

A MORPHOMETRIC EXAMINATION OF SEXUAL DIMORPHISM IN THE *HYLOPHILUS*, *XENOPS*, AND AN *AUTOMOLUS* FROM SOUTHERN VERACRUZ, MEXICO

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Abstract.—Two tropical vireonids (*Hylophilus o. ochraceiceps* and *H. d. "decurtatus"*) and two furnariids (*Xenops minutus mexicanus* and *Automolus ochrolaemus cervinigularis*) were examined using external measurements of museum specimens. All four species are sexually monochromatic. Degrees of sexual dimorphism are described, and discriminant equations are presented as a method for determining the sex of captured birds. Correct use of these equations is discussed. Clues to aging are offered when possible; juvenal plumages are summarized. In all four species males are larger than females in wing and tail lengths, but no significant differences were found in body mass. Tarsus length is longer in male *A. ochrolaemus*, and probably shorter in male *H. ochraceiceps*. Bill length is longer in male *H. decurtatus*. At present there are no functional explanations for the observed dimorphisms. The congeneric vireonids, which show geographic and some habitat overlap, show very little overlap in morphological space.

ESTUDIO MORFOMÉTRICO SOBRE EL DIMORFISMO SEXUAL EN *HYLOPHILUS*, *XENOPS*, Y *AUTOMOLUS* EN EL SUR DE VERACRUZ, MÉXICO

Sinopsis.—Se llevó a cabo un estudio morfométrico de dos especies de vireónidos (*Hylophilus o. ochraceiceps* y *H. d. "decurtatus"*) y de dos de furnáridos (*Xenops minutus mexicanus* y *Automolus ochrolaemus cervinigularis*) al sur de Veracruz, México. Las cuatro especies resultaron ser sexualmente monocromáticas. Se describe el grado de dimorfismo sexual entre las especies y se presenta una ecuación discriminativa que permite identificar el sexo de individuos capturados. Se discute la utilización correcta de la ecuación. En los machos de todas las especies la longitud de las plumas de las alas y la cola resultaron ser de mayor tamaño que en las hembras; aunque no se encontró diferencia significativa en el peso corporal. La longitud del tarso es mayor en los machos de *A. ochrolaemus*, y probablemente más corto en los machos de *H. ochraceiceps*. El pico es más largo en los machos de *H. decurtatus*. Al presente no hay una explicación funcional para el dimorfismo observado en las especies estudiadas. Los vireónidos congénéricos, que muestran solapamiento geográfico y de habitat, muestran muy poco solapamiento en espacio morfológico.

Cryptically dimorphic bird species, those in which the sexes look alike by plumage but show small differences in size and shape, are difficult to study in the field at levels below the population because sex classes are indistinguishable during most of the year. This paper has two goals. The first is to initiate a survey of sexual dimorphism among sexually monochromatic tropical passerines. The second is to provide tropical workers with the best means possible to identify the sex of captured birds for field study (e.g., banding and behavioral studies). Workers in the neotropics lack reliable methods for distinguishing the age and sex of most resident

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species. As current rates of habitat alteration threaten neotropical populations and species, accumulation of accurate data regarding these groups becomes critical. To this end, analysis of museum specimens may prove useful in field studies of living birds. In addition, morphometric analyses may indicate areas where examination of geographic variation might be fruitful. Juvenal plumages are summarized and methods for aging birds are offered where they might be useful. The latter remain tentative pending thorough study of marked birds. All four of the species considered here were recently listed by Ramos (1985) as forest-dwelling species whose populations in Mexico and Central America may be in danger due to deforestation.

METHODS

Our analyses are based on recent series of museum specimens collected in the vicinity of Cerro Balzapote (near Volcán San Martín), Sierra de Los Tuxtlas, Veracruz, Mexico. Specimens were collected in primary rainforest and second growth. For a more thorough description of the habitats in this area, see Ramos and Warner (1980). The Veracruz samples were supplemented with additional material from other localities in Mexico and Central America where noted. We did not use specimens with heavily worn plumage. Sex of specimens was taken directly from labels; in most cases gonad size had been noted. Obviously mis-sexed specimens did not appear in our analyses of these particular samples, although they are often a problem (see Clench 1976). Subspecific names (after Blake 1968; Parkes, *in* Phillips 1991; and Peters 1951) are included to emphasize the importance of considering geographic variation in size when measuring birds in the field. Full consideration of this variability within the subspecies examined is not within the scope of this paper, but we do examine small samples from other geographic localities for some indication of the extent of within-sex differences. Measurements included the lengths of wing chord (unflattened wing), tail, tarsus, bill (from tip to anterior edge of nostril), and length of the eighth primary (P8), with number 10 being the outermost. Measurements were made to the nearest 0.1 mm with vernier calipers following Baldwin *et al.* (1931), except for P8, which was measured to the nearest 0.5 mm using a highly flexible insert (Jenni and Winkler 1989). All measurements were performed by a single observer (GAV). Body mass was determined from specimen labels (when possible).

Discriminant analyses were performed on untransformed data using a stepwise selection for "good" predictor variables through the minimization of Wilks' lambda. Multivariate normality (indirectly) and equality of group covariance matrices were examined using Box's *M*-test (Norušis 1988). Discriminant equations are derived from unstandardized canonical discriminant function coefficients (Norušis 1988:B-7). The ability of these equations to accurately identify males and females is generally reported here as the percent of individuals correctly classified from the sample that generated the discriminant equation. Large numbers of specimens from restricted localities are not yet generally available for neotropical birds,

TABLE 1. Comparative measurements (mm) and body mass (g) of male and female *Hylophilus o. ochraceiceps* from Los Tuxtlas, Veracruz.

