowers (*Ipomopsis aggregata* and closely related species), whose color, morphology, and nectar reward either varied naturally or, in some tests, were manipulated. When color was varied, but reward held constant, the initial preference for red disappeared in all birds (see also [Elam and Linhart, 1988](#), who found no discrimination by hummingbirds among differently colored *I. aggregata* flowers in the field). When color was held constant, birds preferred *I. aggregata* flowers to *Ipomopsis tenuituba*, and it

was assumed that birds were making this discrimination on the basis of variation in morphological features such as corolla width. Grant and Temeles (1992) showed that these birds extract more nectar from flowers with wider corollas (see also Lange *et al.*, 2000). These data, then, offered support for the notion that coevolution between hummingbirds and their flowers may be focused on flower morphology and content rather than color.

However, field experiments in which the same manipulations were carried out (Meléndez-Ackerman and Campbell, 1998) did not yield the same result. Birds preferred to visit red flowers throughout these tests, and when color was held constant, they did not discriminate among flowers on the basis of their morphological differences. The authors themselves raise the possibility that there is a “learning and memory” explanation for the difference between the results. Unlike the earlier study, in which individuals were tracked and birds were allowed to make more than 20 visits to each flower type, in this later experiment, not only were birds unmarked (although there were at least 2 of them as data were collected from 2 species) but only 11–18 visits were recorded in total. The suggested explanations for this difference were that (1) the birds in the first study had not had prior experience of one of the flower types used in the test, as that plant species did not occur in the area from which the birds were caught, or (2) the birds in the second experiment did not have enough experience with the test flowers to learn to discriminate between the flower types on the basis of their different morphological features. Neither of these possibilities can be excluded. In spite of these plausible explanations for the difference in outcome between the experiments, the authors effectively dismiss them by concluding that the color–nectar reward relationship is more important than morphological variation among flowers of different species.

This conclusion has potentially important implications for on-going discussions of plant–pollinator coevolutionary relationships, about the specificity of which there is a dispute (Aigner, 2001; Johnson and Steiner, 2000). If pollinators pay more attention to the color of flowers and/or learn this feature better or more quickly than morphological features, then one might also expect to see selection acting more strongly on color, a rather nonspecific floral feature. However, to determine whether the discrepancy between the experiments is a biological or a logistical one requires marking birds and following each individual’s choices, coupled with providing birds with equal experience of the two experimental set-ups.

Whatever the interpretation put on the data of Meléndez-Ackerman *et al.*, they are consistent with the suggestion by Grant (1966) that birds with brief access to flowers, such as when they are simply passing through

an area on migration, will use the most conspicuous cue to make flower choices. With increasing experience, however, birds will both use additional cues and learn to ignore the color information if it is incompatible with reward outcome.

Ironically, one of the studies with the largest sample of individually marked birds (22 wild black-chinned hummingbirds *Archilochus alexandri*) did not take individual performances into account when assessing discrimination abilities (Goldsmith *et al.*, 1981; Goldsmith and Goldsmith, 1979). In spite of this, the authors discuss whether the birds learned associations with reward, and whether red and green were learned at the same rate, as well as whether birds can simultaneously learn two conflicting color associations. They, too, seem to have found that birds developed strong location preferences and that the position of the feeder easily overrode the value of the color of the feeder to the birds. The authors claim that the birds learned red–reward associations at the same rate as green–reward association and that brightness was not used as a major cue. However, because the birds have a striking position bias and because individual data were not analyzed separately, these conclusions cannot be substantiated. Learning rates cannot be summed across individuals in this way—group data may mask wide variation in individual performance such that a majority of birds that learn rapidly, for example, may obscure the fact that some of the birds never learned or made the discrimination at all. At this stage, then, wavelength discrimination by black-chinned hummingbirds (or, indeed, any hummingbirds) has yet to be adequately investigated.

Another study that also used marked birds and assessed learning of cues was that carried out by Sandlin (2000a; see also Sandlin, 2000b) to investigate the relationship between cue use and competitor density in foraging decisions made by males and females of three species of hummingbird (black-chinned hummingbirds, *Archilochus alexandri*; blue-throated hummingbirds, *Lampornis clemenciae*; and magnificent hummingbirds, *Eugenes fulgens*). However, just as in the studies by Goldsmith and co-authors, surprisingly, effort was put into marking the birds and then these marks were not used to distinguish the data within and between birds. It is not clear whether the data presented are fair representations of the behavior of the birds, or how many birds participated in the experiments, even though the experiment purports to investigate the role of reliable versus ambiguous cues in foraging decisions, yet another question that is reliably addressed only by collecting data from individuals. The reliable cues were given by blue symbols on feeders providing a rich (30%) sucrose source and yellow symbols on a poorer (15%) sucrose source while the ambiguous cues were symbols with quarters in blue and

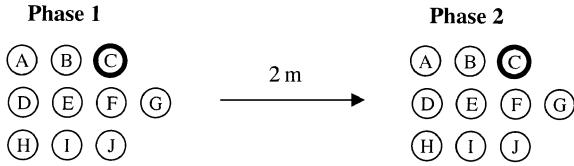
yellow. The birds were presented with arrays of 10 feeders for several 30-min periods each day. The arrays had either 5 yellow and 5 blue feeders or 10 “ambiguous” feeders. The colors were kept constant both across days (six trials in a day) and through the field season. Locations, however, were changed at the beginning of each trial, so birds were trained, effectively, to pay more attention to the color rather than to spatial cues. Nonetheless, although the birds were less likely to feed from the rich feeders when the visual cues were ambiguous, when competition was low their performance was conspicuously better than by chance.

One explanation for this result is that, rather than differentiating between reliability and ambiguity, as was the intention, the birds were being offered feeders that, by their color, required no additional learning of the color–reward association after the first trial or feeders that were differentiated only by their locations, which had to be learned anew on each trial. Even though the responses of the birds were sorted only by species, they appear to have learned the color–reward association rapidly and well, as they nearly always chose the blue feeders when these were offered, a result that is consistent across trials and days and one to be expected if the cue is reliable across time. However, in the ambiguous color trials the birds also seemed to have learned the location–reward associations, information about which was available only during the half-hour of testing. This experiment, therefore, seems to have added at least as much to the literature on the rapid rate at which these birds learn information about reward locations, irrespective of the location’s color, as it has to the role of reliability in information acquisition during foraging (see also [Biegler and Morris, 1996](#); [Roberts and Pearce, 1998](#)).

