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Discrimination of Colors by the Black-Chinned Hummingbird, *Archilochus alexandri*

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Summary. The color vision of a population of black-chinned hummingbirds was studied by behavioral methods. Birds were attracted to feeders equipped with tungsten lamps and interference filters. Results are based on counts of approximately 5700 visits by 92 ± 5 birds. Population size was estimated by mist-netting and marking 29 hummingbirds, 22 of which could be recognized individually during the course of the experiments.

Following experience with red (620 nm) at all feeders, the birds showed a modest tendency to visit red (620 nm, 650 nm) and blue (490 nm) rather than intermediate greens and yellows. When sugar was presented at only one wavelength, however, choices became much sharper.

When positions of the feeders were randomized, trained birds selected feeders on the basis of hue. Brightness was not used as a significant cue. This finding thus provides a more rigorous demonstration of color vision in hummingbirds than has heretofore been available.

Either position or color could be learned in several hours (6–22 visits). Red (620 nm) and green (546 nm) were learned at the same rate. Two different (and opposing) color associations could be learned simultaneously at sites approximately 30 m apart.

Discrimination of hue was measured following training to each of four wavelengths: 620, 590, 546, and 480 nm. Light from interference filters with transmission maxima at 546 and 550 nm were differentiated by the birds to a statistically significant extent. 546 and 590 nm appear to lie near the boundaries of hues; a boundary near 540 nm is found in pigeon but not human color vision.

Introduction

Red is the commonest color of hummingbird pollinated flowers, at least in temperate latitudes (Graenicher, 1910; Pickens, 1930, 1941; Grant and Grant, 1968), and there persists a common belief that hummingbirds are preferentially attracted to red. Moreover, this "preference" is frequently assumed to reflect some specialized sensory or neural apparatus and therefore a genetic basis. Thus, for example, one can find recent reference "...to the color preference (known to every observer) of trochilids, moreover to...researches on birds proving their high sensitivity to red and their much lower sensitivity to blue" (Faegri and van der Pijl, 1971).

The facts tell another story. Sherman (1913), Pickens (1941), Béné (1941), Wagner (1946); Lyerly et al. (1950), Grant (1966), and Miller and Miller (1971) found that red was not preferentially visited at artificial feeders. On the other hand Collias and Collias (1968), Poley (1968) and Stiles (1976) have reported instances where it was; in the latter case, however, choices correlated with the color of the birds' most recent natural food source. There is general agreement among the more recent authors that position of the feeder in an array (Lyerly et al., 1950; Collias and Collias, 1968; Miller and Miller, 1971) and concentration of sugar (Collias and Collias, 1968; Stiles, 1976) can have an overriding influence on the choices of feeder made by hummingbirds.[1]

Béné (1945), on the basis of observations of a pair of recently fledged black-chinned hummingbirds, concluded that they had to learn by trial and error to associate flowers with sugar sources, and that they were not preferentially attracted to any particular color of flower. Wagner (1946), fed several species of Mexican hummingbirds from flasks covered with colored papers, concluding that "the flask most frequently visited was always the same color as the flower most visited at the particular season." Wagner

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[1] The position effect was not recognized by Sherman (1913) and Pickens (1941), and to an uncertain extent by Béné (1941). The outcome of Pickens' first experiment appears to have been molded by a position preference, and the results of his second do not survive a test of statistical significance. His conclusion that violet was preferred by ruby-throated hummingbirds is therefore suspect. Similarly, the results of the first experiment of Béné (1941) on black-chinned hummingbirds do not show a statistically significant preference for yellow

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did not present his data, however, so his report had relatively little impact. Hummingbirds have been shown to learn color-food associations in several experimental situations (Scheithauer, 1967; Collias and Collias, 1968; Poley, 1968; Miller and Miller, 1971; Stiles, 1976). What, then, does one make of the correlation between red color and pollination by hummingbirds? In our judgement the most plausible explanation is that in the evolution of a predominately red hummingbird-pollinated flora, the initiative has fallen to the plants. It is not that red can play a unique role in attracting hummingbirds, but rather that it is the color least likely to attract competing Hymenoptera (Grant and Grant, 1968; Raven, 1972).[2] Red has also been assumed to contrast with green foliage (Pickens, 1930; Miller and Miller, 1971), a view for which there has been little direct evidence but which is supported by the present experiments. Red serves as a flag, but its association with nectar sources is learned (Stiles, 1976).

From the standpoint of visual physiology, all of the previous experiments on hummingbird vision suffer a dual drawback: they employed broad band stimuli of (usually) unspecified spectral content (food dyes, paints), and none addressed the relative roles of hue and brightness. The results therefore provide no useful information on wavelength discrimination and are difficult to interpret in terms of known (or knowable) retinal functions. As a consequence there is little basis for such conclusions as "recent work suggests that the ability of flower birds to distinguish shades of color in the red-orange area may greatly exceed our own" (Raven, 1972).

The following experiments were planned as a pilot study to explore the feasibility of using a wild population of hummingbirds in experiments capable of testing wavelength discrimination and related visual processes. On the basis of these results, the approach appears promising.

Methods

Location. These experiments were performed on a population of wild birds at the Southwestern Research Station of the American Museum of Natural History in the Chiricahua Mountains in southeastern Arizona. This location was selected for two reasons. First, three species of hummingbird are abundant in the area: the black-chinned (*Archilochus alexandri*), blue-throated (*Lampornis clemenciae*), and the magnificent (or Rivoli's) (*Eugenes fulgens*). Second, the months of May and June are virtually without rain, the birds are feeding on insects, and there are few if any natural sources of nectar to compete with artificial feeders.

Feeders. Four feeders were employed. Each consisted of a lamp housing 20 cm wide × 18 cm high × 25 cm deep, containing a 500 watt projection lamp, collimating lenses, heat filter, a small cooling fan, and a six-position wheel holding a selection of interference filters (Ditric, three cavity, half band width 7 ± 2 nm depending on the filter). Except around the transmission peak, the filters were blocked to $<0.01\%$ at all wavelengths from the ultraviolet through the infrared. The $\lambda_{\max}$ was within 1 or occasionally 2 nm of the nominal value indicated by the manufacturer. The front of the housing contained a 22 mm diameter ground glass port uniformly irradiated from behind by narrow spectral bands of light, appearing as a bright luminous disk on the matte black background of the exterior finish of the box. A 250 ml plastic wash bottle was suspended in front of the lamp housing in an inverted position. The tube was trimmed to form a 25 mm "corolla" centered in front of the luminous disk, and the birds could draw solution by hovering in front of the feeder and inserting the bill into the tube. The feeders contained either 0.5 M sucrose or water, as specified in the description of individual experiments.

The feeders were mounted in pairs on photographic tripods at a height of 1 m and separated laterally by about 62 cm. In most experiments all four feeders were used in a linear array; in a few experiments they were used as pairs. The birds fed readily and were not disturbed by the soft hum of the fan motors.