	Males (19)			Females (17)			Dimor- phism ¹	F ²	P ²
	\bar{x}	SD	Min.-Max.	\bar{x}	SD	Min.-Max.			
Wing chord	59.5	2.02	(56.0-62.7)	57.4	1.45	(56.4-60.3)	1.04	12.42	0.001
Primary 8	44.3	1.56	(41.5-47.0)	42.7	1.80	(39.0-45.5)	1.04	8.50	0.006
Bill	8.6	0.36	(8.1-9.3)	8.6	0.27	(8.2-9.2)	1.00	0.21	0.653
Tail	46.0	1.90	(42.7-49.5)	44.3	1.50	(42.4-48.6)	1.04	9.17	0.005
Tarsus	17.0	0.54	(16.1-17.9)	17.4	0.62	(16.9-18.7)	0.98	3.88	0.057
Mass ³	11.0	0.95	(9.4-12.8)	10.7	1.06	(9.6-12.7)	1.03	0.76	0.390

¹ Index of dimorphism calculated by dividing mean male value by mean female value.

² Univariate *F*-ratio and corresponding *P*-value, here essentially the results of a two-sample *t*-test (Norušis 1988:B-4). For these tests, *df* = 1, 34.

³ Data from 17 males and 14 females.

preventing a thorough test of the discriminant equations. "Jackknifing" samples, a parametric statistical technique that allows a reduction in bias for estimates of population values (Sokal and Rohlf 1981:795), is another approach for evaluating the discriminating power of discriminant models. By using this technique we were able to make the most use of available specimens and at the same time arrive at a reasonable estimate of how well the final discriminant equations perform (see Norušis 1988:B-12).

SPECIES ACCOUNTS

Vireonidae (10-primaried *Oscines*)

Hylophilus ochraceiceps ochraceiceps (Tawny-crowned Greenlet).—This bird of forest understory is common in the lowland rainforest of S Veracruz. The species is found from SE Mexico to N Bolivia and Amazonian Brazil (American Ornithologists' Union 1983, Ridgely and Tudor 1989). The Andes cause a break in this distribution (Ridgely and Tudor 1989). The subspecies *ochraceiceps* is distributed through the Caribbean slope of SE Mexico and Guatemala, and apparently intergrades with *H. o. pallidipectus* in S Yucatan Peninsula, Belize, and probably N Guatemala (Blake 1968; Parkes, *in* Phillips 1991). Our measurements showed males significantly larger than females in wing, P8, and tail ($P = 0.001-0.006$), and females probably larger than males in tarsus length ($P = 0.057$; Table 1). Discriminant analysis on a sample of 19 males and 17 females from southern Veracruz yielded the equation:

$$D = 0.3407TL + 0.3667WCH - 1.3053BL - 25.6353 \quad (\text{Equation 1})$$

where *D* is the discriminant score, TL is tail length, WCH is wing chord, and BL bill length. When this equation was applied to the sample that generated it, the sexes of 16 males and 14 females (a total of 30 individuals, or 83% of the sample) were correctly classified. Fifteen specimens (12 males, three females) of *H. o. ochraceiceps* from other localities in Mexico (Oaxaca: two males, one female; Chiapas: three males, one fe-

male; Campeche: two males; "Veracruz": two males, one female), and Guatemala (Izabal: three males) were also examined. The ability of Equation 1 to predict the sex of these birds was poor: only nine of 15 were correctly classified (60% of the sample), suggesting geographic variation in size of tail, bill and wing chord lengths. A discriminant analysis of the entire sample (31 males, 20 females) resulted in the following discriminant equation:

$$D = 0.3155TL + 0.3699WCH - 36.0767. \quad (\text{Equation 2})$$

When applied to the sample from which it was generated, this equation had an overall success rate of 72.6%, misclassifying 10 males and four females (misclassified: 25% of Los Tuxtlas birds, 33% of the other 15 individuals). The range of the discriminant scores of the misclassified individuals is broad (-1.9-1.3) in relation to the range of scores of the correctly classified birds (-2.0-2.4), suggesting that confidence can only be placed in the sex of the individuals with the most extreme scores. Assumptions of multivariate normality and equality of covariance matrices do not seem to be violated in the second discriminant analysis (Box's $M = 4.99$, $F = 1.59$, $df = 3$, 73,415, $P = 0.19$), suggesting that geographic variation of wing and tail length in *H. o. ochraceiceps* is not extreme. Despite its limited predictive ability, Equation 2 should have wider geographic applicability than just S Veracruz. Note, however, that the predictive ability of Equation 1 was stronger for the Los Tuxtlas point sample (i.e., there is probably geographic variation in size), and that we had only a very small sample of females from outside of Los Tuxtlas.

