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Differential response to colour tasks on resident and migratory hummingbirds: a field test

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Foraging performance of different hummingbird species was quantified by experimentally simulating changes in the environment, and we tested the hypothesis that species of migratory hummingbirds are more likely than resident to adjust their behaviour to changes in the environment. Colour discrimination tasks were designed to explore how 120 recently captured hummingbirds perform when the expected rewarding floral colour is not profitable. Hummingbirds were presented with an array consisting of 36 randomly distributed artificial flowers of two contrasting colours, where 18 were empty and either pink, orange or red, and 18 were filled with a sugar solution and were either green, yellow or orange. Although a few individuals failed or gave up visiting the experimental array after few non-rewarding foraging bouts (28%), most hummingbirds foraged continuously (72%). Out of those that foraged continuously, 36% consistently visited non-rewarding flowers and 64% switched to the rewarding colour. On average, migrants visited proportionally more rewarding flowers and were more willing to forage than residents, except the poor performance of one migratory species. Both migratory and resident hummingbirds performed better than chance when foraging on red/orange arrays, but their foraging performance differed on pink/green and orange/yellow arrays. Our results showed that some individuals thrive on risk and novelty while others shrink from the same situation, and that these differences are due to intrinsic differences among individuals in their tendency to switch, or a differential sensitivity to different colour combinations, regardless of their migratory status.

KEY WORDS: colour preference, discrimination tasks, foraging behaviour, hummingbirds, Mexico.

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INTRODUCTION

Dichotomies such as specialization and generalization have been useful but poorly understood central debating points in behavioural ecology. In this sense, a hummingbird using a broad range of floral resources would be considered the prototype of a generalist forager. However, this generalization is problematic because individual foragers are remarkably plastic in their foraging behaviour (EWALD & CARPENTER 1978; FEINSINGER et al. 1985). The responses of individuals to a given task, although a possible fundamental axis of hummingbird behavioural variation, have been investigated only in a few hummingbird species, particularly *Selasphorus* species. To date, most studies have explored species differences in their abilities to discriminate colour (LYERLY et al. 1950; COLLIAS & COLLIAS 1968; MILLER & MILLER 1971; STILES 1976; GOLDSMITH & GOLDSMITH 1979; GOLDSMITH 1980; MITCHELL 1989), learning spatial cues to find food (COLE et al. 1982; HAINSWORTH et al. 1983; GASS & SUTHERLAND 1985; MILIAR et al. 1985; WOLF & HAINSWORTH 1986; BROWN & GASS 1993; BROWN 1994; HEALY & HURLY 1995; SUTHERLAND & GASS 1995; HURLY 1996; IRWIN & BRODY 1999) and memory use for location and/or visual cues for tracking changes in the environment (GASS & SUTHERLAND 1985; TAMM 1987, 1989; HURLY & HEALY 1996; PÉREZ et al. 2011). However, there is scanty evidence of whether they make use of their foraging experience to solve foraging tasks, and modify their foraging behaviour based on their past experience (BACON et al. 2010), the taste of food (BACON et al. 2011), the variance of nectar volume and concentration (LARA et al. 2011) and/or the use of floral resources by conspecifics and heterospecifics (ALTSHULER & NUNN 2001; LARA et al. 2009), and which species of hummingbirds perform more precisely in such behavioural tasks. The existence of such variation is particularly important to understand information use to assess generality among cognitively advanced pollinators such as hummingbirds.

Environmental changes occur continuously and, to deal with change, many bird species can either migrate to another location or stay and develop new ways to adapt to the change (LEMEL et al. 1997). It makes sense for resident birds to collect and keep track of information about their floral resources rather than migrants, since the residents will use that information to make decisions about long-term habitat suitability and to discover and take advantage of new resources. Migrants, on the other hand, are repeatedly confronted with unfamiliar environments in which they must quickly discover food resources. For instance, North American hummingbirds undergo considerable long-distance migrations, during which time they have to learn new rewarding flowers at each stage of the round-trip journey back to the breeding habitat. As, usually, they are only in a given area for a short time, the collected information is no longer useful in the next stopover area of the journey (METTKE-HOFMANN et al. 2009). In this way, the difference in migratory behaviour among hummingbirds may influence decision-making processes to explore unfamiliar or novel floral resources (BRODBECK 1994). In nature, during their local altitudinal or long-distance migratory movements, migratory hummingbirds forage on diverse assemblages of flowers varying in shape, colour and accessibility, facing new floral resources used by resident species assemblages that vary spatially and temporally (ARIZMENDI 2001; HEALY & HURLY 2003; LARA 2006). Thus, they must constantly make foraging decisions about which patches, plants and flowers to visit, partly as a function of quality of the nectar reward (MELÉNDEZ-ACKERMAN et al. 1997). The uncertainty of these decisions in a novel environment may possibly be reduced if an individual can quickly associate a rewarding flower with its colour and discriminate non-rewarding flowers to avoid their

revisitation (MILIAR et al. 1985; PÉREZ et al. 2011), as this colour use by individuals affects not only their foraging choices but also population-level responses to competition (SANDLIN 2000a, 2000b). Although hummingbirds typically pollinate primarily red, tubular flowers, they also feed from flowers that are neither tubular nor red throughout their ranges (GRANT 1966; ALTSHULER 2003), and they are flexible in moving quickly to rewarding colours other than red once they are sampled (MILLER & MILLER 1971; STILES 1976; GOLDSMITH & GOLSMITH 1979; MELÉNDEZ-ACKERMAN et al. 1997; LARA et al. 2009; GONZÁLEZ-GÓMEZ et al. 2011). Many tropical hummingbird species migrate altitudinally (ORNELAS & ARIZMENDI 1995), and these annual bird movements up and down mountain slopes reflect spatial and temporal variation in floral resources (STILES 1988; ORNELAS & ARIZMENDI 1995; ARIZMENDI 2001; LARA 2006). Based on this, we hypothesize that hummingbird migratory behaviour linked to the more pronounced spatial and temporal variation in floral resources has evolved with different behavioural plasticity in exploratory and foraging abilities as compared with resident hummingbirds. If this is correct, we expect that migratory hummingbirds should be able to quickly change and adjust their colour preferences of the flowers they visit due to the short time spent in a given novel environment, whereas resident hummingbirds should prefer visiting their natural red flower type and will take longer to change their colour preferences.

Here we investigated whether migratory hummingbirds (short- and long-distance migrants) show more flexibility in changing preference when their naturally preferred red colour flags an unrewarding flower. We tested two resident and four migratory hummingbird species with colour discrimination tasks using artificial flowers of two contrasting colours and measured a number of behavioural variables during the tasks. Because the colour discrimination tasks were performed using recently captured individuals performing the same task without training, the observed variation in their preferences for responding to colour cues was likely to be an expression of normal cue use during foraging behaviour rather than a response learned within the context of the experiment. Specifically, our goal was to test whether or not hummingbirds will move their natural preferences away from red flowers when exposed to a situation in which red flags non-rewarding flowers, and to explore possible differences between migratory and resident hummingbirds in the number of flowers birds visit of the empty sort before testing flowers with an unexpected rewarding colour.

METHODS

Study site

Fieldwork was conducted from June to December 1992 at Las Joyas field station (19°35'–19°37'N 103°15'–104°37'W; at 1952 m above sea level). This 1245-ha preserve is located in the Sierra de Manantlán Biosphere Reserve, between the Mexican states of Jalisco and Colima. Mean annual precipitation is 1610 mm (JARDEL 1991), most of it falling between June and October when hurricanes occur. A short dry season extends from March to May. Mean annual temperature is 14.6 °C, with freezing temperatures occurring only for a few days during the winter (November to February). The vegetation is a mosaic of wet coniferous, pine-oak, and fragments of cloud forest along ravines, and secondary vegetation (VÁZQUEZ et al. 1995).

Hummingbirds and their flowers

Las Joyas holds 21 hummingbird species, the richest hummingbird fauna reported at this latitude (ORNELAS & ARIZMENDI 1995). Our study focused on six of the most abundant hummingbird species in the study area, two resident species, *Hylocharis leucotis* (HL) and *Lampornis amethystinus* (LA), and four migratory species, *Colibri thalassinus* (CT), *Amazilia beryllina* (AB), *Eugenes fulgens* (EF) and *Selasphorus rufus* (SR), which include different points along the continuum from truly resident hummingbirds through short-distance migrants, through altitudinal and local migrants to long-distance or latitudinal migrants (RAPPOLE & SCHUCHMANN 2003). HL and LA are year-round residents at Las Joyas, whereas CT, AB and EF are altitudinal migrants, and SR latitudinal migrants (ORNELAS & ARIZMENDI 1995). At Las Joyas, HL breed during the rainy season and LA early in the rainy season; CT nest at the end of the rainy season (August) and, after breeding, they move to higher elevations; AB and EF are most abundant from the end of the rainy season to the dry season at Las Joyas and breed earlier at higher elevations, and SR arrive at the study area in October and establish territories in forest edges until their departure by March to breeding grounds in the USA and Canada. These species vary in body size and foraging behaviours as well (Table 1). Flower availability for hummingbirds in the area varies seasonally (ARIZMENDI 2001). The higher abundance of hummingbird flowers occurs during wintertime, which coincides with the peak abundance of hummingbirds. Highly dense herbaceous plants take over recently opened and burned areas, and bloom copiously and asynchronously from the arrival of latitudinal migrants (September–October) to their departure (March–April). The peak abundance during the winter (December–March) coincides with the arrival of latitudinal migrants in large numbers. A more detailed description of floral resources used by hummingbirds in the area throughout the year is given by ORNELAS & ARIZMENDI (1995) and ARIZMENDI (2001).

