

IRIDESCENT POLYCHROMATISM IN A FEMALE HUMMINGBIRD: IS IT RELATED TO FEEDING STRATEGIES?

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ABSTRACT.—Conspicuous coloration may evolve through aggressive competition either for mates, in sexual selection, or for any limiting resource, in social competition. Most species of hummingbirds (Trochilidae) have polygynous (promiscuous) mating systems, bright male plumage, and conspicuous sexual dichromatism. These patterns have led to the view that their iridescent plumage has evolved by sexual selection. I report an iridescent polychromatism in females of the Andean hummingbird *Heliangelus exortis exortis* that suggests the evolution of iridescent plumage via aggressive feeding behavior. Female *H. e. exortis* vary within and among populations in the development of the large iridescent gorget characteristic of males. I document a regular north-south pattern of geographic variation in the polychromatism. In samples from northern Colombia, female gorgets vary from a noniridescent (femalelike) to a fully iridescent (malelike) condition, whereas females from southern Colombia have only the discrete noniridescent and fully iridescent morphs. Samples of females from Ecuador are comprised predominantly of the noniridescent morph. The color forms are not due to seasonal plumage differences or ontogenetic changes. A significant negative correlation between bill length and degree of iridescence in the largest geographic sample suggests that females with iridescent gorgets are more aggressive territorial foragers than less iridescent females. Received 16 July 1984, accepted 8 April 1985.

NUMEROUS factors have been proposed to explain the evolution of conspicuous coloration in animals. These include predator warning and avoidance (Curio 1976, Baker and Parker 1979, Endler 1979), thermoregulation (Watt 1968, Clark 1974, Walsberg et al. 1978), and behavioral communication as influenced by the biotic (Nobel and Vogt 1935, Tinbergen 1951, Murray 1981) or physical (Burtt and Gatz 1982) environment. Evaluation of the relative importance of these potential influences presents a major challenge to evolutionists.

Within the category of behavioral communication, the effects of nonsexual social competition are particularly difficult to distinguish from those of sexual selection. Darwin (1871) proposed that conspicuous sexually dimorphic features evolve via sexually selected competition for mates, through the advantage these features confer either in mate choice (epigamic selection) or in aggressive interactions among members of one sex that determine access to the other (intrasexual selection). The theory of

social competition (Crook 1972; West-Eberhard 1979, 1984) recognizes that analogous interactions may extend to competition over limiting resources other than mates, and promote the elaboration of conspicuous signals used in nonsexual contexts.

The effects of sexual selection and of nonsexual social competition are difficult to distinguish in practice because both phenomena lead to the prediction that increased dominance and aggressive behaviors can lead to the elaboration of conspicuous signals such as bright coloration. Moreover, the effects of sexual selection are difficult to control in sexually reproducing animals. Specifically, variation in male coloration (e.g. Rohwer and Niles 1979, Dominey 1980, Ewald and Rohwer 1980, Gross and Charnov 1980, Rohwer et al. 1980, Procter-Grey and Holmes 1981, Edwards 1982, Flood 1984) often fails to distinguish these hypotheses because male dominance and territoriality invariably are tied to breeding activities (Wilson 1975, O'Donald 1977). This ubiquitous correlation makes it difficult to determine whether nonsexual social competition is a sufficient explanation for the evolution of conspicuous coloration in males.

The occurrence of intraspecific variation in

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female coloration provides a natural control of this difficulty that has gone unappreciated. In many species, especially those in which males mate promiscuously, females are less aggressive sexually, thereby providing some control for the influence of sexual selection. Variation in female plumage is particularly relevant for determining the evolutionary significance of iridescent plumage in the largely promiscuous hummingbirds (Trochilidae), which exhibit some anomalous female plumages that are difficult to explain by sexual selection.

Male hummingbirds employ their iridescent plumage in a variety of contexts, including nuptial displays, aggressive sexual displays, and aggressive displays associated with nectar-centered feeding territoriality (Stiles 1973, 1982). Because promiscuous breeding systems are thought to be associated with high levels of sexual selection (Payne 1984), the bright male plumage and sexual dichromatism characteristic of most hummingbirds are consistent with sexual selection theory (Selander 1972). However, sexual selection does not explain the evolution of "bright monomorphic" species characterized by a brilliant female plumage similar to that of the male (e.g. in the genera *Panterpe*, *Eulampis*, *Amazilia*). Bright monomorphic species do not show a consistent reduction in the intensity of sexual selection as inferred from their breeding systems (Wolf and Stiles 1970, Wolf 1975a). Rather, both sexes in bright monomorphic species exhibit nonbreeding nectar-centered feeding territoriality (Wolf 1969, 1975a, b; Ingles 1976). Feeding territoriality is usually lacking in the dull-colored females of most sexually dichromatic species (Wolf 1969, 1975a, b; Linhart 1973). Therefore, the correlation between bright female plumage and feeding territoriality strongly suggests that conspicuous iridescence may evolve solely for its importance as a nonsexual aggressive signal (Pitelka 1942, Wolf and Stiles 1970, Stiles 1973).

