Asymmetrical expression of transsexual phenotypes in hummingbirds

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I present evidence for asymmetry in the expression of transsexual traits in adult hummingbirds. Among females, individuals with male-like plumage are common and define a continuous range of variation. Among males, individuals with female-like plumage are rare and define discontinuous plumage morphs. Quantitative characters also distinguish transsexuals from other members of their sex, but the characters involved differ for male-like females (bill length) and female-like males (bill, wing and tail length). Gonadal development is correlated with transsexuality only in males; female-like males have significantly smaller testes than male-like males. Both sexes demonstrate a significant negative association between plumage brightness and bill length. This association suggests an ecological basis for transsexuality because differences in plumage and bill morphology are associated with differences in foraging behaviour within and between hummingbird species. Morphological differences between transsexuals and non-transsexuals imply that plumage sexual dimorphism is more likely to evolve through changes in the frequency of female, rather than male, transsexual variants.

Keywords: asymmetry; hummingbird; plumage coloration; polymorphism; sexual dimorphism; transsexuality

1. INTRODUCTION

Considerable interest has always attended the occurrence of transsexuality in nature because of its potential relevance to humans (Thornhill & Gangestad 1996). 'Transsexual' phenotypes arise when members of one sex express secondary sexual attributes more typical of the other sex, resulting in the occurrence of male-like females (MFs) or female-like males (FMs), in addition to more typical female-like females (FFs) and male-like males (MMs), within the same population (Stamps & Gon 1983; Bleiweiss 1985; Robertson 1985; Gross 1996). An important question about such variation that has not been addressed is whether MFs and FMs are 'equivalent' phenomena; that is, do both transsexual forms resemble members of the opposite sex in the same way? Here, I show that MFs and FMs in hummingbirds are not equivalent in this sense. Rather, both the frequency and the exact form of transsexuals differ between males and females. In hummingbirds, the different transsexual forms are independent of age and can occur within the same interbreeding population, so that growth patterns and phylogenetic influences that might otherwise cause transsexuals to differ are factored out. Thus, the hummingbird example provides particularly convincing evidence for the biological asymmetry of transsexuality.

2. MATERIAL AND METHODS

(a) Scope of the study

Earlier studies of the Andean hummingbird genus *Helianthus* demonstrated that adult females of most species typically vary in their expression of a male-like gorget, with a complete range of variation from non-iridescent (female-like) to fully iridescent (male-like) females (Bleiweiss 1985, 1992a,b, 1994). These studies also found a few (approximately 6 out of 822) specimens with female-like plumage but with small testes noted on the specimen label (see table 4 in Bleiweiss 1992a). To compare

and clarify the apparent variation both within and between the sexes, I augmented my earlier data for *Helianthus* by assessing plumage and morphological variation among adults and immature birds of both sexes in several related Andean 'Brilliant' genera including *Eriocnemis*, *Haplophedra*, *Heliodoxa* (including *Polyplancta*, *Clytolaema*, *Hylonympha*) and *Coeligena* (Gerwin & Zink 1989; Bleiweiss *et al.* 1994, 1997; del Hoyo *et al.* 1999). I examined all specimens in the focal taxa from 15 museum collections (see Acknowledgements for list of museums). To ensure accurate assessment of sex, I characterized variation both for all specimens with sex indicated on the specimen label, and for just those specimens with gonad data. As the two data sets gave qualitatively similar results, I report the more inclusive analyses.

(b) Morphology

Morphology was quantified as before (Bleiweiss 1985, 1992a,b). Plumage variation was summarized by assigning individuals to four exclusive colour classes based on the average number of male-like feathers of the variable trait (usually the gorget) in MMs: class I = 0%; class II $\leq 25\%$; class III $\leq 50\%$; class IV $> 50\%$. Immature birds were distinguished by the presence of striations on their bills (Ortiz-Crespo 1972); these striations gradually disappear with ontogeny and are absent in adults (approximately one year of age and older), thus providing a quantitative scale for assessing the ontogeny of immature plumage (Bleiweiss 1985, 1988, 1992b). All meristic traits were quantified by using a camera lucida to trace and then count the number of elements (feathers or striations; see Bleiweiss (1985) for details).