The lamps were run from a stabilized power supply. Fluxes were measured with a calibrated photodiode (United Detector Technology), and except where otherwise indicated in the Results, they were adjusted on a quantum basis for equal photopic luminosity for the pigeon (further details in Results). Intensity was controlled by the insertion of neutral density filters and by trimming the voltage supplied to the lamp. In the latter case it was necessary to compensate for the change in color temperature of the lamp by calibrating the output flux vs lamp voltage at several wavelengths. Energy flux fell in the range 5×10^{14}–5×10^{15} photons s^{-1} cm^{-2} in a plane just external to the ground glass disk. Contrast was maintained approximately constant during the course of the day by placing the feeders in the shade of a canvas tarpaulin. The relative roles of brightness and hue are described in the Results.

Marking of Birds. In order to be able to recognize individuals, 70 hummingbirds were mist-netted and coded with small marks of colored paint on the mid dorsum. This marking, which was done between May 7 and May 16, involved 29 *Archilochus*, 20

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[2] According to Schimper (1903), the first adequate description of pollination by hummingbirds dates from 1870. The possibility is not mentioned in Gould's (1861) monograph on the Trochilidae. Darwin (1877) was aware of only a few cases of pollination by birds, and gives red no special mention. Ten years later, in 1887, however, Kerner von Marilaun had some remarkable things to say on the subject in his popular treatise "Pflanzenleben" (English edition, Kerner, 1895). "[Scarlet-red] flowers in particular affect the hummingbird. Indeed it seems that this tiny bird ... prefers scarlet flowers" (Vol. 2, p. 196). Unfortunately one cannot tell from Kerner's account whether he is summarizing a concept that had become so widely accepted in the preceeding decade that documentation was thought to be unnecessary, or whether the idea was original with him. In either event he also made the cautious suggestion that "further observations in tropical regions are required to ascertain whether there are not other flower-visiting animals besides hummingbirds and butterflies, especially flies and beetles, which can distinguish scarlet flowers ...; for certain plants ... with large scarlet spathes ... have no honey, and are consequently disregarded by hummingbirds and butterflies." Moreover, Kerner also recognized that in general Hymenoptera are drawn to flowers with colors at the short wavelength end of the spectrum, leaving the reds to butterflies and hummingbirds (Vol. 2, p. 195). The principal contribution of more recent authors to this subject has therefore been to restate the correlation in neo-Darwinian language.

Although Schimper (1903) cited Kerner for claiming "an essential connection between ... the wealth of the American flora in plants with red blossoms, and ... the presence of hummingbirds" he was in agreement about the senses of hummingbirds. "Undoubtedly [hummingbirds] show a preference for red, especially for fiery red colors." The idea that red plays a special role in the visual behavior of hummingbirds therefore seems to have become firmly entrenched before the turn of the century

Lampornis, 20 *Eugenes*, and 1 *Selasphorus platycerus*. The sites for netting were between 40 and 100 m from the location of the experimental feeders, which were in operation between May 13 and June 3.

General behavior of feeding birds. The feeders were placed in an open area, and although all three of the common species of hummingbird visited them regularly, the black-chins were the most numerous, presumably because they are more likely to leave wooded areas to forage. All of our quantitative results are therefore based on *A. alexandri*, but we have no reason to believe that more extensive observations of the other species would have led to different findings.

Male blue-throated hummingbirds occasionally attempted to dominate the feeding area, chasing away other individuals of the same or other species. Among the black-chinned hummingbirds, however, the females were clearly dominant. The black-chins frequently visited the feeders in small groups, noisily stirring about and chasing each other. Females frequently displaced males from feeders; males seldom displaced females. Females often chased each other, but pairs of females would frequently share a feeder for a few moments, alternately drinking, then hovering several cm away while the second bird took a turn. We have not observed two males sharing a feeder in this manner, and only once or twice, a male and a female.

Scoring of Visits. Except for the first few experiments, two observers scored the visits together, viewing the birds with 7 × binoculars and a 15 × spotting scope from distances of 8–10 m. One observer was situated directly in front of the feeders and could therefore see the identification marks on the backs of the birds. The second viewed the birds from the side and was thus in a position to determine whether they had inserted their bill into the feeding tube in the process of selecting a feeder. This latter precaution was necessary, because frequently the birds' decisions were accompanied by a head nod, and careful observation was required to determine whether the contents of the feeder had been sampled. In almost all cases the observer on the side could make this determination without ambiguity. In a few instances, where the tip of the bill approached the orifice of the "corolla" but did not quite enter it, the tongue might have flicked into the tube without having been seen. These cases were tabulated as though the bill had entered the tube and the contents tasted.

Having fed, birds frequently explored the other feeders. This behavior is important in helping birds accommodate to shifting sources of nectar. In the first experiments all visits were counted, primary choices as well as secondary exploratory visits. After training to specific colors was started, however, only primary choices were considered, and unless stated otherwise, these are the data reported in the Figures.

When birds arrived at the feeders in groups, only the initial arrivals were scored; the results are therefore not knowingly distorted by birds following each other to the same feeder. Moreover, if more than one feeder was occupied, visits were not scored until the crowd had cleared. The one exception to these latter stipulations occurred in experiments where the discriminations were so easy for the birds that individuals would repeatedly reject the "wrong" feeder – without tasting the contents – while waiting for the correct feeder to become free.

The results are based on approximately 5,700 scored visits of *A. alexandri*.

Training to Specific Wavelengths. During training to specific wavelengths, water without sugar was supplied simultaneously in association with one or two other colors, and positions were altered regularly. Further details appear with descriptions of specific experiments.

Analysis. Frequency distributions were analyzed by the χ^2 test to determine their statistical significance. Further details will be found in the Results and in the figure captions.

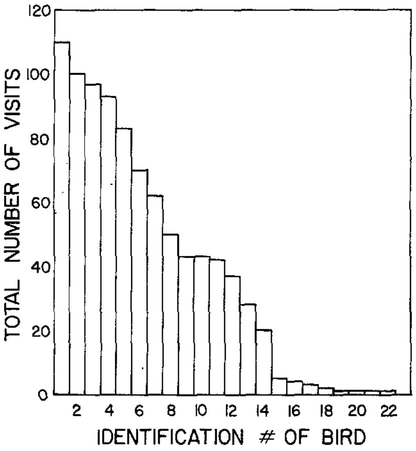

Fig. 1. Total number of recorded visits by each of 23 individually recognizable black-chinned hummingbirds during a period of approximately 2 weeks duration. Individual birds visited the feeders at very different frequencies

Results

Characteristics of the Population

Individual birds visited the feeders at different frequencies. Of the 29 marked *A. alexandri*, 22 individuals were subsequently identified as they visited the feeders; six others were recognizable, but due to preening and wear of the paint marks, identification of the individual members of this group was ambiguous; and one bird was not seen at the feeders. Visits by the 22 identifiable visitors are shown by the histogram in Fig. 1, where the birds are rank-ordered along the abscissa according to the number of visits that were observed. Individuals varied by a factor of approximately 100 in the frequency at which they came to the feeders. The reason for the great variation between individuals is not known, but it is not related to sex. Statistically equal numbers of males and females of both marked and unmarked black-chins visited the feeders.