Color is, undisputedly, a cue that these birds use when foraging. However, from these rather uncontrolled experiments, as well as from experiments we have carried out (detailed below), color seems to be used in a way that fits well with the suggestion by [Grant \(1966\)](#) that the use of this cue by these birds is context dependent. When birds are in unfamiliar territory, such as on migration, they depend heavily on flower color when making decisions about which flowers to visit.

However, territorial birds, such as the rufous hummingbirds resident throughout the breeding season in the foothills of the Rocky Mountains in Canada, pay little attention to color, at least under some circumstances. Some of the evidence we have to support this comes from a series of experiments we carried out with a 10-flower array. In some testing situations, there was a single rewarded flower (containing 20% sucrose solution) and nine flowers that were either empty or contained water (which the birds find somewhat aversive and will spit out), while in other experiments there were three rewarded and seven unrewarded flowers (see

(a) One rewarded flower



(b) Three rewarded flowers

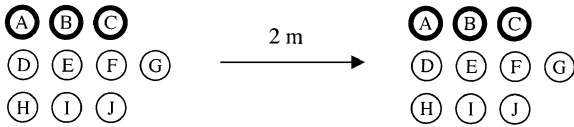


FIG. 1. Schematic array of 10 flowers used to determine the role of color pattern in rufous hummingbird memory for flowers. In (a) 10 flowers were presented, each with a different color pattern (designated by the different letters). One of the flowers contained sucrose (designated by the boldface circle) while the other flowers contained water. Once the bird had learned which was the rewarded flower (phase 1), the array was moved 2 m (edge to edge) and the bird observed until he had learned which flower contained reward (phase 2). In this example, the flowers are the same color patterns and in the same array positions in phase 2 as they were in phase 1. In (b) the same procedure was followed, but three nearest neighbor flowers contained reward and seven contained water. (From Hurly and Healy, 2002.)

Fig. 1; Hurly and Healy, 2002). Each bird tested was an individually marked territorial male.

During testing only the focal male visited the array of flowers and he received each set of trials consecutively. We found that when flowers each bore a unique color pattern (two colors in geometric patterns), the birds learned with fewer errors which were the rewarded flower(s). Once the bird had learned which were the rewarding flowers we shifted the array 2 m from the original location and presented him with either exactly the same array (as depicted in Fig. 1) or an array with either the flowers' color patterns, the position of the rewarded flowers, or both, altered. We reasoned that, if the bird remembered both what the flower looked like and where it was in the array, then if neither had changed (apart from the location of the entire array) he would learn which were the rewarded flowers with fewer errors in this second phase of a trial than in the first phase.

In some tests birds did learn with fewer errors in phase 2 but only when either position alone or both color and position were unaltered. We tried a number of different array manipulations (e.g., leaving rewarded positions the same, changing flower colors, rearranging the flowers within the array) in order to show that the birds did remember flower color pattern, but

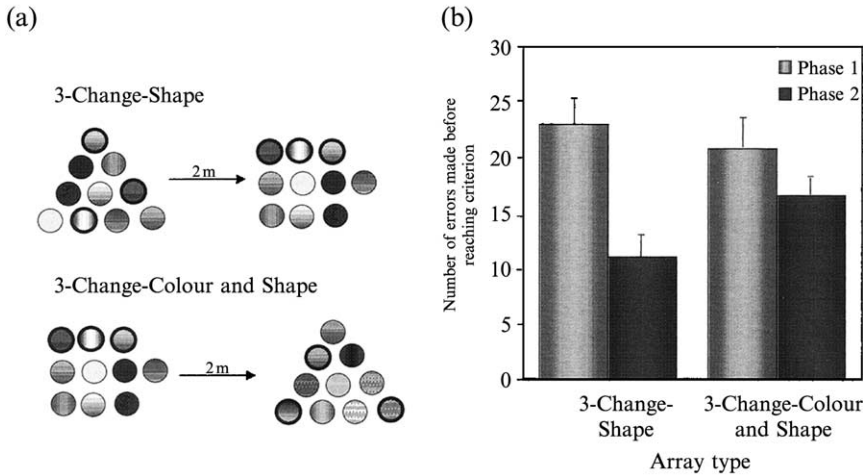


FIG. 2. (a) Schematic of two arrays designed to prevent any spatial information used in phase 1 from being used when learning which were the rewarded flowers (three, designated by boldface circles) in phase 2. In the first array, flowers retained the same color patterns between the phases while in the second array, the flower color patterns were unique in the second phase. (b) Mean number of errors (\pm SE) made before reaching criterion in the two phases for each array. Phase 1 is represented by the shaded columns and phase 2 by the solid columns ($n = 10$ males). The difference between the phases was significant for 3-Change-Shape ($p = 0.001$) but not for 3-Change-Colour and Shape ($p = 0.10$). From Hurly and Healy (2002).

these were all to little avail if there was any kind of spatial cue available. To show that birds do remember color information in these kinds of tests, we had to present the birds with arrays containing the same flowers but in differing array shapes (see Fig. 2).

We had found a similar result in a previous test, in which the bird had to learn the positions of 8 rewarded flowers in an array of 16. Arrays contained flowers that were either all the same color or were all of different colors. In half the arrays the flowers were 10 cm apart, and in the other half they were 80 cm apart. When the flowers were all different colors the birds learned which contained rewards with fewer errors than when the flowers were all of the same color. The distance between the flowers had no effect on the speed of acquisition. Once a bird had learned which were the rewarded flowers, the arrays were moved as shown in Fig. 3, such that half the flowers were in new locations but the remainder were in previously occupied locations. When the bird returned to the array his visits were recorded. There was an effect of having moved the array in all four array types but the major effect was due to the distance between the flowers. Birds did not appear to use information pertaining to flower color