A discriminant equation is tailored to be optimal for the sample used to generate it. Misclassification rates, then, are overly optimistic for applications to individuals taken from outside the sample generating the discriminant function. As we saw above, Equation 1, generated from the Los Tuxtlas sample, is hardly useful for specimens taken elsewhere. Given the reality of geographic variability, however, this is not an adequate test of the first discriminant function (Equation 1). An alternate (and more realistic) way to test the efficacy of Equation 1 is to perform a jackknifing procedure (Norusis 1988). In this series of analyses, each analysis excludes one individual; this individual is then classified based on the function generated by the rest of the sample. For *H. o. ochraceiceps* from Los Tuxtlas ($n = 36$), these analyses resulted in the misclassification of nine birds (five males, four females), which gives us a more realistic successful classification rate of 75%.

Descriptions of the juvenal plumage of *H. o. ochraceiceps* (Brodkorb 1943:75) and *H. o. pallidipectus* (Bangs 1907:305) appear similar; Ridgway (1904) did not describe the juvenal plumage of this species. Three specimens in juvenal plumage from Los Tuxtlas (from 16 Aug. 1973) appear to fit Brodkorb's description. Juvenal plumage differs from that of the adult in having cinnamon-buff underparts (uniform to chin; nearest Smithe's [1975, 1981] No. 123A), lighter back and head (Light Raw Umber, No. 23), faint gray under eyes, along cheek and edges of lower man-

dible, and only a slight yellow-green tinge at nares (more green in adult). Wings lack the distinct yellow coloration on the leading edge of the wrist. Skulls become completely ossified, but at least some individuals (second-year [SY] birds only?) can retain skull "windows" into February.

Hylophilus decurtatus "decurtatus" (Lesser Greenlet).—This bird is regular to relatively common in the mid to upper levels of lowland rainforest in S Veracruz, and can be found at lower levels in second growth and edge habitats. The species occurs from E Mexico (SE San Luis Potosi, C Veracruz) south through Central America (along both slopes from Chiapas) through N-central and W Columbia, W Ecuador, and into NW Peru (American Ornithologists' Union 1983, Phillips 1991, Ridgely and Tudor 1989). Our analyses preceded the recognition that *H. d. decurtatus* of Blake (1968) constituted four races (Parkes, in Phillips 1991). Specimens representing three of these races are included in our sample: *H. d. dickermani* (from Los Tuxtlas), *phillipsi* (from Campeche), and Parkes' *decurtatus* (from Guatemala, El Salvador, Costa Rica, and Panama). Parkes noted, however, that size variation was negligible among the four races formerly considered *decurtatus*, a view our analyses support. The subspecies *dickermani* occurs on the Gulf slope of S Mexico (S Veracruz through Tabasco and N Chiapas to W Campeche; see Parkes, in Phillips 1991).

Our total sample of *H. d. "decurtatus"* showed more sexual dimorphism than *H. o. ochraceiceps*, with the sample from Los Tuxtlas (*dickermani*; Table 2) showing no overlap in male and female ranges for measurements of wing chord (WCH), primary eight (P8) and bill (BL). As a result of our limited sample, however, measurement of a single character should probably not be used to sex birds in the field. The tails of females were also significantly shorter ($P < 0.0001$). The sample from southern Veracruz (*H. d. dickermani*; 13 males, six females) yielded the following discriminant equation:

$$D = 0.8945P8 + 3.5022BL - 67.2511 \quad (\text{Equation 3})$$

which accurately sexed 100% of this sample. Our sample of females is small, however. A larger sample of birds from areas in Central America outside of Los Tuxtlas was used to test the success rate of Equation 3. This sample included 16 males (from Campeche, Veracruz, Guatemala [four], El Salvador, Costa Rica [eight], and Panama), and nine females (from Guatemala [two], El Salvador, and Costa Rica [six]). Three of these birds (two males, one female) were misclassified when scored using Equation 3, a success rate of 88%. The complete sample ($n = 44$; 29 males and 15 females) yielded the discriminant equation

$$D = 0.5067WCH + 0.3688TS + 0.8757BL - 41.3851 \quad (\text{Equation 4})$$

where WCH is wing chord, TS is tarsus, and BL is bill length. Using this equation, one male from Guatemala (Parkes' *decurtatus* by distribution) was misclassified, yielding an overall success rate from this sample of 97.7%. The assumptions of the test (equality of group covariance matrices) are violated in this analysis (Box's $M = 19.75$, $F = 2.99$, $df = 6$,

TABLE 2. Comparative measurements (mm) and body mass (g) of male and female *Hylophilus d. dickermani* from Los Tuxtlas, Veracruz.

	Males (13)			Females (6)			Dimor- phism ¹	<i>F</i> ²	<i>P</i> ²
	\bar{x}	SD	Min.–Max.	\bar{x}	SD	Min.–Max.			
Wing chord	56.5	1.29	(54.6–58.6)	52.1	0.52	(51.2–52.7)	1.08		***
Primary 8	43.7	1.32	(42.0–46.0)	39.9	0.80	(39.0–41.0)	1.09		***
Bill	8.5	0.30	(8.2–9.1)	8.0	0.11	(7.8–8.1)	1.06		***
Tail	40.8	1.54	(38.0–42.9)	37.0	1.08	(36.4–38.6)	1.10	29.91	<0.0001
Tarsus	16.9	0.74	(15.9–18.8)	16.7	0.42	(16.3–17.3)	1.01	0.19	0.67
Mass ⁴	9.0	0.61	(8.0–9.9)	9.0	0.63	(8.5–10.2)	1.00	0.01	0.93

¹ Index of dimorphism calculated by dividing mean male value by mean female value.

² Univariate *F*-ratio and corresponding *P*-value, here essentially the results of a two-sample *t*-test (Norušis 1988:B-4). For these tests, *df* = 1, 17.

