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Source: The Condor, 110(3) : 569-574

Published By: American Ornithological Society

URL: https://doi.org/10.1525/cond.2008.8482

The Condor 110(3):569–574
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PHENOTYPIC VARIATION IS CLINAL IN THE YELLOW-THROATED WARBLER

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Abstract. Subspecies are assumed to have unique evolutionary histories, but molecular data sometimes contradict subspecies designations based on morphology. A recent genetic survey of the Yellow-throated Warbler (*Dendroica dominica*) found that none of its three continental subspecies qualified as evolutionarily significant units. I performed a range-wide morphological assessment of the continental Yellow-throated Warbler subspecies in an effort to quantify their differences and examine if and how subspecific differences related to geography. Results indicated much overlap in the morphological characters most important in diagnosing Yellow-throated Warbler subspecies (bill length and the proportion of yellow in the lores), and discriminant function analysis failed to correctly assign most individuals, especially those collected near a subspecies border. There was a strong west-to-east clinal change in bill length and the proportion of yellow in the lores and no evidence of discrete morphological groups. I recommend eliminating the subspecies *D. d. albilora* and *D. d. stoddardi* because they cannot be reliably diagnosed by morphology or mtDNA.

Key words: Dendroica dominica, *geographic variation, subspecies, Yellow-throated Warbler.*

La Variación Fenotípica es Clinal en *Dendroica dominica*

Resumen. Se asume que las subespecies tienen historias evolutivas únicas, pero en algunos casos los datos moleculares contradicen las designaciones de subespecies que se basan en la morfología. Un estudio genético reciente sobre *Dendroica dominica* encontró que ninguna de las tres subespecies continentales cualificó como una unidad con significancia evolutiva. Realicé una evaluación de la morfología de las subespecies continentales de *D. dominica* a través de toda su área de distribución con la intención de cuantificar sus diferencias y examinar, sí y como las diferencias entre las subespecies se relacionan con la geografía. Los resultados indicaron una alta sobreposición en los caracteres morfológicos más importantes para la diagnosis de las subespecies de *D. dominica* (largo del pico y la proporción de amarillo del área loreal), y la mayoría de los individuos no fueron asignados de forma correcta con un análisis de función discriminante, especialmente aquellos individuos que fueron colectados en los bordes de distribución de las subespecies. Hubo un cambio clinal fuerte desde el oeste hacia el este en el largo del pico y en la proporción de amarillo del área loreal, y no hubo evidencia de grupos morfológicos discretos. Recomiendo eliminar las subespecies *D. d. albilora* y *D. d. stoddardi* debido a que éstas no pueden ser diagnosticadas por morfología ni por ADNmt de forma confiable.

The rise of the biological species concept during the mid-twentieth century fostered an increase in the number of described avian subspecies, and, though the utility of the subspecies rank was questioned (Wilson and Brown 1953), it was believed that variation within species represented local adaptations of evolutionary significance (Mayr 1982). The assumption that subspecies have unique evolutionary histories has led to the use of subspecies in roles that require their evolutionary independence, such as taxonomy, comparative studies, and conservation plans (Zink 2004). Many of the morphological traits used to designate subspecies, however, can be directly affected by the rearing environment (James 1983), and when morphological subspecies are subjected to independent tests of evolutionary isolation (i.e., neutral molecular markers), they often fail to meet the requirements of evolutionarily significant units (Ball and Avise 1992, Zink 2004).

The above situation is exemplified by the Yellow-throated Warbler (*Dendroica dominica*), which is a midsized warbler with a black face, white supercilium, and bold yellow throat patch. It is a Neotropical migrant that breeds in the southeastern United States and is divided into three continental subspecies (a fourth subspecies is confined to the Bahamas and will not be considered here; Hall 1996). These subspecies were not named following any rule, and their description is based on approximately 15–20 individuals per subspecies taken from the extreme eastern or western portion of their ranges (Ridgway 1902, Sutton 1951). The subspecies differ in morphology, ecology, and plumage. The eastern *dominica* is reported to have a long bill (12.4–15.0 mm, sexes combined; Curson et al. 1994) and yellow lores, breed in mixed forests or cypress (*Taxodium* spp.) swamps, and to winter mainly in the Caribbean (Curson et al. 1994, Hall 1996). The western *albilora* is reported to be larger than *dominica* (Ridgway 1902), have a short bill (10.9–12.7 mm, sexes combined; Curson et al. 1994), have white lores, breed in sycamore (*Platanus* spp.) bottomlands or cypress swamps, and to winter mainly in Central America (Hall 1996). *D. d. stoddardi* is confined to coastal Alabama and the panhandle of Florida, where it may be resident (Hall 1996). It is reported as being indistinguishable from *dominica* (Curson

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Manuscript received 17 October 2007; accepted 30 June 2008.