Measurements of wing (chord of unflattened first primary), bill (culmen from the flange of the nasal operculum) and tail (chord of unflattened fifth rectrix) length were taken on each specimen when possible; I omitted measurements on particular specimens if a feature was obviously in moult, worn or damaged. Data on body mass were not available for many specimens, but linear measurements of the wing and tail lengths are highly correlated with mass (R. Bleiweiss, unpublished data). Therefore, wing and tail measurements are also used as proxy

Table 1. *Presence-absence distribution of transsexual variability among adults by sex across species*

	females ^a	
	not variable	variable
males		
not variable	24 ^b	9 ^c
variable	2 ^d	7 ^e

^a Gorget colours of males and male-like females may differ slightly (in *Heliodoxa branickii*, for example, gorgets are chrome-orange in females versus spectrum red in males).

^b *Haplophaedia aureliae*, *H. lugens*, *Eriocnemis luciani*, *E. glaucopoides*, *E. mosquera*, *E. cupreiventris*, *E. alinae*, *E. mirabilis*, *E. derbyi*, *E. godini*, *E. nigrivestis*, *Heliodoxa xanthogonys*, *H. rubricauda*, *H. imperatrix*, *H. aurescens*, *H. schreibersii*, *H. jacula*, *H. macrocerca*, *Coeligena iris*, *C. phalerata*, *C. helianthea*, *C. prunellei*, *C. wilsoni*, *C. coeligena*.

^c *Helianthus clarisse*, *H. mavors*, *H. micraster*, *H. regalis*, *H. spencei*, *Heliodoxa gularis*, *H. branickii*, *H. rubinoides*, *Coeligena bonapartei*.

^d *Coeligena torquata*, *Heliodoxa leadbeateri* (females differ in the extent of male-like crown iridescence among populations).

^e *Helianthus amethysticollis*, *H. strophanus*, *H. exortis*, *H. viola*, *Eriocnemis vestitus*, *Coeligena lutetiae*, *C. violifer*.

variables for overall size. Colour names follow those provided for standards in Smithe (1975).

(c) Analyses

To detect general characteristics of transsexual phenotypes across all taxa, it was desirable to pool all individuals for most analyses. To remove mean size differences among taxa from these analyses, I first converted size data for each species to standard normal deviates (z -scores of zero mean and unit variance) of $\log_{10}$ measurements, thereby translating data to units of standard deviation. All analyses were conducted in SAS (SAS Institute 1983) for UNIX[®] on a SparcStation 20 (Palo Alto, CA, USA).

3. RESULTS

(a) Survey of variation

My survey of plumage variation among 2252 adult specimens in the focal taxa identified transsexual phenotypes in 18 out of 42 species (tables 1 and 2). All four possible combinations of intraspecific variation in male and female plumage were detected (table 1), including species in which the plumage of either one or both sexes varied within populations. Failure to detect variation in some species may reflect inadequate sampling (rare taxa) or actual absence.

I focus here on species with transsexual variation in one or both sexes (total sample: 1293 adults and 269 immature birds). In these species, the sexes differ significantly in the frequencies of colour classes for both adults ($\chi^2 = 1311.3$, d.f. = 3, $p < 0.0001$) and immature birds ($\chi^2 = 73.34$, d.f. = 3, $p < 0.0001$); data for males and females of these taxa are summarized together (tables 3, 4 and 5) to facilitate comparisons.

(b) Male-like females

Adult MFs were frequent and taxonomically widespread, occurring in 16 out of 42 species (38.1%) across

the taxa examined (table 1 and figure 1). In most cases, the characteristics of MFs conformed to those described in earlier studies of *Helianthus*. Maleness typically varied continuously between the extreme female-like (class I) and male-like (class IV) female morphs. The one variable *Eriocnemis*, *Eriocnemis vestitus*, was atypical because FFs were also iridescent, with glittering yellow-green to golden underparts and a scaly turquoise-blue gorget. However, MFs were identical to males in their more striking iridescent plumage, which included a larger violet gorget, darker green body plumage and a contrasting glittering yellow-green lower back. Across all taxa, iridescent male-like feathers (classes II–IV) were present in 288 out of 548 adult females (52.6%) and the most male-like females (classes III and IV) occurred at moderate to high frequency (34.3% across all taxa), particularly in *Helianthus* and *Heliodoxa*.