In this paper I address a previously unanalyzed color pattern that involves the variable expression of iridescent malelike features in females of an Andean hummingbird, the Tourmaline Sunangel (*Heliangelus exortis exortis*). Subtle examples of this "polychromatic" variation in hummingbirds have been noted in the temperate species *Calypte anna* (Williamson 1956) and in several tropical genera, including *Heliangelus* (Berlioz 1944, 1949), but distinctive female variants in iridescent male plumage are

recorded only for the tropical White-necked Jacobin (*Florisuga mellivora*; Zimmer 1950b, Monroe 1968, Elgar 1978). Although *H. e. exortis* is considered to be sexually dichromatic, with a highly iridescent gular patch or "gorget" in males and a white gorget in females (e.g. Meyer de Schauensee 1964), Chapman (1917) noted that some females of *H. e. exortis* from the Western Cordillera of Colombia had fully iridescent gorgets like those of males. I show here that female *H. e. exortis* vary dramatically both within and among populations in the malelike iridescence on their gorgets, and I argue that the polychromatic variation supports the origin of iridescent coloration in hummingbirds through selection for aggressive signals associated with foraging behavior.

MATERIALS AND METHODS

In *Heliangelus exortis*, the violet-chinned and rose-throated nominate form, *H. e. exortis*, occurs throughout the three Andean Cordilleras of Colombia and through the Ecuadorian Andes, primarily on the eastern slope. Two orange-throated forms, *H. e. micraster* and *H. e. cutervensis*, occur in the Andes of southwestern Ecuador and northern Peru, respectively (Peters 1945, Zimmer 1951), but are rare in collections and are not treated here. I examined 275 individuals from the entire range of *H. e. exortis* in this study. Sample size and geographic distribution of specimens are given in Table 1. A more complete description of the geographic relationships among localities can be found in Bleiweiss (1985).

Determination of age and sex.—Only two specimens, both immatures, had gonad data noted on their labels. Therefore, alternative methods had to be used to determine age and sex. To distinguish immatures from adults, I relied on the presence of corrugations on the culmens of immature birds (Ortiz-Crespo 1972, Stiles and Wolf 1974). Specimens were examined under a Bausch and Lomb zoom dissecting microscope (7–30 \times) to look for the presence of corrugations. A specimen was considered adult if the bill was perfectly smooth outside the nasal depression. The inverse relationship between the number of bill corrugations and age of immature birds permits one to study plumage ontogeny (Ortiz-Crespo 1972, Ewald and Rohwer 1980). To determine the relative age of immatures, bill corrugations were counted with the aid of a Wild microscope with camera lucida attachment. Wing and tail measurements are considerably larger in males of many except the smallest hummingbird species (Zimmer 1950a, 1952; Stiles 1983; Payne 1984). I have verified this relationship for *Heliangelus* with large series of *H. amethysticollis* for which gonadal data were available (Bleiweiss in prep.). To determine the sex of *H. e. exortis* specimens, I em-

TABLE 1. Distribution and sample size for *Heliangelus exortis exortis* specimens examined.

Locality	Pooled ^a	Cordillera ^b			Adults	Immatures
		West	Central	East		
1. El Peñón	A			West	1	
2. La Aguadita	A			West	1	
3. El Roble	A			West	6	1
4. Fusugasugá-Silvania	A			West	4	
5. Hacienda Zuliaba			East		7	1
6. Santa Elena			East		2	
7. Páramo de Sonsón			West		6	2
8. El Zancudo	B		West		17	1
9. Santa Isabel	B		West		1	1
10. Laguneta			West		43	15
11. Toche; Tolima			West		7	6
12. Puracé			West		1	
13. Coconuco			West		1	
14. Paletara			West		2	
15. Almaguer			West		6	3
16. Hacienda La Ilusión		West			8	1
17. La Florida	C	East			1	
18. Coast Range	C	East			3	
19. Cerro Munchique	C	East			25	1
20. Munchique-El Tambo	C	East			2	1
21. Tijeras-Moscopán			East		7	4
22. Guanderal	D			East	3	
23. Cerro Pax	D			East	8	5
24. Papallacta	E			East	8	
25. Cuyujúa	E			East	14	4
26. Baeza	E			East	3	1
27. Volcán Sumaco				Isolated peak	10	1
28. San Antonio	F			East	1	1
29. Ambato	F			East	1	
30. Baños	F			East	6	1
31. Volcán Tungurahua	F			East	4	
32. Planchas	F			East		2
33. Corazón				West		1
34. Pallatanga				West	6	3
35. Macas	F			East	4	
Total					219	56

^a Letters A-F designate pooled localities used for analysis of geographic variation (see text).

^b East and west designations under each Cordillera refer to the slope of the range.

ployed the two measurements that best separated the sexes in *H. amethysticollis*: length of unflattened outer primary from point of emergence from skin, and length of outer tail feather (rectrix 5) from point of emergence from skin. The extrapolation from *H. amethysticollis* to *H. e. exortis* is justified because they are congeners. There is no reason to assume that what holds for *H. amethysticollis* and many other hummingbirds does not also hold for *H. exortis*.

Morphological variation.—I use the term "gorget" to denote the entire gular region, and "chin" and "throat" to denote its uppermost and remaining portions, respectively. The color variation described involves iridescent structural colors that vary in intensity: "glittering" indicates intense, mirrorlike iridescence, while "shining" indicates less intense iridescence with a metallic luster (Greenewalt 1960).