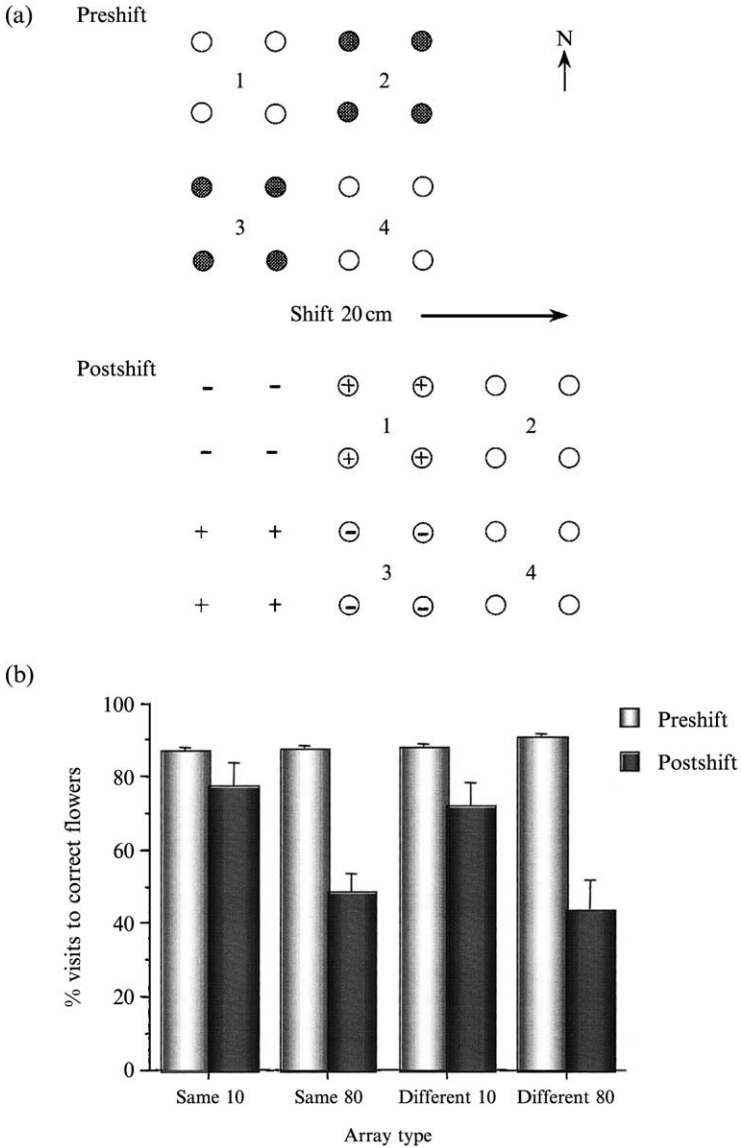


FIG. 3. (a) Schematic of an array of 16 flowers, in which 8 flowers contained sucrose (shaded circles) while 8 flowers contained water (open circles). Once a bird had learned which flowers contained reward to a criterion of 80% or greater, the array was shifted such that half of it occupied half of the locations of the preshift array (designated by the circles overlying half of the plus symbols and half of the minus symbols). The plus symbols represent locations (relative to landmarks outside the array) of flowers that had been previously rewarded and the

pattern once the rewarded locations were known (see Fig. 3 and discussion later).

This clear use of color information to learn locations more rapidly but not to improve, or to be required for, subsequent recall of those locations, is somewhat akin to the phenomenon of potentiation (Batsell *et al.*, 2001). Potentiation has also been invoked to explain the coupling of nonaversive odorants with bright coloration in aposematic insects (Guilford *et al.*, 1987; also see Rowe, 2002). Naive predators encountering a novel, brightly colored unpalatable prey that also smells (not necessarily unpleasantly) learn to avoid the new prey faster than if the prey is odorless. Once the association is learned the odor does not have to be present for prey avoidance to be observed. Investigation of potentiation in the psychological literature has also typically been with odor as the potentiating stimulus (e.g., Durlach and Rescorla, 1980; Rusiniak *et al.*, 1979; Slotnick *et al.*, 1997). The color augmentation of location learning seen in our hummingbird experiments is, to our knowledge, the first example of a visual cue potentiating a spatial location–reward association.

The question as to whether hummingbirds might have innate color preferences has not yet been properly addressed. The evidence that, like butterflies (Weiss, 1997, 2001), hummingbirds will learn associations between color and reward readily (Hurly and Healy, 1996) does not rule out the possibility that there are innate preferences as well. Given the greater likelihood of coevolution between hummingbirds and plants in the tropics, perhaps species from this region or further south would be more profitable to test. Given the requirement for captive raising in order to properly address this question, however, it is likely to remain unanswered for the foreseeable future.

II. SPATIAL LEARNING AND MEMORY

It seems odd that the role that color plays in both hummingbird foraging and, by extension, plant–hummingbird pollination syndromes continues to

minus symbols represent locations of flowers that previously contained water. (b) The proportion of visits to correct flowers (means \pm SE) by birds before the shift (lighter columns) and following the shift (darker columns). There were four array types: two in which all the flowers bore the same color pattern (Same 10 and Same 80) and two in which each flower bore a unique color pattern (Different 10 and Different 80); two arrays had flowers 10 cm apart while the other two arrays had flowers 80 cm apart ($n = 4$ males). Postshift performance was significantly more affected ($p = 0.01$) when flowers were 80 cm apart than at a spacing of 10 cm. (From Healy and Hurly, 1998.)

attract attention, given that the most consistent finding in hummingbird foraging is that they pay much more attention to the location of a flower. [Miller *et al.* \(1985\)](#), testing rufous hummingbirds in a laboratory, found that even striking changes to the visual aspects of feeders did not affect which ones the birds preferred to feed from. A common anecdote is also that migrant hummingbirds appear at locations where feeders had been supplied the previous year, thus providing the stimulus for the feeder to be retrieved from the cupboard in which it has spent the winter, filled, and made available to the birds.

One possible explanation for the emphasis on the use of color cues, to the neglect of memory for spatial locations, may be that optimal foraging theory (OFT) has played an important and influential role in setting the questions asked about foraging decision making in a range of pollinators, so that the kinds of information use incorporated even into more recent models has been rather simplistic. In addition, much of the modeling has focused on decision rules that birds might use to decide when to leave a patch rather than which patch to visit next [see, e.g., [Gass and Montgomerie \(1981\)](#) and [Armstrong *et al.* \(1987\)](#)]. It may also seem unparsimonious to assume that animals may remember many locations, rather than use some computationally simpler technique such as movement rules or to visit all conspicuous objects. Some models have also assumed that birds retained memories for flowers in a patch only until they began foraging in the next patch (e.g., [Armstrong *et al.*, 1987](#)). Color is simply a much more obvious cue to investigators than is memory of the location of a flower. However, all the attempts to show that the hummingbirds use the kinds of rules that have featured in OFT models have failed, and the consistent outcome is always that the birds use information gained on previous visits ([Pyke, 1981](#); [Valone, 1992](#); [Wolf and Hainsworth, 1990](#)).