³ No overlap in the ranges of male and female values for this character.

⁴ Data from 12 males and 5 females.

5213.9, *P* = 0.006), suggesting that geographic variability exists in this broad sample. We suggest, then, that this equation is probably not as useful as simply making a scatter plot of WCH versus BL from any point sample for which sex information is desired. Alternatively, measurements of P8, WCH, and BL can probably be compared to the ranges of our sample to identify sex with great accuracy. This suggestion presumes that male and female size will covary geographically (such that the degree of dimorphism in these characters remains roughly the same). Such covariation seems to occur in at least some avian species (e.g., *Bubo virginianus*, McGillivray 1989; *Geospiza* spp., Price 1984; *Tyrannus tyrannus*, Van Wynsbeghe et al. 1992).

Although Ridgway (1904:217) described the juvenal plumage of this species, we re-examined a single male *H. d. decurtatus* in juvenal plumage (U.S. National Museum [USNM] 34673, Angostura, Costa Rica, 12 Jun. 1864) for this paper. In the juvenal plumage the crown and hindneck are a rather drab, olive brown (between Smithe's [1975, 1981] No. 27 and 28), rather than mouse or slate gray as in the adult. The remaining dorsal body surface is browner than in the adult, washed with the same color that is in crown. The underparts are white (much more than in adult), although flanks and sides show a tinge of grayish and traces of yellow-olive. Under-tail coverts are light olive-yellow, as opposed to sulphur yellow in the adult. Although the skull becomes completely ossified in this species, the precise timing of ossification is unknown.

Furnariidae (10 *Primaries*, *Suboscines*)

Xenops minutus mexicanus (Plain *Xenops*).—This species is uncommon to regular in S Veracruz, where it is found in the mid to upper levels of lowland rainforest, or, less commonly, at lower levels in edge habitats and second growth near rainforest. The species has a broad distribution, occurring in wooded areas on the Gulf and Caribbean slopes of Mexico and

TABLE 3. Comparative measurements (mm) and body mass (g) of male and female *Xenops minutus* from Mexico and Central America.

	Males (20)			Females (11)			Dimor- phism ¹	F ²	P ²
	\bar{x}	SD	Min.-Max.	\bar{x}	SD	Min.-Max.			
Wing chord	64.5	1.62	(61.4-67.0)	60.3	0.97	(58.7-62.0)	1.07	62.69	<0.0001
Primary 8	47.7	1.51	(45.0-50.0)	43.6	0.97	(42.0-45.0)	1.09	66.81	<0.0001
Bill	9.9	0.33	(9.3-10.5)	9.9	0.44	(9.1-10.5)	1.01	0.25	0.62
Tail	50.9	2.10	(47.2-55.3)	46.7	1.03	(44.5-48.2)	1.09	39.79	<0.0001
Tarsus	14.2	0.59	(13.4-15.7)	14.1	0.39	(13.3-14.6)	1.01	0.97	0.33
Mass ³	11.2	0.86	(10.4-11.9)	11.0	0.68	(9.8-12.4)	1.01	0.07	0.80

¹ Index of dimorphism calculated by dividing mean male value by mean female value.

² Univariate *F*-ratio and corresponding *P*-value, here essentially the results of a two-sample *t*-test (Norušis 1988:B-4). For these tests, *df* = 1, 29.

³ Data from Los Tuxtlas specimens: 15 males and 4 females.

Central America south to Nicaragua, then on both slopes into South America (American Ornithologists' Union 1983), where it is widespread to E Peru, C Bolivia, and N-central Brazil, with a disjunct population occurring along the Atlantic slope of E Brazil southwest to S Paraguay (Dunning 1987). The subspecies *mexicanus* occurs in the humid tropics of S Mexico (Veracruz, Oaxaca, Chiapas, Tabasco, Campeche, Yucatán and Quintana Roo), and in Guatemala, Belize and Honduras (Peters 1951). Our sample of *X. m. mexicanus* (*n* = 31) is composed of specimens from Guatemala (Izabal: two females) and Mexico: Veracruz (Los Tuxtlas: 15 males, five females), Campeche (Pacaitun: three males, two females), and Oaxaca (Futla: two males, two females).

Discriminant analyses suggest that geographic variability within *mexicanus* is minor (e.g., for the Los Tuxtlas sample, Box's *M* = 1.21, *F* = 1.11, *df* = 1, 382, *P* = 0.29; for the total sample, Box's *M* = 4.70, *F* = 1.43, *df* = 1, 11,376, *P* = 0.23). As a result, we include the complete sample in further discussion and in Table 3. Although lengths of wing chord, tail, and P8 showed significant differences between the sexes (*P* < 0.0001; Table 3), discriminant analysis selected P8 as the best discriminating variable. The equation

$$D = 0.7422P8 - 34.3322 \quad (\text{Equation 5})$$

where P8 is the length of primary eight, correctly classified 90.3% of the sample used to generate it. A jackknifing procedure, wherein a series of 31 discriminant analyses were performed (see discussion under *Hylophilus o. ochraceiceps*), yielded the same success rate (90.3%), with three males misclassified. Analogous results between the two categorization procedures are probably caused by the fact that only one character is used in the discriminant models. The same three males were misclassified in all cases. As individuals of this species can be sexed relatively easily using a single character, a procedure such as that outlined by Mewaldt and King

(1986) might prove very effective for determining the sex ratio of large samples.