The violet chin and rose throat feathers are always glittering in both sexes of *H. e. exortis*. Nonglittering chin and throat feathers vary geographically from white (eastern and southern Colombia through Ecuador) to white with a shining green to dusky terminal dot (northern and central Colombia) [see Bleiweiss (1985) for a discussion of this variation]. The female polychromatism involves variation in the number of glittering gorget feathers. I quantified the polychromatic variation either by directly counting the number of glittering iridescent feathers or, when very numerous, by estimating their numbers by counting the tracings of all glittering gorget feathers made with the camera lucida.

To quantify the pattern of geographic variation in glittering gorget iridescence, I divided the variation in glittering feather counts into four gorget color

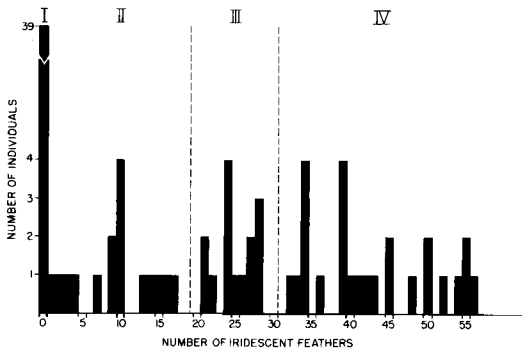


Fig. 1. Distribution of glittering gorget feather counts for all adult females. Qualitative gorget color classes II-IV were designated on the basis of the two largest distributional gaps in feather counts (between 18 and 20 and between 29 and 32, as indicated by dashed lines).

classes (I-IV) based on the number of glittering feathers. Class I denotes absence of glittering iridescence. The frequency distribution of glittering feather counts among all adult females ($n = 94$) reveals an uneven distribution, with gaps at 18-20, 29-31, and 46-49 (Fig. 1). The first two gaps help divide the sample into three qualitative categories (little, moderate, and full iridescence) and permit the assignment of individuals to different count classes (class II = 1-17, class III = 21-28, class IV = 32+). These classes are consistent with a subjective impression of differences in appearance. Classes II and III have both glittering and nonglittering feathers. Class I has only nonglittering feathers, and class IV usually only glittering ones.

Mensural characters may be correlated with differences in feeding behavior between the sexes and among different hummingbird species (Feinsinger and Colwell 1978). I used such characters as an indirect test of the relationship between polychromatic variation and feeding behavior in the absence of behavioral observations. Territorial species in general, and males in particular, often have shorter bills, and shorter wings relative to body mass (wing disc loading), than nonterritorial species and females, which are less aggressive (Stiles 1973, Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978, Snow and Snow 1980). These differences in morphology are thought to increase the energetic efficiency of territorial and nonterritorial foraging strategies (Wolf et al. 1972, Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978, Ewald and Williams 1982). Similar morphological differences therefore may evolve together with evolutionary divergence in foraging behavior among individuals.

I used six characters to examine the possible rela-

tionship between polychromatic variation and feeding behavior: (1) length of exposed culmen (EC), (2) length of culmen from flange of the nasal operculum to tip (CF), (3) length of outer primary (FP), (4) chord of unflattened wing from the bend to the tip (WB), (5) length of inner (IT) tail feather (rectrix 1), and (6) length of outer (OT) tail feather (rectrix 5) (see Baldwin et al. 1931). I used the two measures of wing length as indices of wing disc loading (assuming equal weights among females) because weights were not available. Specimens were measured under the Bausch and Lomb zoom dissecting microscope with needle-point dividers, that were then remeasured with dial calipers. I omitted individual measurements when feathers were molting or very worn.

Statistical analysis.—Because of small sample sizes, specimens from several localities were pooled for statistical analysis of geographic variation (pooled localities are designated by letters A-F in Table 1). Close geographic proximity and absence of obvious physical barriers between localities were the criteria used for pooling (Bleiweiss 1985). Geographic variation in gorget color classes was analyzed by $R \times C$ contingency tables using Chi-square statistics with at least one expected observation per cell (Snedecor and Cochran 1969: 235, 241). I calculated Spearman rank correlation coefficients between mensural characters and gorget coloration for each geographic sample separately because there is significant geographic variation in most of the measurements (Bleiweiss 1985).

RESULTS

Sexual variation in adult Colombian and Ecuadorian samples.—Adult Colombian *H. e. exortis* show continuous variation in glittering gorget iridescence. Adult *H. e. exortis* from Ecuador exhibit only two gorget conditions: glittering violet chin and rose throat, or pure white chin and throat. Because variation in Ecuador is simplified, I used these samples as the standard for determining sex in the variable Colombian samples. A bivariate scatter plot of wing length (FP) vs. tail length (OT) for all adult specimens from Ecuador (localities E, F, 27, 34) separated adults into two groups (Fig. 2A). Individuals with wing and tail measurements greater than 45.5 mm have highly iridescent gorgets, which are violet on the chin and rose on the throat. Smaller individuals have pure white, noniridescent chins and throats in 24 of 25 individuals. This clear morphological division in the Ecuadorian sample reflects sexual differences in measurements. Thus, all males have highly ir-