As described in more detail below, in most experiments blocks of 25 visits were tabulated between changes in the positions of the colored lights. The number of visits by any individual during one of these blocks is therefore of importance in analyzing the results of these experiments (see also the Discussion). Table 1 shows some additional information on the frequency of visits, organized in terms of these blocks of 25 counts. On the average, an individual bird made less than 0.3 visits per block of 25 counts, and even the most frequent visitors averaged less than 0.7 visits per block.

Stability of the Population. Figure 2 shows for a 16 day period the percentage of daily visits by *A. alexandri* that is accounted for by marked birds. The line is a least squares fit of the data to a linear regres-

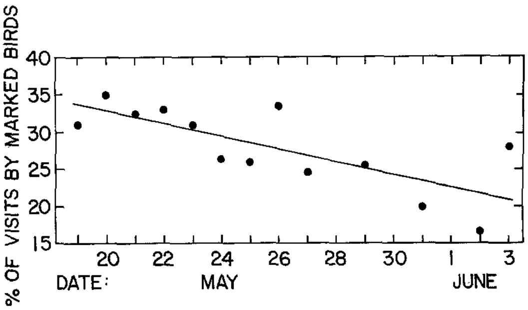

Fig. 2. Per cent of total visits of *A. alexandri* by marked individuals during a 16 day period. The straight line is a least squares fit with a slope of -0.8% per day

Table 1

No. of visits of single birds per block of 25 counts	Time required for 25 counts (min); marked and unmarked	Visits per hour	% of all visits that are repeats within a block of 25 counts
Average for 22 marked birds			
0.284 ± 0.047	12.46 ± 3.96^{a}	1.37 ± 0.49^{a}	11.5
Average for 5 most frequent visitors			
0.680		3.27	14.8

[a] ±S.D. of temporal variation. The principal source of variation is due to differences between birds, as emphasized by the second row of entries as well as Fig. 1

sion. The curve has a slope of -0.8%/day, and the decrease in the proportion of marked birds visiting the feeders with time is statistically significant (correlation coefficient $= 0.747$, $P < 0.01$). The cause of this shift in composition of the population has not been studied; however, it seems not to be caused by total disappearance of individual birds. On the other hand, the shift occurred slowly enough not to interfere with experiments of one or a few days duration. It is doubtless caused in part by the appearance of juveniles, as this species fledges in late May (Bent, 1940).

Size of the Feeding Population. On the assumption that the marked birds are representative of the larger group of black-chins, the population is estimated to consist of 92 ± 5 birds. Using the figures in Table 1, one can calculate that the birds made 1700–1800 individual visits in a 14 h day, only a fraction of which were tabulated.

Visits by blue-throated hummingbirds accounted for $9.3\% \pm 1.8$ SD of all visits; by magnificent hummingbirds, $4.9\% \pm 2.6$. Neither of these species showed a significant change in the frequency of visiting with time.

Spontaneous Choices

The first experiments were addressed to the question of whether with this equipment wild hummingbirds

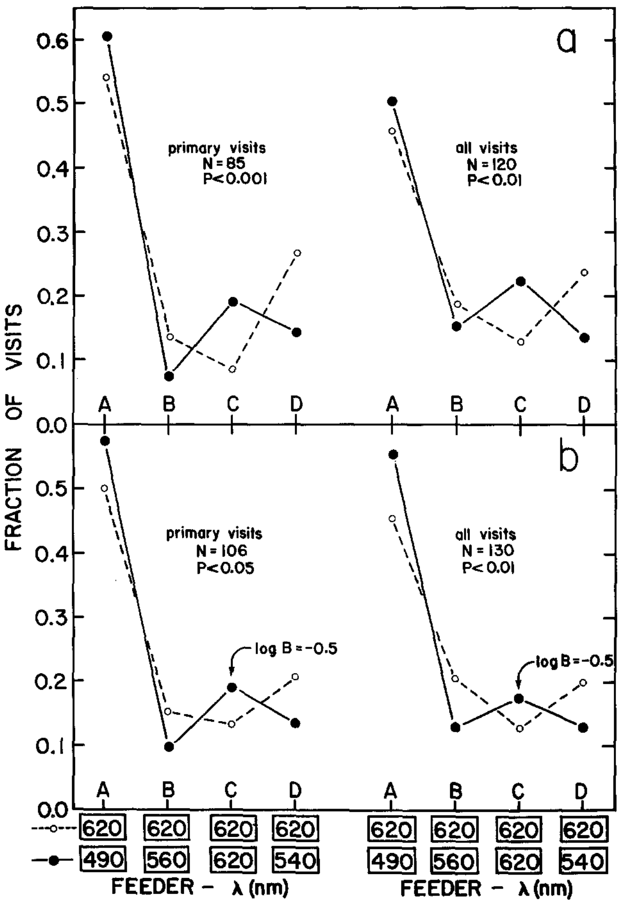

Fig. 3a and b. Distribution of visits at the 4 feeders when all were illuminated with red (open circles, broken curves) and with 4 different wavelengths (filled circles, solid curves). **a** All lights adjusted for equal photopic luminosity for the pigeon. **b** Brightness of 620 nm at feeder C reduced 0.5 log units during the period that 4 different wavelengths were displayed. Open circles show the position effect that was present during this experiment; filled circles differ significantly in χ^2 test, as indicated by the values of P. All feeders supplied with 0.5 M sucrose

show a preference for red if they have been feeding on red sources. Figure 3a shows the results. When 620 nm was displayed at all four feeders, the visits were distributed across the array as shown by the open circles and broken line. Not all feeders were equally favored; the one on the left end (A) received the most visits, the third from the left (C) fewest. This *position effect*, seen here in an extreme form, occurred regularly, although as will be described below, it was subject to alteration, and under certain conditions it disappeared. Similar preference for the end feeders has been noted by other workers (Collias and Collias, 1968; Miller and Miller, 1971). In this instance the left end was presumably preferred because it was closest to the woods from which most of the birds arrived.

When four different wavelengths were presented at the feeders (490 nm at A, 560 nm at B, 620 nm at C, 540 nm at D), the distribution of visits differed

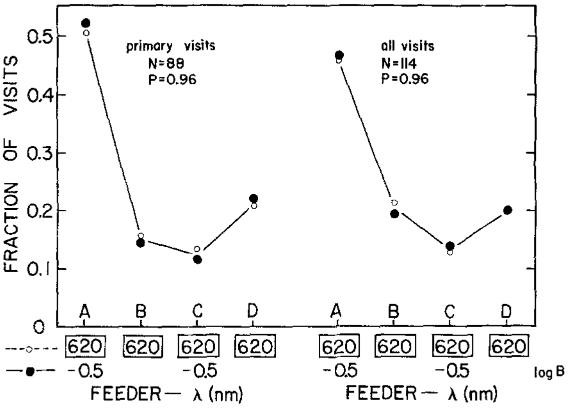

Fig. 4. Position effect evident when all feeders were illuminated with lights of identical wavelength and intensity (open circles) was unaltered by changes in brightness of two of the lamps (filled circles). Sucrose present at all feeders