The juvenal plumage in this species is apparently similar to that of the adult (Ridgway 1911:173). We have not seen specimens in complete juvenal plumage. One female *X. m. ridgwayi* (USNM 485830, Panama, El Volcán, 16 Mar. 1965) in first prebasic molt appears a bit yellower (Smithe's [1975, 1981] No. 53-153) on the wrist and lower neck/upper breast areas than does the adult. It is also duller and less rufescent on the back. For in-hand identification purposes, the juvenal plumage includes the white malar streak of the adult, as well as the distinctive wing and tail patterns (although bill shape alone should enable relatively easy identification). Skulls become completely ossified, but some individuals (probably second-year [SY] birds) retain unossified "windows" at least until May.

Automolus ochrolaemus cervinigularis (*Buff-throated Foliage-gleaner*).—This species of forest understory has a range similar to that of *Xenops minutus* in Mexico and Central America (American Ornithologists' Union 1983). In South America its range is also similar to that of *Xenops minutus*, except that it is absent from SE Brazil and much of the Atlantic slope of Venezuela and Colombia (Dunning 1987). The subspecies *cervinigularis* is found in S Mexico (Veracruz, Oaxaca, Tabasco and Chiapas), W Belize, NW Honduras and Nicaragua (Peters 1951).

Our sample of 33 birds is composed of specimens from El Salvador (one of each sex), Nicaragua (one female) and Mexico: Veracruz (nine males, 12 females), Oaxaca (one male, three females) and Chiapas (three males, two females). Sexual dimorphism in this species is significant in

TABLE 4. Comparative measurements (mm) and body mass (g) of male and female *Automolus ochrolaemus cervinigularis* from Mexico and Central America.

	Males (14)			Females (19)			Di- morph- ism ¹	F ²	P ²
	\bar{x}	SD	Min.–Max.	\bar{x}	SD	Min.–Max.			
Wing chord	91.1	2.83	(87.8–96.9)	87.8	2.32	(84.4–92.5)	1.04	13.34	0.001
Primary 8 ³	64.4	2.29	(61.5–68.0)	62.0	2.18	(56.5–64.5)	1.04	5.14	0.038
Bill ¹	17.4	0.82	(15.6–19.1)	17.3	0.84	(15.6–18.7)	1.00	0.00	0.944
Tail	76.7	1.91	(73.0–79.5)	73.0	3.08	(67.5–79.0)	1.05	15.73	0.0004
Tarsus	24.9	0.87	(23.1–26.5)	23.6	0.79	(22.2–24.7)	1.05	19.63	0.0001
Mass ³	48.1	5.20	(40.8–57.8)	45.5	5.17	(40.1–56.5)	1.06	1.20	0.289

¹ Index of dimorphism calculated by dividing mean male value by mean female value.

² Univariate *F*-ratio and corresponding *P*-value, here essentially the results of a two-sample *t*-test (Norušis 1988:B-4). For these tests, *df* = 1, 31.

³ These values are from the Los Tuxtlas, Veracruz portion of sample (nine males, nine females).

⁴ Bill length in the Los Tuxtlas population (nine males, nine females) shows more dimorphism. For males, \bar{x} = 17.3 mm (SD = 2.29), and for females \bar{x} = 18.0 mm (SD = 2.18; *F* = 3.10, *df* = 1, 16, *P* = 0.097).

tail, wing chord, tarsus and P8 ($P = 0.0001$ – 0.038 ; Table 4). In a discriminant analysis of the full sample (14 males, 19 females), the equation

$$D = 0.2356TL + 0.8691TS - 38.5904 \quad (\text{Equation 6})$$

(where TL is tail and TS tarsus length), correctly categorized 81.8% of the birds (two males and four females were misclassified). The assumption of multivariate normality was not violated (Box's $M = 4.07$, $F = 1.26$, $df = 3$, 125,014, $P = 0.29$), suggesting that geographic variation in tail and tarsus is not pronounced in this sample. A separate analysis of the 18 individuals from Los Tuxtlas (nine males, nine females) resulted in the equation

$$D = 0.4862TL + 0.9473TS - 1.1516BL - 39.0554 \quad (\text{Equation 7})$$

(where BL is bill length), which successfully categorized 94.4% of the sample used to generate it (Los Tuxtlas birds; one female misclassified) and 78.6% of the 14 remaining, geographically more widespread individuals (three females misclassified). The inclusion of bill length in Equation 7 is a consequence of the greater degree of dimorphism for this character exhibited by the Los Tuxtlas population, a difference that is not apparent in the broader geographic sample (Table 4). Testing the efficacy of these two equations by jackknifing showed that both give similar results. A jackknife analysis of all 33 birds (33 discriminant analyses on 32 birds each) resulted in the misclassification of six individuals, yielding an 81.8% success rate, the same result as with the single, full-sample discriminant analysis (Equation 6). As with *Xenops minutus*, these analogous results are explained by the use of few characters in the discriminant equation. A similar jackknife examination of the Los Tuxtlas sample (18 discriminant analyses on 17 birds each) resulted in the misclassification of three birds (one male and two females; an 83.3% success rate). Thus, the use of a third character (bill; Equation 7) is not warranted unless one is examining birds from Los Tuxtlas.