Gonadal development did not differ significantly between female plumage variants (table 3). Moreover, immature females expressed the complete range of plumage variation observed in adult females and the differences in colour-class frequencies between adult and immature females were only marginally significant ($\chi^2 = 8.67$, d.f. = 3, $p < 0.05$). The amount of male-like iridescence was not correlated significantly with age (as indexed by the number of bill striations, table 4). Thus, maleness expressed in females was not correlated in any simple way with physiological status or age. On the other hand, extreme female colour classes differed significantly in bill length, reflecting a general pattern for bills to be longer in female-like (I–II) compared with male-like (III–IV) individuals (table 5 and figure 2).

(c) Female-like males

Whereas females vary greatly in their expression of iridescent male-like plumage, the vast majority of adult males were MMs. However, 18 out of 745 sexed adult males from nine (ten if *Coeligena torquata inca* is split from *C. torquata*; del Hoyo *et al.* 1999) species across all taxa were virtually identical in plumage to female-like (class I, rarely class II) females of that species (tables 1 and 2 and figure 1). The disparity in relative frequency of FMFs (classes I and II) compared with MFs (classes III and IV) was striking; FMFs comprised only *ca.* 2% (most species) or 10% (*Coeligena lutetiae*) of adult males, whereas MFs often exceeded 50% of adult females in some species. Both MFs and FMFs may occur in the same population (*Helianthus exortis*, *Helianthus amethysticollis*, *E. vestitus*, *Coeligena violifer*), although the rarity of FMFs may have precluded their detection in all samples (table 1).

The rare FMFs cannot be dismissed as improperly sexed females. Label data for most of the FMFs specifically indicated the presence of testes; for instance, drawings of paired testes accompanied label data for five of these specimens and the presence and dimensions of testes were indicated for eight more (table 2). Gonad data were lacking for FM *C. lutetiae*, for which only sex was indicated on the labels. However, the existence of FMFs was well-supported for two congeners (tables 2). Remarkably, the gonadal development of FMFs appeared to be atypical, as the testes were smaller than those of MMs but similar in size to those of immature males (indicated to be ≤ 1 mm,

Table 2. Sexing data for adult (smooth bills) female-like males

taxon	specimen number ^a	colour ^b	gonads ^c	collection date
<i>Helianthus amethysticollis</i>	ZMK 26.8.83.24	0	testes minute	3 August 1983
<i>Helianthus strophianus</i>	USNM 173977	10	labelled male	July 1898
<i>Helianthus exortis</i>	AMNH 121639	3	testes not enlarged	24 March 1913
<i>Helianthus exortis</i>	AMNH 109494	17	testes not enlarged	10 July 1911
<i>Helianthus viola</i>	AMNH 171120	0	testes not enlarged	5 September 1921
<i>Eriocnemis vestitus</i>	MCZ 298715	46 ^d	testes minute	5 August 1965
<i>Heliodoxa leadbeateri</i>	AMNH 322935	0	testes minute	12 November 1937
<i>Heliodoxa leadbeateri</i>	LSUMZ 87402	0	testes minute	14 June 1978
<i>Coeligena torquata</i>	LSUMZ 91823	0	testes < 1.00 mm	19 October 1979
<i>Coeligena torquata</i>	LSUMZ 91824	0	testes < 1.00 mm	19 October 1979
<i>Coeligena torquata</i>	LSUMZ 95760	0	testes 1 mm × 1 mm	30 May 1980
<i>Coeligena lutetiae</i>	USNM 173690	2	labelled male	December 1898
<i>Coeligena lutetiae</i>	USNM 173702	0	labelled male	July 1898
<i>Coeligena lutetiae</i>	USNM 173701	0	labelled male	July 1898
<i>Coeligena lutetiae</i>	USNM 173717	0	labelled male	February 1898
<i>Coeligena violifer</i>	LSUMZ 87465	0	testes minute	11 September 1978
<i>Coeligena violifer</i>	LSUMZ 113535	3	single testis 0.5 mm × 0.5 mm	25 July 1983
<i>Coeligena violifer</i>	LSUMZ 101788	7	testes 1 mm × 1 mm	29 July 1981

^aAMNH, American Museum of Natural History; LSUMZ, Louisiana State University Museum of Zoology; MCZ, Museum of Comparative Zoology; USNM, United States National Museum; ZMK, Zoologiske Museum, København.

^b Number of glittering male-like feathers.

^c Minute as determined from drawing of paired testes on specimen label.

^d FFs and FMFs have scaly turquoise-blue gorgets.