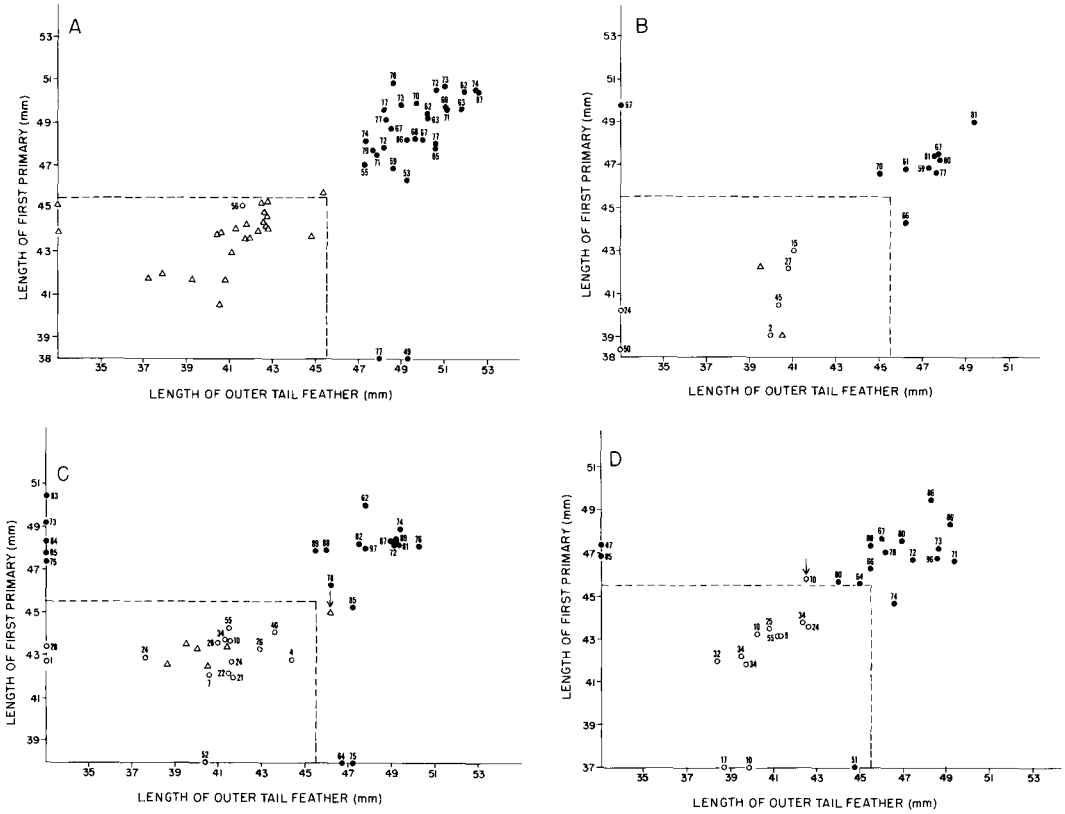


Fig. 2. Scatter plots of lengths of outer tail feather (OT) vs. first (= outer) primary (FP) for Ecuadorian localities E, F, 27, 34 (A), and the three largest Colombian samples: B = loc B (El Zancudo region), C = Laguneta, D = loc C (Munchique region). Solid symbols are males; open symbols are females. The number of glittering gorget feathers is indicated above each circle. Triangles are females with no glittering gorget feathers. Specimens for which only one of the measurements could be taken are also plotted; they fall on the appropriate axis. Arrows indicate questionable females (see text). Scatter plots of additional localities can be found in Bleiweiss (1983).

idescent gorgets and all females but one have pure white gorgets.

In addition to the gorget color differences, the sexes also differ in body coloration in Ecuador. Although both sexes are predominantly shining green, males are much darker than females, with a bronze cast on the back and upper tail coverts. Male crowns look blackish when seen from the front and have a highly contrasting glittering green forecrown. Female crowns are green, with less contrasting glittering forecrowns. Female belly feathers are broadly edged with tan, and their outer tail feathers have light tips, features that are absent in males.

Colombian specimens were first sexed by

body coloration. Plots of Colombian specimens for wing length (FP) and tail length (OT) fall, like Ecuadorian ones, into two groups that are roughly separated by a size of 45.5 mm for FP and OT (Fig. 2B-D). Larger individuals (males) have the same gorget color as males from Ecuador. The female portion of each sample, however, is highly variable, with from 0 to 55 glittering iridescent gorget feathers. For individuals sexed by body plumage, 2 of 75 females (indicated by arrows in Fig. 2C, D) and 7 of 104 males had one of the two measurements larger or smaller than expected based on their plumage. Of these, the sex of 4 of the males and the class I female from Laguneta (Fig. 2C) are probably correct because my evaluation agrees with