A total of 186 adult hummingbirds were captured using mist nets around the field station compound for this study. Each bird was measured, weighed and banded with a numbered individual band to avoid re-utilization of the same individuals during the study. Hummingbirds were captured as needed for the experiments, and handled kindly using the required permits and approved animal welfare protocols before housing.

Table 1.

Data summary of the sample size (n = number of captured individuals) and main features and migratory status of each hummingbird species used in the study. AB = *Amazilia beryllina*; CT = *Colibri thalassinus*; EF = *Eugenes fulgens*; HL = *Hylocharis leucotis*; LA = *Lampornis amethystinus*; SR = *Selasphorus rufus*. Body measurements were taken from ORNELAS (1994, 1995).

Species	n	Migratory status	Foraging behaviour	Bill shape	Bill length (mm)	Wing chord (mm)	Body mass (g)
AB	30	Altitudinal migrant	Highly territorial	Straight	19.5–19.7	53–54	4.2–4.5
CT	21	Altitudinal migrant	Territorial	Slightly curved	20.9–21.0	65–61	4.5–5.0
EF	53	Altitudinal migrant	Trapliner	Straight	26.3–29.5	68–71	6.8–7.5
SR	16	Latitudinal migrant	Territorial	Straight	16.5–18.0	44–40	3.4–3.2
HL	29	Resident	Territorial males	Straight	17.2–17.3	52–55	3.1–3.4
LA	37	Resident	Territorial males	Straight	21.2–22.5	62–69	5.2–6.4

Housing conditions

After capture, naïve hummingbirds were allowed to acclimate to captivity for 1 or 2 days before experimental trials began. Hummingbirds were housed individually (or in groups of four or five individuals of smaller HL and SR within one cage) for 1–2 days in field-collapsible cages (61 × 61 × 61 cm; BioQuip®, Gardena, California, USA). Two to four feeders (Perky-Pet cat. No. 214, Laguna Hills, California, USA) with red bases were placed in cages housing several individuals to prevent domination of the feeders by few birds. Dominant or aggressively territorial individuals of AB were housed in individual cages but visually in contact with birds in the other cages. All cages were placed in a room illuminated with ambient light and temperature. Migratory hummingbirds may exhibit hyperphagia (overeating to increase fat deposition) just before and during migration periods. By contrast, resident birds do not become hyperphagic and do not deposit fat at all, or they do so at different times than migrants (e.g., during winter or breeding). For this reason, and in order to control the possibility that differences in motivation to eat would mask the colour of the flowers as a foraging cue, hummingbirds had free access to 20% (by mass) sugar solution, and ca 20 live *Drosophila* flies introduced to the cage two or three times a day. Most hummingbirds acclimated to captivity within a day (LARA & ORNELAS 1998). We could not detect any housing or cage effects of individually or group-caged hummingbirds on their foraging performance in the outdoor aviary flowers (see also LARA & ORNELAS 2001). The research reported here was performed with the approval of an independent local committee (Universidad de Guadalajara) that reviewed and approved our protocols regarding housing conditions and ethical issues, and we followed the Guidelines for the Use of Wild Birds in Research proposed by the North American Ornithological Council.

Response to colour tasks

Experimental array and foraging task. The experiment was designed to test hummingbird fidelity to a colour similar to one that has previously been rewarding under new conditions. A green aluminium grid (2.5 × 2.5 m) was built to place artificial flowers inside a portable, outdoor aviary (4 × 8 × 2 m) where all trials were performed. The aviary was permanently installed in a forest edge, near the field station compound. The grid was constructed of two 2.5-m poles set into the ground 2.5 m apart with six aluminium poles extending horizontally between them, each 0.25 m above or below the next. Artificial flowers were made of conical plastic micropipette tips (4 cm length) and simulated 'petals' with plastic material (flagging tape) of different colours. Six 'flowers' were secured to each horizontal pole approximately 0.25 m apart, as shown in Fig. 1. The distribution of flowers in the array was randomly selected each time a bird was tested. An identification number was assigned to distinguish the position of each flower within the array by randomizing its position in each trial. Original vegetation was not removed to give a more natural setting for the bird being tested. A perch was placed inside the aviary 3 m away from the observer.

Three colour pairs were used in this experiment (R/O = red and orange; O/Y = orange and yellow; P/G = pink and green). In each colour preference trial, hummingbirds were presented with an array of 36 artificial flowers of two colours, where 18 empty flowers were either red, orange or pink, and 18 rewarding flowers were either orange, yellow or green (Fig. 1). Diffuse reflectance measurements were obtained for six colour types of flagging tape (Forestry Suppliers, Jackson, Mississippi, USA) using a VARIAN-CARY 2415 spectrophotometer calibrated to measure reflected light in the range of 300–500 nm. Colour combinations were chosen based upon the similarity of reflectance (%) of each pair member (Fig. 2). For example, the reflectance of pink and green colours is obviously different to the human eye at above 500 nm, but perhaps very similar to hummingbirds below 400 nm since they are suspected to have colour vision extending to the near UV (GOLDSMITH 1980). The colour models used in this study differ in hue (the major wavelength reflected from a substrate) but often also in intensity (the amount of light reflected from surface at a given wavelength). Hummingbirds could be attending to either or both of these characteristics when they choose a particular substrate as rewarding, but this was not addressed in this study.

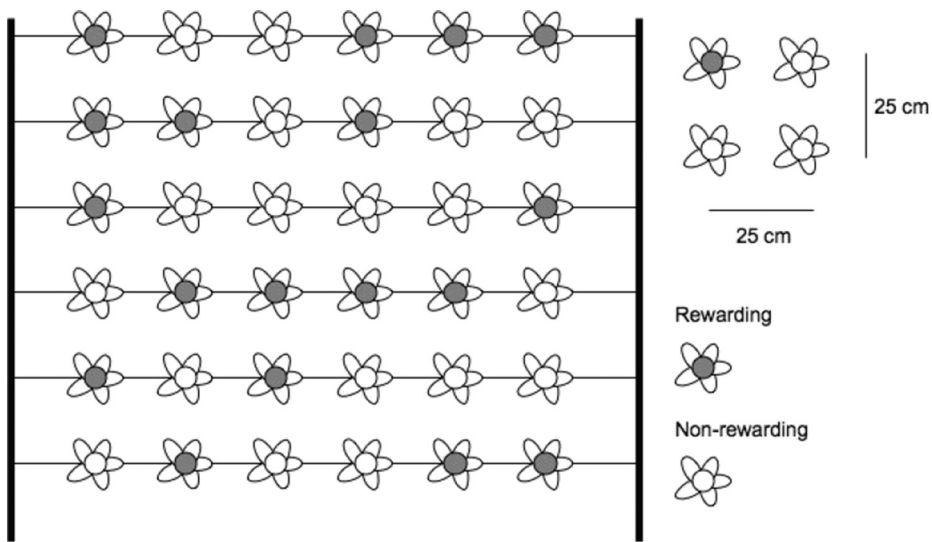


Fig. 1. — Diagram of the experimental setup used in this study. Two experimental groups of flowers (rewarding and non-rewarding) were randomly located in the experimental grid used in the experiments (see text).

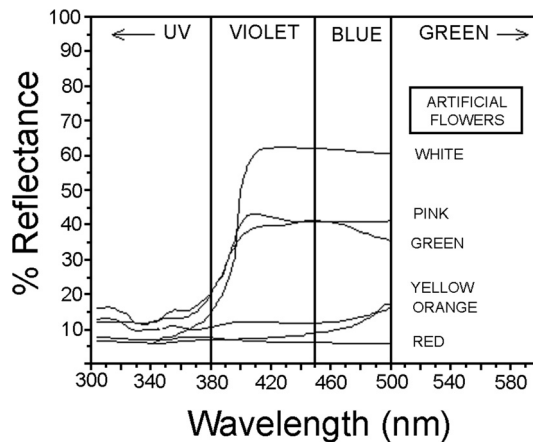


Fig. 2. — Spectral reflectance curves for ‘petals’ of artificial flowers made out of flagging tape. Diffuse reflectance measurements were obtained using a spectrophotometer calibrated to measure reflected light in the range of 300–500 nm to plot the relative reflectance at each wavelength. All reflectance curves are similar in their general shape. All colours have a broad peak of reflectance in the long-wavelength end of the spectrum, falling off rapidly to low reflectance at shorter wavelengths. Colours differ mainly in the location where the reflectance drops from high to low reflectance. The shortest wavelength for which hummingbirds have been tested is around 390 nm.