Table 3. Descriptive statistics for gonad size (largest linear dimension noted on specimen label) across colour classes in females and males of all age classes and species

(Colour classes as defined in § 2(b). All values are given as means ± s.d.; the number of specimens is given in parentheses.)

	gonad dimensions			
	class I	class II	class III	class IV
adults				
females ^a	4.18 ± 1.70 (63)	4.20 ± 1.85 (20)	4.17 ± 1.00 (9)	5.04 ± 2.40 (11)
males ^b	1.00 ± 0.00 (3)	0.75 ± 0.35 (2)	none	2.40 ± 0.67 (126)
immature birds				
females ^c	2.80 ± 1.30 (5)	2.25 ± 0.90 (9)	2.33 ± 0.52 (6)	2.60 ± 0.42 (5)
males ^d	1.00 (1)	1.25 ± 1.06 (2)	1.50 ± 1.17 (5)	0.84 ± 0.39 (24)

^a ANOVA, $F = 0.78$, $p > 0.5$.

^b ANOVA, $F = 12.22$, $p < 0.0001$.

^c ANOVA, $F = 1.80$, $p > 0.17$.

^d ANOVA, $F = 0.53$, $p > 0.66$.

or drawn that small; tables 2 and 3). Adult FMFs had longer bills and shorter wings and tails than adult MMFs; these characteristics are more like those of females, in general, and of FFs in particular (table 5 and figure 2). Among immature birds, the allometry expressed in bivariate plots of either wing or tail on bill length suggests a strong influence of growth on size at this stage of development (figure 2; hence statistical differences between classes were not tested for immature birds). However, both immature and adult FMFs have longer bills than MMFs of similar age (table 5 and figure 2).

FMFs do not appear to be an earlier stage in a plumage ontogeny of MMFs. Iridescent male features develop in immature birds and increase with ontogeny, as assessed as a function either of colour-class frequencies in adults compared with immature birds ($\chi^2 = 155.604$, d.f. = 3, $p < 0.0001$) or of bill striations among immature birds

(negative associations in the largest samples (table 4); see also Bleiweiss 1985, 1992b). Thus, the occurrence of FMFs among immature and adult birds (figure 2) indicates that two distinct ontogenies (MMFs and FMFs) occur in individuals of roughly equal age. There was no evidence that FMFs were moulting into male-like plumage or that they were collected during particular seasons or years (table 2). Their rarity alone suggests that FMFs are not part of the typical male ontogeny.

4. DISCUSSION

The reciprocal expression of transsexual phenotypes in interbreeding hummingbirds (same species and/or population) reveals that the presence or absence, frequency, morphology and physiology of transsexual phenotypes differ between males and females. Moreover, MFs

Table 4. *Ontogeny of male-like iridescence as indicated by association of numbers of iridescent feathers with numbers of bill striations (which decrease with increasing age)*

(Negative associations indicate an increase in iridescent plumage with age. Data are only for taxa with female-like males. n.s., not significant.)

taxon	females			males		
	<i>n</i>	r_s^a	p^b	<i>n</i>	r_s^a	p^b
<i>Helianthus amethysticollis</i>	14	-0.13782	n.s.	34	-0.38881	*
<i>Helianthus strophianus</i>	6	-0.65714	n.s.	11	0.05923	n.s.
<i>Helianthus exortis</i>	23	-0.10557	n.s.	36	-0.46945	**
<i>Helianthus viola</i>	0	—	—	16	-0.13456	n.s.
<i>Eriocnemis vestitus</i>	9	-0.49373	n.s.	18	-0.40538	*
<i>Heliodoxa leadbeateri</i>	0	—	—	6	-0.46382	n.s.
<i>Coeligena lutetiae</i>	12	0.22050	n.s.	12	-0.21518	n.s.
<i>Coeligena violifer</i>	11	0.19263	n.s.	10	-0.56177	*

^a Spearman's rank correlation coefficient.

^b One-tailed significance, * $p < 0.05$, ** $p < 0.01$.

