

Reversed plumage ontogeny in a female hummingbird: implications for the evolution of iridescent colours and sexual dichromatism

ROBERT BLEIWEISS

Department of Zoology and the Zoological Museum, University of Wisconsin, Madison, WI 53706, U.S.A.

Received 15 November 1990, accepted for publication 18 April 1991

In polygynous birds, bright plumage is typically more extensive in the sexually competitive males and develops at or after sexual maturity. These patterns, coupled with the importance of male plumage in sexual displays, fostered the traditional hypothesis that bright plumages and sexual dichromatism develop through the actions of sexual selection on males. This view remains problematic for hummingbirds, all of which are polygynous, because their bright iridescent plumages are also important non-sexual signals associated with dominance at floral nectar sources. Here I show that female amethyst-throated sunangels [*Helianthus amethysticollis* (d'Orbigny & Lafresnaye)], moult from an immature plumage with an iridescent gorget to an adult plumage with a non-iridescent gorget. This 'reversed' ontogeny contradicts the notion that iridescent plumage has a sexual function because sexual selection in polygynous birds should be *lowest* among non-reproductive immature females. Moreover, loss of iridescent plumage in adult females indicates that adult sexual dichromatism in *H. amethysticollis* is due in large part to changes in female ontogeny. I suggest that both the ontogeny and sexual dichromatism evolved in response to competition for nectar.

KEY WORDS:—Hummingbird – moult – ontogeny – iridescence – sexual selection – feeding ecology.

CONTENTS

Introduction	183
Materials and methods	184
Results	186
Sexing	186
Age and gonad condition	186
Female ontogeny	187
Comparison with males	190
Discussion	190
Evolution of the immature stage	191
Evolution of the adult stage	192
Conclusions	193
Acknowledgments	193
References	193

INTRODUCTION

The status of sexual selection as an evolutionary process distinct from natural selection can be difficult to evaluate from a functional analysis of display

structures. By definition, natural selection acts on any trait that influences the number of offspring whereas sexual selection acts on only those traits that influence an individual's ability to acquire mates. In practice, however, many display structures function in both mate acquisition and other contexts. These complications can obscure the original basis for the evolution of the trait (cf. Gould & Vrba, 1982).

For example, circumstantial evidence supports both sexual and non-sexual origins for the brightly coloured plumages of birds. The sexual selection hypothesis is consistent with the observation that many birds acquire a brightly coloured plumage with the advent of sexual maturity, the time when reproductive activities and mate competition commence. Furthermore, immatures often wear drab plumages, whereas adults of migratory species often lose their colourful plumages during the non-breeding season (Lyon & Montgomerie, 1986). This interpretation is reinforced by the frequent association of the most elaborate male ornaments and pronounced sexual dichromatisms with polygyny, a mating system in which the intensity of sexual selection is believed to be greater on males. Yet the possibility exists, as with any correlation, that factors other than those considered actually provide the causal link. Indeed, predation pressures, non-sexual social interactions and diet also change with age, season and breeding system. One or more of these non-sexual factors could be responsible for the evolution of conspicuous plumage (e.g. Baker & Parker, 1979; West-Eberhardt, 1983; Slagsvold & Lifjeld, 1985). If a plumage ornament has sexual and non-sexual functions, it becomes difficult to distinguish its initial function from those it may have acquired subsequently. The challenge is to find natural experiments that serve to discriminate among causal mechanisms.

Here I describe a novel moult pattern that accomplishes this aim for one typical hummingbird plumage ornament, the brightly coloured iridescent gorget. Traditionally, gorgets are considered products of sexual selection because they typically develop at sexual maturity and only in the males of this uniformly polygynous family (Aldrich, 1956; Williamson, 1956; Stiles, 1982). However, the male gorget functions both as a sexual display signal and as a non-sexual aggressive signal for defence of nectar-providing flowers (Stiles, 1982), so one cannot say for which function it evolved. I demonstrate that females of the amethyst-throated sunangel [*Heliangelus amethysticollis* (d'Orbigny & Lafresnaye)] moult from a *bright* to a *dull* gorget at sexual maturity. I argue that such a 'reversed' ontogeny provides evidence that non-sexual selection alone is sufficient to explain the evolution of iridescent plumage and sexual dichromatism in some hummingbirds.

MATERIALS AND METHODS

The nine currently recognized sunangel species (Peters, 1945; Fitzpatrick, Willard & Terborgh, 1979) are common residents of forested and scrubby Andean habitats. My study of *H. amethysticollis* is based on an examination of museum skins collected from Ecuador to Bolivia. I follow Peters (1945) and Fitzpatrick *et al.* (1979) in considering populations from Venezuela and central Colombia to comprise a distinct species, *H. clarisse*. Most specimen labels contained gonad information (95 of 146 adults and 37 of 65 immatures). I sexed

the remaining specimens by application of discriminant function analysis (DFA), which is a powerful tool for sexing hummingbirds from various linear measurements (Bleiweiss, 1992). I used a jackknife validation procedure on a stepwise analysis of four measurements that proved sexually dimorphic in adult birds sexed by their gonads: length of outer primary (P), length of exposed culmen (EC), length of culmen from base of nasal operculum (CB) and length of outer tail feather (OT) (Baldwin, Oberholser & Worley, 1931). The inclusion of specimens sexed by DFA augments substantially both the sample size and geographic coverage of my study. Further details of these analyses are given elsewhere (Bleiweiss, 1992).