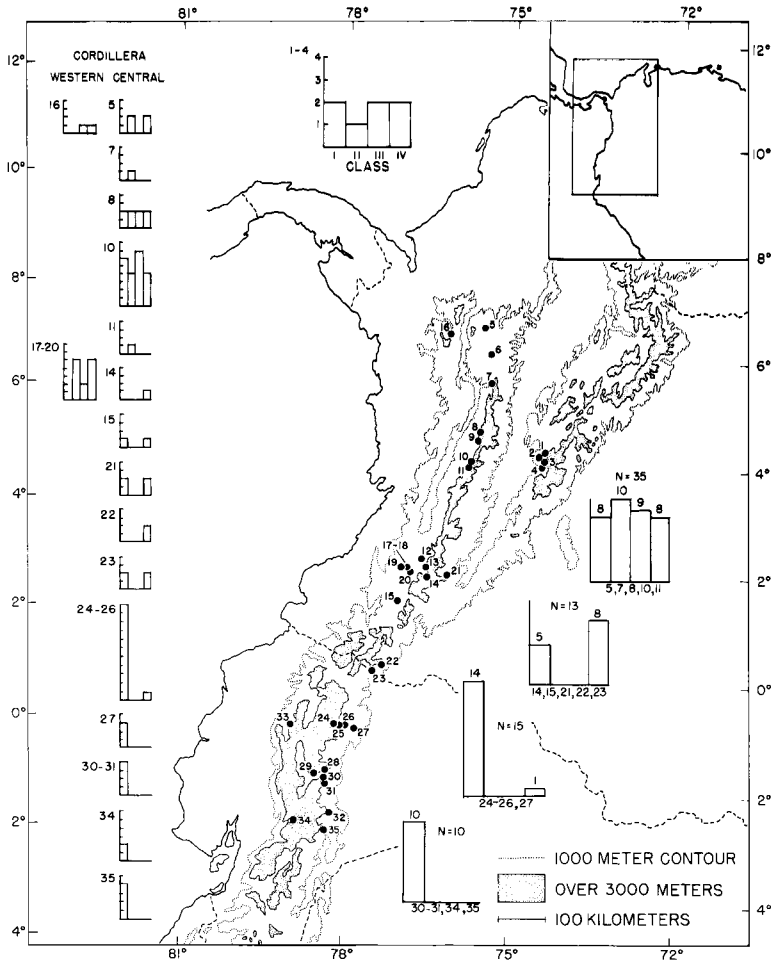


Fig. 3. Geographic variation in glittering gorget iridescence in adult female *H. e. exortis*. Gorget color classes are based on Fig. 1 and are as described in text. Separate histograms for each locality are on the left side. The principal geographic pattern is summarized by the histograms on the right side. The Bogotá sample (top center) has all four gorget color classes and is used as a key for the other histograms. Localities were plotted with the aid of ornithological gazetteers (Paynter and Traylor 1977, 1981). Numbers under histograms refer to samples included (see Table 1). There was no significant differentiation among localities in the central sections of the Central and Eastern cordilleras (A, B, and loc 10; 3×4 contingency $\chi^2 = 0.809$, $v = 6$, NS).

the sex noted on labels by the collectors, who sexed birds by examining their gonads (Chapman 1917: 304–305). The other three problematical males are all fully iridescent and do not affect the general conclusions.

Females with the highest counts of glittering gorget feathers have gorgets that are malelike in color, but this color is more limited in extent (maximum count 56 vs. a range of 43–95 for males). Iridescent gorgets in females differ in detail from those of typical males in frequently

having broad white or light gray concealed bases, and in having violet chin feathers only when the glittering gorget iridescence is extensive. Although the number of glittering gorget feathers in males also varies, this variation is not related to qualitative changes in gorget color and pattern. Within the accuracy of the sexing criterion, adult males from all geographic regions have the gorget color and pattern described for males from the Ecuadorian sample. The variation in number of glittering gorget

feathers for combined adult female samples was significantly greater than that for males [F-test of $\ln(\text{number of glittering feathers} + 1)$ (Sokal and Rohlf 1981: 421), $F = 14.88$, $v_1 = 93$, $v_2 = 113$; $P < 0.001$ (one-tailed test)].

Geographic variation in female coloration.—The pattern of geographic variation in all four classes of glittering iridescence among adult females is summarized in Fig. 3. There is striking geographic differentiation in the best-sampled region from the Central Cordillera of Colombia southward into Ecuador. Samples are highly variable (classes I-IV) in the north, but exhibit decreased variability southward, with only the extreme noniridescent and fully iridescent morphs present in southern Colombia and with decreasing frequency of the iridescent morph (class IV) in Ecuador. Differences among samples within this region were highly significant (3×4 contingency table, $\chi^2 = 48.265$, $v = 6$, $P < 0.001$). The occurrence of only the two extreme gorget classes I and IV in the southern section of the Central Cordillera of Colombia, though based upon small individual collections, is repeated for the several contiguous localities. Other small collections from elsewhere in the range do not show this pattern.

Two other relatively well-sampled regions also exhibit suggestive patterns. The sample of female *H. e. exortis* with accurate locality information from the Bogotá region was limited ($n = 7$), but the high variability of females from this region (classes I-IV) is further supported by their high variability among the numerous Bogotá trade skins. Trade skins were not included in the analysis because they lack specific locality information. These collections generally were made in the Bogotá region or, less frequently, in the central part of the Central Cordillera (Chapman 1917, Berlioz and Jouanin 1944). Bogotá trade skins also exhibit all four gorget classes. Unlike all other large samples of females, the samples from the Cerro Munchique region (loc C) lack individuals in the noniridescent class (I).