While the incorporation of learning and memory into these models has taken some considerable time, the idea that an ecological approach might provide insight into learning and memory has been around and productive for at least two decades. [Garcia *et al.* \(1966\)](#) found that rats could learn to avoid a novel food that had been associated with an aversive outcome (long delay taste aversion learning). This association was a precise pairing between the novel taste and smell of the food with the ensuing illness. Psychologists subsequently termed such specific associations “constraints on learning.” This label was used in recognition that the general principles of learning assumed to underlie all learning, did not always apply. It has since been developed into the notion of “adaptive specializations” of learning and memory, that is, the evolution of ways of processing, storing, and using information in a functionally appropriate manner ([Krebs, 1990](#); [Shettleworth, 1998](#)).

The most thoroughly worked example of an adaptive specialization to date is that centered around the hypothesis that food storing is associated both with an enlarged hippocampal region (the area of the brain subserving spatial memory) and with enhanced spatial memory (Krebs *et al.*, 1989; Olson *et al.*, 1995; Shettleworth, 1990). But an ecological adaptation approach was first applied to hummingbird cognition by Cole *et al.* (1982). Given that flowers do not immediately replace their nectar once emptied, they suggested that hummingbirds might use their memory for recently visited flowers to avoid them in the near future. They predicted that these birds might find it easier to learn to visit a flower in a new location (win-shift) than to return to a flower in the same location (win-stay). Cole *et al.* tested three species and all the birds learned to win-shift much faster than to win-stay. Even on the first day of training the birds were more ready to shift than to stay and the subsequent rate of improvement on shift trials was also faster.

In a field version of equivalent tasks, including both a delayed nonmatching-to-sample task and a delayed matching-to-sample task, we found similar results (Healy and Hurly, 2001). This ability to acquire a win-shift rule more readily than a win-stay rule is not, however, confined to hummingbirds. Rats, pigeons, pigs, and tits are also much faster to learn a nonmatching-to-sample rule than a matching-to-sample rule (e.g., McGregor and Healy, 1999; Mendl *et al.*, 1997). It has been argued that animals should respond flexibly to whether or not a food patch depletes and to the scale over which resource depletion occurs. Cole *et al.* (1982) suggested, for example, that, as birds might view patches of inflorescences as a resource that was effectively not depleting, they may more readily learn to win-stay in such situations.

The birds do, clearly, learn to return to profitable locations both over shorter time periods than a normal flower would take to refill and also after intervals that are considerably longer (witness their fidelity to artificial feeders, both within a season and even after a winter spent in Mexico). They also pay attention to spatial scale. In 2 field experiments using arrays of 5 or 16 flowers, we found that birds used a different spatial scale to remember which flower(s) contained reward depending on how close these flowers were to each other (Healy and Hurly, 1998; Hurly, 1996; see also experiments on scale in relation to spatial associative learning: Brown and Gass, 1993; Brown, 1994). Birds were presented with arrays in which there were either 1 of 5 flowers containing sucrose or 8 of 16. In different trials, flowers were presented at different distances from each of the nearest neighbors. Once the bird had learned which were the rewarded flower(s), the array was shifted such that half of it overlapped previous flower locations. When the flowers were separated by 40 cm or

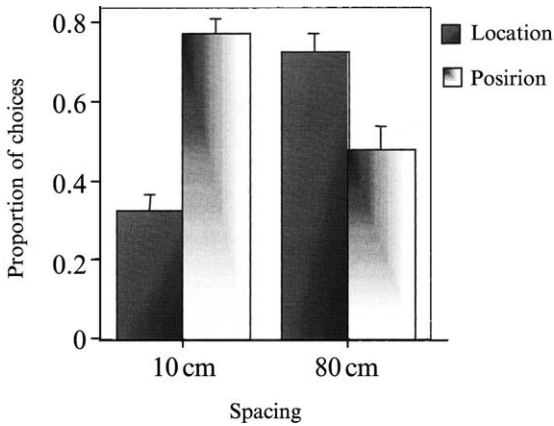


FIG. 4. Proportion of choices (means \pm SE) to visit flowers in either the location (darker columns) or in the position (lighter columns) they occupied in phase 1. When flowers were spaced 10 cm apart, birds were more likely to visit flowers in the appropriate position and when flowers were 80 cm apart, birds were more likely ($p < 0.0001$) to visit flowers in the appropriate location (as defined by landmarks outside the array; $n = 4$ males). (From Healy and Hurly, 1998.)

less, the birds visited flowers in the shifted array that were in the appropriate position in the array (i.e., using other flowers in the array to make flower choices), but when the flowers were more distant, they visited the flowers in the appropriate location (i.e., using landmarks outside the array to make flower choices; see Fig. 4 and Hurly and Healy, 1996).

The fact that the birds appear to pay attention to, and/or remember, cues based on their spatial scale may have an ecological basis: some of the flowers they feed on are close together, such as inflorescences on a single stalk, whereas others are somewhat further apart, such as flowers found on bushes, and still others are single flowers separated by tens or hundreds of centimeters. It would seem “sensible” for the birds to use a hierarchy of spatial scale if the flowers are close together, such as “encode and remember where the plant is in the field, then remember roughly where on the plant flowers have been visited.” In one experiment we presented birds with arrays in which the rewarded flowers either were nearest neighbors or were dispersed around the array with at least one intervening flower between them (Hurly and Healy, 2002). The birds learned more quickly which were the rewarded flowers when the flowers were nearest neighbors than when the rewarded flowers were dispersed around the array (see Sutherland and Gass, 1995, for a laboratory demonstration of this effect). It is not clear whether this is because the birds learn to fly a simple pattern from one flower to another or whether it is due to them “chunking,” or

grouping, the rewarded locations together in memory, perhaps as a particular pattern or simply a general region of the array (Dallal and Meck, 1990; Macuda and Roberts, 1995).