Table 5. *A posteriori contrasts on standardized and transformed morphometric data for adult sex-morph classes pooled across all variable species*

(1, male-like male; 2, female-like male; 3, class I female; 4, class II female; 5, class III female; 6, class IV female. n.s., not significant.)

morph	first primary						culmen from flange						outer tail feather					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
1	—						—						—					
2	*	—					*	—					*	—				
3	*	n.s.	—				*	n.s.	—				*	n.s.	—			
4	*	n.s.	n.s.	—			*	n.s.	n.s.	—			*	n.s.	n.s.	—		
5	*	n.s.	n.s.	n.s.	—		*	n.s.	n.s.	n.s.	—		*	n.s.	n.s.	n.s.	—	
6	*	n.s.	n.s.	n.s.	n.s.	—	*	*	*	n.s.	n.s.	—	*	n.s.	n.s.	n.s.	n.s.	—

* $p < 0.05$ by Tukey's Studentized range test (HSD).

resemble other females more than FMs resemble other males. These findings imply that transsexuality is expressed and controlled differently in males and females. Thus, hummingbirds provide an excellent model for understanding patterns of transsexuality in the animal kingdom, especially in higher vertebrates.

Data presented here and elsewhere (Bleiweiss 1985, 1992a,b) indicate that adult plumage variation cannot be attributed simply to changes in colour and form with age, season or year. For both sexes, immature birds (by gonads and bill striations) express a profile of variation similar to that observed in adults. Thus, intrasexual variation is not defined by age-class structure within populations (contra delayed plumage maturation; Rohwer *et al.* 1980; Hill 1996). FMs could be a rare conditional phenotype in which a few adult males delay the acquisition of iridescent plumage. However, the differences in quantitative characters between MMs and FMs suggest that FMs are rare morphs that retain their distinctive features throughout life. In either case, MFs and FMs differ in many characteristics. Thus, comparisons of MFs and FMs seem justified even if all possible age-related and other facultative changes cannot be ruled out. Here, I examine some of the implications of the hummingbird pattern for birds and for animals generally.

(a) *Proximate mechanism*

The expression of male-like traits in females has often been attributed to a correlated response in females to selection on males because the sexes share most of their genomes. The coincident but asymmetrical expression of transsexual morphs, as documented here, provides several new insights into this hypothesis. First, the existence of transsexual males indicates that a genetic correlation may also produce female-like traits in males. In this regard, however, the genetic-correlation hypothesis predicts that both sexes should express transsexual traits in the same way, through the shared portion of their respective genomes. In the most extreme such case, MFs should be the size and colour of males and FMs the size and colour of females. My evidence that transsexual morphologies are expressed differently in the sexes implies that the unshared portion of the genome also strongly regulates the expression of secondary sexual traits.

For hummingbirds, expression of FMs as discrete plumage morphs suggests that genetic correlations may be stronger when female traits are expressed in males than vice versa. However, the frequency of transsexualism is greater in females than males. These seemingly contradictory properties could occur if transsexuality is controlled, at least in part, by genetic factors located on the sex

Figure 1. Frequency of plumage variants for (a) adults and (b) immatures of the 'Brilliant' taxa examined (variable species only). Plumage classes are defined by the percentage of the mean number of glittering feathers of the adult male-like male feature (class I = 0%; class II $\leq 25\%$; class III $\leq 50\%$; class IV $> 50\%$). In *Eriocnemis vestitus*, adults are assigned only to class I (iridescent female-like) or class IV (iridescent male-like), as described in § 3(b).

chromosomes. Unlike mammals, birds lack dosage compensation (Baverstock *et al.* 1982; Ellegren 2000) and females are the heterogametic sex (ZW). Control of maleness through the dose of Z-linked genes is consistent with the polymorphic expression of transsexual phenotypes in males, which suggests the operation of a threshold mechanism; the karyotypes of FMs would be of great interest in this regard. Nevertheless, some autosomal control of transsexuality in hummingbirds is suggested by the graded expression of male-like plumage in females and by the associations in both sexes between plumage and morphometric variation (see also Hogan-Warburg 1966; Lank *et al.* 1995). Moreover, the smaller testes of FMs implicate hormonal differences as either a cause or an effect of transsexuality (Owens & Short 1995). Such patterns reinforce the general conclusion that both sex-linked and autosomal genetic factors must generate the complicated and asymmetrical patterns of transsexuality observed in hummingbirds.

