

Sexual dimorphism in the birds from southern Veracruz, Mexico, and other localities. III. Wilson's Warbler (*Wilsonia pusilla*)

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ABSTRACT. Using museum specimens from Mexico, Canada, and the western United States, we examined sexual dimorphism in the Wilson's Warbler (*Wilsonia pusilla*), a Nearctic-Neotropic migrant (Passeriformes: Parulidae). On average, males had longer tails, wing chords, and eighth and ninth primaries than females. Three methods for quantifying cap plumage showed that differences in cap size and pattern alone could not definitively separate the sexes. Discriminant functions are presented for sexing individuals using cap category, cap length, wing chord, tail length, and ninth primary length. More specific functions are provided for samples from Alaska and eastern Mexico. For each group, equations are included for assigning individual probabilities of belonging to either sex.

SINOPSIS. **Dimorfismo sexual en aves de la parte sur de Veracruz, México y otras localidades III. *Wilsonia pusilla***

Utilizando especímenes de museos de México, Canadá y la parte oeste de los Estados Unidos examinamos el dimorfismo sexual del migratorio *Wilsonia pusilla*. Los machos, en promedio, tenían la cola, tamaño del ala y tamaño de la octava y novena primaria más largas que las hembras. Tres métodos utilizados para cuantificar el plumaje de la capucha mostró que la diferencia en tamaño y el patrón de ésta, utilizando como único parámetro, no era suficiente para separar los sexos. Se presenta un análisis de función discriminativa para sexar los individuos utilizando la longitud de la capucha y tamaños del ala, rabo y longitud de la novena primaria. Se provee de una ecuación matemática más específica para muestras de Alaska y el este de México. Para cada grupo se provee una ecuación que asigna probabilidades individuales para cada sexo.

Key words: discriminant function, morphometrics, sexual dimorphism, *Wilsonia pusilla*

The Wilson's Warbler (Parulidae: *Wilsonia pusilla*) is a Nearctic-Neotropic migrant passerine with a broad breeding range in northern North America and a wintering range from southern Texas and Baja California south to Costa Rica and western Panama (AOU 1998). This small warbler is recognizable by its olive-green upperparts and yellow underparts and forehead. Males generally have a distinctive black cap, but females can also have dark crowns, although their caps, when present, tend to be shorter or more patchy than those of males. Ridgway (1902) concluded that females of the three subspecies may have duller plumage, a more restricted black crown-patch, and smaller average tail and wing measurements than males, but the sexes are often not distinguishable. Dwight (1900) also found little de-

finite difference between female and male plumages.

The current protocol for determining the sex of captured Wilson's Warblers prepared by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service (1980) advocates separation by size differences in cap length and wing chord, following Stewart (1972). Pyle (1997) offered a combination of cap lengths and patterns to discern males from females. However, the examination of plumage differences cannot reliably sex all breeding-season adults (Chase et al. 1997).

This study was undertaken to explore sexual size dimorphism in Wilson's Warblers, to critically examine plumage dimorphism (dichromatism), and to create discriminant functions to help distinguish the sexes in the field. The approach has been used successfully in other species in which plumage or external soft parts have been inadequate for distinguishing males from females (e.g., Anderson 1975). This study is also the third in a series of morphometric

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examinations of birds collected primarily in southern Veracruz, Mexico (Winker et al. 1994, 1996).

METHODS

Our analyses are based on 255 *W. pusilla* museum specimens collected during breeding, wintering, and migration. Specimens were collected from Mexico, the United States, and Canada from 1952 to 1998. Over half (180) were collected in Veracruz, Mexico, in the mid 1970s (for site description see Rappole and Warner 1980). Two were collected in Morelos, Mexico, and four in British Columbia, Canada. Of the 69 specimens from the United States, 47 are from Alaska, 11 from Texas, eight from Minnesota, two from Wisconsin, and one from Arizona. Some 17% of the total sample was identified as subspecies *pusilla*, 60% as *pileolata*, and 1% as *chryseola*; 22% of the sample was not identified to subspecies. Determination of subspecies was based on label annotations, with the exception of all Alaska and northern British Columbia birds, which were designated *pileolata* (AOU 1957).