When the flowers are in close proximity, the costs of revisiting a flower that has not yet refilled or missing a flower that has not been visited is probably minimal. When the flowers are far apart, however, the cost of making a mistake is likely to be higher. We suggested this as an explanation for a counterintuitive result we found when we tested birds in the following way: they were presented with a red or a yellow flower (half the birds got red, the others got yellow) that contained too much sucrose to empty on a single visit (Hurly and Healy, 1996). When each bird had left the flower, we refilled it and added a second. The second flower was either 3, 40, or 80 cm from the original flower, and it was either the same color or the alternative color. This second flower contained water. The counterintuitive result was that, when the flowers were of the same color, birds were more likely to choose correctly the original flower the closer the flowers were together (Fig. 5). This was particularly striking given that the closest distance was 3 cm, which meant the flowers were actually touching each other, implying high levels of spatial accuracy. When the flowers were 80 cm apart the birds tended to be more likely to choose the new flower, even though they were never rewarded for doing so (see Fig. 5).

We suggested that the birds knew which was the flower that definitely contained a reward, but it was to their advantage en route to the known source of food to check out new, distant flowers (sampling) when they appeared. Plants may use the spacing of flowers as a way of manipulating their hummingbird pollinators. When flowers are close together, the plant could present empty as well as rewarding flowers, which would not dissuade the bird from continuing to forage on that plant because of the small price paid by moving to another nearby flower.

On the other hand, widely spaced flowers may be more noticeable (in the sense of being surprising rather than literally more conspicuous) and thus more likely to be visited than flowers seen on previous occasions. We tested whether male rufous hummingbirds treat new and seen but previously unvisited flowers differently by presenting them with three different types of array: “free,” “forced,” and “mixed” (Henderson *et al.*, 2001). This experimental design was a variation on an open-field radial maze we had first used to show that rufous hummingbirds could remember, and avoid, flowers (Healy and Hurly, 1995). In free arrays, the bird was faced with eight flowers arranged in a circle and each containing 15 μ l of sucrose (an amount that requires the bird to visit several flowers before his crop is filled), and he was allowed to visit four flowers before being chased

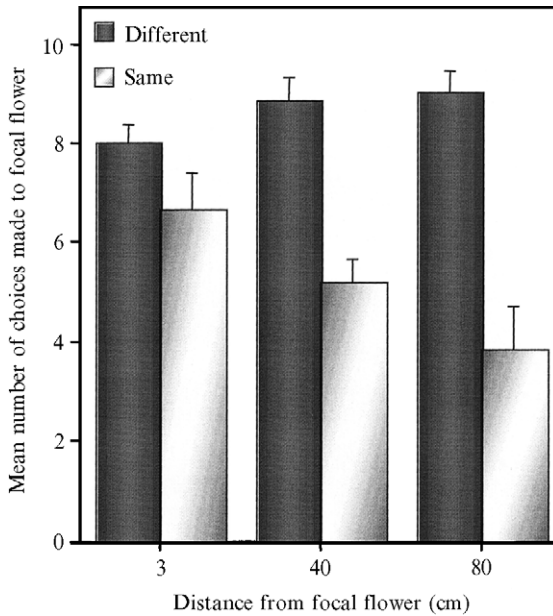


FIG. 5. Mean number of choices (\pm SE) made to visit the focal flower when the alternative flower was either of the same (lighter columns) or different (darker columns) color and either 3, 40, or 80 cm from the focal flower ($n = 6$ males). There was a significant interaction between color and distance ($p = 0.0001$). When the distracter flower was a different color, there was a significant negative relationship between distance and performance ($p < 0.05$). (From Hurly and Healy, 1996.)

from the array. In forced arrays, there were only four flowers containing $15 \mu\text{l}$ of sucrose, so he was forced to visit the flowers we chose for him. In mixed arrays, he was presented with six flowers all containing $15 \mu\text{l}$ of sucrose, but allowed to visit only four. In all array types he was prevented from returning for at least 5 min (this was the minimum retention interval; he could return at any time after 5 min), and his choice of flowers on this return visit was recorded. When he did return he was presented with eight flowers, four containing sucrose and four empty. In the free trials, the sucrose-containing flowers were the four flowers he had seen previously but not visited; in the forced trials, the rewarded flowers were all new; in mixed trials, two of the rewarded flowers were ones he had seen and not visited while two were new. There were no differences in the performances of the birds on the different trial types, but on the mixed trials birds were much more likely to visit new flowers than flowers they had seen but not visited on their earlier trip to the array. It appears as if birds are not only remembering and avoiding recently emptied flowers, they are also taking

note of flowers in the vicinity that have yet to be visited. It may be that not only are new flowers more noticeable but they, by their very recency, are less likely to have had their contents reduced or lost to dehydration or to other nectarivores.

Once the location of the flowers is learned, radical visual changes can be made and the bird ignores them (e.g., Miller *et al.*, 1985; Healy and Hurly, 2001; Hurly and Healy, 1996). Although we have not quantified it, we saw a dramatic example of how major the visual changes could be: when arrays with the flowers spaced at 80-cm intervals were moved in the experiments described in Healy and Hurly (1998), on a number of occasions birds flew to, and hovered, at apparently the appropriate (in x , y , and z coordinates) place for a rewarded flower that was now some 160 cm distant. After failing to gain reward at this location, the bird often flew off, apparently oblivious to the presence of the shifted array, even though there were no visual obstacles to prevent him seeing it.