The juvenal plumage of this species is apparently similar in coloration to that of the adult (Ridgway 1911:217). We did not examine a specimen in complete juvenal plumage, but note that a young male *cervinigularis* (USNM 302,709, Oaxaca, Mexico, 29 Jul. 1967) in first prebasic molt displayed some dorsal juvenal feathers much lighter than in the adult. "Downy," or loosely structured, juvenal-type undertail coverts may be retained until well after the attainment of first basic plumage on the rest of the body. Breast "scalloping" decreases with plumage wear. Angle of outer rectrix tip is probably a useful aging criterion (for measuring this character, see Collier and Wallace 1989), but must be confirmed with marked birds. Skulls become completely ossified, but the rate of ossification is unknown.

Comparison of the Two Hylophilus

The congeneric greenlets (*H. decurtatus* and *H. ochraceiceps*) are sympatric through much of their ranges, and show some overlap in micro-

habitat use in the rainforest of southern Veracruz (Los Tuxtlas; KW, pers. obs.). This sympatry suggests that they occupy different ecological niches, and it might be predicted that they differ morphologically. Indeed, this is the case. Our samples of the two species from Los Tuxtlas (36 *ochraceiceps*, 19 *decurtatus*) show very little overlap in morphological space. In the characters wing chord, tail, tarsus, and bill lengths, *ochraceiceps* is significantly larger than *decurtatus* ($F > 4.5$, $df = 1, 53$, $P < 0.04$, univariate F -ratio). In the length of P8 the two species are also nearly significantly different at the $\alpha = 0.05$ level ($F = 3.7$, $df = 1, 53$, $P = 0.059$). In a discriminant analysis of these birds (using direct, rather than stepwise inclusion of variables), group centroids were 3.6 standard deviations apart in discriminant space, an overlap between the two species of about 3.6% each. Two individuals were misclassified (a success rate of 96.4%, as predicted by examination of group centroids), one male *decurtatus* and one female *ochraceiceps*. The smallest *ochraceiceps* females thus appear to overlap to some degree the morphological space occupied by the largest male *decurtatus*. The overlap is small, however.

DISCUSSION

The data sets of Ridgway (1904, 1911) notwithstanding, our data constitute the first detailed examination of sexual dimorphism that we know of in the species considered. All four of these species are cryptically dimorphic, with males tending to be larger than females. Of the measured characters, wing chord, P8 and tail were significantly larger in males of all four species; tarsus length was significantly longer in male *A. ochrolaemus cervinigularis*, but is probably shorter in male *H. o. ochraceiceps*. Bill length was significantly longer in male *H. d. decurtatus*, and mass was not significantly different between the sexes of any of the four species (Tables 1-4).

Sexual size dimorphism may be present due to selective pressures corresponding to sexual or natural selection (e.g., Jehl and Murray 1989, Johnston and Selander 1973, Price 1984). Ralls (1977) and Price (1984) suggested that an advantage to large males due to sexual selection and a reproductive advantage to small females could produce and maintain sexual dimorphism. Insofar as all four of the species considered here have larger males, either or both of these selective pressures could be operating in these species. In the absence of plumage dimorphism, however, it might be presumed that sexual selection has a relatively minor influence on the body plan of these species. Although we found no significant differences between the sexes in body mass, our samples were relatively small, and with larger samples differences may be found in this parameter (e.g., Tables 1 and 4).

A brief review of the known life histories of these four presumably monogamous species gives little insight to potential environmental factors causing or maintaining the dimorphisms observed. In *H. ochraceiceps*, both parents feed the young, but only one parent (sex unknown) was found brooding (Skutch 1960). In *H. decurtatus*, females finish the nest

(at least), incubate, and brood the young. Males may assist with brooding and do assist in feeding the young. Skutch (1960:29) had one observation that suggested they remained paired in December. Males of these *Hylophilus* species are unlikely to incubate (Skutch 1960). Skutch (1969) found *Automolus ochrolaemus* in pairs at all seasons. The sexes apparently share in the digging of the nest burrow, incubation, and feeding and brooding of the young. In *Xenops minutus*, Skutch (1969) found that although sometimes going in pairs, they were more often alone or with mixed-species flocks. Both members of the pair will excavate the nest hole if they do not use an already existing hole. Both sexes also participate in lining the nest hole, incubating, and in feeding the young. In all four species the female sings, although in *H. decurtatus* female song is shorter than that of the male, and this statement needs verification in *H. ochraceiceps*. Skutch (1960, 1969) felt that in *ochraceiceps* "song" consisted solely of their common, nasal call notes. Ridgely and Tudor (1989:160) noted that the presumed song ("a loud, clear, penetrating 'tee-yeeé'") is heard much less frequently than the call.

There appears to be no pattern between these life history observations and the observed dimorphisms. How the latter might be related to sexually different behaviors and/or uses of the environment must await further study.

Some qualifications for our morphometric analyses are required. For one, data from museum specimens are a potential source of error. It is well known that specimen labels can be wrong with regard to the sex of the individual (e.g., Clench 1976). We did not directly inspect the gonads of the measured birds, and thus do not know whether our sample included mis-sexed individuals. Further, museum specimens shrink when they dry. Although this is unlikely to affect an examination of sexual dimorphism, it will affect the application of museum-derived mensural data to living (or freshly dead) birds. For this reason it is important to apply a correction factor to measurements of live birds (excluding P8, which does not show significant shrinkage; see Jenni and Winkler 1989) before using the discriminant equations presented here (Winker 1993). Although shrinkage has not been examined in the taxa considered here, living measurements in these four species might be multiplied by correction factors averaged from other studies of shrinkage: wing chord (0.983), tail (0.988), bill (0.989) and tarsus (0.976). These correction factors are crude, but nothing better can be done until more data on shrinkage become available (see Winker 1993).