We only used specimens for which sex had been determined by gonadal inspection ($N = 255$). By only using specimens with gonadal descriptions, we reduced the possibility of using specimens for which the sex was uncertain or transcribed in error, and eliminated those for which the sex was determined by plumage. Specimens of questionable or unknown sex were excluded, regardless of external morphological characteristics. Of the specimens we examined, nine from the University of Alaska Museum and 80 from the Bell Museum of Natural History (25.9% of the specimens in those two collections) did not have gonadal information on their labels and were not included in any analyses. Degree of skull ossification was determined when skulls were available or from the specimen labels when recorded. *Wilsonia pusilla* generally reach complete ossification between 15 September and November of their first year (Pyle 1997). However, this study included specimens with incomplete ossification that had been collected through November to as late as 23 December.

Measurements taken were the lengths of the wing chord (unflattened wing), tail, tarsometatarsus (tarsus), and bill (from tip to anterior

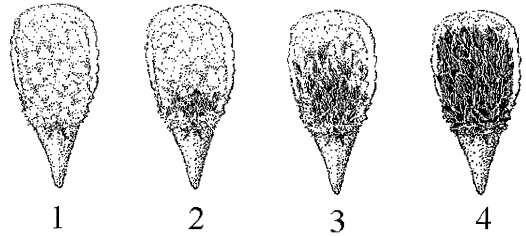


Fig. 1. The four cap categories for Wilson's Warblers. The categories are (1) all olive with no black feathers; (2) black feathers in anterior half of crown only; (3) black feathers in posterior half of crown, regardless of presence of black feathers in anterior half; and (4) solid black cap with no olive feathers. Caps in categories 2 and 3 may have olive feathers interspersed with the black ones.

edge of nostril), bill width and height (at the anterior edge of nostrils), and the length of the eighth (P8) and ninth (P9) outermost primaries (Baldwin et al. 1931; Jenni and Winkler 1989). To avoid bias, all measurements were completed before noting and recording the sex of each individual. Specimens with heavy feather wear or damage that would preclude accurate measurement were excluded. Measurements were made to the nearest 0.1 mm with vernier calipers, except for primaries P8 and P9, which were measured to the nearest 0.5 mm with a highly flexible insert (Jenni and Winkler 1989). To assure consistency, all measurements were performed by a single observer (JJW). Body mass was determined from specimen labels when possible, although the utility of this character is limited without an associated indication of body fat, gut contents, or breeding condition.

Caps were evaluated in three ways. First, the extent of black feathers from the front to the back of the head was measured to the nearest 0.1 mm with vernier calipers. This measurement, called "cap length," is the distance from the front of the anterior-most dark feather to the back of the posterior-most dark feather, regardless of the dark feathers' positions on the crown and the amount of olive feathers interspersed. Second, caps were assigned a "cap category." This value separated caps into one of four classes, ranging from solid olive-green to solid black (Fig. 1). Third, caps were evaluated for their level of demarcation or distinctiveness at the trailing, or posterior, edge. They were divided into three classes: those showing no black, those with a gradual transition from

black to green, and those with a strong, even demarcation between the posterior end of the black feathers and the beginning of the green feathers. Ranking and measurements of caps were done independently of other measurements and blindly with regard to the sex of the bird.

Means of male and female measurements were compared using t -tests (SPSS for Windows 1995). For two of the analyses, specimens of different subspecies were pooled because it can be difficult or even impossible to distinguish these accurately based on subtle plumage characteristics, especially during migration. However, a separate analysis was performed on those specimens for which the subspecies *pileolata* could be confidently ascertained using both geography and plumage characters, those of Alaska and northern British Columbia (AOU 1957). Age classes were pooled to accommodate the uncertainty in assessing a bird's age in the field, which can be particularly difficult after ossification is completed. Of the 255 specimens in our sample, 130 had data on skull ossification or reproductive condition which, combined with the time of year, could positively confirm their status as after-hatching year birds. Equality of variance was not assumed for the t -tests unless Levene's Test was satisfied for that condition (Levene 1960).

Discriminant analyses were performed on untransformed data using a stepwise selection for "good" predictor variables through the minimization of Wilks' lambda. Specimens with missing values were excluded from analyses requiring those variables. The variable with the most missing values was mass, which had not been recorded for 27 (10.6%) of the specimens. Other variables with missing values, with the number of specimens in parentheses, included bill height (12), bill width (8), bill length (6), tarsus (5), and tail length (1).

In calculating the discriminant scores of individuals, the sex ratios of the samples were used rather than assuming a 1:1 ratio. These ratios varied slightly, from a 1.38 to 1 male skew in the Alaska and northern British Columbia breeding season sample, to a 0.98 to 1 female skew in the Mexico sample, with an overall sex ratio near unity of 1.06 to 1. The sex ratios of the different geographic samples reflect the imbalanced ratios encountered in field work in the different localities. Although

unwise to confound relative sample sizes with prior probabilities in nature (Williams 1983), for analytical reasons it is important not to add incorrect information, such as a sex ratio of unity where none exists.

Multivariate normality (indirectly) and equality of group covariance matrices were examined using Box's M Test (Norusis 1988). Discriminant equations were derived from unstandardized canonical discriminant function coefficients (Norusis 1988:B7). 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 function. In addition, we used the jackknife approach to estimate how well the final discriminant functions performed (Sokal and Rohlf 1981:796).

RESULTS

Male Wilson's Warblers, on average, have significantly longer tails, wing chords, eighth and ninth primaries, and caps (Table 1). We found no difference between the sexes in mass, tarsus, or bill measurements.

The distribution of cap categories (Fig. 2) differed between males and females (Mann Whitney $U = 1845.5$, $Z = -11.237$, two-tailed significance = 0.000). Of the 131 males examined, 60.3% (79) had Category 4 caps, 38.9% (51) had Category 3 caps, none had a Category 2 cap, and 0.8% (1) had a Category 1 cap. Of the 124 females examined, 4.8% (6) had Category 4 caps, 37.9 (47%) had Category 3 caps, 25% (31) had Category 2 caps, and 32.3% (40) had Category 1 caps.

The proportion of individuals whose cap had a distinctive trailing edge also varied between males and females. Of 131 males, 48.9% (64) had a strong posterior line of demarcation on the cap, 50.4% (66) did not, and 0.8% (1) had no dark cap at all. Of 124 females, 62.1% (77) had no distinct trailing edge to their caps, 5.6% (7) did have strong delineation, and 32.3% (40) had no dark caps to be evaluated.

Discriminant analysis of the entire sample correctly assigned the sex to 91.3% of the specimens (117 of 125 males and 103 of 116 females). However, this function required nine variables, which would be onerous to measure in the field. Removing four weak predictor variables (eighth primary length, bill length, bill

Table 1. Comparative measurements (mm) and body mass (g) of male and female *Wilsonia pusilla*.

	Males		Females		Dimorphism ^a	F-test	
	\bar{x} (N)	SD	Min.-Max.	SD		Min.-Max.	t
Cap length	12.8 (131)	1.87	0.0-16.6	4.88	0.0-14.2	13.98	0.000
Wing chord	54.8 (131)	2.04	47.9-59.2	1.85	47.6-57.4	9.10	0.000
Primary 9	38.7 (131)	2.15	34.5-45.0	1.99	31.5-46.5	7.18	0.000
Primary 8	41.3 (131)	2.00	36.5-46.5	1.85	36.0-48.0	7.83	0.000
Tail length	46.4 (131)	1.63	41.8-50.1	2.05	39.3-50.7	5.75	0.000
Mass ^b	6.9 (111)	0.65	5.4-9.0	0.89	5.3-10.4	1.52	0.131
Tarsus	16.9 (129)	0.69	14.8-19.3	0.69	15.3-19.2	0.29	0.774
Bill length	6.0 (128)	0.28	5.4-6.9	0.31	5.3-7.0	-0.12	0.904
Bill height	2.8 (126)	0.24	2.0-3.5	0.21	2.3-3.5	-0.14	0.886
Bill width	3.0 (128)	0.25	2.4-3.7	0.24	2.2-3.5	-0.03	0.976

^a Index of dimorphism calculated by dividing mean male value by mean female value.

^b Includes individuals in migration with substantial fat deposits.

height, and bill width) yielded the following discriminant function, which correctly sexed 89.8% of the specimens (a 1.5% loss in discriminating ability):

$$D = 0.5977\text{CAPC} + 0.1172\text{CAPL} + 0.0646\text{P9} + 0.0454\text{TL} + 0.1805\text{WCH} - 17.0779 \quad (1)$$

where *D* is the discriminant score, CAPC is the cap category, CAPL is cap length, P9 is ninth primary length, TL is tail length, and WCH is wing chord. When applied to the sample that generated it, this equation correctly classified 93.9% of the males (123 of 131) and 85.4% of females (105 of 123). The sample size here is larger because with fewer characters there were fewer missing values. Jackknifing the data yielded a success rate of 88.6%, correctly classifying 92.4% of the males and 84.6% of the females. The assumptions of multivariate normality and equality of covariance matrices were violated in this analysis (Box's *M* = 137.20, approximate $F_{15,253496} = 8.95$, *P* = 0.0000).

Focusing on birds from Mexico (mostly from Veracruz), we were able to classify 87.9% of the 182 specimens using the following discriminant function:

$$D = 0.6423\text{CAPC} + 0.0938\text{CAPL} + 0.0467\text{TL} + 0.2632\text{WCH} - 18.8946 \quad (2)$$

This equation correctly sexed 88.9% males (80 of 90) and 85.9% females (78 of 92). Jackknifing these data gave an 86.8% success rate, correctly classifying 90.0% of the males and 83.7% of the females. The assumptions of multivariate normality and equality of covariance matrices were also violated in this analysis (Box's *M* = 72.23, approximate $F_{10,154728} = 7.05$, *P* = 0.0000).

When specimens collected in Alaska and northern British Columbia (all of the same subspecies, *pileolata*) were pooled, they yielded a discriminant function with a much higher success rate of 96.0%:

$$D = 0.9189\text{CAPC} + 0.1800\text{CAPL} + 0.0977\text{TL} + 0.0938\text{WCH} - 13.9426 \quad (3)$$

This function correctly classified 100% of the

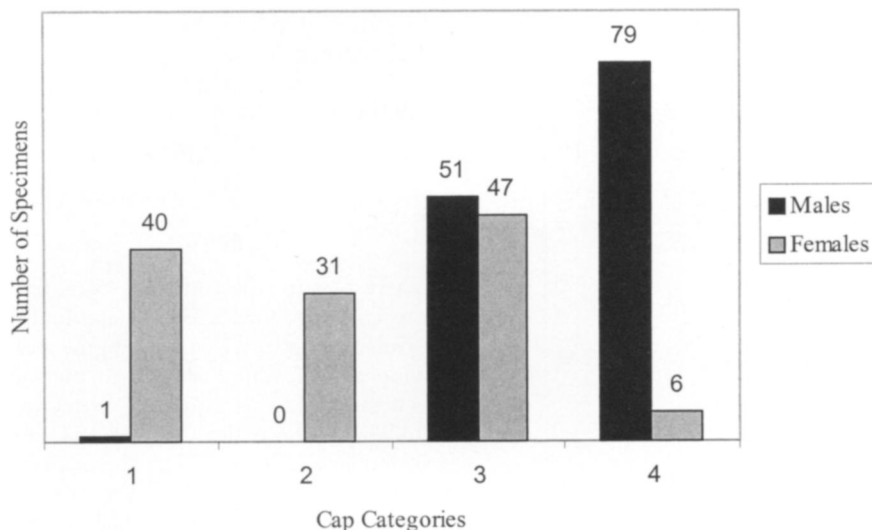


Fig. 2. The distributions of males and females across the four cap categories. The total number of males and females examined are 131 and 124, respectively.

males in the sample (29) and 90.5% females (19 of 21). The jackknife procedure yielded the same success rates. Again, the standard assumptions were violated (Box's $M = 46.82$, approximate $F_{10,8720} = 4.24$, $P = 0.0000$).

Cap length, cap category, and demarcation level were all significantly different for males and females, but none of these variables could effectively differentiate the sexes alone or in combination. At best, cap length alone correctly classified 80.0% of the entire sample, whereas the other cap-related variables were less successful. Using just one cap variable had the added disadvantage of disparate success rates for the two sexes. Cap length, when applied alone, misidentified 37.9% of the females compared to misidentifying only 3.1% of the males. In contrast, using level of demarcation alone misidentified 51.9% of the males but only 5.6% of the females.

DISCUSSION

Using dimorphism to determine the sex of Wilson's Warblers is not as straightforward as is generally assumed. For instance, U.S. Fish and Wildlife Service and Canadian Wildlife Service (1980) guidelines classify birds with a black cap greater than 11 mm and wing chord 53 mm or greater as male and those with a cap length less than 8 mm as female. This method would in-

correctly classify 1 of the males and 6 of the females in our sample ($N = 255$), a failure rate of 2.7%. Moreover, it would leave more than a third unknown, thus achieving an overall success rate of just 62%. Although Pyle (1997) stated that all males after August of their hatching year (i.e., in first basic plumage) have caps of 12 mm or greater, 26% of the male specimens in this study had caps under 12 mm, often retaining short caps into their second year. Black-capped females exist; one in this study had a solid cap of 14.2 mm (Table 1). The idea that males can be differentiated by a stronger demarcation between black and green feathers in the crown is also unreliable, misidentifying nearly a third of the specimens when used as the sole criterion.

Although only gonadally sexed specimens were used, the possibility of missexed specimens remains (Clench 1976). The examination of the ten longest-capped females and shortest-capped males revealed a steady gradation of cap lengths in both sexes, suggesting a natural and plausible progression within each sex to the extremes exhibited in cap coloration. However, one specimen (Bell MNH 33458) labeled as male with a cap length of 0.0 mm represented a marked break from the next shortest-capped male at 8.8 mm. The preceding discriminant functions classified it as female with a likelihood of over 99%, suggesting an error in sex-

Table 2. Statistics for the individual discriminant scores (D) generated by Eqn. 1–3.

Region	Sex	Equation	N	Mean	SE	Min.–Max.	95% CI ^a	Eigenvalue ^b
North America	Males	1	131	1.06	0.07	–2.28–2.87	–1.32–4.01	1.2186
	Females	1	123	–1.13	0.11	–3.31–2.06	–4.11–1.84	1.2186
Mexico	Males	2	90	0.96	0.08	–2.20–2.29	–1.80–3.73	0.9219
	Females	2	92	–0.94	0.12	–3.14–2.22	–3.71–1.82	0.9219
Alaska and British Columbia	Males	3	29	1.75	0.12	0.61–2.78	–2.85–6.35	4.4033
	Females	3	21	–2.42	0.29	–3.98–0.75	–7.02–2.18	4.4033

^a 95% confidence interval; mean \pm 2 SD, where SD is that of the population.

^b Ratio of between-groups to within-groups sums of squares. Generally, the larger the value, the better the discriminant function.

ing. Removing this anomalous specimen from the study would lower the success rate by 0.5% in the Mexican sample yet would improve it by 0.5% in the overall sample. Because excluding it does not alter the functions or their discriminating ability significantly, this specimen was included in all analyses.

Two other specimens (that appear to be correctly sexed) warranted attention for their unusual colorations. One immature October male from Veracruz, Mexico (Bell MNH 33567), lacks the deep black pigment usually seen in dark crowns. Instead of having deep Black feathers, its crown is Citrine, with some feathers edged and shafted in Olivaceous Black (color standards of Ridgway 1912). Adjusting for the paler variation of dark crown feathers, its cap measurements were not unusual for a male. Another specimen, an immature August female from Alaska (UAM 6372), displays a striking lack of yellow pigment, or a hypoxanthic condition. Although its wings and tail are much like those of other Wilson's Warblers, its belly and undertail coverts are Olive-Buff, washed with Baryta Yellow on the throat and sides. Its back is a Dark Olive-Gray, changing to Olive Citrine at the crown; the superciliary line and eye ring are Barium Yellow. Its identification as a *Wilsonia pusilla* lacking yellow pigment was confirmed by K. C. Parkes in 1993, and its measurements are within expectation for a female of the species.

The differences in the discriminant functions (eqs. 1–3) may reflect morphological variation between the sampled populations due to environmental effects (such as feather wear from migration) and/or heritable geographic variation in phenotype. It is likely that the different rates of success of the sexing algorithms may be

attributed to varying levels of heterogeneity within the sampled populations. The Mexico sample, representative of the migrant stream encountered in eastern Middle America, is comprised of three different subspecies of all age classes. The eigenvalue for that group's discriminant function is therefore lower than that for the homogeneous Alaska-British Columbia group, which is all one subspecies, *pileolata*, and contains more adult birds (Table 2). A higher proportion of adult birds improves the success rate, as adults have all undergone a partial prealternate head molt (Dwight 1900), which can increase the cap length, an important character. The functions appear robust despite the lack of multivariate normality. The violations of multivariate normality stem from the categorical nature of some characters, the sexually bimodal nature of the data, and the within-sex lack of normality in all of the individual morphological characters except wing chord and tail length even when males and females were considered separately (not shown).

The discriminant functions presented can be used to determine an individual's probability of being male (p_m) with the following equation:

$$p_m = (1 + e^q)^{-1}, \quad (4)$$

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

$$q = -D \times [1.9 + |\ln(r^4)| - (r \times \ln(r))]. \quad (5)$$

The probability that an individual is female is $p_f = 1 - p_m$. These equations allow the close approximation of the posterior probabilities generated with the more complex Bayes' theorem (see discussion in Winker et al. 1994). It is optimized for Eqn. 1. To estimate probabil-

ities for the Mexican sample, substitute the following value of:

$$q = -D \times [1.75 + \ln(r^*)] - (3r \times \ln(r)). \quad (6)$$

To estimate probabilities for the Alaska-British Columbia group, replace the constant 1.75 in Eqn. 6 with 1.0. Sex ratios are calculated from Table 2. Readers can review an example of how to use discriminant functions to calculate probabilities in Winker et al. (1994).

The value r can be modified in Equations 5 and 6 to reflect different sex ratios if such are found to occur in one's sample (through examination of gonads, or cloacal protuberances and incubation patches during the breeding season). Although the ratios of the samples used here are unbiased and approximate what mistnetters might encounter, habitat and season may call for an adjustment in the sex ratio if evidence supports it. For example, Chase et al. (1997) reported a male bias of 2:1 in summer breeding-ground captures. On the wintering grounds the sex ratio is closer to unity (Ramos 1986), but there are deviations depending on habitat. Rappole (1986) found males to be less common in Veracruz seral stages and females to be rare in primary rain forest. Timing is also a factor; for example, males migrate north significantly earlier in the spring than females, which might result in a stronger male bias earlier during spring in northern regions (Ramos 1986; Otahal 1995).

Modifications in the equations may also be made to account for shrinkage in museum specimens (Winker 1993; Winker et al. 1994). A subsample of 27 Wilson's Warblers were measured before preparation as museum specimens and then again four or more weeks later after they had dried. The measurements were performed by a single observer (JJW) and included wing chord, tail length, tarsus length, and bill height, width, and length. Although limited by small sample size, paired t -tests showed statistically significant shrinkage in two measurements. The mean tail length shrank by 3.3%, and the mean bill width shrank by 2.5%. Investigators applying these sexing algorithms to living or recently dead birds may wish to multiply values for tail length by the correction factor of 0.967. Slight shrinkage in the other bill measurements and slight increase in wing chord and tarsus were not significant. Shrinkage in the

measured characters may have been affected by freeze-drying, however, because not all specimens were fresh. Mean ninth primary length and mean cap length were not examined for shrinkage. Primary feathers have been shown not to shrink (Jenni and Winkler 1989), and shrinkage in cap length may be difficult to determine precisely, depending on whether specimens were prepared with skull in or out of the skin.

Sexual size dimorphism observed in the lengths of wing chord, tail, and eighth and ninth primaries may be influenced by a number of factors, including sexual selection, fertility selection, and survival selection. Sexual differences in microhabitat preference on the wintering grounds may also explain the evolution of size dimorphism in this species (Rappole 1986). Because *W. pusilla* demonstrates size differences in morphological characters associated with flight (e.g., wing chord, primaries, tail) rather than in mass or bill size, it is possible that these characters reflect differences in flight styles demanded by spatial differences in microhabitats. However, this study cannot differentiate among the possible reasons for the observed dimorphism or determine any functional explanation.

Instead of being considered sexually dimorphic, *W. pusilla* may be more properly termed polymorphic, as suggested by Rappole (1986). Males have larger black caps on average, but there is an intergradation between the sexes. This "andromimesis" may provide females with a competitive edge in agonistic displays on the wintering grounds (Rappole 1986). There is some evidence that dark head plumage in females of the congener *Wilsonia citrina* is not related to age (Morton 1989), but the development and adaptive value of dark caps in some female Wilson's Warblers remain poorly understood. Regardless, the overlap between male and female plumage characteristics is substantial, and size dimorphism also shows enough sexual overlap to defy complete separation.

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