Age and temporal variation in gorget iridescence.—The ontogeny of plumage coloration in *H. e. exortis* indicates that the adult plumage, and the complete range of variability in gorget coloration among smooth-billed females, is attained before the bill corrugations disappear (Fig. 4). Adult males have a single gorget color that immatures acquire gradually before their

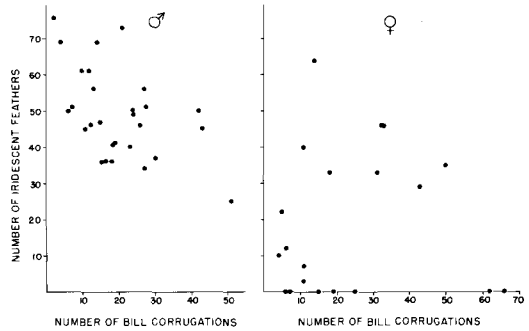


Fig. 4. Ontogenetic variation in glittering gorget iridescence among immature male (left) and female (right) *H. e. exortis* from combined geographic samples.

bill corrugations disappear. Males with < 20 corrugations already have gorgets similar to those in smooth-billed males (immature range 36-76, adult range 43-95). Immature females with comparable numbers of bill corrugations (< 20) exhibit the full range of variation observed among smooth-billed females. Taken as a whole, this information does not rule out age-related or other facultative changes in adult female gorget coloration, but it does indicate that any gorget coloration may exist at the inception of maturity.

I found no evidence of significant seasonal or annual changes in gorget color class frequencies. Within localities, the range of polychromatic variants in subsamples collected over a brief time interval is similar to that for the entire sample and for other large subsamples collected during different months and years (Table 2). For example, most of the large, variable Laguneta sample (locality 10) comprises two collections obtained in different months and years, one from August to September 1911, the other from March to April 1942. There was no significant difference (by Chi-square) in the frequency of the different gorget color classes between these two samples. Similarly, the predominantly white-gorgeted samples from Ecuador have been collected in various months and years (see Table 2), indicating that the prevalence of class I is not due to temporal sampling bias. This particular pattern was stable over at least 41 years (see Table 2). These data also indicate that the basic pattern of geographic variation is not the result of temporal sampling bias (Table 2).

TABLE 2. Temporal sampling of adult polychromatic variants with respect to month and year.^a

Locality	n	Month	Year	Total classes		
				for locality	Total classes for sample	
A. Bogotá region	7	24 Mar-6 Apr	1913	I-IV	I-IV	(2, 1, 2, 2)
8. El Zancudo	7	2-31 Aug	1918	I-IV	I-IV	(2, 2, 1, 2) ^b
10. Laguneta	9	4 Aug-6 Sept	1911	I-IV	I-IV	(5, 1, 2, 1) ^c
	9	17 Mar-15 Apr	1942	I-IV	I-IV	(1, 1, 5, 2)
15. Almaguer	2	11-16 Mar	1912	I, IV	I, IV	(1, 0, 0, 1)
C. Munchique region	4	15-22 Apr	1957	II-IV	II-IV	(0, 2, 1, 1)
21. Tijeras-Moscopán	2	23 Feb-3 Mar	1952	I, IV	I, IV	(1, 0, 0, 1)
23. Cerro Pax	4	20-23 Dec	1950	I, IV	I, IV	(2, 0, 0, 2)
24. Papallacta	2	Feb	1899	I	I	(2, 0, 0, 0)
25. Cuyujúa	2	Aug	1932	I, IV	I, IV	(1, 0, 0, 1)
	5	19 June	1928	I, IV	I	(5, 0, 0, 0)
26. Baeza	3	2-10 Nov	1922	I	I	(3, 0, 0, 0)
27. Volcán Sumaco	2	12-14 June	1924	I	I	(2, 0, 0, 0)
31. Volcán Tungurahua	2	June	1939	I	I	(2, 0, 0, 0)
34. Pallatanga	2	19-20 Oct	1931	I	I	(2, 0, 0, 0)

^a Locality letters and numbers refer to designations in Table 1. Numbers in parentheses are the number of individuals in each of the four gorget color classes (I-IV).

^b Locality 8 vs. locality 10, Aug; Yates corrected for continuity $\chi^2 = 0.29$, $v = 3$, NS at 0.05 level.

^c Locality 10, Aug vs. locality 10, Mar-Apr; Yates corrected for continuity $\chi^2 = 2.57$, $v = 3$, NS at 0.05 level.

Trophic morphology.—In the largest polychromatic female sample, from Laguneta (locality 10, $n = 21$; all other polychromatic localities, $n < 10$), bills vary by more than 2 mm in length (EC 15.3-17.6), and both measures of bill length were significantly negatively correlated with numbers of glittering feathers (Table 3). There were no significant correlations between gorget color and the other four measurements at Laguneta or in any character from other large samples ($n > 4$). Male and female class IV individuals from Laguneta were also similar in bill length (for example, for EC, Mann-Whitney U -test; $U_s = 52$, $t_s = 0.77$, $v = 23$; two-tailed test, $P > 0.5$), while bills of class I females were significantly longer than bills of males ($U_s = 94$, $t_s = 2.69$, $v = 24$; one-tailed test, $P < 0.01$). Thus, in the Laguneta sample, individuals with iridescent gorgets in either sex have comparable bill lengths that are shorter than in females with nonglittering gorgets (class I).