(b) Ecology

In hummingbirds, several lines of evidence indicate that brighter, more colourful plumages and shorter bills occur in the more dominant species, sex and individual (Wolf 1969, 1975; Ewald & Rohwer 1980; Bleiweiss 1985, 1992a,b, 1999). Plumage–bill covariation appears to result from selection associated with priority of access to nectar, which may require subordinates (individuals, females and species) to evolve duller plumage and longer bills to improve their abilities as exploitation competitors. Transsexual individuals further support and extend this hypothesis because they highlight the same associations between more colourful plumage and shorter bills among adults within either sex (table 5 and figure 1; see also Bleiweiss 1985, 1992b). Moreover, as plumage–bill covariation is independent of body mass (Bleiweiss 1999), the expected differences in feeding ecology should prove robust to considerations of mass-dependent energetic costs of flight and of sexual size dimorphism (Feinsinger & Chaplin 1975; Feinsinger *et al.* 1979; Carpenter *et al.* 1993; Stiles 1995). Remarkably, the pattern of longer bills in FMs compared with those of conspecific females parallels the pattern for males and females in species whose sexes share the same female-like plumage and non-territorial feeding behaviours; the longer male bills in these dull monochromatic species are associated with breeding behaviours that may constrain male priority at nectar sources (Bleiweiss 1999). Thus, some ecological behaviours associated with transsexuality may depend on gender. Whether, in the context of feeding or breeding behaviour, the restriction of small gonads to FMs also suggests that the fitness of a transsexual form depends on the sex in which it occurs.

(c) Evolution

Although male hummingbirds are often brighter than females, the sexes share either dull (female-like) or bright (male-like) plumage in many species (Wolf 1969, 1975; Bleiweiss 1992a, 1999). In principle then, the extent of plumage sexual dimorphism could evolve through shifts in the relative frequencies of different male or female (bright or dull) colour forms (Bleiweiss 1992a). Indeed, the frequency of MFs changes dramatically across the

Figure 2. Mean standardized (z -scores; zero mean and unit variance) $\log_{10}$ -transformed wing length (left) and tail length (right) versus bill length in plumage classes across all variable taxa for (a) adults and (b) immature birds. The ordinate is in standard-deviation units. The few male-like females (three adults) and female-like males (one adult, one immature bird) of *Eriocnemis vestitus* are distinguished because all colour classes in this species have iridescent gorgets, which are more well developed in MMs and MFs (see § 3(b)).

populations of several Brilliant species, reflecting intraspecific shifts between sexually dimorphic and bright monomorphic plumage: *Helianthus* (Bleiweiss 1992a) and *Heliodoxa* (*H. rubinoides* and the allospecies *H. gularis-branickii*; table 6). The occurrence of just the two extreme female colour morphs (classes I and IV) in some populations also appears to arise through changes in the modal distribution of continuous variation (Bleiweiss 1992a). Covariation between plumage coloration and bill length implies that such changes in sexual dichromatism reflect corresponding changes in feeding ecology.

Given that FMs are so rare and have underdeveloped gonads, the evolution of dull monomorphism through fixa-

tion of FMs may be unlikely to occur without substantial additional changes. This inference is consistent with evidence that males of dull monomorphic and bright dimorphic hummingbirds have similar patterns of tail-length sexual dimorphism (Bleiweiss 1999; R. Bleiweiss, unpublished data), whereas fixation of FMs would produce sexual monomorphism for tail length. Thus, the proximate mechanisms leading to evolution of bright and dull monomorphisms in hummingbirds may differ. In turn, these differences in mechanism may eventually help to explain the different contributions that each sex makes to the evolution of sexual dimorphism (Bleiweiss 1992a,b, 1999; Amundsen 2000).

Table 6. Geographical variation in frequency of colour classes leading to shifts in sexual dichromatism

species group	morph			
	class I	class II	class III	class IV
<i>Heliodoxa gularis-branickii</i> superspecies ^a				
<i>H. gularis</i> (eastern Ecuador–Peru)	0	2	8	4
<i>H. branickii</i> (southeastern Peru)	16	1	1	3
<i>H. rubinoides</i> polytypic species				
<i>H. r. rubinoides</i> (Colombia)	0	0	3	3
<i>H. r. cervinigularis</i> (eastern Ecuador–Peru)	1	7	6	3
<i>H. r. aequatorialis</i> (western Ecuador)	10	0	0	1

^a See Gerwin & Zink (1989) for molecular evidence of sister relationship.

5. CONCLUSIONS

The intense intrasexual ecological competition that appears to promote the evolution of transsexuality in Brilliant hummingbirds occurs in many members of the family (reviewed in Bleiweiss 1992b, 1999). Thus, transsexuality is probably widespread in hummingbirds, highlighting the need to characterize intrasexual variation as a component of sexual dimorphism in these birds. Indeed, typological approaches to secondary sexual characteristics may prove biologically unrealistic for any organisms in which similar patterns of strong intrasexual ecological competition exist.

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