Before trials, each flower was filled with 200 μL of a 20% (by mass) sugar solution based on the 10–200 μL /flower nectar production range known for hummingbird-visited flowers at Las Joyas (ARIZMENDI 2001; ORNELAS et al. 2007) and the wide range in morphology and metabolism among species (GASS & ROBERTS 1992), minimizing hunger effects in the choice of flowers (TAMM 1987). Locations of food sources that birds do not deplete can require multiple posterior visits, and this can confound the bird's accuracy in the discrimination task. Because we were not able to quantify the amount of nectar consumed by hummingbirds in the aviary, we measured volume of nectar removal in a flower visit indirectly for all six species, and determined whether a hummingbird could empty a high-volume experimental flower in a single visit. This information was necessary to determine whether a hummingbird could empty a flower in a single visit. A lower revisitation rate should be expected in the aviary if nectar in artificial flowers was emptied completely in its first visit. The average extraction volume of each of the six species was separately measured using wild-caught individuals, naïve to the array. We put them one by one in a field collapsible cage ($61 \times 61 \times 61$ cm) containing a perch and one red artificial flower made as described above. The flower was filled with 200 μL of a 20% (by mass) sugar solution and hung at the center of the cage. Then a hummingbird was released into the cage to drink from the flower. Once the hummingbird visited the flower, we measured the distance from the tip of the micropipette tips to the bottom of the meniscus of the remaining volume with a digital caliper. The same procedure was repeated 10 times. Refilling the flower usually took us ca 40 sec. Micropipette tips were calibrated to then use distance measures to calculate volume extracted per flower visit [(volume = $-1.2077 + 2.1951 \times \log(\text{distance})$); $r^2 = 0.993$]. Sixty-six individuals were used in this experiment. Total variance in the removal of 'nectar' per visit was partitioned among species using one-way repeated-measures analysis of variance (ANOVA). In the model, hummingbird species was considered as a fixed effect, and nectar volume extracted over time was the repeated measure. Data were \log_{10} -transformed before analysis. Extraction of sugar solution from artificial flowers differed between species (mean \pm SE, AB: 48.2 ± 0.4 μL /bout, $n = 6$ individuals; CT: 99.7 ± 0.8 μL /bout, $n = 9$ individuals; EF: 139.8 ± 0.8 μL /bout, $n = 16$ individuals; SR: 44.8 ± 0.5 μL /bout, $n = 5$ individuals; HL: 46.1 ± 0.5 μL /bout, $n = 9$ individuals; LA: 46.6 ± 0.4 μL /bout, $n = 11$ individuals; repeated-measures ANOVA, $F_{5, 450} = 13.82$, $P = 0.0001$). No significant differences were observed within bouts ($F_{9, 450} = 0.85$, $P = 0.564$), and the bout \times species interaction was also not significant ($F_{45, 450} = 0.57$, $P = 0.987$). EF, with the longest bills, were able to empty flowers in one visit to the flower. On average, EF extracted three times more than the other species, except CT. LA extracted less nectar than one would expect given its bill length (second longest bill), and CT extracted two times more given its bill length. These results are not surprising given the variation in body mass (metabolism), bill length and wing chord (see Table 1), but show that EF individuals might empty artificial flowers with more than 200 μL in a single visit.

Observational procedures. A total of 120 adult hummingbirds were used in this experiment. Hummingbirds were released one by one into the aviary to visit the artificial flowers for 1 hr. The observer was located outside the aviary behind the perch, in the opposite direction from the grid (ca 7–9 m). We recorded for each hummingbird: (1) the time (min) at end of each foraging bout, with a stopwatch, (2) the identity of each flower probed (colour and position within the array) and (3) the sequence of visits within a bout. A foraging bout began when the bird flew from the perch to forage in the array, and ended when it next returned to the perch (GASS & ROBERTS 1992). With recorded information, we generated the following variables: the time they take to discover the floral array (first visit), the number of foraging bouts, the time they take to probe the first rewarding flower, the total number of flowers visited, the proportion of rewarding flowers visited, the number of different flowers visited, the number of different rewarding flowers visited and the proportion of different rewarding flowers visited. Observations were conducted from 06:00 to 12:00, and subject hummingbirds had access to food before trials and were assumed to have similar hunger levels when facing the colour task. Depriving subjects of food for experimental 'willingness' might introduce biases. During trials, hummingbirds typically caught insects, and/or took baths on leaves of, and/or mosses on branches of, small shrubs inside the aviary. The occurrence of these behaviours indicated to us low levels of stress among the hummingbirds. After each trial was completed, the hummingbird was removed from the aviary and released.

Pre-trial training and exposure to the experimental protocol is recommended to attempt to eliminate previous expectations hummingbirds have about colour, and to ensure that they willingly use the experimental floral array. However, this type of training requires several weeks to eliminate differences among phenotypically plastic individuals, and ecological and social isolation may introduce more experimental bias. We minimized possible confounding factors by using hummingbirds that were (1) naïve to the experimental array, (2) recently captured and all from one season, (3) tested only once and then released and (4) kept in captivity for few days with access to food before trials. This approach allowed us to detect the persistence of their foraging experience before behavioural convergence. Individuals of a given species were not tested sequentially and not all two-colour comparisons could be completed for all hummingbird species. Difficulties such as the arrival time of hummingbirds at the station, capturing new birds of the same species at the right time and their maintenance in captivity caused these asymmetries in the experimental design.

Data analysis. Differences among species and groups of species (migratory vs residents) in the behavioural outcomes in all three colour combinations were assessed using contingency tables. Behavioural differences among species and between migrants versus residents in the time they took to discover the floral array (first visit), the number of foraging bouts, the time they took to probe the first rewarding flower, the total number of flowers visited, the proportion of rewarding flowers visited, the number of different flowers visited, the number of different rewarding flowers visited and the proportion of different rewarding flowers were analyzed using nested ANOVAs, with species nested within migratory status (migrant vs resident) and colour treatment as a blocking variable. Hummingbirds were categorized as either migrants or residents. Because individuals were tested at different times of day, we used one-way ANOVA to test for time-related differences among individuals in their energetic state and motivation. Time variables were \log_{10} -transformed, proportions were arcsine-transformed and counts were square root transformed before analysis to conform more closely to a normal distribution.

To test whether the exploration of new rewarding flowers (first visit to each flower) by hummingbirds was different from random, we used a probability function to count the number of ways in which a given number of rewarding flowers could be visited by hummingbirds that probed rewarding flowers at least once. The hyper geometric distribution (ROBINSON 1985) was used as a null distribution to determine whether the distribution of rewarding flowers visited was random. The probability values then were used to determine which individuals switched to rewarding flowers on the basis of colour. Hummingbirds can deal simultaneously with memory of floral characteristics (colour) and memory of place (SUTHERLAND & GASS 1995; PÉREZ et al. 2011); we do not distinguish the two groups.

We assessed performance of each individual subject in all three-colour combinations as the number of individual flowers visited before locating the first rewarding flower. If subjects searched for the rewarding flowers without previous cues to guide them, up to 18 non-rewarding visits might be needed to discover the first rewarding flower. Thus, under both random and systematic searching, the expected number of visits due to chance in all experiments is 18. Deviations from the expected value for migrants and resident species were assessed using one-sample *t*-tests. The tests were two-tailed because there are two alternative hypotheses. The subjects may remember the rewarding colour and hence find other rewarding flowers with fewer than 18 visits. Alternatively, birds may remember spatial cues and thus be drawn to switch location but would make more than 18 non-rewarding visits.

Lastly, we recorded the cumulative number of rewarding and non-rewarding flowers selected by each subject tested. We split the data into three blocks of 20 min within each feeding trial. If a bird switched to rewarding flowers (non-random visitation), its cumulative visits should perform a gradual switching among the three colour treatment arrays. The comparisons between resident and migratory species were done using a two-way, repeated-measures ANOVA, with migratory status (migratory vs resident) and colour treatment combinations as fixed factors and the proportion of different rewarding flowers over time as the repeated measures. Data were arcsine or square root transformed before statistical analysis to achieve normality.

RESULTS

General responses to the array

Hummingbirds failed to search the array, gave up soon after non-rewarding foraging attempts, continuously visited flowers with the non-rewarding colour or began visiting the non-rewarding colour and then switched to the rewarding colour. Six out of 120 individuals (5%) failed to visit the array, 28 (23%) gave up visiting the experimental array after few non-rewarding foraging bouts and the remaining 86 (72%) hummingbirds foraged continuously. Out of those that foraged continuously, 26 (30%) consistently visited non-rewarding flowers (gained no reward) and 60 (70%) switched to the rewarding colour. A summary of these behavioural responses is presented in Table 2.