Hummingbirds can be aged by external characters of the bill. Immatures have minute corrugations that are lost in adults, whose bills are smooth (Ortiz-Crespo, 1972; Stiles & Wolf, 1974; Ewald & Rohwer, 1980). In several North American hummingbirds, Stiles (1972) found that the bills of fledged immatures are shorter than those of adults, presumably because the bills of immatures have not completed growth. To further validate ageing by bill corrugations for *H. amethysticollis*, I examined correlations between bill texture and bill length. I also tested whether individuals with textured bills have smaller gonads (noted in millimetres on many specimen labels), as would be expected if the corrugations are an accurate guide to reproductive stage. The relative ages of immatures can be determined roughly from the number of bill corrugations (Ortiz-Crespo, 1972; Ewald & Rohwer, 1980), which disappear gradually during the bird's first year (Ortiz-Crespo, 1972; Stiles & Wolf, 1974). I estimated the number of corrugations with the aid of a camera lucida. Individuals that lacked corrugations outside the nasal depression were considered to be adult.

Structural modifications of the feather barbules determine the presence and intensity of iridescent colours in hummingbird feathers, and provide a physical basis for qualitative descriptions such as 'bright' and 'dull'. I used Greenewalt's terminology (1960): "glittering" refers to the most intense mirrorlike reflection, "shining" to a duller metallic lustre. Colour terminology used here follows that of Smithe (1975). I quantified the amount of glittering colouration by counting camera lucida tracings of the glittering feathers on the gorget of each specimen (for details see Bleiweiss, 1985). Females were divided into four plumage colour classes based on the percentage of the average number of glittering feathers in adult males of the species ($\bar{X} = 86.6$; class I = 0%, class II = < 25%, class III = < 50%, class > 50%).

I determined the moult pattern of the gorget by noting patterns of feather replacement. Incoming feathers could be recognized by the presence of a sheath entirely surrounding the new feather, or at the base of an unfurling feather. New feathers were identified as either glittering (purple to magenta) or non-glittering (rufous or rufous with a shining green dot). Feathers hidden within a sheath could not always be identified, but the sheath could be teased apart in some cases, revealing the identity of the nascent feather.

The four skin measurements (P, EC, CB, OT) adhered to the assumption of normality and homogeneity of variance for parametric uni- (Student's *t*) and multi- (DFA) variate statistical tests. Appropriate non-parametric methods were used for variables that did not meet these assumptions (gonad size, bill corrugations, glittering gorget feathers). All statistical analyses were conducted using SPSSx (SPSSx Inc., 1988) or BMDP (Dixon, 1983).

RESULTS

Sexing

The discriminant function constructed for each age group (adults, immatures) was highly significant, and accurately classified most individuals of known sex (BMDP P7M, Dixon, 1983; Table 1). Posterior probabilities of assignment to sex for immatures lacking gonad data exceeded 0.95 for 22 of 25 specimens or 88.0%. The results of DFA on adults, which gave similar levels of reliability, are discussed elsewhere (Bleiweiss, 1992). Subsequent analyses conducted with and without individuals whose sex was less certain ($P < 0.95$) gave qualitatively similar results. I discuss the more inclusive analyses.

Age and gonad condition

Bill length and gonad size correlate with age/reproductive class as defined by the presence (immature) or absence (adult) of bill corrugations. For both sexes, immatures have shorter bills than adults for each of the two different measures of bill length ($P < 0.05$ in three of four comparisons; Table 2). Moreover, analysis of gonad data bears out the *a priori* expectation that the gonads' mean largest dimension among individuals with smooth bills is significantly larger than those with textured bills [males: \bar{X} adults = 2.11, \bar{X} immatures = 0.90 (Mann-Whitney $U = 44.5$, one-tailed $P < 0.0001$); females: \bar{X} adults = 3.64, \bar{X} immatures = 2.19 (Mann-Whitney $U = 51.5$, one-tailed $P < 0.0005$)]. Size of ovarian follicles was minute (physiologically quiescent) in all immatures where it was noted on the specimen label. Thus, individuals with textured bills are indeed physiologically immature.

TABLE 1. Results of jackknifed stepwise discriminant function analysis on immature and adult *H. amethysticollis*. Percentages refer to the proportion of individuals classified as male or female

Actual group	N	Predicted group ^a		χ^2 ^b (d.f.)
		Male	Female	
<i>Immatures</i>				
Sex				
Male	23	21 (91.3%)	2 (8.7%)	36.78***
Female	14	1 (7.1%)	13 (92.9%)	(2)
Unknown	25	11 (44.0%)	14 (56.0%)	
<i>Adults</i>				
Sex				
Male	54	49 (90.7%)	5 (9.3%)	119.10***
Female	41	1 (2.4%)	40 (97.6%)	(4)
Unknown	51	35 (68.6%)	16 (31.4%)	

^aEquality of the covariance matrices was verified by non-significant values ($P > 0.05$) for Box's modification of Bartlett's test (Williams, 1983) and by insensitivity of results to analysis on log transformed measurements (Pimental & Frey, 1978).