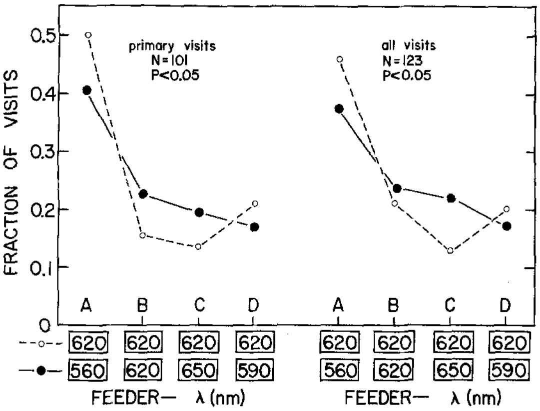

Fig. 5. Association of food with 620 nm can be generalized to 650 nm. Distribution of visits when all feeders displayed 620 nm (open circles, broken curves) was significantly different when 4 different wavelengths were present (filled circles, solid curve). See the caption to Fig. 3 for further details

significantly (Fig. 3a, filled circles), regardless of whether all visits or only primary visits were considered. The red light, which now appeared only at the position that was originally least favored (C), received twice as many primary visits as before. Visits to both the green and yellow-green light were correspondingly fewer, but visits to the blue light were slightly increased. We shall return to this latter point again when discussing the experiments on color discrimination.

In the experiment of Fig. 3a, the four wavelengths were adjusted for equal photopic luminosity for the pigeon. We used the average curve compiled by Bowmaker (1977) based on the data of Granit (1942), Donner (1953), Blough (1957), Ikeda (1965), Graf (1969), Blough et al. (1972), and King-Smith cited by Muntz (1972). This is a broad function that drops only 0.5 log units from the λ_{max} at the edges of the wavelength band 485–640 nm.[3] The corresponding curve for hummingbirds has not been measured and could differ somewhat, so the possibility existed that feeders were being selected on the basis of residual brightness differences that were not accurately neutralized in the adjustments of intensity. Figure 3b shows an experiment that makes this interpretation unlikely. For this test the intensity of the 620 nm light at position C was decreased 0.5 log units during the test period, when the birds had four wavelengths from which to choose. The same pattern of departure of the filled circles from the measured position effect was again observed: significantly more visits at A and C; fewer at B and D.

The position effect was likewise unaltered by similar changes in brightness (Fig. 4). When all feeders showed 620 nm but the intensities at the most and least favored positions (A and C) were each lowered 0.5 log units, there was no effect on the frequency distribution of visits. This is a second piece of evidence that moderate differences in brightness have little or no effect on the birds' choices.

Figure 5 shows the distribution of visits when two reds (620 and 650 nm) were presented in the array. In this experiment blue (490 nm) was not present, and the 546 nm green was replaced by 590 nm yellow. Both of the reds received more than the expected number of visits; the 560 and 590 nm feeders, fewer.

The experiments indicate some preference for red, but in what follows we shall see that this required an association of red with food in the immediate past experience of the birds. Even so, the effect was modest, and other factors such as the position preference, successful experience at other colors, and perhaps the birds' natural tendencies to explore kept up the frequency of visits at the other feeders.

Colors Can Be Learned

The distribution of visits shown in Fig. 5 was radically altered when a 0.5 M sugar solution was available at the middle positions (B and C) but only water was present at the end feeders (A and D) (Fig. 6). After 6 h experience only 6% of the visits occurred at what had originally been the most favored feeder (A, 560 nm), and nearly 80% of the visits were at the two 620 nm feeders where sugar was supplied. An intermediate number of visits were recorded at the fourth feeder (D), which was associated with an intermediate wavelength (590 nm).

Unsorting Position and Wavelength Effects. In order to prevent the birds from cueing on position and to be certain that color was learned, the following

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[3] The pigeon appears to have two distinct photopic sensitivity curves, depending on whether the stimulus projects onto the red or yellow field of the retina (Romeskie and Yager, 1976)

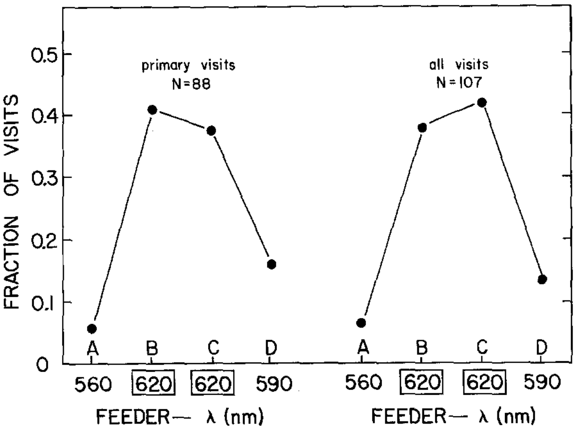

Fig. 6. Distribution of visits is strongly altered by learning. Sucrose was supplied only at 2 feeders (wavelength value enclosed in box on abscissa); visits were scored after 6 h

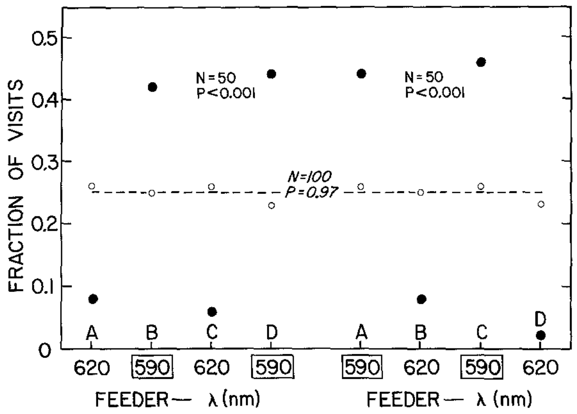

Fig. 7. Distribution of primary visits following training to 590 nm, with only water supplied at 620 nm. Feeder positions regularly shifted to prevent learning of position, as described in the text. Small open circles: all visits ($N=100$), color randomized. Note absence of a position effect in this experiment (for observed deviation from equal frequency of 0.25, $P=0.97$). Large filled circles: right and left halves of the figure show the distribution of visits for the two configurations of test and training lights. Configurations were changed at the start of every 25 visits, thus four times during the course of tabulating 100 visits. Observed deviations from equal distributions of visits is highly significant ($P<0.001$ for both sets of data). Twelve visits to 620 nm divided by 88 visits to 590 nm yields a discrimination ratio of 0.14, as plotted in Fig. 15

paradigm was employed, except where otherwise specified. Two of the feeders displayed the training wavelength and were supplied with sugar solution, whereas the other two, generally with another wavelength, were filled with water. Training and test feeders alternated in the array, and except as specified otherwise, the positions were interchanged at intervals during both training and testing.

For a test session, 100 visits were tabulated in blocks of 25, with interchange of the test and training feeders at the start of the session and between blocks. Each feeder was therefore associated with the test and training colors for an equal number of visits. If there was a position effect, it was revealed in the frequency of visits at each feeder. If there was a preference for one color, that was readily revealed by pooling the data from pairs of blocks in which the training lights occurred at the same positions. To clarify further this method of procedure, two examples are shown in Figs. 7 and 8.