Comparisons of behavioural responses (never tried, gave up, colour consistency, colour switching) in different colour combinations using contingency tables showed that these behavioural responses are not independent of species ($\chi^2 = 45.7$, $df = 15$, $P < 0.01$), colour combination ($\chi^2 = 67.3$, $df = 6$, $P < 0.01$), or migratory status ($\chi^2 = 11.3$, $df = 3$, $P < 0.01$). Most individuals (114/120 individuals) visited at least one flower, and visited the floral array for the first time within the first 10 min.

Migrants vs residents

There were no significant differences between residents and migrants in discovery time, number of bouts and number of different flowers visited per bout (Table 3). However, migrants had a higher proportion of rewarding flowers visited, higher proportion of different rewarding flowers visited and longer giving up time than residents, except the poor performance of CT (Table 3). After removing CT data from the analysis, differences between migrants and residents remained significant (results not shown). In summary, migrants (except CT) visited proportionally more rewarding flowers and were more willing to forage than residents; migrants AB, EF and SR had the highest values (Table 3).

Results of nested ANOVAs showed no significant differences between resident and migratory species in their performance for most of the variables analyzed except for the giving-up time (Table 4), which was longer for migratory species (Table 3). The colour combination, as a blocking variable, had a significant effect on all variables except the discovery time (Table 4). There were no time-related differences in variables related to the energetic state (and by inference, motivation to feed) between residents and migrants. However, the proportion of rewarding flowers visited by individuals tested from 07:00 to 08:00 (48%) and from 11:00 to 12:00 (62%) was statistically higher (one-way ANOVA, $F_{3, 114} = 6.37$, $P = 0.0005$) in relation to those tested from 08:00 to 11:00 (21–29%). The proportion of different rewarding flowers was also statistically higher (one-way ANOVA, $F_{3, 110} = 6.71$, $P = 0.0002$) among those tested from 07:00 to 08:00 (45%) and from 11:00 to 12:00 (60%) than among those tested in between (21–26%). The same pattern was observed for the time they took to discover the first rewarding flower, but the differences were marginally significant ($P = 0.0468$). The finding that some individuals performed better from 07:00 to 08:00 and from 11:00 to 12:00 is intriguing. However, this result is not simply due to the fact that they had lesser fat reserves or were more hungry since all other values of response variables directly related to their energetic state (discovery time, number of bouts, number of flowers visited and giving-up time) were not statistically different between time periods ($P > 0.05$).

Table 2.

Data summary of general behavioural responses of hummingbirds to experimental arrays (n = number of individuals; NTR = never tried the array; GUP = gave up; CON = colour consistency; SWI = switching; R/O = red/orange; O/Y = orange/yellow; P/G = pink/green; AB = *Amazilia beryllina*; CT = *Colibri thalassinus*; EF = *Eugenes fulgens*; HL = *Hylocharis leucotis*; LA = *Lampornis amethystinus*; SR = *Selasphorus rufus*.

Species	<i>n</i>	NTR	GUP	Foraged continuously	
				CON	SWI
R/O					
AB	10	0	0	0	10
EF	18	0	0	0	18
CT	–	–	–	–	–
SR	–	–	–	–	–
HL	5	0	2	0	3
LA	9	1	0	0	8
O/Y					
AB	6	2	1	0	3
EF	6	0	1	0	5
CT	5	1	3	1	0
SR	7	0	2	1	4
HL	6	0	5	0	1
LA	6	0	5	0	1
P/G					
AB	8	0	2	4	2
EF	8	0	1	7	0
CT	6	0	0	6	0
SR	2	1	0	0	1
HL	8	0	3	3	2
LA	10	1	3	4	2
Total	120	6	28	26	60

Non-random exploration

According to the null model of a hyper geometric distribution, seven out of 45 individuals that probed rewarding flowers at least once visited different rewarding flowers non-randomly (Table 5). These individuals were mostly AB (five AB, one EF, and one HL). A marginal tendency was observed among other three AB individuals and one EF. These results suggest that 15% of the individuals incorporated colour cues as they foraged different rewarding flowers.

Table 3.

Behavioural differences of hummingbirds visiting the floral arrays by species, migratory status and colour combination. Data are mean \pm SE values. Letters indicate differences after post hoc mean comparisons (Games-Howell procedure, $P < 0.01$). n = number of individuals. AB = *Amazilia beryllina*; CT = *Colibri thalassinus*; EF = *Eugenes fulgens*; HL = *Hylocharis leucotis*; LA = *Lampornis amethystinus*; SR = *Sceloporus rufus*. R/O = red/orange; O/Y = orange/yellow; P/G = pink/green. DT = discovery time (min); FB = number of foraging bouts; FR = first rewarding flower (min); NF = number of flowers visited; PRF = proportion of rewarding flowers visited; NDF = number of different flowers visited; NDRF = number of different rewarding flowers visited; PDRF = proportion of different rewarding flowers visited; GUP = giving up time (min).

Variables	Hummingbird species						Migratory status			Colour combination		
	Residents			Migrants			Residents	Migrants	R/O	O/Y	P/G	
	HL	LA	AB	CT	EF	SR						
n	19	25	24	11	32	9	44	76	42	36	42	
DT	11.3 \pm 1.5a	12.0 \pm 3.2a	17.7 \pm 3.5a	21.1 \pm 5.4a	9.5 \pm 1.4a	18.6 \pm 5.8a	11.7 \pm 1.9a	14.9 \pm 1.7a	10.3 \pm 1.7a	16.0 \pm 2.5a	15.1 \pm 2.3a	
FB	12.2 \pm 3.7a	9.0 \pm 1.6a	16.3 \pm 2.4a	8.4 \pm 2.7a	14.6 \pm 2.0a	20.0 \pm 6.2a	10.3 \pm 1.8a	14.9 \pm 1.4a	14.1 \pm 1.6a	11.0 \pm 2.4a	14.2 \pm 2.0a	
FR	38.3 \pm 5.0a	33.3 \pm 5.0a	30.0 \pm 4.9a	40.9 \pm 6.9a	25.7 \pm 4.0a	34.2 \pm 8.5a	35.4 \pm 3.6b	30.3 \pm 2.7a	13.8 \pm 0.2a	37.4 \pm 3.9b	46.1 \pm 2.7c	
NF	22.9 \pm 5.9a	18.2 \pm 3.0a	31.3 \pm 3.0a	16.4 \pm 4.5a	27.9 \pm 3.5a	28.7 \pm 9.6a	20.3 \pm 3.1a	27.4 \pm 2.7a	29.9 \pm 3.4a	20.1 \pm 4.5a	23.5 \pm 2.9a	
PRF	0.24 \pm 0.7a	0.25 \pm 0.6a	0.47 \pm 0.7b	0.11 \pm 0.6c	0.47 \pm 0.6b	0.45 \pm 0.1ab	0.25 \pm 0.4a	0.41 \pm 0.4b	0.65 \pm 3.7a	0.24 \pm 0.5b	0.11 \pm 0.4c	
NDF	10.4 \pm 2.0a	9.9 \pm 1.4a	12.9 \pm 1.8a	7.9 \pm 1.5a	12.2 \pm 1.2a	9.1 \pm 2.0a	10.1 \pm 1.2a	11.4 \pm 0.8b	13.7 \pm 1.2a	8.6 \pm 1.4b	10.1 \pm 0.8bc	
NDRF	3.6 \pm 1.3a	3.1 \pm 0.9a	6.3 \pm 1.2b	0.3 \pm 0.1c	4.8 \pm 0.7b	4.4 \pm 1.4ab	3.3 \pm 0.7a	4.6 \pm 0.5b	7.6 \pm 0.6a	3.4 \pm 0.8b	1.3 \pm 0.4c	
PDRF	0.21 \pm 0.1a	0.25 \pm 0.6a	0.42 \pm 0.1b	0.19 \pm 0.1c	0.44 \pm 0.1b	0.33 \pm 0.1ab	0.23 \pm 0.1a	0.39 \pm 0.1b	0.55 \pm 0.1a	0.27 \pm 0.1b	0.17 \pm 2.4ac	
GUP	35.1 \pm 4.7a	36.0 \pm 4.0a	52.4 \pm 3.0b	38.9 \pm 5.0ab	52.2 \pm 1.8b	50.4 \pm 5.3ab	35.5 \pm 3.0a	500.2 \pm 1.6b	51.5 \pm 1.8a	34.9 \pm 3.6b	46.5 \pm 2.5ac	

Table 4.

Results of nested analyses of variance (ANOVAs), with species nested within migratory status and colour treatment as a blocking variable.