^bThe statistical significance of each discriminant function was tested by transforming Wilks' lambda into a χ^2 statistic (Marascuilo & Levin, 1983). *** $P < 0.001$.

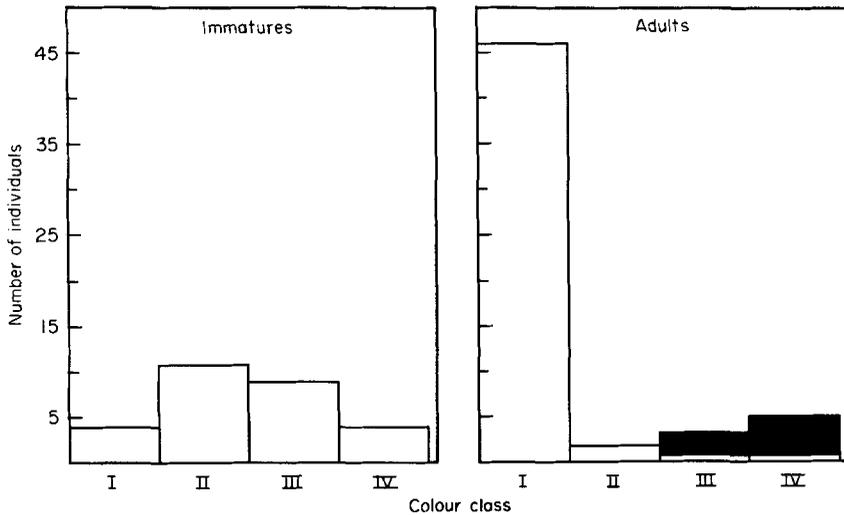


Figure 1. Difference in the amount of glittering iridescence between immature and adult females. The iridescent colour classes (II-IV) are significantly more frequent among immatures. Black histograms represent females from a population whose adults are predominantly male-like (see text).

Female ontogeny

Geographic variation among populations of adult *H. amethysticollis* has been discussed in a survey of the entire genus (Bleiweiss, 1992). The gorgets of adult males are glittering magenta to rose, whereas those of adult females are typically non-iridescent rufous, sometimes with shining green dots. Although adult females of many *Helianthus* species often have glittering gorgets, such polychromatism is greatly reduced in *H. amethysticollis* (only 11 of 57 specimens, or 19.3%, have glittering gorget feathers; Fig. 1). In contrast, most immature females have a few to many glittering gorget feathers (24 of 28 specimens or

TABLE 2. Age-related bill length differences in male and female *H. amethysticollis*: EC = exposed culmen; CB = culmen from base of nasal operculum

Character	Age class	mm ($\bar{X} \pm SE$)	<i>t</i> ^a	d.f.	<i>P</i> ^b
Male					
EC	Immature	15.39 ± .19	4.85	104	***
	Adult	16.48 ± .11			
CB	Immature	18.61 ± .18	2.66	107	**
	Adult	19.12 ± .09			
Female					
EC	Immature	15.95 ± .20	3.36	72	***
	Adult	16.74 ± .12			
CB	Immature	19.06 ± .17	1.32	74	*
	Adult	19.34 ± .11			

^aUnpaired Student's *t*-test.

^bSignificance levels are one-tailed on the *a priori* assumption that immatures have shorter bills than adults.

P* < 0.1; *P* < 0.01; ****P* < 0.001.

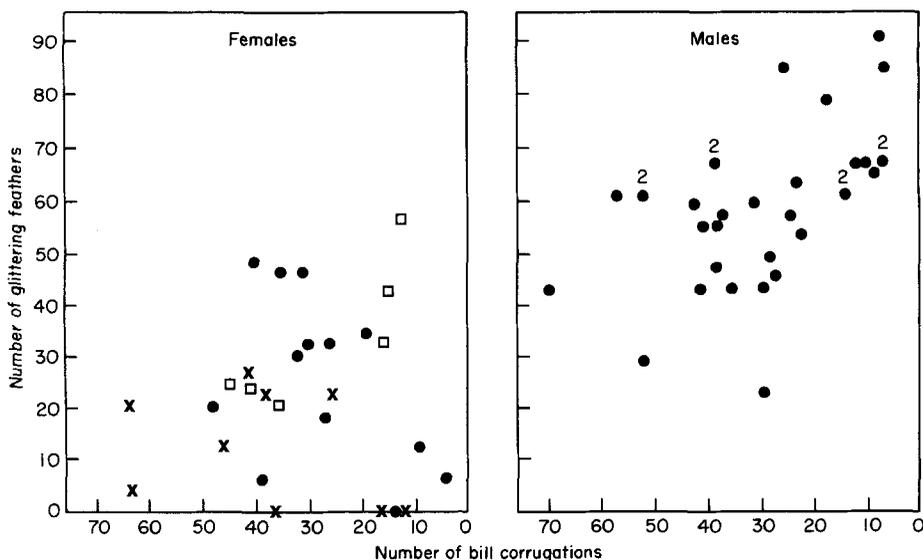


Figure 2. Gorget ontogenies of immature females and males. The amount of glittering iridescence clearly increase with age in males. Absence of the expected negative trend among females is due to geographic variation in the relationship between numbers of bill corrugations and glittering feathers. □, Ecuador—northern Peru; X, central Peru; ●, southern Peru—Bolivia. Males from all localities plotted as filled dots.

85.7%; Fig. 1). This significant age-related difference in colour (Pearson $\chi^2 = 39.7$, d.f. = 3, $P < 0.0001$) demonstrates that most females moult from a glittering to a duller non-glittering gorget at sexual maturity. The feather replacement pattern in moulting individuals supports this conclusion; significantly, only non-glittering feathers were found growing on the gorgets of moulting females (65 emerging feathers from among 17 individuals).

Among females, the progressive loss of glittering feathers is indicated also by the fact that most older (by fewer bill corrugations) immatures have duller non-glittering gorgets. One might expect an overall negative relationship between the numbers of bill corrugations and glittering throat feathers because glittering feathers are lost in adults. The absence of such a relationship in the pooled sample is apparently due in part to geographic differences in the relationship between bill and feather development (Table 3, Fig. 2). Numbers of glittering

TABLE 3. Spearman's coefficients of rank correlation between numbers of glittering male-like feathers and of bill corrugations

Sex	Groupings ^a	r_s	P^b	N
Males	Pooled	0.5339	***	33
Females	Pooled	0.010		28
Females	Loc. 1	0.8117	**	6
	Loc. 2	-0.4087		9
	Loc. 3	-0.4231	*	13

^aPooled: all samples; Locality 1: Ecuador and northern Peru; locality 2: central Peru; locality 3: southern Peru—Bolivia.

^bOne-tailed significance levels: * $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$.