DISCUSSION

In promiscuous mating systems, which are characteristic of most hummingbird species (Stiles and Wolf 1979), the potential for sexual selection as measured by variance in reproductive success is high in males but low in females (Payne 1984). This makes sexual selection an

unlikely explanation for the origin of polychromatic variation in female hummingbirds. By contrast, aggressive competition for nectar may occur in both sexes in hummingbirds, and it helps explain the evolution of the brilliant female plumage of bright monomorphic species (Wolf 1969, Wolf and Stiles 1970). These considerations suggest that competition for nectar is a more plausible basis for the origin of polychromatic variation in female *H. e. exortis* than is sexual selection. Social competition is defined in terms of intraspecific competition, whereas aggressive competition for nectar in hummingbirds may include interspecific interactions (Moynihan 1979). I therefore refer to the hypothesis for the evolution of polychromatic variation via nonsexual competition for nectar as the "feeding strategy hypothesis" in order to include the possible effects of interspecific aggression.

The principal prediction of the feeding strategy hypothesis is that polychromatic variation in the gorget of female *H. e. exortis* reflects variation in foraging behavior. Iridescent females of bright monomorphic hummingbirds actively defend their territories and are codominant with males (Wolf 1969, Stiles and Wolf 1970, Wolf and Stiles 1970). On this basis, I further predict that increasing gorget iridescence should be positively correlated with increasing

TABLE 3. Spearman rank correlation coefficients for female gorget iridescence and six mensural characters for the Laguneta sample (locality 10).^a Sample sizes are given in parentheses.

EC	CF	FP	WB	IT	OT
-0.59** (21)	-0.51* (21)	0.32 (20)	0.37 (17)	0.29 (20)	0.21 (19)

^a EC = length of exposed culmen, CF = length of culmen from flange of nasal operculum to tip, FP = length of outer primary, WB = chord of unflattened wing from bend to tip, IT = length of inner tail feather, OT = length of outer tail feather. * $P < 0.02$, ** $P < 0.01$ (two-tailed tests).

dominance and degree of feeding territoriality among female *H. e. exortis*. There is as yet no direct proof of these predictions from field observations. However, aggressive territorial exploitation of nectar is characteristic of male *H. e. exortis* (Moynihan 1979, Hilty and Brown in press). In other territorial hummingbird species where males have a glittering gorget, the gorget is used in aggressive displays associated with feeding territoriality (Ewald and Carpenter 1978). Feeding territoriality in male *H. e. exortis* therefore provides a necessary condition for my inference that female *H. e. exortis* with iridescent gorgets are territorial nectar feeders.

The negative correlation between bill length and the degree of gorget iridescence in females from Laguneta supports the predicted association of an iridescent gorget with aggressive feeding territoriality (in light of the possible general relationship between decreasing bill length and increased territoriality discussed in the Materials and Methods). However, this correlation is not consistent among all localities. Perhaps, variation in bill length is not necessary for the evolution of individual differences in the degree of feeding territoriality.

The only direct observations of behavioral correlates of intrapopulational variation in gorget coloration involve ontogenetic variation in male *Calypte anna*. Adult male *C. anna* have glittering red crowns and gorgets that develop gradually with age. As is consistent with the predictions for polychromatic variation in *H. e. exortis*, adult male *C. anna* are territorial during the nonbreeding season while the less iridescent juveniles hold poor-quality territories or are not territorial (Ewald and Rohwer 1980). It is difficult, however, to assess the evolutionary significance of polychromatisms using ontogenetic variation because individuals differ in age (experience) and sexual maturity. These two factors can determine the outcome of aggressive interactions even in the absence of color

variation. The polychromatic variation described in this paper differs from ontogenetically developed color variation in at least three important respects: (1) occurrence within broad age categories of immatures and adults, (2) temporal stability in the relative frequencies of the gorget color classes at some localities such as Laguneta, and (3) female sex-biased pattern (polychromatic variation limited to females). I explore below the possible implications of these characteristics for the feeding strategy hypothesis to provide a specific framework for future research.

Age independence. — Age independence of polychromatic variants contrasts with the strong ontogenetic component of many cases of variable male plumage ascribed to sexual selection (Gilliard 1969, Wilson 1975). Dull, unornamented males are often subordinate immatures that do not achieve full ornamentation or reproductive potential until they move up the dominance hierarchy. Such males may even delay attempts to reproduce until they are older, but may gain in lifetime reproductive fitness by achieving greater reproductive success at an older age. Thus, sexually selected plumage variation in males may arise out of its reflection of age rather than from the selective value of different levels of ornamentation *per se* (Price 1984). The appearance of polychromatic variation early in the ontogeny of *H. e. exortis*, and its persistence in adults, suggests that the different phenotypes are viable at any age. Competition for nectar may produce age-independent polychromatic variation in females; unlike competition for mates among males, females have no apparent fitness payoff for delaying access to nectar.