Variable	Migratory status (species)				Colour combination			
	degrees of freedom	Mean Square	<i>F</i>	<i>P</i>	degrees of freedom	Mean Square	<i>F</i>	<i>P</i>
Discovery time (min)	5	0.361	1.357	0.2458	2	0.325	1.220	0.2991
Number of bouts	5	5.921	2.102	0.0703	2	8.520	3.025	0.0526
Time to discovering first rewarding (min)	5	0.139	0.790	0.5591	2	5.111	29.045	0.0001
Number of flowers visited per hour	5	5.705	1.069	0.3816	2	18.364	3.440	0.0355
Proportion of rewarding flowers	5	0.330	2.625	0.0277	2	3.355	26.715	0.0001
Number of different flowers	5	0.652	0.395	0.8513	2	6.695	4.056	0.0199
Number of different rewarding flowers	5	2.403	1.983	0.0865	2	37.070	30.070	0.0001
Proportion of different rewarding flowers	5	0.154	1.079	0.3758	2	1.408	9.883	0.0001
Giving up time (min)	5	0.240	6.285	0.0001	2	0.451	11.800	0.0001

The performance of subjects was heterogeneous depending on their migratory status and the confronted colour combination (Fig. 3). Note that flower revisitation was much higher on average when hummingbirds switched to rewarding flowers (Table 5), which presumably increased their foraging efficiency. On P/G arrays, the average foraging performance of resident hummingbirds was significantly better than chance ($t = -2.70$, $df = 17$, $P = 0.015$) compared to migratory hummingbirds ($t = -1.03$, $df = 23$, $P = 0.312$). However, when they were confronted with O/Y arrays, the performance of migratory species was better and differed significantly from chance ($t = -4.64$, $df = 23$, $P < 0.0001$) compared to resident species ($t = -1.72$, $df = 11$, $P = 0.112$). Both migratory ($t = -52.77$, $df = 27$, $P < 0.0001$) and resident hummingbirds ($t = -6.52$, $df = 13$, $P < 0.0001$) performed significantly better than chance when foraging on R/O arrays.

Table 5.

Flower revisitation for individuals that probed at least one rewarding flower, and hyper geometric distribution used as a null distribution to determine whether hummingbirds choose new rewarding flowers at random or whether they use colour. Flower revisitation was measured for non-rewarding flowers before the switch and for rewarding flowers after the switch. Means \pm SD correspond to the number of times a given flower was revisited. To test whether the exploration of flowers was random (first visit to each flower), we used a probability function to count the number of ways in which a given number of rewarding flowers was visited by hummingbirds that probed flowers of the rewarding colour at least once. Individuals that probed flowers on the basis of colour were considered switchers ($P < 0.01$). AB = *Amazilia beryllina*; CT = *Colibri thalassinus*; EF = *Eugenes fulgens*; HL = *Hylocharis leucotis*; LA = *Lampornis amethystinus*; SR = *Selasphorus rufus*. R/O = red/orange; O/Y = orange/yellow; P/G = pink/green. * $P < 0.05$, ** $P < 0.01$.

Species	Colour treatment	Flower revisitation		Hyper geometric distribution		
		Before switch	After switch	Total different flowers	Total different rewarding flowers	$P\left[n_i \geq h\left(i\right)\right]$
AB						
1	R/O	0	1.11 ± 1.21	27	17	0.008**
2	R/O	0	2.25 ± 2.91	10	9	0.003**
3	R/O	0	3.85 ± 4.65	26	13	0.644
4	R/O	0	0.60 ± 0.69	15	9	0.249
5	R/O	0.25 ± 0.50	1.63 ± 2.73	16	12	0.008**
6	R/O	–	–	12	6	0.637
7	R/O	0	0.85 ± 0.94	24	14	0.144
8	R/O	0	0.70 ± 0.67	13	10	0.017*
9	R/O	0	0.85 ± 0.89	9	7	0.060
10	R/O	0	0.20 ± 0.42	17	10	0.252
1b	O/Y	0	0.83 ± 0.75	12	10	0.005**
5b	O/Y	–	–	6	4	0.329
7b	O/Y	0.09 ± 0.30	4.00 ± 4.27	29	15	0.500
1c	P/G	–	–	4	4	0.051
2c	P/G	1.33 ± 1.87	1.75 ± 2.06	16	4	0.998
3c	P/G	–	–	4	4	0.051
EF						
12	R/O	–	–	7	5	0.200
26	R/O	0.33 ± 0.81	0.12 ± 0.35	16	7	0.842
27	R/O	0.25 ± 0.50	1.42 ± 1.39	23	15	0.017*
29	R/O	1.00 ± 0.00	0.55 ± 1.13	17	8	0.747
31	R/O	0	0.75 ± 1.16	18	7	0.952

(Continued)

Table 5.
(Continued)

Species	Colour treatment	Flower revisitation		Hyper geometric distribution		
		Before switch	After switch	Total different flowers	Total different rewarding flowers	$P [n_I \geq h(i)]$
32	R/O	0	1.22 ± 1.71	13	9	0.082
22	O/Y	1.62 ± 1.74	2.00 ± 1.87	22	7	0.999
28	O/Y	0	1.36 ± 1.50	24	11	0.855
33	O/Y	0.83 ± 0.83	0.25 ± 0.75	21	7	0.997
34	O/Y	0	1.28 ± 1.25	12	6	0.637
SR						
1	O/Y	0	7.87 ± 4.18	15	8	0.500
4	O/Y	1.57 ± 1.98	4.40 ± 5.68	14	5	0.957
5	O/Y	0	7.33 ± 8.04	10	6	0.355
6	O/Y	0	2.00 ± 2.50	12	8	0.144
HL						
11	R/O	0	1.50 ± 1.22	18	6	0.990
13	R/O	0	0.78 ± 1.12	27	15	0.221
15	R/O	0	4.00 ± 3.25	24	13	0.362
22	O/Y	0	0.64 ± 0.74	25	13	0.500
3	P/G	0	6.00 ± 7.33	13	10	0.017*
8	P/G	0	2.00 ± 2.89			
LA						
1	R/O	0	1.16 ± 1.32	11	5	0.764
3	R/O	0	2.66 ± 1.52	8	3	0.885
4	R/O	0	5.00 ± 3.53	15	5	0.979
5	R/O	0	0.70 ± 0.67	18	10	0.369
6	R/O	0	1.50 ± 2.06	20	12	0.157
8	R/O	0	0.83 ± 1.43	21	11	0.500
9	R/O	–	–	15	5	0.979
14	O/Y	0	0	12	2	0.999
18	P/G	0.37 ± 0.74	2.60 ± 2.07	11	5	0.764
29	P/G	0.58 ± 0.79	0.80 ± 1.22	25	10	0.986

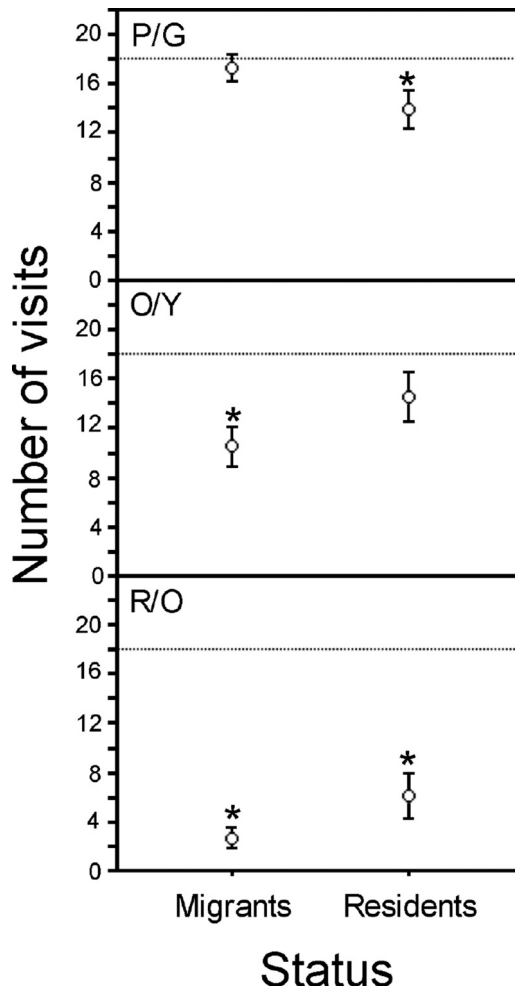


Fig. 3. — Foraging performance of migrant and resident hummingbirds when confronted with rewarding and non-rewarding flowers in three flower colour combinations (R/O: red/orange; O/Y: orange/yellow; P/G: pink/green). Each open symbol represents the mean (\pm SE) number of different flowers visited of the non-rewarding colour until the switch to visiting flowers of the rewarding colour. The horizontal dashed line refers to chance level of performance, and asterisks denote performances that were significantly different from chance ($P < 0.05$). The rewarding colours in each trial were orange (O), yellow (Y) and green (G), respectively.

Examination of cumulative choices across the 20-min blocks within each feeding trial showed that resident and migratory hummingbirds differ in their preferences for a flower colour type. The proportion of rewarding flowers visited over time varied depending on the migratory status and the confronted colour combination (Fig. 4); resident and migratory species marginally differed in the proportion of rewarding flowers visited over time (repeated-measures ANOVA, $F_{1, 226} = 2.81$, $P = 0.097$). Significant differences were observed within colour treatments ($F_{2, 226} = 38.59$, $P = 0.0001$), and the migratory status \times colour combination interaction was also significant ($F_{2, 226} = 3.12$, $P = 0.048$).