Figure 7 shows an experiment in which the position effect was absent. Frequency of visits at the four feeders – regardless of color – is shown by the small open circles and does not deviate significantly from equal probability (broken line; 0.25 of all visits at each feeder). The right and left sides of Fig. 7 show the frequency of visits partitioned according to whether the training wavelength (in this case 590 nm) appeared at positions B and D (left) or A and C (right). Visits to the training color and to the test λ (in this case 620 nm) are shown by the large filled circles. χ^2 analyses performed on each half of the data separately indicate that the deviations from the dashed line are highly significant (for such a distribution by chance, $P<10^{-3}$).

The same kind of analysis can be performed in the presence of a significant position effect. In the example of Fig. 8, the left end of the feeder array was again favored, as shown by the frequency distribution for total visits (dashed line). A χ^2 test shows that this distribution is significantly different ($P=0.03$) from equal numbers of visits at each feeder. Using this observed distribution as the expected distribution, χ^2 tests of the two halves of the experiment indicate that there is a powerful effect of λ: the data points for the training color lie significantly above the curve, and for the test wavelength, significantly below it (for chance $P<10^{-3}$).

The Hummingbirds Cue on λ, Not Brightness. Additional controls were undertaken to explore the role of luminosity differences in influencing the birds' choices. The birds were taught to associate food with one wavelength (λ_{train}) when viewed in conjunction with a second wavelength (λ_{test}) of presumably equal photopic brightness, and the effect of varying the brightness ratio on the fraction of visits to each wavelength was then determined. Figure 9 shows the results of two experiments involving pairs of wavelengths close together (triangles) and farther apart (circles). The filled symbols indicate the fraction of visits to λ_{train} when the lights were adjusted for equal photopic luminosity for the pigeon. As shown by the open symbols, there is not a significant effect of subsequently varying the brightness ratio over a 30-fold range. (The values of P give the probability that the vertical positions of the open circles deviate from the y-coordinate of the filled circle by chance alone.) This experiment is therefore in agreement with those described in the section on spontaneous choices in

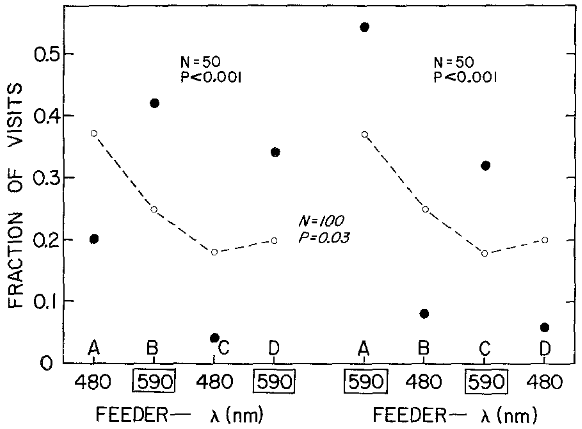

Fig. 8. An experiment similar to that of Fig. 7, but exhibiting a position effect. Training wavelength indicated by the boxes. Distribution of total visits differs significantly from equal probability at each feeder ($P<0.05$); distribution of visits by wavelength differs significantly from the measured position effect ($P<0.001$ for each half of the data). See caption to Fig. 7 and text for further details

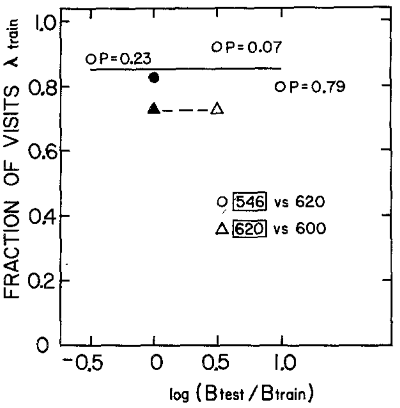

Fig. 9. Hummingbirds do not use relative brightness as a significant cue in making choices between feeders, for the degree to which pairs of wavelengths are discriminated following training at equal (pigeon) brightness does not vary with moderate changes in the brightness ratio. P values give the probability that the observed fraction of visits differs by chance from that measured at equal brightness (filled symbol)

indicating that relative brightness is not a significant parameter influencing the birds' choices of feeder.

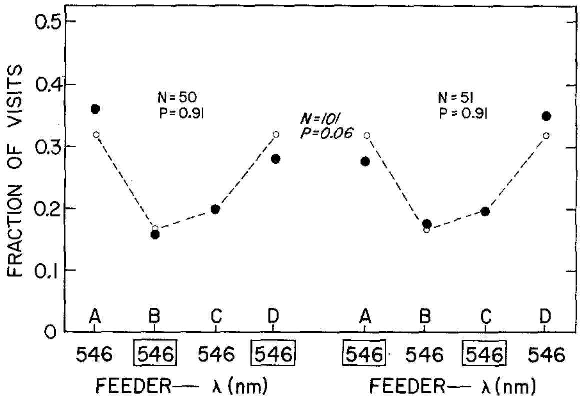

Fig. 10. The birds were unable to discriminate between sugar and water bottles (without tasting the contents) when difference in wavelength was reduced to zero. Discriminations are therefore based on $\Delta\lambda$. Boxes around the wavelength indicate presence of sugar. See captions to Figs. 7 and 8. Probability of position effect due to chance = 0.06; deviation of visits from position effect is not significant ($P=0.91$)

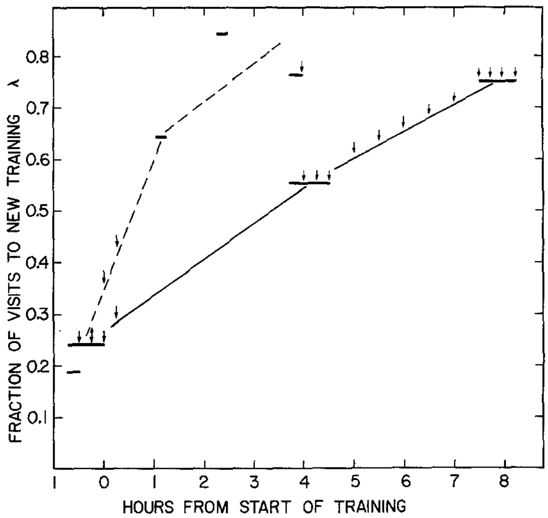

Fig. 11. Learning of a new wavelength. When both feeder position and color could serve as cues, the birds abandoned previous association with wavelength and cued on position (broken curve). Data points for the broken curve are based on counts of only 25 visits, and the last two points are not significantly different from each other ($P=0.34$). In order to strengthen a new association with wavelength, position of the feeder was eliminated as a consistent cue beginning at about 4 h on the abscissa. Small vertical arrows: times at which the feeder positions were shifted. Horizontal extent of data marks indicates time required to sample birds' choices: short marks, 25 counts; long marks, 100 counts. Training wavelength was shifted from 620 to 546 nm at $t=0$; test wavelength was simultaneously shifted from 546 to 620 nm. See text for further details

Choices Are Based on $\Delta\lambda$. Controls were also done to demonstrate that the selection of one feeder over another was based on the difference in λ and not some unidentified parameter such as odor. Figure 10 shows one of these experiments, in which during testing the wavelength displayed with the water bottle was identical to that appearing with the sugar solution. As can be seen by the broken curve, a position effect was present, favoring the end feeders. It was assumed to be significant ($P=0.06$) and was used to calculate the expected frequency in the χ^2 test. The birds were totally confused as to which bottles contained sucrose ($P=0.91$ for deviation of the "correct" choices from the expected distribution). This experiment was performed with similar results when the birds were trained to a red light.