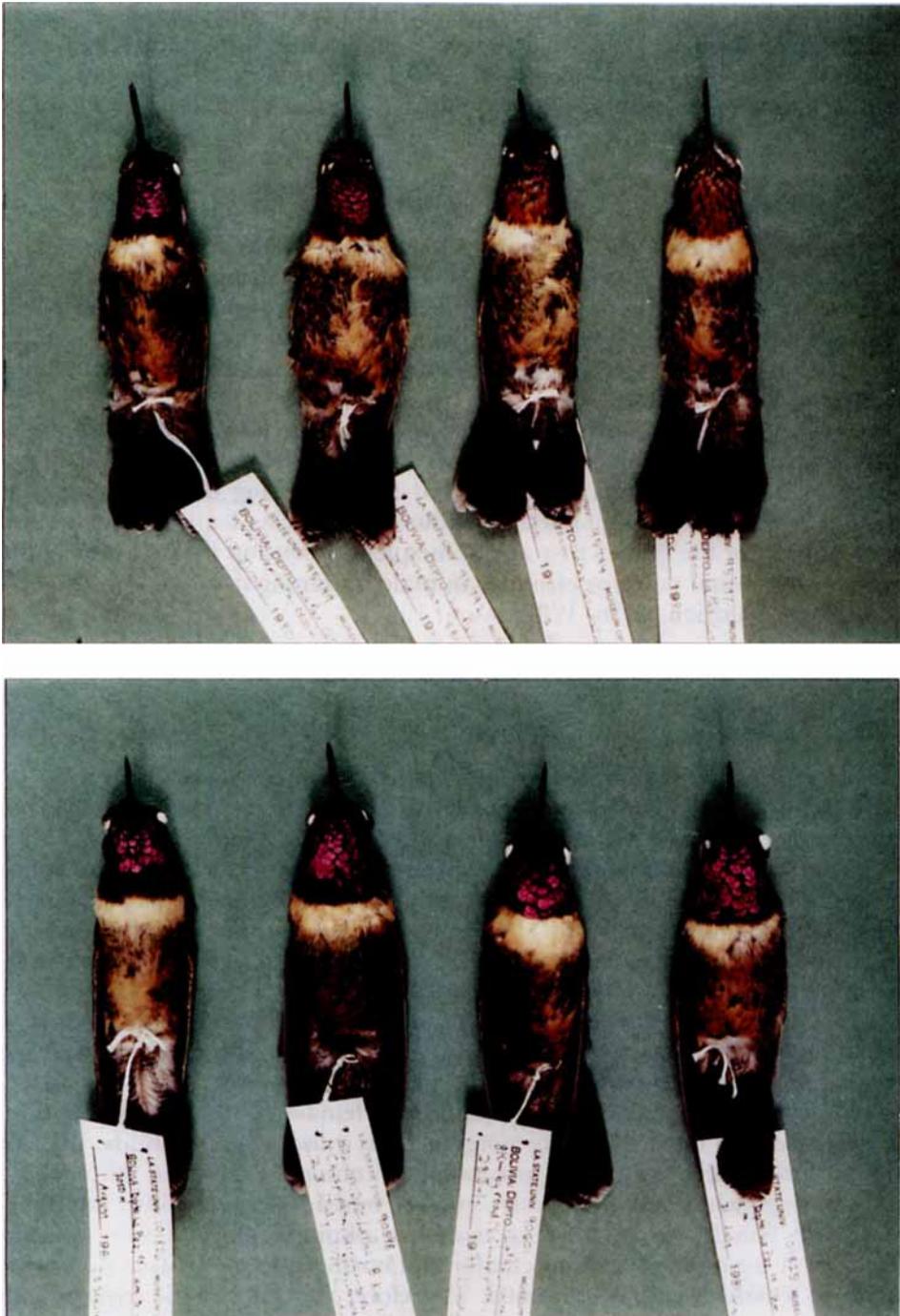


Figure 3. Plumage ontogeny of immature females (top) and males (bottom) as indicated by a series collected at Chuspipata, Bolivia from 1979 to 1981 (Louisiana State University Museum of Zoology). In each grouping, the youngest bird is on the left, and the moult stages advance to the right.

feathers and bill corrugations are negatively correlated in the larger Peruvian and Bolivian samples, but positively correlated in the northernmost sample from Ecuador and northern Peru. The aberrant relationship in the north may reflect the small size of the sample available for this region, or a different ontogenetic trajectory among these subspecifically distinct (Zimmer, 1951) populations.

Comparison with males

Immature females with few or no rufous gorget feathers are very similar in appearance to immature males (Fig. 3). In both, glittering gorget feathers are restricted to the chin and upper half of the throat. The remaining lower portion of the throat is dark shining green, bordered below by the light coloured chest band present in both immatures and adults (which varies clinally from white in Ecuador to rufous in Bolivia).

In marked contrast to the pattern among females, however, the number of glittering feathers in the gorgets of males increases with age (Table 3, Fig. 2), and only glittering feathers were observed to be growing on their gorgets (40 emerging feathers from among ten individuals). Glittering feathers appear on the upper portion of the gorget first and subsequently develop in the lower border. These are the usual patterns of moult in male hummingbirds with an iridescent adult gorget (Aldrich, 1956; Williamson, 1956).

DISCUSSION

Evidence that female *H. amethysticollis* moult from a brighter glittering to a duller non-glittering gorget at maturity is supported by two patterns: most immature females have glittering gorgets whereas most adult females have duller non-glittering gorgets; all feathers emerging on the gorgets of immature females are non-glittering. This moult apparently is not unique to *H. amethysticollis* among hummingbirds, as Elgar (1978) reports that an immature female white-necked jacobin (*Florisuga mellivora*) in his aviary molted over a 14-week period from an iridescent blue plumage typical of males to a white and shining green one. Inadequate nutrition or other unnatural conditions might produce an anomalous moult in a captive bird. The existence of the same pattern in a natural population, however, cannot be so readily dismissed.

The one caveat to this 'reversed' pattern in female *H. amethysticollis* is that a few *adult* females have glittering gorgets. This raises the possibility that two different ontogenies exist; the predominant ontogeny is from glittering to non-glittering, while less frequently, gorgets remain glittering into adulthood. Most adult females with glittering male-like plumage (Fig. 1) were collected from a small region in southern Ecuador and northern Peru, an area from which immature females were not obtained. Therefore, the ontogenetic sequence that ends with a glittering adult female plumage remains undocumented. Nevertheless, moult from a glittering to a duller non-glittering gorget is clearly the norm over most of the species' range. Below, I consider the significance of the female ontogeny for understanding the evolution of iridescent plumage and the development of sexual dichromatism.

Evolution of the immature stage

Although glittering plumages are typical of many male hummingbirds, the immature plumage described here adds to the variety of glittering plumages documented in female hummingbirds. Previous work has shown that adult females of many species develop monomorphic or polymorphic glittering male-like plumages (Wolf, 1969; Wolf & Stiles, 1970; Bleiweiss, 1985, 1992). These plumages are unlikely to be products of sexual selection acting on females because hummingbirds are polygynous, a breeding system in which females should enjoy low levels of mate competition (Darwin, 1871). Nonetheless, as these are adult plumages and thus occur in reproductively mature birds, a sexual origin cannot be ruled out.

The reversed ontogeny provides conclusive support for a non-sexual function for glittering female gorgets because the bright plumage develops in non-reproductive immature females, which should enjoy the lowest levels of sexual selection (West-Eberhardt, 1983; Lyon & Montgomerie, 1986) and disappears when they mature. Moreover, the apparent rarity of reversed plumage ontogenies implies that the bright immature stage evolved for this non-sexual function. Thus, speculations as to the possible non-sexual origin of the glittering immature plumage are justified.

Among non-sexual factors, predation may account for the origin of some bright colours that are hard to explain as products of sexual selection (Baker & Parker, 1979). The bright colours of immature invertebrates and small terrestrial vertebrates, for example, appear to serve as warning or distraction signals to potential predators (e.g. Cooper & Vitt, 1985). I exclude predation as an important influence on the bright plumage of immature *H. amethysticollis*, however, because predation levels are very low on non-breeding hummingbirds (Miller & Gass, 1985). Diet *per se* can influence plumage colour because the amount of pigment deposited in feathers can depend on the quantity of pigment present in the bird's food (Slagsvold & Lifjeld, 1985). However, iridescent colours are produced by structural modifications to the feather, so their development is independent of the ingestion of specific biochromes.

Alternatively, the glittering gorget of immatures may serve as an aggressive signal associated with the defence of nectar resources. Field studies have demonstrated a direct relationship between iridescent plumages in adult hummingbirds and socioecological behaviours associated with foraging. Specifically, females of sexually dichromatic species are usually less territorial nectar feeders than their more highly iridescent male conspecifics, whereas females of monochromatic species with iridescent plumage are as territorial as their respective males (Wolf, 1969, 1975; Wolf & Stiles, 1970; Stiles & Wolf, 1970, 1979). One would predict, therefore, that immatures with glittering plumage are more aggressive than the relatively dull-coloured adult females in their exploitation of nectar sources.

Two lines of indirect evidence make this an attractive explanation for the reversed ontogeny. First, male *Helianthus* are notably aggressive and territorial (Fitzpatrick *et al.*, 1979; Moynihan, 1979; Snow & Snow, 1980), so the glittering gorget is presumably an important territorial signal in this genus. Second, immature hummingbirds, unlike the immatures of many vertebrates, are widely reported to exhibit aggressive behaviours and territoriality associated with

exploitation of nectar (Stiles, 1973; Feinsinger, 1976; Gass, Angehr & Centa, 1976; Gass, 1978, 1979; Ewald, 1985).

When compared with those of adults, the shorter bills of immatures are intriguing in view of a general correlation among hummingbirds between bill length and feeding strategy (Paton & Collins, 1989). Across adults of many species, shorter bills are associated with more aggressive feeding strategies both between the sexes (male bills are shorter) and interspecifically (Wolf, Stiles & Hainsworth, 1976; Feinsinger & Colwell, 1978; Feinsinger *et al.*, 1979). This association may be a causal one, as bill length affects how much and how fast a hummingbird can extract nectar from a flower. Specifically, shorter-billed hummingbirds can probe only short flowers efficiently and legitimately (through the flower's natural opening). Conversely, longer-billed hummingbirds have access to nectar of long flowers that shorter-billed individuals cannot fully exploit. Thus, short-billed individuals must defend their food plants against longer-billed competitors if they are to secure an adequate nectar supply (Feinsinger *et al.*, 1979). The economics of foraging may also dictate these patterns among different age classes; shorter-billed immatures may defend flowers against adults on some occasions. Though seemingly small, the age-related differences in bill length (1–2 mm) are of the same magnitude as some sex-related differences in bill length (Paton & Collins, 1989).

Finally, feeding ecology provides a plausible basis for the remarkably similar form of the glittering gorget in immatures of both sexes. Species of birds that compete aggressively for food have often converged on the same aggressive signal (Cody, 1969; Cody & Brown, 1970; Moynihan, 1979). It is, therefore, potentially significant that immature male and female hummingbirds often forage in the same habitat where they interact aggressively (Feinsinger, 1976; Gass, 1978). This association could lead both sexes to evolve similar aggressive signals.

Evolution of the adult stage

Sexual selection theory leads to the expectation that sexual dichromatism in polygynous species develops through the elaboration of male morphology (Darwin 1871). It is remarkable, therefore, that in *H. amethysticollis*, adult sexual dichromatism develops in part because immature *females* lose their iridescent gorgets at sexual maturity.

Analysis of the underlying basis for this colour change in adults is complicated because one is again faced with the possible roles of sexual and natural selection. For example, females sporting aggressive releasers may have difficulty attracting a mate (Nobel, 1936; Robertson, 1985). Predation might select for dull-coloured adult plumage in females because they conduct all of the duties associated with nesting, a time when they are probably most vulnerable to predators (Miller & Gass, 1985). However, the evolution of permanent bright plumages in adult females of many hummingbird species implies that other factors take precedence. In view of these facts, I propose that feeding ecology is the most reasonable and unifying explanation of the entire ontogeny. As emphasized above, there are many reasons to expect the social milieu of hummingbirds to permit immature females to develop aggressive non-sexual signals. Moreover, dull-coloured plumage may benefit a hummingbird that exploits nectar by a non-territorial

strategy (Rohwer, 1982; Ewald, 1985), as do the dull-plumaged adult females of many species (Wolf *et al.*, 1976; Feinsinger & Colwell, 1978; Snow & Snow, 1980).

CONCLUSIONS

The most important question raised by the reversed ontogeny described here is whether it represents an interesting exception, or a key to the underlying causal basis for the evolution of bright colour. Ontogenies characterized by a bright social signal restricted to immatures are not unique to hummingbirds, but are also found in coral reef fishes (Lorentz, 1966; Barlow, 1974) and woodpeckers (Bent, 1939; Goodwin, 1968; Short, 1982). These other groups share with hummingbirds a social system characterized by heightened aggression among immatures (Myrberg & Thresher, 1974; Short, 1982). This basic similarity suggests that the development of bright colours through non-reproductive competition is taxonomically widespread.

Although bright colours and aggression are equated traditionally with greater age because older individuals are usually dominant, some recent theories suggest that aggression and dominance may be selected whenever the net value of resource defence outweighs its cost. Such an asymmetry does not necessarily favour the development of bright colours and aggression in older individuals (Ewald, 1985). Indeed, immature hummingbirds have been observed to dominate adults in contests over nectar resources (Ewald, 1985). The evolution of reversed ontogenies suggests that foraging behaviour provides a potent selective force whose role in shaping patterns of colouration among animals has not been fully appreciated.

ACKNOWLEDGEMENTS

Peter Cotton, Dana Geary and Kurt Frstrup made many helpful suggestions on a draft of the manuscript. I thank the curators of the following museums for providing me access to specimens under their care: Academy of Natural Sciences, Philadelphia; American Museum of Natural History, New York; British Museum, Tring; Louisiana State University Museum of Zoology, Baton Rouge; Museum of Comparative Zoology, Cambridge; United States National Museum, Washington D. C.; Western Foundation of Vertebrate Zoology, Los Angeles; Universitetets Zoologiske Museum, Kobenhavn. Bill Feeney drafted the figures and Adam Steinberg took the photographs. This work was supported by a Frank M. Chapman Postdoctoral Fellowship from the American Museum of Natural History.

REFERENCES

- ALDRICH, E. C., 1956. Pterylography and molt of the Allen hummingbird. *Condor*, 58: 121-131.
- BAKER, R. R. & PARKER, G. A., 1979. The evolution of bird coloration. *Philosophical Transactions of the Royal Society of London*, 287B: 63-130.
- BALDWIN, S. P., OBERHOLSER, H. C. & WORLEY, L. G., 1931. Measurements in birds. *Scientific Publications of the Cleveland Museum of Natural History*, Vol. 2.
- BARLOW, G. W., 1974. Contrasts in social behaviour between Central American cichlid fishes and coral-reef surgeon fishes. *American Zoologist*, 14: 9-34.

- BENT, A. C., 1939. Life histories of North American woodpeckers. *United States National Museum Bulletin*, 174: 1-334.
- BLEIWEISS, R., 1985. Iridescent polychromatism in a female hummingbird: Is it related to feeding strategies? *Auk*, 102: 701-713.
- BLEIWEISS, R., 1992. Widespread polychromatism in female sunangel hummingbirds (*Heliangelus*: Trochilidae). *Biological Journal of the Linnean Society*, 45: 291-314.
- CODY, M. L., 1969. Convergent characteristics in sympatric populations: a possible relation to interspecific territoriality. *Condor*, 71: 222-239.
- CODY, M. L. & BROWN, J. H., 1970. Character convergence in Mexican finches. *Evolution*, 24: 304-310.
- COOPER, W. E. & VITT, L. J., 1985. Blue tails and autonomy: enhancement of predation avoidance in juvenile skinks. *Zeitschrift für Tierpsychologie*, 70: 265-276.
- DARWIN, C. R., 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- DIXON, W. J., 1983. BMDP-83. *Biomedical Computer Programs P-series*. Berkeley: University of California Press.
- ELGAR, R. J., 1978. Dimorphism in a captive female white-necked jacobin (*Florisuga mellivora*). *Avicultural Magazine*, 84: 147-149.
- EWALD, P. W., 1985. Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Animal Behaviour* 33: 705-719.
- EWALD, P. W. & ROHWER, S., 1980. Age, coloration and dominance in nonbreeding hummingbirds: a test of the asymmetry hypothesis. *Behavioral Ecology and Sociobiology*, 7: 273-279.
- FEINSINGER, P., 1976. Organization of a tropical guild of nectarivorous birds. *Ecological Monographs*, 46: 257-291.
- FEINSINGER, P. & COLWELL, R. K., 1978. Community organization among neotropical nectar-feeding birds. *American Zoologist*, 18: 665-681.
- FEINSINGER, P., COLWELL, R. K., TERBORGH, J. & CHAPLIN, S. B., 1979. Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. *American Naturalist*, 113: 481-497.
- FITZPATRICK, J. W., WILLARD, D. E. & TERBORGH, J. W., 1979. A new hummingbird species from Peru. *Wilson Bulletin*, 91: 177-186.
- GASS, C. L., 1978. Rufous hummingbird feeding territoriality in a suboptimal habitat. *Canadian Journal of Zoology*, 56: 1535-1539.
- GASS, C. L., 1979. Territory regulation, tenure, and migration in rufous hummingbirds. *Canadian Journal of Zoology*, 57: 914-923.
- GASS, C. L., ANGEHR, G. & GENTA, J., 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. *Canadian Journal of Zoology*, 54: 2046-2054.
- GOODWIN, D., 1968. Notes on woodpeckers. *Bulletin of the British Museum (Natural History) Zoology*, 17: 1-44.
- GOULD, S. J. & VRBA, E. S., 1982. Exaptation—a missing term in the science of form. *Paleobiology*, 8: 4-15.
- GREENEWALT, C. H., 1960. *Hummingbirds*. Garden City, New York: Doubleday & Co.
- LORENTZ, K., 1966. *On Aggression*. New York: Harcourt, Brace and World.
- LYON, B. E. & MONTGOMERIE, R. D., 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? *Evolution*, 40: 605-615.
- MARASCUILO, L. A. & LEVIN, J. R., 1983. *Multivariate statistics in the social sciences*. Monterey, California: Brooks/Cole Publishing Co.
- MILLER, R. S. & GASS, C. L., 1985. Survivorship in hummingbirds: is predation important? *Auk*, 102: 175-178.
- MOYNIHAN, M. M., 1979. Geographic variation in social behavior and in adaptations to competition among Andean birds. *Publications of the Nuttall Ornithological Club*. No. 18.
- MYRER, A. A. Jr. & THRESHER, R. E., 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fish. *American Zoologist*, 14: 81-96.
- NOBEL, G. K., 1936. Courtship and sexual selection of the flicker (*Colaptes auratus luteus*). *Auk*, 53: 269-282.
- ORTIZ-CRESPO, F. I., 1972. A new method to separate immature and adult hummingbirds. *Auk*, 89: 851-857.
- PATON, D. C. & COLLINS, B. G., 1989. Bills and tongues of nectar-feeding birds: A review of morphology, function and performance, with intercontinental comparisons. *Australian Journal of Ecology*, 14: 473-506.
- PETERS, J. L., 1945. *Check-list of the Birds of the World, Vol. 5*. Cambridge; Harvard University Press.
- PIMENTEL, R. A. & FREY, D. F., 1978. Multivariate analysis of variance and discriminant analysis. in P. W. Colgan (Ed.), *Quantitative Ethology*: 247-274. New York: John Wiley & Sons.
- ROBERTSON, H. M., 1985. Female dimorphism and mating behavior in a damselfly, *Ischnura ramburi*: Females mimicking males. *Animal Behaviour*, 33: 805-809.
- ROHWER, S., 1982. The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, 22: 531-546.
- SHORT, L. L., 1982. *Woodpeckers of the World*. Delaware Museum of Natural History.
- SLAGSVOLD, T. & LIFJELD, J. T., 1985. Variation in plumage color of the great tit *Parus major* in relation to habitat, season, and food. *Journal of Zoology (London)*, 206A: 321-328.
- SMITHE, F. B., 1975. *Naturalist's Color Guide*. New York: The American Museum of Natural History.
- SNOW, D. W. & SNOW, B. K., 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. *Bulletin of the British Museum (Natural History) Zoology*, 38: 105-139.