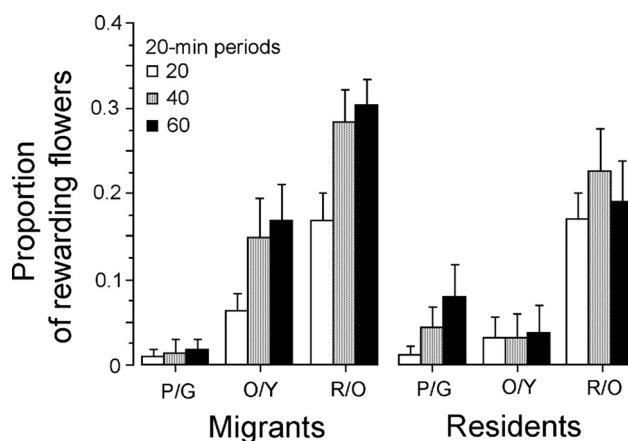


Fig. 4. — Examination of cumulative choices of migrant and resident hummingbirds across 20-min blocks within each feeding trial using three flower colour combinations (R/O: red/orange; O/Y: orange/yellow; P/G: pink/green). The rewarding colours in each trial were orange (O), yellow (Y) and green (G), respectively.

DISCUSSION

Migrants and residents responding to environmental changes

In this aviary study, some individuals gave up soon after non-rewarding foraging attempts (23%). Most of these responses (61%) to experimental arrays observed among resident species in the O/Y and P/G colour combinations (Table 2) occurred because they had a first non-rewarding foraging attempt or because they were faithful to red or close-to-red colours (flower colour constancy). This inflexible behavioural response may indicate that individuals of resident species perceived only red (or reddish colours) as an acceptable rewarding colour. The fact that some individuals (21.6%; Table 2) continuously visited non-rewarding flowers is intriguing as they incurred greater energetic expenses in hovering by visiting non-rewarding flowers for 1 hr. Individuals that consistently visited the same non-rewarding colour, and starved for 1 hr, showed a limited perception for rare or new colours as rewarding (or they have been minoring on red flowers), as most of the responses (92%) occurred in the P/G colour combination.

Switching was the most efficient behavioural response to environmental changes in the aviary as they gathered the reward in the experimental array. GRANT & GRANT (1968) suggested that resident tropical hummingbirds could readily locate food without the aid of a uniform flower colour as they live in an environment where food supply is predictable throughout the year. In contrast, migrant hummingbirds and highly mobile hummingbirds (*sensu* FEINSINGER 1980) experience environmental changes during migration and should sample novelties more often (ALTSHULER & NUNN 2001; LARA et al. 2009). These individuals would be exposed to different colour cues that they can use to discriminate between rewarding and non-rewarding food sources. Thus, the flexibility to switch would be more adaptive for migrants than would be a fixed colour preference, as their environments change unpredictably. Unexpectedly, migrants did not perform better in their response to a given task (proportion of rewarding flowers

visited, proportion of different rewarding flowers, giving-up time) than residents, challenging the usefulness of dichotomies such as that of migratory and resident hummingbirds in the response to a given task. AB and EF did, however, switch colours in the face of unexpected changes in the environment. There are two possible explanations for this result. Firstly, different species (or individuals) may have different ways of responding to environmental changes (KREBS & INMAN 1992; SANDLIN 2000a). A fixed foraging behaviour can be favoured when the environment is constant and easy to predict (e.g., one rewarding colour), but it may also be best if change is unpredictable or when spatial variation is so complex that it cannot be learned. On the other hand, the ability to shift from colour consistency to colour switching should improve hummingbirds' foraging rate in the face of unexpected changes in the environment. The basic assumption that migrants should switch more readily than residents could be argued the other way around. That is, migrants should use cues that will most rapidly lead them to rewarding flowers upon arriving at a new site, and resident hummingbirds are 'keeping tabs' on a long list of local floral resources of various colours and add new ones to their repertoire at the moment they come into bloom. These hypotheses require explicit further testing.

The second, more plausible, explanation is that although hummingbirds can detect changes in the environment using colour cues, they require further information to assess the colour and location of the unexpected rewarding colour. Experimental studies on colour discrimination by hummingbirds have shown that individuals quickly associate colour with food rewards in arrays of artificial flowers, and can discriminate between colours with a high degree of spectral sensitivity (MILLER & MILLER 1971; GOLDSMITH & GOLDSMITH 1979; GOLDSMITH 1980). The results of our experiment suggest that hummingbirds switched more easily from red to orange (93%) than any other colour combination used in the experiment (< 40%). Red flowers are common among hummingbird-pollinated plants (GRANT 1966; WEISS 1991). Red colour provides information on the location of nectar over space and time, but also it represents a stimulus that could provide a different kind of information. The plant uses these signals presumably to exploit the sensitivity of certain lineages of hummingbirds to red, but nothing is known on the ontogeny of this preference.

The differential behaviour of CT with respect to other migratory species is intriguing. However, phenological differences between hummingbird species used in our study entailed the overlap of some of our experiments with the breeding season of CT. This may explain the different behaviour recorded in this species, but further studies are required to test this possibility.

Differential sensitivity to colour

In this study, we showed that both migrant and resident hummingbirds switched more easily from red to orange than any other colour combination used in the experiment, and their performance in this colour combination was better than chance. The observation that hummingbirds are strongly attracted to red in nature (GRANT 1966; STILES 1976; FAEGRI & VAN DER PIJL 1979), and the reinforcement imposed by the nectar feeders previous to the test, could explain why hummingbirds in this study were more faithful to red or reddish colours; hummingbirds have experience in their lives to associate red/orange colours with rewards. However, the performance of migrants was better than chance when confronted with the O/Y combination and residents did better than chance in the P/G combination. Given the existing evidence suggesting that colour

and spectral sensitivities vary among species (GOLDSMITH 1980; JACOBS 1992; VARELA et al. 1993), it is likely that hummingbirds perceived the differences in reflectance between red colours used in the three-color combinations.

Individuals that repeatedly foraged on few rewarding flowers might have memorized their spatial location in the array. There is evidence indicating that hummingbirds are more influenced by the position of the nectar source than its colour (BENÉ 1945; COLLIAS & COLLIAS 1968; MILLER & MILLER 1971; MILIAR et al. 1985; BROWN & GASS 1993; BROWN 1994; SUTHERLAND & GASS 1995), and that hummingbirds use both location and visual cues (HURLY & HEALY 1996) to remember previously rewarding flowers hierarchically or independently depending on environmental conditions (PÉREZ et al. 2011). Therefore, our interpretation of differential sensitivity to colour must be interpreted with caution. STILES (1976) pointed out that being able to discriminate within a flower clump is more relevant for the birds than being able to find a feeder. By remembering the location of each flower, hummingbirds can discriminate through multiple visits which individual flowers or inflorescences are the most profitable (and preferentially return to them); they can avoid revisiting an area or flowers they have previously emptied (STILES 1976; HAINSWORTH et al. 1983), or they can associate rewarding flowers with other stimuli in the visual field (BROWN 1994). The use of spatial memory has two advantages: (1) it enables a bird to recall which flowers were visited most recently (and thus were emptied of nectar) and (2) it provides reliable information to use to decide which flowers or patch of flowers to visit on the next foraging flight (STILES 1976), or the next foraging day (GASS & SUTHERLAND 1985). Therefore, it is possible that hummingbirds used both location and colour cues to remember which flowers they visited and emptied to avoid them in the next foraging bout (HURLY & HEALY 1996).

Differences in information processing

There are at least two alternative interpretations of the origin for the species differences in switching. First, high-volume flowers used for this experiment represent different things to different species (e.g. differences in extraction rates; MONTGOMERIE 1984; SANDLIN 2000a). Morphological differences among the studied hummingbirds (body mass, wing-disc loadings, crop size) make the interpretation of our results difficult since the benefits and costs of a high volume differ among species (e.g., hummingbirds could not adjust meal size to the high-volume flowers offered in this study; TAMM 1989). High-volume artificial flowers such as those used in this study (200- μ L) offered more food than most of the birds could consume in a visit, and normally more than North American, territorial hummingbirds would encounter in nature. Across a wide range of hummingbird territories, nectar standing crop means per flower are usually less than 4 μ L (GASS & ROBERTS 1992). The situation is different among more tropical, traplining hummingbirds, which come across flowers that produce nectar copiously and accumulate standing crops of up to several hundred microliters (GASS & ROBERTS 1992). Most species of hummingbirds in our study have been observed in other geographic areas foraging on plants pollinated mainly by bats and perching birds (HERNANDEZ & TOLEDO 1979; CRUDEN et al. 1983; EGUIARTE & BURQUEZ 1987; EGUIARTE et al. 1987; MARTÍNEZ DEL RIO & EGUIARTE 1987; ORNELAS et al. 2002). In all cases, flowers accumulate standing crops of up to 300 μ L (ORNELAS et al. 2007). Therefore, it is possible that hummingbirds at Las Joyas have experienced some of these high-volume flowers, as they do in other geographic areas.