This observation led us to investigate the use of a spatial component that has rarely been examined in any animal: the use of the z coordinate when encoding or remembering a spatial location. Wolf and Hainsworth (1990) and Blem *et al.* (1997) both found that hummingbirds preferred higher rather than lower flowers. Blem *et al.* favored a predation avoidance interpretation, but we suggested that higher flowers might be more conspicuous as they were less likely to be visually impeded by undergrowth. We also suggested that height variation among flowers might make each more discriminable as well as memorable. As a preliminary investigation into the role that flower height plays in hummingbird foraging, we presented birds with either four or eight flowers, in forced or free trial types as described above, in four x - y locations at one of two heights, in another variation of the open-field radial maze (Henderson *et al.*, 2001). In both trial types the expectation was that, if the bird could remember which flowers he had recently emptied, he would avoid those four and visit the four remaining flowers (in the free trials) or the four new ones (in the forced trials). In support of the finding by Blem *et al.*, we found a slight preference for visiting the higher flowers when the bird returned to the array in free trials, but this was not the case in forced trials. Birds were, however, significantly better than random chance at avoiding the flowers they had recently emptied, a result that would have been obscured if the birds had strong height preferences. Although they tended to avoid emptied flowers slightly more on free trials than on forced, this difference was not significant. As the bird can choose when to return to the array (in this case, the range was between 5 and 32 min), we also looked at whether or not performance was affected by the length of retention interval. For this range of durations at least, performance did not decline with increasing time since the bird's first

visit. If the birds do remember which flowers have been recently emptied, it would be advantageous to avoid them at least until the flower has refilled to a significant level. In this experiment we did not have control trials in which height was not varied, so we cannot determine whether birds are better able to remember a three-dimensional (3-D) location than a two-dimensional (2-D) one.

A direct comparison of performance on 2-D and 3-D mazes has not been carried out in any species as yet, although [Brown \(1994\)](#) and [Brown and Gass \(1993\)](#) presented birds with vertical arrays of feeders and we have presented birds with horizontal arrays of flowers. This may be, in part at least, because the classic animal used to investigate spatial memory, the rat, lives a largely two-dimensional life. This 2-D life notwithstanding, when [Grobéty and Schenk\(1992\)](#) tested rats in a 3-D maze and also compared performance in 2-D mazes that were either horizontal or vertical, they found that in both the maze types with a vertical component, the rats appeared to pay more attention (measured as making fewer errors) to the vertical dimension than to either of the horizontal dimensions. This they interpreted as being due to an increase in the energetic demands of climbing up or down for these animals, which it would pay them to minimize relative to moving in the horizontal plane.

This problem of energetic cost is also one faced by flying birds. In species such as hummingbirds it is enormously costly to hover ([Chai *et al.*, 1999](#); [Chai and Millard, 1997](#)), while for other avian species in flight it is costly to climb ([Piersma *et al.*, 1997](#); [Thomas and Hedenstrom, 1998](#)) as it may well also be for terrestrial arboreal animals. In fish, except for bottom dwellers such as catfish, however, moving up and down in the water column entails no more energetic effort than moving in the horizontal plane. Alternatively, it may be that moving vertically is novel for the rats and they pay more attention to novel information than do animals that regularly traverse a 3-D environment.

It remains to be seen, then, whether there is a difference between aerial/terrestrial animals and fish in the amount of attention they pay to the vertical dimension relative to the horizontal dimensions and whether this is related to novelty or to energy expenditure. Ecological and morphological variation aside, it seems plausible to us that locations that are differentiable in three dimensions rather than just two should be more memorable. However, all these possibilities require experimental testing.

It seems plausible that, like the horizontal components, the vertical component to a location may be encoded with regard to spatial scale, that is, flowers that are close together are remembered relative to other flowers on the plant while flowers that are vertically far apart may be remembered relative to landmarks beyond the plant. [Wiegmann *et al.* \(2000\)](#)

investigated relational and absolute height learning in bumble bees (*Bombus impatiens*), by training two groups of bees to forage from a flower at the same height. For the bees in one of these groups the rewarded flower was presented alongside a higher, empty flower. The test was the presentation of two unrewarded flowers, one at the trained height and the other at a lower height. The bees with experience of flowers at only one height chose the higher flower, that is, the one at the training height. Of the bees in the group exposed to flowers of two different heights, those that had never visited the unrewarded flower during training also visited the higher flower in the test, but those bees that had visited both during training chose the lower flower in the test. Some of the bees, then, appeared to have encoded the correct height of the flower in relation to its immediate surroundings. This is somewhat akin to the way in which the hummingbirds seem to encode locations that are less than 40 cm apart horizontally (as were these bee flowers vertically). We have yet to test whether the hummingbirds treat the vertical component to a flower's location in the way these bees did.

III. COGNITIVE MAPS

One of the aspects of spatial cognition we have not dealt with explicitly in our experiments on hummingbirds is that of cognitive mapping. There are a number of methods by which animals may navigate from one location to another. The methods for which there is the most convincing evidence are those that might be generally labeled as "route retracing," for example, following a chemical trail, or path integration, which does not require literal retracing but does entail use of distances and directions from the outward journey to calculate the current position.

Occupying something of a superior position in the hierarchy of navigation methods is cognitive mapping (see [Healy *et al.*, 2003](#), for a review). Many aspects of cognitive mapping have been debated, not least its definition, but most agree that a cognitive map is a neural representation of the spatial aspects of an animal's familiar environment. The especial advantage of possessing such a map of one's environment, over other navigation techniques, is that an animal is able to plan optimal routes, and, more especially, to take shortcuts and detours.

Whether nonhuman animals have, or use, cognitive maps has been hotly disputed, particularly in the hymenopterans, sparked off by the claim that bees used cognitive maps during foraging ([Gould, 1986](#); and see, e.g., [Dyer, 1991](#); [Kirchner and Braun, 1994](#); [Menzel *et al.*, 1998](#)). Thus far we claim that rufous hummingbirds use spatial memory. We might also claim that the ability to take short cuts and to plan routes around his territory, before

foraging flights, would also be advantageous to a male whose days are consumed by watching out for females and in intense territorial defense. The result we discussed earlier, that birds more readily learn rewarded locations when these are nearest neighbors, however, is consistent with an alternative possibility, which has been proposed for navigation in the hymenopterans. This is that these insects use “snapshots” or visual images of their environment, either alone or in a series, to return to rewarded locations or home (Cartwright and Collett, 1983). Each snapshot is paired with a compass direction and therefore when the current view matches a snapshot in the album, the animal knows which way to go, either to reach home or the next snapshot.