Rate of Learning: Either Position or Color Can Be Learned. Figure 11 shows the transfer of birds from an association of food with red (620 nm) to green (546 nm). During the first several hours of the proce-

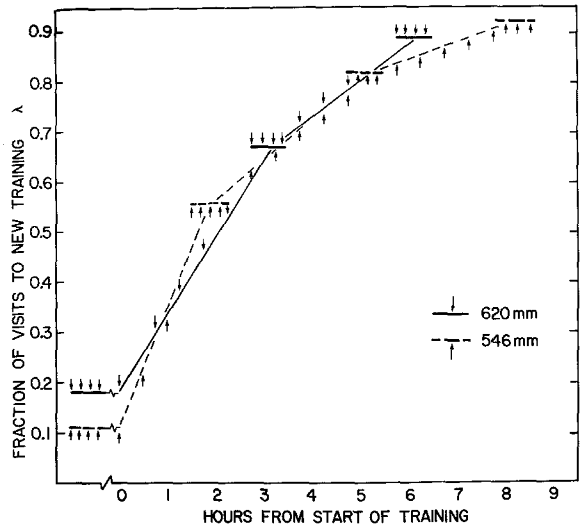

Fig. 12. Red (solid lines) and green (broken lines) associations are learned with equal facility. In order to randomize the positions at which each color appeared, feeders were shifted at times indicated by the small vertical arrows, as described in the text. Horizontal extent of data marks indicates time required to record 100 visits. Test wavelength was 546 nm when training wavelength was 620 nm, and vice versa

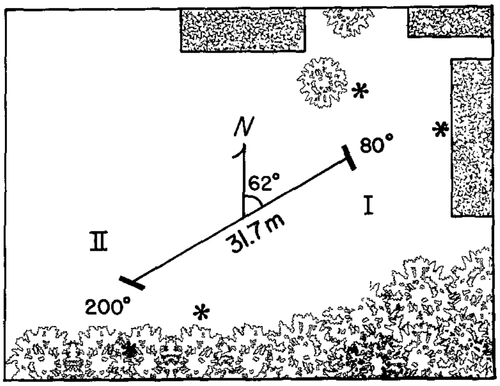

Fig. 13. Schematic diagram of positions and orientations of feeders in an experiment designed to test the birds' capacity to learn conflicting color associations at two different sites. Site I was the original location of all 4 feeders where birds were first trained to 590 nm. Two of the feeders were moved to site II, and training to 480 nm was effected at site I. Stippled areas indicate trees and edges of buildings. Site I was about 2 m higher than Site II. Observation points indicated by asterisks

dure the positions of the feeders with sugar (546 nm) were not switched with those containing water (620 nm), and sample counts of 25 visits suggested that learning was complete after 2.5 h (broken curve). Between 3.75 and 4.5 h the full count of 100 was performed, in blocks of 25, with the positions of the lights changed between blocks. The result of this measurement made it clear that during the first 2.5 h the birds had simply learned to associate the sucrose solution with two of the feeder positions, for their response to the new training color was scarcely better than chance. The experiment then continued with a regular interchange of the positions of the two colors with time (times indicated by the small arrows), and after several more hours the birds had formed an association between the green stimulus and the sucrose solution. This experiment indicates that either position or color can provide the cue for association with food, and that the former can take precedence (see also Miller and Miller, 1971).

Red and Green Are Learned at the Same Rate. Collias and Collias (1968), having obtained evidence that hummingbirds are not genetically programmed to respond preferentially to red, suggested that they nevertheless might learn to associate red with food faster than other colors. As natural nectar sources are unlikely to be associated exclusively with green, we measured both the rate of transfer of association from green (546 nm) to red (620 nm) and from red to green. Figure 12 shows that either wavelength can be learned with equal facility, and that if the positions at which the colors appear are regularly changed during the learning process, the rate at which the new association is formed is almost as fast as the learning of position shown by the dashed curve in Fig. 11.

The number of visits required for relearning is treated in the Discussion.

Two Conflicting Color Associations Can Be Learned Simultaneously at Different Locations. In order to determine whether the birds' memory for color could be site specific, two of the feeders were relocated at a distance of 32 m, as shown by the diagram in Fig. 13. In order to lose as few of the visiting birds as possible, the feeders were moved in increments of approximately a meter over a period of about 12 h. During most of the period of movement, the birds were feeding at 590 nm but seeing 480 nm at the water-filled bottles. Toward the end of the time required to move one pair of the feeders to the new site, retraining to 480 nm (with 590 nm at the water-filled bottles) began at the original feeding site.

At each feeding site the birds selected the appropriate color to a much greater extent than predicted by chance (Fig. 14). It therefore appears that they can remember more than one color association at a time.

This interpretation assumes that the same birds were feeding at both sites. We cannot say that the two sub-populations were identical, but we observed some of the same marked birds visiting both sites, and noted that many of the unmarked birds appeared to fly directly from the original feeding area to the feeders that had been moved. We therefore believe the interpretation to be valid.

Alteration of the Position Effect. In experiments utilizing all four feeders in a row, the position effect seemed

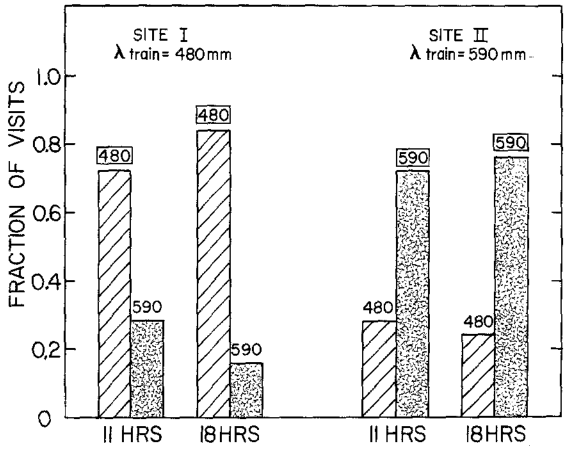

Fig. 14. Results of the experiment on site-specific color training. The birds visited the color appropriate to the site. Deviations from equal distribution are highly significant by the χ^2 test: At site I, $P<0.001$ at both times; at site II, $P<0.01$ at 11 h, $P<0.001$ at 18 h. Note that this experiment involved a pair of wavelengths that did not yield the highest discrimination ratios (cf. Fig. 15)