Second, intrinsic differences among species could explain the observed tendency to switch among migrants. However, the observation that not all migrant hummingbirds switched to the rewarding colour in the floral array, as hypothesized, indicates that some individuals may rely on other cues while foraging (e.g., smell; IOALÉ & PAPI 1989). A certain degree of curiosity and occasional exploration for colour novelties can potentially benefit an individual forager, particularly a migrant hummingbird (ALTSHULER & NUNN 2001). TAMM (1989) showed that the Calliope Hummingbird (*Stellula calliope*), a latitudinal migrant species, not only uses multiple sources of information, but integrates them over multiple time scales simultaneously into foraging decisions. On a phylogenetic scale, a 'hard-wired' network, in which only certain colours are perceived as acceptable rewards, may be an evolutionary consequence of specialization resulting in the loss of the ability to switch, or they might never have had that ability. If our hypothesis is correct, ancestral members of a given hummingbird lineage (e.g., mangoes, CT) would be somehow less flexible in their foraging (constancy) than switching among those more derived members (e.g., emeralds, AB). This hypothesis cannot be tested yet because of the lack of detailed foraging behaviour data for most hummingbird species; however, it would be worthwhile to examine cognitive abilities and sensitivity to colour in a phylogenetic context, particularly to determine if differences between ancestral and more derived members of hummingbird lineages in sensitivity to colour are related to the inability to learn novel resources.

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REFERENCES

- ALTSHULER D.L. 2003. Flower color, hummingbird pollination, and habitat irradiance in four Neotropical forests. *Biotropica* 35: 344–355.
- ALTSHULER D.L. & NUNN A.M. 2001. Observational learning in Hummingbirds. *The Auk* 118: 795–799. doi:[10.1642/0004-8038\(2001\)118\[0795:OLIH\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2001)118[0795:OLIH]2.0.CO;2).

- ARIZMENDI M.C. 2001. Multiple ecological interactions: nectar robbers and hummingbirds in a highland forest in Mexico. *Canadian Journal of Zoology* 79: 997–1006. doi:[10.1139/z01-066](https://doi.org/10.1139/z01-066).
- BACON I., HURLY T.A. & HEALY S.D. 2010. Both the past and the present affect risk-sensitive decisions of foraging rufous hummingbirds. *Behavioral Ecology* 21: 626–632.
- BACON I., HURLY T.A. & HEALY S.D. 2011. Hummingbirds choose not to rely on good taste: information use during foraging. *Behavioral Ecology* 22: 471–477.
- BENÉ F. 1945. The role of learning in the feeding behavior of Black-chinned Hummingbirds. *The Condor* 47: 3–22. doi:[10.2307/1364444](https://doi.org/10.2307/1364444).
- BRODBECK D.R. 1994. Memory for spatial and local cues: a comparison of a storing and a non-storing species. *Animal Learning & Behavior* 22: 119–133. doi:[10.3758/BF03199912](https://doi.org/10.3758/BF03199912).
- BROWN G.S. 1994. Spatial association learning by Rufous hummingbirds (*Selasphorus rufus*): effects of relative spacing among stimuli. *Journal of Comparative Psychology* 108: 29–35. doi:[10.1037/0735-7036.108.1.29](https://doi.org/10.1037/0735-7036.108.1.29).
- BROWN G.S. & GASS C.L. 1993. Spatial association learning by hummingbirds. *Animal Behaviour* 46: 487–497. doi:[10.1006/anbe.1993.1217](https://doi.org/10.1006/anbe.1993.1217).
- COLE S., HAINSWORTH F.R., KAMIL A.C., MERCIER T. & WOLF L.L. 1982. Spatial learning as an adaptation in hummingbirds. *Science* 217: 655–657.
- COLLIAS N.E. & COLLIAS E.C. 1968. Anna's hummingbirds trained to select different colors in feeding. *The Condor* 70: 273–274. doi:[10.2307/1366705](https://doi.org/10.2307/1366705).
- CRUDEN R.W., HERMANN S.M. & PETERSON S. 1983. Patterns of nectar production and plant-pollinator coevolution, pp. 80–125. In: Bentley B. & Elias T., Eds. *The biology of nectaries*. New York, NY: Columbia University Press.
- EGUIARTE L.E. & BURQUEZ A. 1987. Reproductive ecology of *Manfreda brachystachya*, an iteroparous species of Agavaceae. *The Southwestern Naturalist* 32: 169–178. doi:[10.2307/3671560](https://doi.org/10.2307/3671560).
- EGUIARTE L.E., MARTÍNEZ DEL RIO C. & ARITA H. 1987. El nectar y el polen como recursos: el papel ecológico de los visitantes a las flores de *Pseudobombax ellipticum* (H.B.K.) Dugand. *Biotropica* 19: 74–82. doi:[10.2307/2388462](https://doi.org/10.2307/2388462).
- EWALD P.W. & CARPENTER F.L. 1978. Territorial responses to energy manipulations in the Anna hummingbird. *Oecologia* 31: 277–292. doi:[10.1007/BF00346248](https://doi.org/10.1007/BF00346248).
- FAEGRI K. & VAN DER PIJL L. 1979. *The principles of pollination ecology* (3rd ed.). Oxford, UK: Pergamon Press.
- FEINSINGER P. 1980. Asynchronous migration patterns and the coexistence of tropical hummingbirds, pp. 411–419. In: Keast A. & Morton E.S., Eds. *Migrant birds in the Neotropics: ecology, behaviour, distribution, and conservation*. Washington, DC: Smithsonian Institution Press.
- FEINSINGER P., SWARM A. & WOLFE J.A. 1985. Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. *Ecological Monographs* 55: 1–28. doi:[10.2307/1942523](https://doi.org/10.2307/1942523).
- GASS C.L. & ROBERTS W.M. 1992. The problem of temporal scale in optimization: three contrasting views of hummingbird visits to flowers. *The American Naturalist* 140: 829–853. doi:[10.1086/285443](https://doi.org/10.1086/285443).
- GASS C.L. & SUTHERLAND G.D. 1985. Specialization by territorial hummingbirds on experimentally enriched patches of flowers: energetic profitability and learning. *Canadian Journal of Zoology* 63: 2125–2133. doi:[10.1139/z85-313](https://doi.org/10.1139/z85-313).
- GOLDSMITH T.H. 1980. Hummingbirds see near ultraviolet light. *Science* 207: 786–788. doi:[10.1126/science.7352290](https://doi.org/10.1126/science.7352290).
- GOLDSMITH T.H. & GOLDSMITH K.M. 1979. Discrimination of colors by the Black-chinned hummingbird, *Archilochus alexandri*. *Journal of Comparative Physiology (A)* 130: 209–220. doi:[10.1007/BF00614607](https://doi.org/10.1007/BF00614607).
- GONZÁLEZ-GÓMEZ P.L., VÁSQUEZ R.A. & BOZINOVIC F. 2011. Flexibility of foraging behavior in hummingbirds: the role of energy constraints and cognitive abilities. *The Auk* 128: 36–42. doi:[10.1525/auk.2011.10024](https://doi.org/10.1525/auk.2011.10024).
- GRANT K.A. 1966. A hypothesis concerning the prevalence of red coloration in California hummingbird flowers. *The American Naturalist* 100: 85–97. doi:[10.1086/282403](https://doi.org/10.1086/282403).