We have explored this issue little to date, due, in part, to the difficulty of presenting birds with hidden goals, the most common method of determining the mechanism by which the animal reaches a goal. Some clever testing on the possible use of cognitive maps by animals has been done using Clark’s nutcrackers, *Nucifraga columbiana* (Gibson and Kamil, 2001; see also review in Healy *et al.*, 2003). In these experiments, the birds were trained to locate a goal hidden within a large (diameter, 132 cm; height, 154 cm) steel cylinder that had an opening along 90° of its wall to allow the bird to enter. The cylinder was placed in a larger experimental room (4.4 × 3.0 m), such that the birds, when at the goal in the cylinder, could see only some of the landmarks placed around the room. The test involved turning the cylinder such that some, or none, of the landmarks previously seen at the goal, could be seen during the test. The supposition was that if the birds were using a cognitive mapping strategy they would use their memory of room/landmark panorama to localize the goal, even though at test the panorama only partly matched (or did not match at all) the training view. Under most of the test conditions the birds were accurate at locating the goal, but Gibson and Kamil are cautious about concluding that the birds use a cognitive map mechanism, as the birds’ searching patterns are also consistent with calculating distance (from the wall of the cylinder) and direction (from the landmarks outside the cylinder, before entering) independently. The interpretation of the results of this study, beautifully designed as it is, demonstrates the difficulty of determining conclusively whether animals use a cognitive map.

We used a similar kind of apparatus to examine whether our birds used a simpler technique than a mapping strategy to locate the reward flowers in an array, that of a learned route. Birds were trained to fly into a large cage of semirigid netting that enveloped an array of 16 flowers, 40 cm apart, 3 of which contained sucrose solution. In one treatment there was only one entrance to the cage and this remained the same throughout training, while in the second treatment there was an entrance on each of the four sides of

the cage and the birds could choose through which they wanted to enter and leave. Once the birds had reached a criterion level of performance, they were tested with only one of the cage doors open. For the birds trained with only one door open, the test door was a different one. In all cases, the birds could view the surrounding landscape through the walls and roof of the cage. Although these birds do not normally forage in a set movement pattern, it may be that when a location is frequently visited, a similar approach flight path is taken.

The hymenopterans are well known for using stereotyped approach directions when returning to rewarded locations, and we thought it possible that the hummingbirds were doing something similar, even though they do not use the “turn back and look” strategy used by bees when learning both about the location of the have and of rewarding flowers (e.g., Capaldi *et al.*, 2000; Collett and Zeil, 1998). In this experiment we assumed that the birds trained with a single door open would be more disrupted by the test condition (i.e., where they are forced to use a different entrance and therefore final approach direction) than those trained with all the doors open. In fact, all the birds were no better than chance at locating the reward flowers on the test. Whatever the explanation for their behavior, they showed no hint of using a cognitive map strategy (i.e., in this case, using the landmarks surrounding the cage to localize the rewarded flowers).

IV. TIMING

Although we have focused much of our attention on the ability of rufous hummingbirds to learn and to remember visual or spatial information about the flowers they feed on, an integral component of their ability to avoid flowers they have emptied recently is the capacity to remember when it was that they visited that flower. The question of whether animals measure time now encompasses a huge literature, much of which is especially concerned with seasonal changes such as those involved in breeding and migration (for reviews see Aschoff, 1989; Gallistel, 1990; Gwinner, 1986). While hummingbirds undoubtedly carry out some kind of endogenous tracking of circannual changes, it is their ability to time shorter durations in which we are specifically interested.

There are thought to be two different mechanisms for timing such shorter durations: *phase sense* or *timing*, by which the animal can learn the time of day (as in a 24-h period) at which an event regularly occurs, and *interval sense* or *timing*, by which an animal can learn a fixed duration between two events that themselves can occur at any time during the day. The ability to associate time of day with a specific location (time–place

learning) has been seen in foraging both in the field (e.g., oystercatchers, *Haematopus ostralegus*, foraging on tidal mudflats; Daan Koene, 1981) and in the laboratory (e.g., garden warblers, *Sylvia borin*; Biebach *et al.*, 1989). It is possible that this is what hummingbirds are doing if they are defending their territories by exploitation as we discussed earlier, that is, they go to the edges of their territories each morning in order to deplete the flowers there. The question as to whether they might be able to remember when they emptied flowers, especially those that are not on their territory boundaries, seems, however, to be an interval timing problem. Timing of intervals is thought to be used when there is no fixed time of day associated with a significant event, as with, for example, emptying a flower. Rather, when an appropriate interval has elapsed (e.g., 3–4 h), the bird could then return to a refilled flower. Each flower, or plant, would be associated with a timer that is started once the bird leaves the flower.

There are at least two issues that arise here with regard to proposing that hummingbirds use interval timing in deciding which flowers to avoid: (1) a bird doing this accurately would have to keep track of at least several dozen, and possibly as many as several hundred, timers all running concurrently; and (2) as the precision of interval timing is proportional to the interval being timed, the ability of the bird to time flowers that were emptied several hours previously (the time thought to elapse before total refilling; Armstrong *et al.*, 1987) is likely to be quite poor.

That they are able to measure time at all was shown by Gill (1988) in long-tailed hermit hummingbirds (*Phaethornis superciliosus*), which were at least capable of learning 10- and 15-min fixed interval reinforcement schedules. Gill presented birds in the field with up to three feeders, which were refilled at fixed intervals (FI, either 10 or 15 min) after the last successful visit. In addition, Gill doubled the amount of nectar if the FI passed without the feeder being emptied (e.g., at 15 min on a 10-min FI schedule) and emptied the feeder if the bird did not return within 20 min after the FI. One bird that dominated one of the feeders returned after the feeder had been refilled and so obtained nectar on 88% of visits. The return intervals of this bird also increased to longer than the FI schedule, which increased the amount of nectar obtained on each visit. At one of the feeders the dominant male had to compete at reasonably regular intervals with another male. The visits of the dominant male were characterized by losses of two kinds, either losing to his competitor or returning too early so that competitive losses were negatively correlated with timing losses. These hummingbirds, then, under conditions of no competition such as a territorial bird might face, can time intervals of 10 and 15 min, and they learned to do so within a morning.