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The Condor, Vol. 110, Number 3, pages 569–574. ISSN 0010-5422, electronic ISSN 1938-5129. © 2008 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/cond.2008.8482

et al. 1994) except in having a longer and more slender bill (14.0–17.0 mm, sexes combined; Sutton 1951). There is also a migratory long-billed form on the Delaware-Maryland-Virginia ("Delmarva") peninsula (Ficken et al. 1968) that is reported to be indistinguishable from *stoddardi* in appearance (Stevenson 1982), despite a geographical separation of over 1000 km.

Distributions of eastern and western morphological subspecies of the Yellow-throated Warbler correspond spatially to a phylogeographic break reported for several vertebrate species (Soltis et al. 2006), including some fish (Wiley and Mayden 1985, Bermingham and Avise 1986), water snakes (Lawson 1987), and the Carolina Chickadee (*Poecile carolinensis*; Gill et al. 1999). Thus, in a recent evolutionary study of the Yellow-throated Warbler, a genetic division was assumed a priori to correspond to the observed morphological partition, and it was hypothesized that the Yellow-throated Warbler fit temporally into this comparative phylogeographic framework (McKay, in press). Surprisingly, however, mitochondrial DNA (mtDNA) control region sequences indicated a pronounced lack of differentiation between Yellow-throated Warbler continental subspecies (McKay, in press). Potential causes for this discrepancy are that morphological traits have evolved faster than mtDNA or that morphological subspecies in the Yellow-throated Warbler do not correspond to evolutionary lineages. As there has been no range-wide quantitative assessment of phenotypic variation in the Yellow-throated Warbler, it is unknown whether variation in the extent of yellow coloration in the face and variation in bill shape varies discretely or gradually across the species' range. Here, I assess the morphological subspecies of the Yellow-throated Warbler in an effort to quantify their differences and examine if and how differences relate to geography.

METHODS

SAMPLES AND MEASUREMENTS

During the breeding season (April and May) of 2006, I collected 89 specimens from 10 populations located across the Yellow-throated Warbler's continental breeding range (Table 1, Fig. 1). These specimens were the same as those included in the phylogeographic study of this species (McKay, in press) and have been deposited in the J. F. Bell Museum of Natural History, University of Minnesota, St. Paul (BMNH46327-415). I measured seven morphological characters, including those used to differentiate subspecies (i.e., bill length, bill width, and the proportion of yellow in the lore). Bill depth (at the anterior edge of the nare), tarsus length, wing chord, and tail length (at the central rectrix) were also measured. Bill measurements and tarsus length were taken to the nearest 0.01 mm using digital calipers, and wing chord and tail length were measured to the nearest 0.5 mm using a wing rule. I measured tarsus length and all bill characters three times for each individual and used the mean in analyses. The proportion of yellow in the lore was quantified as follows: I loaded close-up photographs of the left lore of each Yellow-throated Warbler specimen into the program ImageJ for Windows^{TM} (available at <http://rsb.info.nih.gov/ij/>) and measured the total area of the lore, considered as the white or yellow area from the posterior end of the bill to the most anterior point of the eye. Using the same procedure, I measured the yellow area of the lore. I divided the yellow area of the lore by the total area of the lore to estimate the proportion of yellow within the lore. Due to damage sustained during collection, 14% of specimens had some missing data, but this resulted in no more than 6% of data missing for any character. Bill measurements (length, width, and depth) from 51 museum specimens (housed at the Louisiana State University Museum of Natural Science; specific museum catalog numbers are available upon request) collected between 7 March and 23 June 1896–1999 were included in subspecies-level analyses but were not assigned to a population. These specimens were included to determine whether any patterns changed when birds from multiple years were added to analyses. I used only measurements from males in all analyses.

STATISTICAL ANALYSES

I tested each morphological character for departures from normality. I then determined two-tailed Pearson correlation coefficients for all pairwise comparisons between body characters. Next, I compared the means of all characters with an analysis of variance (ANOVA), first with samples grouped by population and secondly with samples grouped by subspecies (*dominica*, *albilora*, or *stoddardi*). A Tukey's HSD post-hoc test was used to determine maximum homogeneous groupings of populations and of subspecies for each character. The two characters most diagnostic of subspecies, bill length and the proportion of yellow in the lore, were plotted to determine whether they formed discrete clusters.

To further evaluate the distinctiveness of each subspecies, I grouped specimens by subspecies and applied a stepwise discriminant function analysis using all seven morphological characters. