## SEXUAL SIZE DIMORPHISM IN BIRDS FROM SOUTHERN VERACRUZ, MEXICO. II. THRYOTHORUS MACULIPECTUS AND HENICORHINA [LEUCOSTICTA] PROSTHELEUCA

### KEVIN WINKER<sup>1</sup>

Conservation & Research Center, NZP, Smithsonian Institution, Front Royal, Virginia 22630 USA

## JOHN T. KLICKA

Bell Museum of Natural History, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, Minnesota 55108 USA

## GARY VOELKER

Burke Museum, DB-10, University of Washington, Seattle, Washington 98195 USA

Abstract.—Two monochromatic tropical wrens (*Thryothorus maculipectus* and *Henicorhina* [*leucosticta*] prostheleuca) were examined using external measurements of museum specimens. Although the sexes show overlap in all measured characters, males were larger than females on average. Degrees of dimorphism are described, and discriminant equations are presented as a method for identifying the sex of individuals. The success of these equations for sexing jackknifed samples varies from 93–97%. Clues to aging are offered and juvenal plumages are summarized. Recognition of the retention of some juvenal plumage well into adulthood in *H. "L" prostheleuca* raises questions of species limits in Middle American groups of *H. "leucosticta.*"

#### DIMORFISMO SEXUAL EN EL TAMAÑO DE AVES DEL SUR DE VERACRUZ, MEXICO. II. *THRYOTHORUS MACULIPECTUS* Y *HENICORHINA [LEUCOSTICTA] PROSTHELEUCA*

Sinopsis.—Se examinaron dos especies monocromáticas (*Thryothorus maculipectus y Henicorhina [leucosticta] prostheleuca*) usando medidas externas de especímenes de museo. Aunque los sexos muestran sobrelapamiento en todas los caracteres medidos, por lo general los machos eran más grandes que las hembras. Se describen grados de dimorfismo y se presentan ecuaciones discriminantes para identificar el sexo de individuos. El éxito de estas ecuaciones para identificar el sexo de muestras seleccionadas por el método "jackknife" fluctúa entre un 93–97%. Se ofrecen indicios para determinar edades y se resumen los plumajes juveniles. Al reconocer la retención de algún plumaje juvenil en la adultez avanzada de H. "*l.*" *prostheleuca* levanta preguntas sobre los límites de especies en grupos mesoamericanos de H. "*leucosticta.*"

Sexually monochromatic bird species, those in which the sexes look alike by plumage, are difficult to study intensively in the field because the sexes are indistinguishable during much of the year. This is our second in a series of papers examining sexual dimorphism in monochromatic

<sup>1</sup> Current address: Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 USA. neotropical passerines and providing field workers with guidelines to identify the sex of captured birds for field study. Neotropical field workers lack reliable methods for distinguishing the age and sex of most resident species. We summarize juvenal plumages and offer methods for aging birds where they might be useful. The latter remain tentative pending thorough study of marked birds and/or the accumulation of more modern museum material. Our reports will also be useful for museum workers, who are frequently confronted with old specimens whose utility is limited because they possess few or no data. In addition, morphometric analyses can indicate areas where examination of geographic variation might be fruitful.

As current rates of habitat alteration threaten neotropical birds, accumulation of data regarding these groups becomes critical. Analyses of museum specimens can be useful for field studies of living birds, and field workers should be encouraged to contribute to this important database by preserving voucher specimens.

### METHODS

Our analyses are based on series of museum specimens collected in the 1970's in the vicinity of Cerro Balzapote (near Volcán San Martin), Sierra de los Tuxtlas, Veracruz, Mexico (18°30'N, 95°W). 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 samples from Los Tuxtlas were supplemented where noted with additional material from other localities in Mexico and Central America. 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. Errors in sexing did occur among the specimens measured (apparent through our analyses; see below), and these are often a problem (Clench 1976).

Subspecific names are used to emphasize the importance of considering geographic variation in size when measuring birds in the field or museum. 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 usefulness of the discriminant equations beyond our more concentrated samples. This approach also enables a crude examination of the degree of geographic variation in the taxa considered. Measurements included the lengths of wing chord (unflattened wing), tail, tarsus, bill (from tip to anterior edge of nostril), gonys, 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 wing and tail (measured to nearest 0.5 mm using vernier calipers), and P8 (measured to the nearest 0.5 mm using a highly flexible insert after Jenni and Winkler 1989). All measurements were performed by a single observer (ITK). Body mass was taken from specimen labels

where available. Specimens with missing values (not including mass) were not used in analyses where the missing values were required.

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 were derived from unstandardized canonical discriminant function coefficients (Norušis 1988:B-7). The ability of these equations to identify males and females accurately is 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, preventing a thorough test of the discriminant equations. "Jackknifing" samples, a parametric statistical technique allowing a reduction in bias for estimates of population values (Sokal and Rohlf 1981:795), is another approach for evaluating the separating power of discriminant models. By using this technique we were able to make the greatest 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

Thryothorus maculipectus maculipectus (Spot-breasted Wren).—This species is found in thick cover in many wooded habitats (though uncommon in forest interior), more commonly in lowlands. Activity is mostly within 2 m of the ground, but individuals and pairs will ascend thick vine tangles into 15+ m canopy when foraging. The species ranges from southern Nuevo León and central Tamaulipas south and east along the Gulf and Caribbean slopes through Middle America to northern Costa Rica (American Ornithologists' Union 1983, Phillips 1986). The nominate race occurs from southern Veracruz south and east to central Tabasco (Phillips 1986).

The first analysis of specimens from Los Tuxtlas revealed one specimen that was clearly mis-sexed (posterior probability of being male, although labeled female, was 99.7%). This specimen was not included in further analyses.

The sample from Los Tuxtlas showed that although the measurements displayed overlap between the sexes, males were significantly larger than females in all characters examined (Table 1). Discriminant analysis of the subset of this sample possessing data on body mass (21 males, 15 females) yielded the equation:

$$D = 0.2281 \text{ MASS} + 0.2858 \text{ WCH} + 0.3640 \text{ TL} + 0.9477 \text{ TS} - 56.3579,$$
(1)

where MASS is body mass, WCH is wing chord, TL is tail length, and TS is tarsus length. This equation successfully classified 97.2% of the sample used to generate it, failing to classify correctly one male, whose discriminant score (D) was -0.39.

		Males (26)	26)		Females (17)	(17)	Dimor-		
	x	SD	MinMax.	Ŷ	SD	MinMax.	- phism⁴	$F^{ m b}$	$P^{b}$
Wing chord	57.0	1.44	(54.5-60.5)	53.5	1.20	(52.0-56.5)	1.06	64.19	<0.00005
Primary 8	41.9	1.64	(38.0 - 46.0)	39.2	0.91	(38.0 - 41.0)	1.07	38.28	< 0.00005
Bill	11.9	0.61	(9.3-12.8)	11.1	0.79	(8.9 - 12.3)	1.07	12.93	0.0009
Gonys	10.9	0.54	(8.3 - 12.1)	10.0	0.78	(7.9 - 11.1)	1.09	18.75	0.0001
Tail	47.5	1.63	(42.5 - 50.5)	44.1	1.29	(42.0 - 47.0)	1.08	50.11	< 0.00005
Tarsus	21.9	0.50	(20.9 - 23.2)	20.8	0.47	(19.9 - 21.7)	1.06	55.26	< 0.00005
Mass <sup>c</sup>	16.2	1.11	(13.7 - 18.5)	13.9	1.53	(12.3 - 15.6)	1.16	39.04	< 0.00005
a Indev of dimorphi	rnhism calcula	ted by divid	ism calculated by dividing mean male value by mean female value	ue hv mean	female valu	le.			

TABLE 1. Comparative measurements (mm) and body mass (g) of male and female Thryothorus m. maculipectus from Los Tuxtlas, Veracruz.

ì, -٢ • Data from 20 males and 14 females; df = 1,32.

Vol. 67, No. 2

[239

240]

When examining the sample from Los Tuxtlas as a whole, without considering body mass, three different discriminant functions produced the same classificatory results (including jackknifing results). Because it involves the measurement of fewer characters, the equation we choose to offer is

$$D = 0.3725 \text{ WCH} + 0.2578 \text{ TL} + 1.0830 \text{ TS} - 55.8942,$$
 (2)

which successfully classified 97.7% of the sample used to generate it (26 males, 17 females). Again, one male was misclassified (discriminant score of -0.47; not the same individual misclassified by Equation 1).

How well does the morphology of birds from Los Tuxtlas enable us to categorize successfully the sex of birds from outside this area? Nineteen additional birds from other areas in Mexico were examined in this regard. This sample came from Tamaulipas (six males, one female), San Luis Potosí (two males), Oaxaca (three of each sex), and elsewhere in Veracruz (three males, one female). When applied to this sample, Equation 2 resulted in the misclassification of one bird, a 94.7% success rate on a sample not used in generating the function. This rather high success rate suggests that geographic variation in wing, tail, and tarsus lengths in this region is small (though the sample includes individuals of other subspecies; cf. Phillips 1986). A final discriminant analysis was performed on the entire sample (40 males, 22 females), giving the function

$$D = 0.2596 \text{ WCH} + 0.3103 \text{ TL} + 1.2951 \text{ TS}, \tag{3}$$

which successfully classified 96.8% of the sample used to generate it. Two males were misclassified, with discriminant scores of -0.51 and -0.74. Mensurally, *Thryothorus maculipectus* shows enough sexual dimorphism that a high percentage of captured individuals may be confidently sexed. Individuals misclassified by Equations 1–3 were adult as well as juvenile males. Assumptions of multivariate normality and equality of covariance matrices were not violated in these analyses (Box's M > 8.07, P > 0.27).

Ridgway (1904) described the juvenal plumage as similar to adults, but with anterior and median venter duller white, usually washed with pale brown. Breast spots are much smaller, sometimes streak-like, less sharply defined, and dull grayish instead of dark brown as in the adult (adult spots not black as Ridgway stated, but rather Sepia, between Smithe's [1975, 1981] No. 219 and 119). Markings on the sides of the juvenal head are much less distinct, and the undertail coverts and flanks are nearest Clay Color (Smithe's No. 26). Undertail coverts in the adult become whitish with broad, dusky (Sepia) barring. We note that the juvenal plumage is much duller overall than that of adults. Dorsally, young birds approach Cinnamon Brown (Smithe's No. 33), whereas adults are nearest Raw Sienna (No. 136). This difference probably reflects differences in feather structure, rather than pigmentation.

The breeding season in southern Veracruz is at least 4 mo long, as indicated by specimens in juvenal plumage from 19 April-18 August. Ju-

venile specimens from 13 September and 10 October are just beginning first prebasic molt, so the breeding season may be as long as 5 mo.

Individuals can be aged using two characters. Skull ossification becomes complete during the first year, and may be quite rapid. The latest unossified specimen is from 17 January. Juvenal undertail coverts (Clay Color) are retained after the first prebasic molt. Adult undertail coverts, whitish with Sepia barring, seem to be acquired in first year (hatching year, or HY) birds in autumn (ca. October). The presence of juvenal undertail coverts or an unossified skull indicates a bird in its first year (HY/SY). Additional recent specimens or study of marked birds are needed to determine the timing of ossification and acquisition of adult undertail coverts; for now use of both characters is recommended.

Henicorhina [leucosticta] prostheleuca (White-breasted Wood-Wren).— This species is common in the woodlands of southern Veracruz, from lowland rainforest and second growth to montane rainforest and *Quercus-Liquidambar* forest (though less common at higher elevations). It is a ground dweller, rarely occurring higher than 3 m in forest understory. The group with which we are concerned (see taxonomic notes below) occurs from southeastern San Luis Potosí and northern Veracruz south on the Gulf and Caribbean slopes (not on drier northern half of Yucatan Peninsula) south to perhaps southern Nicaragua, and on the Pacific slope from southeastern Oaxaca to Guatemala (see American Ornithologists' Union 1983, Dickey and van Rossem 1938, Land 1970, Phillips 1986).

As with the last species, the first analysis of specimens from Los Tuxtlas showed that one specimen was mis-sexed; although labeled female, the specimen had a 99.9% posterior probability of being male. This specimen was excluded from further analyses.

The Los Tuxtlas sample showed that although the measurements displayed overlap between the sexes, males were larger than females in all characters (Table 2). Discriminant analysis of the subset of this sample with data on body mass (34 males, 20 females) showed that mass gives no additional discriminatory power over a function that does not include mass (39 males, 21 females). The latter function,

$$D = 0.2266 \text{ WCH} - 0.3142 \text{ TL} + 1.9033 \text{ TS} + 1.0508 \text{ BL} + 0.5874 \text{ P9} - 76.3726,$$
(4)

where BL is bill length and P9 is the length of Primary 9, successfully classified 96.7% of the sample used to generate it, misclassifying a male and a female (*D*-scores -0.97 and -0.32, respectively). These two birds were misclassified in both of these analyses. A less cumbersome function would include fewer variables. By not allowing the stepwise selection of Primary 9, the following function was generated:

$$D = 0.3625 \text{ WCH} + 1.5879 \text{ TS} + 0.9289 \text{ BL} - 63.4712,$$
 (5)

which successfully classified 96.9% of the sample used to generate it (40 males, 24 females; more birds were useful because of fewer missing values due to such factors as molt). In this analysis two males were misclassified

		Males (39)	39)		Females (21)	(21)	Dimor-		
	x	SD	MinMax.	Ϋ́	SD	Min.–Max.	- phism <sup>a</sup>	$F^{ m b}$	$P^{\mathrm{b}}$
Ving chord	52.9	1.71	(48.5-56.0)	50.1	1.16	(48.0-53.0)	1.06	45.55	<0.00005
Primary 9	33.3	1.18	(31.5 - 35.5)	31.3	1.09	(29.5 - 34.5)	1.07	42.55	< 0.00005
rimary 8	39.2	1.55	(35-41.5)	37.2	1.20	(34-42)	1.06	28.43	< 0.00005
Sill	10.8	0.41	(10.0-11.6)	10.1	0.47	(9.1 - 10.9)	1.08	44.89	< 0.00005
Sonys	10.1	0.52	(8.7 - 11.0)	9.3	0.46	(8.6 - 10.4)	1.08	30.81	< 0.00005
lail	24.4	1.26	(22.0-26.5)	23.0	1.03	(21.5 - 25.0)	1.06	18.64	0.001
arsus	22.4	0.43	(21.1 - 23.4)	21.3	0.43	(20.3 - 22.7)	1.05	90.45	< 0.00005
Mass <sup>c</sup>	14.8	1.02	(13.5 - 17.0)	13.6	0.94	(12.2 - 15.2)	1.09	20.38	< 0.00005

## K. Winker et al.

### J. Field Ornithol. Spring 1996

(different individuals from previous misclassifications; D = -0.90 and -0.50).

Twenty-three additional birds from outside Los Tuxtlas were examined to determine how well Equation 5 performed over a wider geographic area. This sample consisted of specimens from Chiapas (four males, two females), Oaxaca (one of each sex), Campeche (one male), Guatemala (four males, one female), and elsewhere in Veracruz (four males, five females). Three of these specimens were misclassified using Equation 5, a failure rate of 13%. A female from Oaxaca (D = 0.04) and a male and female from elsewhere in Veracruz were misclassified (D = -0.90 and 0.08). Given the origins of the misclassified birds, geographic variation probably did not play a strong role in the success rate (87%) of Equation 5 on birds from outside Los Tuxtlas. In this case, then, a function that is geographically more robust can be obtained by including all measured birds (53 males, 30 females):

$$D = 0.2272 \text{ WCH} + 0.2243 \text{ TL} + 1.6222 \text{ TS} + 0.9149 \text{ BL} - 62.4389.$$
(6)

This equation successfully classified 95.2% of the sample used to generate it, misclassifying two birds from Los Tuxtlas (the same two misclassified by Equation 5), a male from Chiapas (D = -0.53), and the same male from elsewhere in Veracruz misclassified by Equation 5.

Henicorhina [leucosticta] prostheleuca shows enough sexual size dimorphism that a majority of captured individuals can be confidently sexed. Our sample included a mixture of adults and first year (HY/SY) birds, so the equations are quite useful. Assumptions of multivariate normality and equality of covariance matrices seemed robust in all analyses (Box's M > 8.54, P > 0.23).

The juvenal plumage was not described by Ridgway (1904), but was briefly (and incompletely) described by Traylor (1949). The juvenal plumage is a generally more subdued and drab version of the adult plumage. Most notably, the juvenal throat and breast are gray (closest to Smithe's [1975, 1981] Glaucous, No. 80), instead of white. This has created some confusion in species-level identification (see notes below on separating this species from *H. leucophrys*). The flanks of the juvenal plumage are nearest Mikado Brown (Smithe's [1975, 1981] No. 121C), compared with the rustier Raw Sienna (no. 136) of the adult. Similarly, the juvenal back is nearest Prout's Brown (No. 121A), while the adult back is a brighter Mars Brown (No. 223A). Facial markings in young birds are similar but much less distinct than those of the adult. The crown and nape of young birds is a uniform Dark Brownish Olive (No. 129), while in the adult these feathers are Sepia (No. 119) with lighter brown tips (approaching Raw Umber [No. 223]).

Finally, an important and previously unrecognized characteristic of the juvenal plumage occurs in the wing coverts. In *prostheleuca* adults, both greater and median secondary wing coverts are Sepia (No. 119), tipped terminally with white (or sometimes only a bright buff). On the closed

wing these tips appear as two parallel rows of spots. In adults, the feather interior is often patterned and of a more chocolate color than in the juvenile. Unlike adults, juvenal greater secondary coverts have a cinnamon (nearest Mikado Brown, No. 121C) fringe along the entire feather edge, and the white tips are conspicuously lacking. Also, the feather interior is a generally solid rufous-brown.

Individuals in juvenal plumage can be found in southern Veracruz from 18 April to 18 September, suggesting a breeding season of at least 5-mo duration.

The first prebasic molt appears to be confined largely to the body (specimen record and pers. obs.), and the juvenal greater and median secondary coverts are retained for some time, providing an excellent character for aging birds. Adult secondary coverts are often acquired gradually, causing many first year (HY/SY) birds in late autumn and winter to have a mixed set of these coverts. The presence of *any* juvenal greater secondary coverts (usually easily recognized by a break in a row of white spots) indicates a bird in its first year.

Ossification is completed in the first year, but the rate of ossification is independent of the rate of acquisition of adult greater secondary coverts, making both characters useful for aging birds (KW, pers. obs.). Ossification may be completed in some individuals by December, but unossified second-year (SY) birds can still be found in April, which is concordant with the long reproductive season. Birds in their first year (HY/SY) can often be distinguished by the retention of at least some juvenal greater secondary coverts until well into April of their second calendar year (these latter are SY birds in which ossification is complete and reproductive activity has begun). Greater secondary covert spotting is not a useful aging character throughout the range of "*leucosticta*" as currently recognized (see taxonomic notes). It is useful, however, for the range described above.

Taxonomic notes.-Inasmuch as our notes on aging H. "leucosticta" include a character that is not useful throughout the range of the species as currently recognized, it is useful to discuss the distribution of this aging character among the subspecies of H. "leucosticta" (sensu lato) and to summarize current taxonomic views. Adults east and south of the Canal Zone in Panamá (subspecies alexandri, darienensis, and all South American subspecies, including the nominate race) essentially do not acquire white greater secondary covert spotting. As in *prostheleuca*, the juvenal coverts in these other groups tend to be retained into adulthood, but are distinguishable largely by the brighter russet-cinnamon edging, which we thought to be a less reliable aging criterion in Mexican individuals because it could either fade or wear away before these feathers were molted. In examining specimens throughout Middle America, it is clear that at least some of the taxonomic confusion in this group arises from the previously unrecognized retention of some juvenal plumage well into adulthood. Ridgway (1904:610), for example, described both the juvenal and adult wing covert conditions as being those of the adult, presumably viewing white spotting as a polymorphism.

Phillips (1986) is the most recent revisor of H. "leucosticta" north of Colombia. He (1986:129) noted that "I reluctantly follow Hellmayr's guess that H. prostheleuca is conspecific with leucosticta, which seems quite dubious..." We are also skeptical of this lumping. Further, we consider that division of the Central American forms may be warranted. Besides the acquisition of white greater secondary covert spotting in adults north and west of (southern?) Nicaragua, there is also a striking difference in the call notes of "leucosticta" between Panamá/Costa Rica and Mexico. The call note in southern Veracruz is a rather bright, almost metallic "tink." In Panamá the call has been described as "bweeer, somewhat reminiscent of a Swainson's Thrush" (Catharus ustulatus, Ridgely and Gwynne 1989:345). Slud (1964:292) described the call of Costa Rican birds as "an antbird-like hoarse 'eerp' or 'rerp'." The presence of a derived (apomorphic) character (greater secondary covert spotting) in northern populations, together with striking call note differences between Panamanian/Costa Rican and Mexican populations, suggests species-level differences.

Because Middle American populations (including populations in western Colombia and northwestern Ecuador) are geographically isolated from the true *leucosticta* group of South America (see Ridgely and Tudor 1989:93), the two major Middle American groups can be considered *pros*theleuca in the north and pittieri/darienensis in the south and east. Exactly where these two major Middle American groups meet and what occurs there remains unresolved. This meeting occurs in the ranges of the subspecies *pittieri/costaricensis*. A geographically rather broad area from at least eastern Costa Rica (in the west) to central Panamá (in the east), in which the incidence of white spotting in adult greater secondary coverts declines as one goes east, may represent a hybrid zone. Regardless of what this zone represents, we can recognize that the prostheleuca group is made up of the nominate race and, in addition, the following subspecies: decolorata (Phillips 1986), tropaea (Bangs and Peters 1927; considered by Monroe [1968] and Phillips [1986] to be part of prostheleuca), and smithei (Dickerman 1973).

At the very least, it appears that *prostheleuca* is a major subspecific group. Further study is needed to determine whether it is simply a major subspecies under the biological species concept (what might be considered a phylogenetic species), or whether it warrants recognition as a full biological species. Because the group is subject to foxing (Dickerman 1973), any comprehensive revision will require new material. Anyone working with "*leucosticta*" should collect representative samples (including tissues) as a matter of course.

Separating Henicorhina [leucosticta] prostheleuca from H. leucophrys.— These two species are often confused, at least in part because the English common names are misleading. H. leucophrys, the Gray-breasted Wood-Wren, is gray below throughout its life. H. leucosticta, the White-breasted

Taxon	Equation	n	No. misclas- sified	% success
Thryothorus maculipectus	1	36	2	94.4
-	2	43	3	93.0
	3	62	3	95.2
Henicorhina [leucosticta]	4	60	2	96.7
prostheleuca	5	64	2	96.9
*	6	83	4	95.2

TABLE 3. Jackknife results for Equations 1-6.

Wood-Wren, is gray ventrally when young (HY birds). The following notes are only useful for birds north of southern Nicaragua. In comparing mostly Henicorhina [leucosticta] prostheleuca and H. leucophrys mexicana, the best characters to use in distinguishing H. leucophrys from H. [leucosticta] prostheleuca are in the wing. H. leucophrys shows an absence of any greater secondary covert spotting and the presence of very pale white spotting in the greater primary coverts (together with gray breast). Juvenile prostheleuca also lack greater secondary covert spotting and are gray below, but generally have bold spotting in the primary coverts. Adult prostheleuca have a bold white venter and bold white spotting in greater primary and secondary coverts. The gray venter of juvenile (HY) prostheleuca can last at least until 18 September. The throat and upper breast of two birds from this date from Los Tuxtlas in partial juvenal plumage (in prebasic molt) are just beginning to show traces of white. Some other general differences between the two species are that the brown on the back is more rufescent in *leucophrys*, and that this species also has less black on the top of the head and on the neck.

Equation performance and the jackknife procedure.—Equations 1-6 are optimal for the samples considered, and the rates of successful classification are therefore overly optimistic for birds from outside these samples. A more realistic estimate of how well a discriminant function will perform can be obtained by doing a jackknifing procedure – a series of discriminant analyses in which each step (analysis) excludes one individual, generates a discriminant function from the remaining birds, then classifies the excluded individual. All birds in the sample are excluded from one analysis; the success rate is calculated by examining what percentage of birds were correctly classified when they were excluded from the sample generating the function. Equations 1-6 generally performed very well (Table 3). In H. "l." prostheleuca the actual efficacy of Equations 4 and 5 may approach 100%. In the two series of jackknife analyses on the Los Tuxtlas birds only two individuals were misclassified, and these in every analysis, suggesting that perhaps they were both mis-sexed in preparation.

### DISCUSSION

The data presented here constitute the first detailed examination of sexual dimorphism in the taxa considered. Both taxa are cryptically di-

[247

morphic (monochromatic, but with size differences present); males are larger than females in all characters examined. Degrees of dimorphism between the two species are roughly similar, except in body mass, where *Thryothorus m. maculipectus* shows greater dimorphism than *Henicorhina* "*l.*" prostheleuca (Tables 1 and 2). Although the two species show some overlap in measured characters (Tables 1 and 2), they show no overlap in morphological space as determined through principal component analysis (not shown). Although in different genera, in the lowland rainforest community of southern Veracruz these two species are each others' closest relatives. They show a rather good degree of macro- and microhabitat segregation, but they often show habitat overlap, as well (KW, pers. obs.). Interactions between the two species (if any) are largely unknown.

Because degrees of sexual dimorphism should be attributable to mating system or life history parameters, it is useful to consider the life histories of these two species, which show a similar level of dimorphism. Remarkably little is known about the life history of Thryothorus maculipectus for a simple reason: it does not occur in the geographic area where the great naturalist Alexander Skutch has conducted many decades of careful work. Much can be inferred, however, from the life history of T. rutilus, which, although now considered a separate species, was at one time considered conspecific (see comments in Phillips 1986, Ridgway and Tudor 1989). Individuals of T. maculipectus and rutilus occur in pairs throughout the year, and both sexes sing, often in a duetting, or antiphonal fashion (Skutch 1960, KW, pers. obs.). Antiphonal singing in these wrens serves the place of contact calls in other species, acting to keep the pair together as they move through the heavy forest they occupy. Although *rutilus* and maculipectus can be found sleeping in dormitory nests occasionally, they have not been observed building them, and may in fact temporarily appropriate the dormitory nests of other species. Skutch (1960) believed that rutilus might use dormitory nests only inconsistently. In rutilus, both sexes build the reproductive nest and care for the young. It is likely that only the female incubates. Courtship and territorial interactions appear to be unknown.

Henicorhina leucosticta (sensu lato) constructs two types of nest: dormitory nests and reproductive nests. Both sexes build both types of nest (Skutch 1960). The two nest types differ substantially, both in placement and construction (though both are fully enclosed structures; Skutch 1960). Only the female seems to incubate, but both parents feed the young (Skutch 1960). The female alone may be responsible for post-fledging care of the young, which includes the sharing of a dormitory nest or nests (Skutch 1960, KW pers. obs.). Courtship appears undescribed, but pairs seem to occupy territories throughout the year, and both sexes sing, although not antiphonally (KW pers. obs., Skutch 1960). Adult males tend to respond more vigorously to tape playback simulations of territory intruders (song and calls), but such playbacks elicit responses from both sexes (KW, unpubl. data). In sum, both species appear to be quite monogamous. Given our limited understanding of their life histories, males

	TABLE 4.	Statistics	for the o	liscriminant s	cores gener	IABLE 4. Statistics for the discriminant scores generated by Equations 1-0.		
		Equa-						Eigen-
Taxon	Sex	tion	u	Mean	SE	MinMax	95% CI <sup>a</sup>	value <sup>b</sup>
Thrvothorus m.	Males	-	21	1.67	0.24	-0.36 - 3.53	-0.53 - 3.86	4.008
maculitectus	Females	1	15	-2.34	0.20	-4.06 - 1.14	-3.86 - 0.81	4.008
4	Males	2	26	1.37	0.21	-0.47 - 3.97	-0.80 - 3.54	3.012
	Females	61	17	-2.10	0.19	-3.70 - 0.66	-3.650.54	3.012
	Males	e0	40	1.20	0.17	-0.74 - 3.87	-0.95 - 3.36	2.727
	Females	3	22	-2.19	0.17	-3.830.64	-3.76 - 0.62	2.727
Henicorhina [leucosticta]	Males	4	39	1.51	0.15	-0.97 - 3.03	-0.30 - 3.33	4.404
trostheleuca	Females	4	21	-2.81	0.24	-5.49 - 0.32	-5.03 - 0.60	4.404
<b>.</b>	Males	5	40	1.32	0.15	-0.90 - 3.21	-0.52 - 3.16	3.000
	Females	5	24	-2.20	0.22	-4.60 - 0.45	-4.370.04	3.000
	Males	9	53	1.17	0.13	-1.13 - 3.12	-0.78 - 3.11	2.461
	Females	9	30	-2.06	0.19	-4.35 - 0.65	-4.090.03	2.461

<sup>5</sup> 30.6 Connected interval, mean - 2.32, much 30 is may or up population.

248]

# K. Winker et al.

J. Field Ornithol. Spring 1996

in these species may be so much larger than females for reasons of territorial defense.

Before employing the discriminant equations presented here, readers are urged to examine our earlier discussion regarding museum specimens, shrinkage, discriminant equations, and sex ratios (Winker 1993, Winker et al. 1994:317–321). Data from other sources (corrected for shrinkage if necessary) can be directly compared to Tables 1, 2, and 4 to determine whether samples are comparable. We recommend that the probability that an individual is male ( $p_m$ ) be calculated as

$$p_{\rm m} = (1 + e^q)^{-1}, \tag{7}$$

where the sex ratio of the sample generating the discriminant equation (r) is incorporated into the equation through the calculation of

$$q = -D_{a} \times [1 + |\ln(r^{6})|] - [(2r \times \ln(r)]].$$
(8)

When used with the discriminant functions given here, this equation enables close approximation of the posterior probabilities calculated using the more difficult Bayes' theorem (see discussion in Winker et al. 1994). Equation 8 only works well for Equations 1, 2, and 6, however. For Equations 3 and 5, replace the  $r^6$  term in Equation 8 with  $r^5$ . For Equation 4 replace the same term with  $r^4$ . Sex ratios are calculated from Table 4. If field work shows a different sex ratio in other samples (with sexes confirmed by direct gonadal examination), sex ratios used in Equation 8 should be modified accordingly. As the sex ratio approaches unity, probabilities will be more conservative (see Winker et al. 1994: Fig. 1). The probability that an individual is female ( $p_{\rm f}$ ) is calculated as  $p_{\rm f} = 1 - p_{\rm m}$ . Readers are urged to examine an example presented in Winker et al. (1994).

The best use of the equations presented will include mensural comparisons with our samples, calculations of individual probabilities of being male, and collection and preservation of some voucher specimens for verification. Although laparotomy might be viewed as a possible alternative to the latter, we stress the dire need for recent neotropical specimens with complete data (date, specific locality, habitat, body mass, gonad condition, stage of skull ossification, molt status). The strength of this need is clear when one considers that a relatively small sample of recent H. "*l.*" prostheleuca specimens enabled us to recognize key age-related plumage differences that shed new light on the diversity of this group in Middle America. Old specimens, those most readily available in collections, often lack the data needed to make such key observations. Only more material will enable the resolution of the evolutionary questions our study raises; such material will prove crucial in other species as well (cf. Phillips 1986). Scientific collecting has a practically insignificant effect on avian populations (Banks 1979, Winker et al. 1991).

### ACKNOWLEDGMENTS

The excellent series upon which our investigations are based were collected and prepared primarily by M. A. Ramos and R. J. Oehlenschlager. Without point samples of this nature

these analyses would not be possible. We thank the curatorial staff of the following institutions for access to specimens in their care: Bell Museum of Natural History (University of Minnesota, St. Paul), Field Museum of Natural History (Chicago, Illinois), and U.S. National Museum of Natural History (Smithsonian Institution, Washington, D.C.). KW thanks Eugene Morton for pointing out the differences in call notes used by *H. "leucosticta*" between Panamá and southern Veracruz. We thank John Rappole for comments on an earlier draft.

#### LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. American Ornithologists' Union, Lawrence, Kansas. 877 pp.
- BALDWIN, S. P., H. C. OBERHOLSER, AND L. G. WORLEY. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 2:1-165.
- BANGS, O., AND J. L. PETERS. 1927. Birds from the rain forest region of Veracruz. Bull. Mus. Comp. Zool. 67:471–487.
- BANKS, R. C. 1979. Human related mortality of birds in the United States. U.S. Fish & Wildl. Serv. Special Sci. Rep., Wildl. No. 215.
- CLENCH, M. H. 1976. Possible pitfalls in museum specimen data. N. Amer. Bird Bander 1: 20-21.
- DICKERMAN, R. W. 1973. A review of the White-breasted Woodwrens of Mexico and Central America. Condor 75:361-363.
- DICKEY, D. R., AND A. J. VAN ROSSEM. 1938. The birds of El Salvador. Zool. Ser. Field Mus. Nat Hist. 23:1-609.
- JENNI, L., AND R. WINKLER. 1989. The feather-length of small passerines: a measurement for wing-length in live birds and museum skins. Bird Study 36:1–15.
- LAND, H. C. 1970. Birds of Guatemala. Livingston Publ. Co., Wynnewood, Pennsylvania. 381 pp.
- MONROE, B. L., JR. 1968. A distributional survey of the birds of Honduras. Ornithol. Monogr. 7:1–458.
- NORUŠIS, M. J. 1988. SPSS/PC+ advanced statistics V2.0. SPSS, Inc., Chicago, Illinois. 343 pp.
- PHILLIPS, A. R. 1986. The known birds of North and Middle America, Part I. Allan R. Phillips, Denver, Colorado. 259 pp.
- RAMOS, M. A., AND D. W. WARNER. 1980. Analysis of North American subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. Pp. 173–180, in A. Keast and E. S. Morton, eds. Migrant birds in the neotropics. Smithsonian Inst. Press, Washington, D.C.
- RIDGELY, R. S., AND J. A. GWYNNE, JR. 1989. A guide to the birds of Panama, Second Ed. Princeton Univ. Press, Princeton, New Jersey. 534 pp.
- ------, AND G. TUDOR. 1989. The birds of South America, Vol. 1. Univ. Texas Press, Austin, Texas. 516 pp.
- RIDGWAY, R. 1904. The birds of North and Middle America, Part III. Bull. U.S. Natl. Mus. 50(3):1-801.
- SKUTCH, A. F. 1960. Life histories of Central American birds, II. Pacific Coast Avifauna No. 34, Cooper Ornithol. Soc., Berkeley, California. 593 pp.
- SLUD, P. 1964. The birds of Costa Rica: distribution and ecology. Bull. Amer. Mus. Nat. Hist. 128:1–430.
- SMITHE, F. B. 1975. Naturalist's color guide, Part I. Amer. Mus. Nat. Hist., New York, New York.
- ——. 1981. Naturalist's color guide, Part III. Amer. Mus. Nat. Hist., New York, New York.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Co., San Francisco, California, USA. 859 pp.
- TRAYLOR, M. A., JR. 1949. Notes on some Veracruz birds. Fieldiana 31:269-275.
- WINKER, K. 1993. Specimen shrinkage in Tennessee Warblers and "Traill's" Flycatchers. J. Field Ornithol. 64:331–336.
  - -----, B. A. FALL, J. T. KLICKA, D. F. PARMELEE, AND H. B. TORDOFF. 1991. The importance of avian collections and the need for continued collecting. Loon 64:238–246.

------, G. A. VOELKER, AND J. T. KLICKA. 1994. A morphometric examination of sexual dimorphism in the *Hylophilus, Xenops,* and an *Automolus* from southern Veracruz, Mexico. J. Field Ornithol. 65:307–323.

Received 11 Jan. 1995; accepted 9 Jun. 1995.