- SPSSx., 1988. *Statistical Package for the Social Sciences, SPSSx Inc.*, 3rd edition. New York: McGraw-Hill.
- STILES, F. G., 1972. Age and sex determination in Rufous and Allen Hummingbirds. *Condor*, 74: 25-32.
- STILES, F. G., 1973. Food supply and the annual cycle of the Anna hummingbirds. *University of California Publications in Zoology*, 97: 1-109.
- STILES, F. G., 1982. Aggressive and courtship displays of the male Anna's hummingbird. *Condor*, 84: 208-225.
- STILES, F. G. & WOLF, L. L., 1970. Hummingbird territoriality at a tropical flowering tree. *Auk*, 87: 457-491.
- STILES, F. G. & WOLF, L. L., 1974. A possible circannual molt rhythm in a tropical hummingbird. *American Naturalist*, 108: 341-354.
- STILES, F. G. & WOLF, L. L., 1979. Ecology and evolution of lek mating behavior in the long-tailed hermit hummingbird. *Ornithological Monographs*, No. 27.
- WEST-EBERHARDT, M. J., 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, 58: 155-183.
- WILLIAMS, B. K., 1983. Some observations on the use of discriminant analysis in ecology. *Ecology*, 64: 1283-1291.
- WILLIAMSON, F. S. L., 1956. The molt and testis cycles of the Anna hummingbird. *Condor* 58: 342-366.
- WOLF, L. L., 1969. Female territoriality in a tropical hummingbird. *Auk*, 86: 490-504.
- WOLF, L. L., 1975. Female territoriality in the purple-throated carib. *Auk*, 92: 511-522.
- WOLF, L. L. & STILES, F. G., 1970. Evolution of pair cooperation in a tropical hummingbird. *Evolution*, 24: 759-773.
- WOLF, L. L., STILES, F. G. & HAINSWORTH, F. R., 1976. Ecological organization of a highland tropical hummingbird community. *Journal of Animal Ecology*, 45: 349-379.
- ZIMMER, J. T., 1951. Studies of Peruvian birds. No. 61. The genera *Aglaeactis*, *Lafresnaya*, *Pterophanes*, *Boissonneaua*, *Heliangelus*, *Eriocnemis*, *Haplophaedia*, *Ocreatus*, and *Lesbia*. *American Museum Novitates*, 1540: 55 pp.