Temporal stability. — Temporal stability of polychromatic variants suggests that they can coexist without evolutionary exclusion. Coexistence of polychromatic variants that differ in foraging behavior is possible if bright plumage

confers different costs and benefits from dull plumage in different social contexts associated with foraging (Ewald and Rohwer 1980, Rohwer 1982). For example, bright plumage, although possibly advantageous in aggressive encounters with conspecifics or other species, may be costly for subordinate birds if it increases the rate and intensity of attacks by dominants. Conversely, dull plumage in subordinates may increase their success at intruding onto nectar territories and reduce the severity of aggressive responses by territorial birds (Ewald and Rohwer 1980). Further morphological evolution for increased efficiency in different foraging strategies by dominants and subordinates should enhance stable coexistence. This possibility is suggested by the correlation between bills and coloration in *Laguna*, where the frequency characteristics of the gorget color classes did not change significantly over at least 30 years. Temporal and geographic shifts in polychromatic variation may be caused by extrinsic shifts in nectar resource availability through changes in the flora or changes in avian nectar competitors such as other hummingbirds or the nectarivorous *Diglossa* (Coeribidae).

Female sex-biased pattern.—Intersexual differences in variability may be due to sexual selection. The sex bias in the polychromatism represents a simple case of reduced male variability documented in many taxa (Pearse and Murray 1982, Stamps and Gon 1983). Stabilizing sexual selection by female choice and intrasexual aggression have been proposed as alternative explanations of this pattern (Pearse and Murray 1982, Rohwer 1982, Stamps and Gon 1983). Both processes may operate in conjunction to reduce variation in aggressive signals in male hummingbirds. Female hummingbirds of some species seem to choose males on the basis of occupancy and quality of a nectar territory (e.g. *Calypte anna*, *Panterpe insignis*; Stiles 1973). This indirect female choice of male aggression can lead to strong selection for aggressiveness and aggressive signals among all males if all males compete for territories during the breeding season without adopting alternative nonterritorial mating strategies (Rohwer 1982). Indeed, these conditions appear to exist in *Calypte anna* (Stiles 1973), where most males are iridescent, but females are polychromatic (Williamson 1956). Conversely, males of promiscuous species

appear to be less discriminating in mate choice (Sibley 1957). Thus, male choice acting on females would be less likely to eliminate female color morphs that evolved through nonsexual selection.

Both proximate mechanisms and broader ecological causes probably will be important for analyzing the evolution of hummingbird polychromatisms. Hummingbirds as a whole meet the requirements for the evolution of intrapopulational variation in conspicuous coloration as outlined by Rohwer (1982): presence of aggressive competition for a resource (nectar), variation in dominance, and frequent aggressive interactions among individuals. The simplest mechanism for the origin of variation in phenotypic traits associated with variation in dominance behavior is a physiological link between coloration and behavior (Keeler et al. 1970, Watt et al. 1984). The final form of the variation may then depend upon how alternative individual strategies of resource exploitation are limited by resource availability. Presence and absence of territoriality in hummingbirds depends upon nectar resource density, with territoriality around denser clumps of nectar. Therefore, female polychromatisms may evolve when females within a population forage over a broad range of nectar densities, while sexually dichromatic and bright monochromatic species may evolve when respective females specialize at low or high densities.

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100 Years Ago in The Auk



From "General Notes" (1885 Auk 4: 382–383):

"On the Feeding Habits of *Phalaenoptilus nuttalli*.—Just without the picket fence that encloses in part the parking of my present residence at Fort Wingate, New Mexico, then [sic] runs a wide board-walk. Beyond this is a broad, well-kept gravel road, standing between the former and an open level plot of ground of about an acre's extent. For a number of evenings past my neighbors have tried to induce me to come out and see a strange-acting bird that disported itself in this roadway, between twilight and dark. I paid little heed to this, as from its description I believed it to be the half-grown young of the *Chordeiles* of this region, which is very abundant in the neighborhood. Last night, however, the bird having been described to me as a small Owl with a white throat, by one of its observers, I took my cane-gun and made a search for it up and down the road-way. I had not far to go, when, as well as I could see by the light of a very young moon, I noticed a small, dark-brownish looking bird apparently amusing himself by making short jumps of two feet or more up in the air, then resting on the road to repeat the performance in a moment or so. Another was going through similar capers on the broad walk. They seemed to be perfectly oblivious to my presence, and, indeed, some children further along were trying to catch them with their hands. As I had never heard the note of the Poor-wills in the vicinity, it did not

strike me at first that it might be this bird; moreover, its action was so odd that I hardly knew what to make of it. At any rate one soon noiselessly lit, like a great, gray moth, directly in front of me in the road, but a few feet distant. It was extremely difficult to see him, and it was more by good luck than good shooting that the little pinch of shot from my cane-gun knocked him over, though the weapon rarely fails me in daytime. I immediately ran up to my study with my prize, where I discovered I had killed a fine specimen of Nuttall's Poor-will. As the skeleton of this bird had long been among my desiderata, the skin and its beautiful plumage was soon stripped off, whereupon I was much surprised to find in its mouth some four or five quite sizable moths, and the upper portion of the oesophagus filled with a wad of a dozen or fifteen more. Fully half of these were yet alive, and two or three managed to fly away when freed from the bodies of their more disabled companions. This, then, is what the bird was up to; instead of flying about as a Nighthawk does, taking his insect prey in a conspicuous manner upon the wing, he captures it in the way I have described above.

"To-night the moon is twenty-four hours older, and the evening proportionately brighter, but a careful search for over half an hour failed to discover a single specimen of the bird on the same ground. I am not aware that any of the other Caprimulgidae have similar habits.—DR. R. W. SHUFELDT, Fort Wingate, New Mexico."