Another factor that probably obscures the true degree of sexual dimorphism in the species considered here is the fact that first-year individuals tend to be smaller in wing length (at least) than adults (e.g., Alatalo et al. 1984). By not being able to recognize age classes in these four species, the necessary inclusion of all age classes in the analyses causes age-related size differences (if they occur here) to cloud purely sexual differences within age classes. From the practical perspective, this lowers the classificatory power of the resultant discriminant equations if these

equations include components showing significant between-age-class variability (Winker, unpubl. data).

How should one use the discriminant equations?—First, these discriminant analyses allow us to “discover” which mensural features give the most power in separating the sexes. These are the measurements that should be taken in the field. To minimize between-investigator variability, measurements of a particular species should be made by the same person. Very worn or molting feathers should not be measured. To determine the approximate sexual structure of a sample, the investigator may wish to use a “powerful” morphological character (or characters; see separate discriminant equations and data in Tables 1–4) in conjunction with a technique such as that outlined by Mewaldt and King (1986; cf. Mueller 1990). Identifying the sex of an individual is best done using the discriminant equations.

An individual bird receives a discriminant score (*D*-value) when the appropriate equation is solved for its particular character values (adjusted for museum shrinkage if needed; see Winker 1993). Extreme *D*-values typify individuals that can be confidently classified as male (high positive values) or female (low negative values). Many individuals will have *D*-values that are intermediate, however, and for these (at least) one should calculate the probability that a particular individual is male.

The statistical software used to generate Equations 1–7 calculates probabilities of group membership based on Bayes’ theorem (Norušis 1988:B-8; however, the theorem is incorrect as printed; see Tatsuoka 1971). Although this technique is powerful, it is difficult to apply. A simpler method (Green and Theobald 1989) calculates the probability of an individual being male as:

$$(1 + e^{-D})^{-1} \quad (\text{Equation 8})$$

where *D* is the discriminant score of the individual of interest and *e* is the constant approximately equal to 2.7182818. This formula has the advantage of being easily solved with a hand calculator or computer spreadsheet, but has the disadvantage of being less powerful than the application of Bayes’ theorem. For example, using Equation 8 rather than Bayes’ theorem causes one more individual to be misclassified in the sample associated with Equation 6 above. Unlike Equation 8, Bayes’ theorem takes into account other information about the sample used to generate the discriminant equation, notably, the sex ratio of that sample and the distributions of its discriminant scores. Nevertheless, the computational difficulties associated with using Bayes’ theorem put it out of reach for most. Modifying Equation 8, however, can give the user an equation for calculating probabilities nearly as powerful as Bayes’ theorem, yet still relatively easy to solve. For discriminant Equations 1, 2, 4, 5 and 6, we recommend that the probability that an individual is male (p_m) be calculated as follows:

$$p_m = (1 + e^q)^{-1} \quad (\text{Equation 9})$$

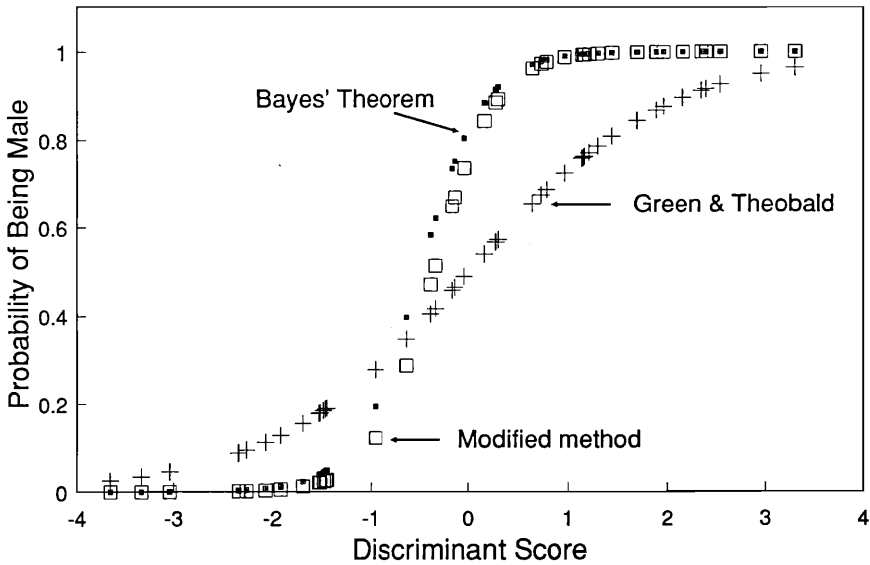


FIGURE 1. The probability that an individual *Hylophilus d. "decurtatus"* is male, based on its discriminant score from Equation 4, as calculated using three different techniques.

where r is the sex ratio of the sample generating the discriminant equation and

$$q = -D_a \times [1 + |\ln(r^4)|] - [r \times \ln(r)]. \quad (\text{Equation 10})$$

In Equation 10 D_a is the discriminant score of individual a . Disregarding the sex ratio of a sample and the distribution of its discriminant scores results in a conservative distribution of calculated probabilities (Fig. 1, "Green and Theobald"). The application of the modification (Equations 9 and 10) is crude and unorthodox, but effective when used with the discriminant functions noted above (e.g., Fig. 1). For Equations 3 and 7 this modification does not improve the classification results obtained by using Equation 8 without modification. A nearly perfect duplication of the Bayes' probabilities for Equation 3 can be achieved by using Equation 9 with $q = -D_a \times 3$, but the use of Equation 3 is discouraged, because it is likely that simply plotting WCH versus BL will accurately sex any sample of *H. decurtatus* (see above). The general modification (Equation 9) is at its poorest for small negative discriminant scores (e.g., Fig. 1), but no method will be able to resolve the sex of these individuals with a high probability of classification.