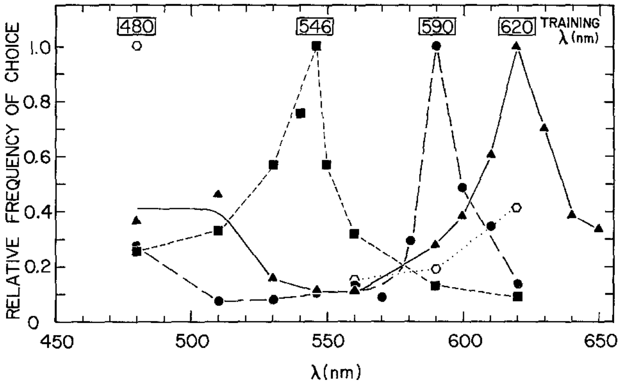

Fig. 15. Color discrimination by black-chinned hummingbirds. The Y-coordinate of each point is the frequency of visits, relative to the training wavelength, referred to in the text as discrimination ratio. The four training wavelengths are indicated above the graphs. Each data point is based on a separate experiment involving (usually) 100 visits, similar to those illustrated in Figs. 7 and 8

to be most pronounced when the birds had no reason to choose between feeders, as in the spontaneous choice experiments in Figs. 3–5 where sucrose was present at all feeders, or where discriminations were difficult (see below). If the ratio of visits to the test and training lights is used as a measure of the ease of discrimination, an analysis of variance of this ratio with the negative log probability that a position effect is present shows a significant correlation ($P=0.045$). There is much scatter in the data, however, suggesting that other factors also influence the position effect. Lyerly et al. (1950) found for a captive bird that the position preference correlated with time of day. We have the impression that another factor may be wind velocity, but the matter has not been studied further.

Wavelength Discrimination

In order to test their capacity to discriminate colors, the birds were trained to specific wavelengths and tested against others, using the paradigm described earlier (Figs. 7 and 8). The four training wavelengths were 620, 590, 546, and 480 nm. The results are summarized in Fig. 15, where relative frequency of choice is plotted vs wavelength. Except at the peak wavelengths, each point in Fig. 15 represents a separate experiment involving usually 100 visits partitioned between the test and training wavelengths. Due to limitations in numbers of certain filters, some of the experiments around 620 nm utilized a single pair of feeders and some around 590 involved simultaneous presentation of the training and two test wavelengths. In each case, the procedure was appropriately modified to compensate for any possible position effect.

620 nm. The birds showed a significant ability to distinguish 620 nm from various neighboring reds and oranges. Discrimination from greens was very pronounced, with a ratio of incorrect:correct choices of approximately 0.1. When tested against blue (480 nm) or even blue-green (510 nm), however, the birds did somewhat less well, as though there were some tendency to confuse wavelengths from the two ends of the visible spectrum. The data for 480 and 510 nm, taken together, are highly significantly different from the discrimination ratios for the next three longer wavelengths tested (530, 546, and 560 nm) ($P<10^{-3}$). This finding suggests an explanation for the observation that in the spontaneous choice experiment of Fig. 3, 490 nm was favored as well as 620 nm.

590 nm. Discrimination around 590 nm appears to be even sharper than around 620, particularly on the short wavelength side. Measurement in this region of the curve required two experiments, one involving 590, 580, and 570 nm, the second 590, 600, and 610 nm. The frequency distributions of visits in these two experiments are highly significantly different ($P<0.001$). An analysis of that part of the data closest to the training wavelength (590, 580 nm compared with 590, 600 nm) also shows a significant difference ($P<0.05$). The discrimination curve is therefore asymmetric around the 590 nm training wavelength.

Discrimination from green is almost complete, but the curve rises somewhat in the blue, although not to quite the same extent as when the training light was 620 nm.

546 nm. Discrimination around this wavelength in the green is also asymmetric. The four "546 nm" interference filters had $\lambda_{\max}$ at 545, 546, 547 and 547 nm. The 550 nm filters (average $\lambda_{\max}=549\pm1$ nm) were seen as different from 546 nm, with a discrimination ratio of 0.56 ($P<0.01$). On the other hand, discrimination of the 540 nm filters (average $\lambda_{max}=541\pm1$ nm) from 546 nm was poorer; the ratio of 0.75 was different from unity but with a much lower level of significance ($P=0.16$). This is the only data point in Fig. 15 that is not different from the normalized frequency at the training wavelength by the usual criteria of statistical significance.

Discrimination of red (620 nm) from 546 nm is very good, confirming in reciprocal fashion the discrimination of 546 nm from the 620 nm training light. The discrimination curve falls in the blue, but not to such low values as in the red.

480 nm. A few experiments were done following training to 480 nm, first to demonstrate that with this equipment hummingbirds can be trained to blue as well as longer wavelengths, and second, to confirm that discrimination of red from blue is less precise than the discrimination of green from blue. As can be seen from Fig. 15, a 560 nm test light was well discriminated from 480 nm, in fact somewhat better than a 480 nm test light was discriminated from a 546 nm training light. Moreover, discrimination deteriorated with a red (620 nm) test light, as was predicted from the results of experiments with a 620 nm training light and a 480 nm test light. The 480 vs 560 discrimination ratio of 0.18 is significantly different from the 480 vs 620 discrimination ratio of 0.41 ($P<0.001$).

Discussion

Spontaneous Choices and Previous Experience

The results of the experiments on spontaneous choices support the view that i) red may serve as an effective stimulus in attracting hummingbirds, at least when the birds have been feeding on sources associated with red, and ii) other factors, such as position of the feeder may influence the birds' choices, so that color is but one of several variables that underpin their selections. Moreover, the relatively weak effect of red in these experiments (see also Poley, 1968) emphasizes the tendencies of the birds both to explore constantly for new food sources and to return to locations that experience has proved rewarding.

We examined spontaneous choices following a period of association of food with red (620 nm), but not with any other color. This is because prior to our arrival in the study area red plastic feeders had been available to be birds, and we decided that the consequent lack of control over the birds' prior experience might complicate the interpretation of experiments with other colors. There is evidence that hummingbirds remember the location of food sources through the winter (Sherman, 1913; Béné, 1945), and much more must be learned about their memory for color. Moreover, when they are dealing with site-specific color associations (Fig. 14), there could be an influence on their exploratory behavior. This, too, should be studied by experiment.

In making spontaneous choices, the birds' experience with 620 nm was generalized to 650 nm, less well to 590 nm (Fig. 5). This suggests that in the long wavelength region of the visible spectrum hues are blocked out in a manner similar to primate color vision. On the other hand, such an experiment tells us nothing about the capacity for hue discrimination, for 620 and 650 nm were well discriminated when a differential reward was present (Fig 15).

To reiterate, these experiments do not support the popular view that hummingbirds are preferentially attracted to red because of either a higher visual sensitivity to red or an innate "releaser". In fact, in the family Trochilidae, which contains more than 300 species, green is by far a commoner color of gorget than is red (Woods, 1927), so it would be astonishing if the visual system were selectively tuned to a restricted band at the long wavelength end of the spectrum. As has been stressed by other authors (e.g. Stiles, 1976) reds and oranges are convenient flags, but their association with nectar sources is both learned and elastic.