- GRANT K.A. & GRANT V. 1968. Hummingbirds and their flowers. *New York, NY: Columbia University Press*.
- HAINSWORTH F.R., MERCIER T. & WOLF L.L. 1983. Floral arrangements and hummingbird feeding. *Oecologia* 58: 225–229. doi:10.1007/BF00399221.
- HEALY S.D. & HURLY T.A. 1995. Spatial memory in rufous hummingbirds (*Selasphorus rufus*): a field test. *Animal Learning and Behaviour* 23: 63–68.
- HEALY S.D. & HURLY T.A. 2003. Cognitive ecology: Foraging in hummingbirds as a model system. *Advances in the Study of Behavior* 32: 325–359. doi:10.1016/S0065-3454(03)01007-6.
- HERNANDEZ H.M. & TOLEDO V.M. 1979. The role of nectar robbers and pollinators in the reproduction of *Erythrina leptorhiza*. *Annals of the Missouri Botanical Garden* 66: 512–520. doi:10.2307/2398843.
- HURLY T.A. 1996. Spatial memory in rufous hummingbirds: memory for rewarded and non-rewarded sites. *Animal Behaviour* 51: 177–183.
- HURLY A.T. & HEALY S.D. 1996. Memory for flowers in rufous hummingbirds: location or local visual cues? *Animal Behaviour* 51: 1149–1157. doi:10.1006/anbe.1996.0116.
- IOALÉ P. & PAPI F. 1989. Olfactory bulb size, odor discrimination and magnetic insensitivity in hummingbirds. *Physiology & Behavior* 45: 995–999. doi:10.1016/0031-9384(89)90227-8.
- IRWIN R.E. & BRODY A.K. 1999. Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* 80: 1703–1712. doi:10.1890/0012-9658(1999)080[1703:NRBBRT]2.0.CO;2.
- JACOBS G.H. 1992. Ultraviolet vision in vertebrates. *American Zoologist* 32: 544–554.
- JARDEL E.J. 1991. Perturbaciones naturales y antropogénicas y su influencia en la dinámica sucesional de los bosques de Las Joyas, Sierra de Manantlán, Jalisco. *Tiempos de Ciencia* 22: 9–26.
- KREBS J.R. & INMAN A.J. 1992. Learning and foraging: individuals, groups, and populations. *The American Naturalist* 140: SS63–SS84. doi:10.1086/285397.
- LARA C. 2006. Temporal dynamics of flower use by hummingbirds in a highland temperate forest in Mexico. *Ecoscience* 13: 23–29. doi:10.2980/1195-6860(2006)13[23:TDOFUB]2.0.CO;2.
- LARA C., GÓMEZ L., VALERO A., ORTÍZ-PULIDO R. & CASTILLO-GUEVARA C. 2011. Risk indifference in white-eared hummingbird (*Hylocharis leucotis*) confronting four foraging options. *Revista Mexicana de Biodiversidad* 84: 630–636.
- LARA C., GONZÁLEZ J. & HUDSON R. 2009. Observational learning in the White-eared hummingbird (*Hylocharis leucotis*): experimental evidence. *Ethology* 115: 872–878. doi:10.1111/j.1439-0310.2009.01668.x.
- LARA C. & ORNELAS J.F. 1998. Forrajeo de artrópodos por dos especies de colibríes mexicanos en condiciones de aviario. *Ornitología Neotropical* 9: 41–50.
- LARA C. & ORNELAS J.F. 2001. Preferential nectar robbing of flowers with long corollas: experimental studies of two hummingbird species visiting three plant species. *Oecologia* 128: 263–273. doi:10.1007/s004420100640.
- LEMEL J.-Y., BELICHON S., CLOBERT J. & HOCHBERG M.E. 1997. The evolution of dispersal in a two-patch system: some consequences of differences between migrants and residents. *Evolutionary Ecology* 11: 613–629. doi:10.1007/s10682-997-1516-z.
- LYERLY S.B., RIESS B.F. & ROSS S. 1950. Colour preference in the Mexican Violet-ear Hummingbird, *Colibri t. thalassinus* (Swainson). *Behaviour* 2: 237–248.
- MARTÍNEZ DEL RIO C. & EGUIARTE L.E. 1987. Bird visitation to *Agave salmiana*: comparisons among hummingbirds and perching birds. *The Condor* 89: 357–363. doi:10.2307/1368488.
- MELÉNDEZ-ACKERMAN E., CAMPBELL D.R. & WASER N.M. 1997. Hummingbird behavior and mechanisms of selection on flower color in *Ipomopsis*. *Ecology* 78: 2532–2541.
- METTKE-HOFMANN C., LORENTZEN S., SCHLICHTS E., SCHNEIDER J. & WERNER F. 2009. Spatial neophilia and spatial neophobia in resident and migratory warblers (*Sylvia*). *Ethology* 115: 482–492. doi:10.1111/j.1439-0310.2009.01632.x.
- MILIAR R.S., TAMM S., SUTHERLAND G.D. & GASS C.L. 1985. Cues for orientation in hummingbird foraging: color and position. *Canadian Journal of Zoology* 63: 18–21. doi:10.1139/z85-004.
- MILLER R.S. & MILLER R.E. 1971. Feeding activity and color preference of Ruby-throated hummingbirds. *The Condor* 73: 309–313. doi:10.2307/1365757.

- MITCHELL W.A. 1989. Informational constraints on optimally foraging hummingbirds. *Oikos* 55: 145–154. doi:[10.2307/3565417](https://doi.org/10.2307/3565417).
- MONTGOMERIE R.D. 1984. Nectar extraction by hummingbirds: response to different floral characters. *Oecologia* 63: 229–236. doi:[10.1007/BF00379882](https://doi.org/10.1007/BF00379882).
- ORNELAS J.F. 1994. Serrate tomia: an adaptation for nectar robbing in hummingbirds? *The Auk* 111: 703–710.
- ORNELAS J.F. 1995. Radiation in the genus *Amazilia*: a comparative approach to understanding the diversification of hummingbirds. *Ph.D. Dissertation, University of Arizona, Tucson, AZ*.
- ORNELAS J.F. & ARIZMENDI M.C. 1995. Altitudinal migration: implications for the conservation of the Neotropical migrant avifauna of western Mexico, pp. 98–112. In: Wilson M. & Sader S., Eds. *Conservation of Neotropical migratory birds in Mexico. Maine, USA: Maine Agriculture and Forestry Experimental Station*.
- ORNELAS J.F., ORDANO M., DE-NOVA A., QUINTERO M.E. & GARLAND T. 2007. Phylogenetic analysis of interspecific variation in nectar of hummingbird-visited plants. *Journal of Evolutionary Biology* 20: 1904–1917. doi:[10.1111/j.1420-9101.2007.01374.x](https://doi.org/10.1111/j.1420-9101.2007.01374.x).
- ORNELAS J.F., ORDANO M., HERNÁNDEZ A., LÓPEZ J.C., MENDOZA L. & PERRONI Y. 2002. Nectar oasis produced by *Agave marmorata* Roezl. (Agavaceae) lead to spatial and temporal segregation among nectarivores in the Tehuacán Valley, México. *Journal of Arid Environments* 52: 37–51. doi:[10.1006/jare.2002.0971](https://doi.org/10.1006/jare.2002.0971).
- PÉREZ G., LARA C., VICCON-PALE J. & SIGNORET-POILLON M. 2011. Memory for location and visual cues in white-eared hummingbirds *Hylocharis leucotis*. *Current Zoology* 57: 468–476.
- RAPPOLE J.H. & SCHUCHMANN K.L. 2003. Ecology and evolution of hummingbird population movements and migration, pp. 39–51. In: Berthold P. et al., Eds. *Avian migration. Heidelberg, Berlin: Springer-Verlag*.
- ROBINSON E.A. 1985. Probability theory and applications. *Boston, MA: D. Reidel Pub. Co.*
- SANDLIN E.A. 2000a. Cue use affects resource subdivision among three coexisting hummingbird species. *Behavioral Ecology* 11: 550–559. doi:[10.1093/beheco/11.5.550](https://doi.org/10.1093/beheco/11.5.550).
- SANDLIN E.A. 2000b. Foraging information affects the nature of competitive interactions. *Oikos* 91: 18–28. doi:[10.1034/j.1600-0706.2000.910102.x](https://doi.org/10.1034/j.1600-0706.2000.910102.x).
- STILES F.G. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. *The Condor* 78: 10–26. doi:[10.2307/1366912](https://doi.org/10.2307/1366912).
- STILES F.G. 1988. Altitudinal movements of birds on the Caribbean slope of Costa Rica: implications for conservation, pp. 243–258. In: Alameda F. & Pringle C.M., Eds. *Tropical rain-forests: diversity and conservation. San Francisco, CA: California Academy of Sciences*.
- SUTHERLAND G.D. & GASS C.L. 1995. Learning and remembering of spatial patterns by hummingbirds. *Animal Behaviour* 50: 1273–1286. doi:[10.1016/0003-3472\(95\)80043-3](https://doi.org/10.1016/0003-3472(95)80043-3).
- TAMM S. 1987. Tracking varying environments: sampling by hummingbirds. *Animal Behaviour* 35: 1725–1734. doi:[10.1016/S0003-3472\(87\)80065-9](https://doi.org/10.1016/S0003-3472(87)80065-9).
- TAMM S. 1989. Importance of energy costs in central place foraging by hummingbirds. *Ecology* 70: 195–205. doi:[10.2307/1938426](https://doi.org/10.2307/1938426).
- VARELA F.J., PALACIOS A.G. & GOLDMITH T.H. 1993. Color vision of birds, pp. 77–98. In: Zeigler H. P. & Bischof H.J., Eds. *Vision, brain, and behavior in birds. Cambridge, MA: Massachusetts Institute of Technology Press*.
- VÁZQUEZ J.A., CUEVAS R., COCHRANE T.S., ILTIS H.H., SANTANA F.J. & GUZMÁN H.L. 1995. Flora de Manatlán. *Forth Worth, TX: Universidad de Guadalajara-University of Wisconsin-Madison-Botanical Research Institute of Texas*.
- WEISS M.R. 1991. Floral colour changes as cues for pollinators. *Nature* 354: 227–229. doi:[10.1038/354227a0](https://doi.org/10.1038/354227a0).
- WOLF L.L. & HAINSWORTH F.R. 1986. Information and hummingbird foraging at individual inflorescences of *Ipomopsis aggregata*. *Oikos* 46: 15–22.