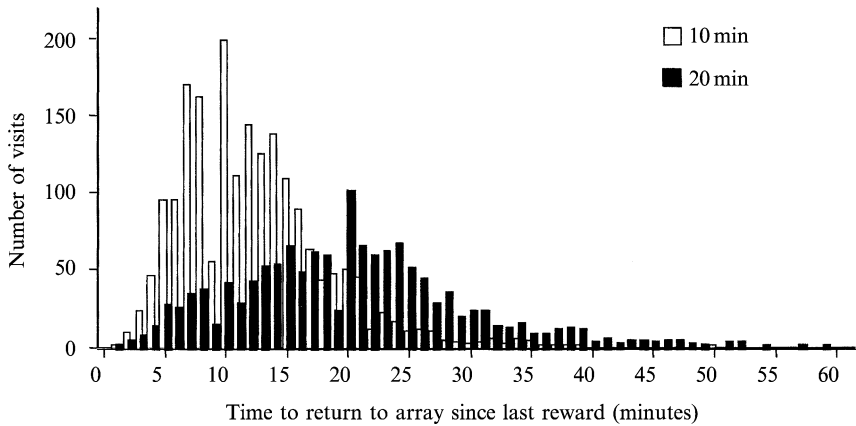


FIG. 6. The time intervals between visits to eight flowers in an array by one bird. Four of the flowers were refilled 10 min (open columns) after the bird had emptied them and four were refilled 20 min afterward (solid columns). The data for this bird were collected for approximately 8–10 h/day for 11 days (number of visits to each type of flower: 10 min, $n = 1937$; 20 min, $n = 1343$).

On the basis of this experiment by Gill, we presented rufous hummingbirds with a similar but slightly more extensive array of eight flowers each containing $20 \mu\text{l}$ of sucrose, four of which were refilled on a 10-min FI schedule and four on a 20-min FI schedule. Depending on the time intervals between visits, a bird can be expected to take at least $100 \mu\text{l}$ on average per visit. The territorial male was allowed to visit the array as and when he wished throughout the day (approximately 8–10 h/day). The experiment continued for 10 days, and three males were tested. All three appeared to have learned the relevant FI schedule (see Fig. 6 for an example of data from one bird; Henderson *et al.*, in preparation) such that, although there is considerable scatter in the data, the peak of return to the 10-min flowers was around or just after 10 min, and for the 20-min flowers around or just after 20 min. As predicted theoretically, the precision of return to the 20-min flowers is much less than for the 10-min flowers. This degree of precision in proportion to the duration of the interval being timed is a feature of interval timing, termed the “scalar property” (Gibbon *et al.*, 1997). It is the case that the birds often return to our experimental arrays (not just the one presented in this experiment) after intervals of approximately 10 min, and this may have made it particularly easy for the birds to learn and to use the shorter time interval. Nonetheless, they were required to keep track concurrently of four flowers with a 10-min FI and four flowers with a 20-min FI. This requires the use of more than one or two timers, although not necessarily as many as eight as birds may have

coupled together flowers visited on the same bout. Keeping track of more than two intervals concurrently has not, to our knowledge, been demonstrated before this experiment although the ability to do so has been implicitly assumed in the literature on episodic memory.

Episodic memory, the memory for distinct episodes in one's life (often described as "what," "when," and "where" memory), has largely been discussed in the context of human learning and memory, not least because it is easier to test for recall of specific episodes in humans than it is in nonhuman animals (e.g., [Aggleton and Pearce, 2001](#); [Morris, 2001](#); [Tulving, 2002](#)). However, it has plausibly been argued that food-storing birds require such multifaceted memories in order to recall locations of caches accurately, and there is some evidence that they can, indeed, remember what they have stored, where they have stored it, and when they stored it ([Clayton *et al.*, 2001a,b](#)). Although we have not yet explicitly tested the ability of hummingbirds to remember what, where, and when in the same experiment, the evidence from the timing experiment is that they seem to be able to remember "when" (at least to some degree). As other experiments by us and a number of others have shown they can remember what and where rewards are located, these hummingbirds seem, in principle, to demonstrate the three components of episodic memory. Although memory for each flower hummingbirds have fed on in the recent past is not the same kind of episode that is typically inferred in the human context, nor would it be efficient for the birds to remember this information over the long term, it would seem advantageous for birds to remember all three components with respect to each of their flower visits. Further testing of episodic or episodic-like memory in animals other than food storerers would be valuable.

IV. CONCLUSION

The major advantage of testing these hummingbirds in the field is that we may eventually gain some insight into their abilities as they use them in their daily lives. We acknowledge that much we have shown to date might have been shown equally clearly in a laboratory setting. However, in a laboratory setting we cannot be sure of the relevance of the results to animals in the field because of the constraints in spatial scale (although not true for testing many invertebrates), in temporal scale (e.g., tests of spatial memory in tits on touch screens), and in other quantitative features (e.g., number of items to be remembered). By testing the hummingbirds in the field we have managed, thus far, to assess their learning and memory abilities by using arrays of flowers on a spatial scale that is comparable to

that they are faced with in everyday foraging. We think, therefore, we now have a better understanding of the way in which a male rufous hummingbird learns and remembers the flowers in his territory. The next steps will involve attempting to test these birds with much greater numbers of flowers so as to assess the extent of their memory capacity, and to test them over a temporal scale that more closely matches real flower-refilling rates.

It would be useful in future to attempt to match our results with comparable data from the laboratory to gain an idea of how well matched the relatively uncontrolled field testing situation and the tightly controlled laboratory situation one. We have little idea as yet of how the quantitative changes in scale (temporal, spatial, or numerical) between the two settings might affect conclusions drawn about learning and memory in any animal from laboratory testing. The rufous hummingbird may be a useful species in which to make such a comparison as they are fairly readily kept and tested in captivity.

V. SUMMARY

Their territory holding, coupled with a number of other important features of the rufous hummingbird, has allowed us to investigate the cognitive abilities of these animals in the field. These birds can remember, so as to subsequently avoid, flowers they have recently emptied. We have also found that, although these birds can learn color-reward associations, when revisiting flowers they pay more attention to the spatial location of the flowers. When flowers are close together, the birds learn flower locations with respect to other nearby flowers. They also learn faster which flowers are rewarded if these flowers are next to each other. When flowers are further apart (>40 cm), however, their locations are encoded relative to landmarks outside of the array. Once the location of a flower has been learned, birds are apparently oblivious to changes in its color pattern.

These birds also pay attention to whether they have seen flowers previously, preferring to visit new flowers before those they have seen and not visited. Not only can these birds remember what they have fed from and where, they may also be able to remember when they visited. We do not know yet how well matched their timing abilities are to relevant flower-refilling rates.

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