Learning Color Associations

Because of the 100-fold variation in the frequency with which individual birds visited the feeders, expressing the rate of learning in terms of number of trials rather than time is not a straightforward conversion. Moreover, to what extent do the infrequent visitors slow down the learning process as it is exhibited by the population? Using the data in the histogram in Fig. 1, one can construct a function that describes how the total number of visits depends on the fraction of the population that has visited (Fig. 16). This exercise shows that 60% of the birds account for 97% of the visits. Moreover, the individuals comprising this 60% come to the feeders at a *minimal* frequency of about 1 visit/hr (see the scale along the top of Fig. 16). Following a 6 h training session, 97% of the counts will therefore be of birds who have visited an average of 6–22 times during the training period. The infrequent visitors will contribute on average but 3 counts out of 100.

Béné (1945) reported that one trial could be sufficient for hummingbirds to learn position. In his experiment the negative reinforcement was salt water. This raises the possibility that position might be learned equally rapidly in our experimental conditions. For this reason it is therefore necessary to ask how many times an individual bird might have made second or third visits during a block of 25 counts. The calcu-

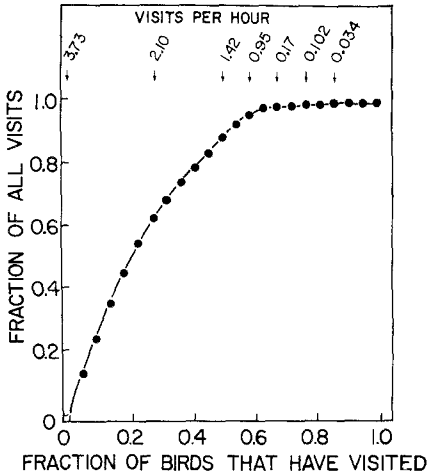

Fig. 16. Normalized function showing the fraction of all visits as a function of the fraction of birds that have visited, calculated from the data of Fig. 1 by summing the contributions of each bird in the order of decreasing frequency of visitation. This treatment shows that 60% of the birds that visited most frequently accounted for 97% of all visits. Scale along the top of the figure shows absolute frequency of visitation (visits/hr) of individual birds according to their ranking on the normalized abscissa. See text for further discussion

lations are in Table 1. For the marked subpopulation of 22 birds, 11.5% of the visits were second (or occasionally third) arrivals, and even for the most frequent visitors (who present the worst possible case), the frequency is not much greater. Therefore, even if position is learned in one trial, the length of the block is not so long as to allow much learning of position. Moreover, the experiment of Fig. 11 suggests that position was not learned much faster than wavelength and therefore required several visits. Another, more direct argument that there can be no significant learning of position in 12.5 min is found in Fig. 10, which demonstrates the absence of cues other than wavelength.

The results of our experiments comparing the rate of learning of 546 and 620 nm lights are not in agreement with the report of Poley (1968), who found that the "preferred" colors (reds) were learned faster than other colors. The reasons for this discrepancy are not clear, but our finding that red and green associations with food can be learned with equal ease demonstrates, at least for this species, that there is no neural mechanism that facilitates learning of one color in preference to another.

Comparison with the Pigeon

The pigeon is the bird whose color vision has been most extensively studied, and there is evidence that its hues differ from those of old world primates. Wright and Cumming (1971), in a matching-to-sample paradigm, found that spectral regions in the neighborhood of 600 and 540 nm were transition zones between hues. In a second experiment Wright (1972) reported minima (smallest value of $\Delta\lambda$) in the hue discrimination function at 600, 540–550, and 500 nm. The 600 and 500 nm points are close to the 590 nm and 490 minima in the human hue discrimination curve, but identification of 540 as a suture between pigeon hues is most interesting, because there is a maximum in the human hue discrimination function at that wavelength (Wright and Pitt, 1934).[4]

These behavioral experiments correlate with recordings from ganglion cells, where narrow-band responses have been found with $\lambda_{\max}$ at 600, 540, and 480 nm (Donner, 1953), as well as thalamic units, with peak response at 600 and 540 nm (Granda and Yazulla, 1971). One might also expect agreement with the excitation-inhibition transitions of color opponent cells, but the values recorded at 500 and 520 nm (Yazulla and Granda, 1973) correspond less well. The underlying retinal mechanisms are not clear. The pigeon has three cone pigments, with $\lambda_{\max}$ at 567, 515, and 460 nm, but the presence of five classes of colored oil droplets creates as many as eight or nine spectral classes of receptor (Bowmaker, 1977). How many distinct input channels exist in the afferent pathway is not yet known.

Is the pigeon's system of hues a general characteristic of diurnal birds, or is it a specialization? As Stiles (1976) has pointed out, the available data on avian vision come almost entirely from granivorous species that rarely encounter brightly colored objects in feeding. Information about species with very different feeding and mating behaviors would therefore help to answer this question.

The present data on wavelength discrimination by black-chinned hummingbirds (Fig. 15) speak to the problem. The asymmetries in discrimination around both the 546 and 590 nm training lights suggest that these two wavelengths lie on or near the borders between hues. The results obtained in the green are particularly interesting. The discrimination of 550 and 546 nm was significant, whereas the discrimination of 540 and 546 nm was not. The sharper discrimination on the long wavelength side of 546 nm is readily compatible with the data of Wright and Cumming (1971) and Wright (1972) on the pigeon, but not so easily reconciled with the human hue discrimination function.

A second point of similarity exists. Blough (1961) and Wright and Cumming (1971) have observed that pigeons trained to peck at a key with a red stimulus showed a propensity to generalize the response to

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[4] There is general agreement about the minima in the pigeon's hue discrimination function at approximately 540 and 600 nm in the work of other authors (Blough, 1972; Riggs et al., 1972; Schneider, 1972; Emmerton and Delius cited in Delius and Emmerton (1979), but rather more uncertainty about the performance of the pigeon's visual system in the blue region of the spectrum

wavelengths in the blue. This corresponds to the hummingbirds' significant tendency to come to 480 and 510 nm feeders when trained to 620 nm, and to visit 620 nm following training to 480 nm. In each case intermediate wavelengths were chosen significantly less frequently (Fig. 15). The spontaneous choice experiment of Fig. 3 can be interpreted as a second manifestation of this phenomenon. Here the frequencies of visits to both 490 nm and 620 nm were greater than chance, as though the red stimulus was generalized to or confused with the short wavelength end of the spectrum. As shown by the experiment of Fig. 5, it is unlikely that the enhanced visitation of the 490 nm feeder was due to its position at the end of the array. A similar closing of the color circle appears in human color naming data (e.g. Boynton and Gordon, 1965). See also Schneider (1972).

The present experiments demonstrate the feasibility of using a wild population of hummingbirds in studies involving visual discriminations. Moreover, they provide some support for the hypothesis that other birds share with pigeons a color vision system that generalizes hues in a manner different from that of humans and old world monkeys. Both the experimental system and the hypothesis deserve further attention.

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