The use of Bayes' theorem and of the proposed general modification (Equations 9 and 10) to the equation proposed by Green and Theobald (1989; Equation 8) assumes that the sex ratios of the analyzed samples represent those to be found in natural populations. The vast majority of

TABLE 5. Statistics for the discriminant scores generated by Equations 1-7.

Species	Sex	Equation	n	Mean	SE	Min.-Max.	95% CI ¹	Eigenvalue ²
<i>Hylophilus o. ochraceiceps</i>	Males	1	19	0.67	0.25	-1.71-2.47	-1.44-2.78	0.534
	Females	1	17	-0.75	0.22	-1.86-1.51	-2.49-0.99	0.534
<i>Hylophilus d. dickermanni</i>	Males	2	31	0.57	0.20	-1.89-2.45	-1.61-2.75	0.527
	Females	2	20	-0.89	0.18	-1.98-1.32	-2.45-0.67	0.527
<i>Hylophilus d. decurtatus</i>	Males	3	13	1.63	0.29	-0.69-2.58	-0.37-3.63	6.418
	Females	3	6	-3.53	0.36	-4.35--2.21	-5.16--1.90	6.418
<i>Xenops minutus mexicanus</i>	Males	4	29	1.06	0.20	-0.95-3.29	-1.07-3.19	2.274
	Females	4	15	-2.05	0.21	-3.66--0.63	-3.61--0.48	2.274
<i>Automolus ochrolaemus</i>	Males	5	20	1.09	0.25	-0.93-2.78	-1.09-3.27	2.304
	Females	5	11	-1.98	0.22	-3.16--0.93	-3.35--0.61	2.304
<i>ceruinigularis</i>	Males	6	14	1.15	0.22	-0.72-2.46	-0.45-2.74	1.031
	Females	6	19	-0.84	0.25	-3.13-1.32	-3.00-1.31	1.031
	Males	7	9	1.51	0.25	0.12-2.79	0.07-2.95	2.558
	Females	7	9	-1.51	0.40	-2.85-0.73	-3.75-0.74	2.558

¹ 95% Confidence interval; mean \pm 2 SD, where SD is that of the population.

² This eigenvalue is the ratio of between-groups to within-groups sums of squares. Generally, the larger the value, the better the discriminant function.

the specimens from southern Veracruz (Los Tuxtlas) were obtained through long-term mist netting, primarily from September through May. The sex ratios of these samples may be representative of the ratios that will be encountered by field workers using mist nets during this period of the year. If these samples do not represent sex ratios found in the field, sex ratios used in Equation 9 can be changed. Changes made in the direction of unity will be more conservative in assigning probabilities. Workers should be aware of possible seasonal and effort-related changes in the sexual structure of samples (e.g., Graves et al. 1983). This area needs further investigation.

An example of using the guidelines presented here might be useful. Suppose that we have captured an individual *Hylophilus ochraceiceps* in southern Veracruz. Equation 1 has the most predictive power for this locality, so we choose to measure the following three body components: TL = 45.5, WCH = 56.9, and BL = 8.9 (all in mm). As all three factors have been found to shrink in museum specimens, we choose to adjust these values before using Equation 1 by applying the correction factors suggested above: (TL = 45.5×0.988 , WCH = 56.9×0.983 , BL = 8.9×0.989). We then solve for Equation 1 to get this individual's D score:

$$D = 0.3407(45.0) + 0.3667(55.9) - 1.3053(8.8) - 25.6353 = -1.2919.$$

Although the negative value suggests this bird is female, males have shown values of this magnitude (Table 5), so we calculate the probability of its being female by first calculating the probability that it is male. To do this, we first solve Equation 10, retrieving the value for the sex ratio found in this region (r) from Table 1: $q = 1.2919 \times [1 + |\ln(1.118^4)|] - [(1.118 \times \ln(1.118))] = 1.7436$. We next solve Equation 9: $p_m = (1 + e^{1.7436})^{-1} = 0.149$. This bird has a 14.9% chance of being male. Its probability of being female (p_f) is $1 - p_m = 0.851$, or 85.1%. If this same individual had been captured in Nicaragua, we would have chosen to use Equation 2. To reduce the probability of error, for large samples we suggest the use of a computer spreadsheet to calculate D -values.

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JOINT MEETING**

The Association of Field Ornithologists and the Federation of New York State Bird Clubs will hold a joint meeting at the Williams Lake Hotel, Rosendale, New York on 23–25 Sep. 1994. The program will include a symposium on owls. Abstracts for the paper session should be sent to Dr. Valerie Freer, Science Department, Sullivan County Community College, Loch Sheldrake, NY 12759.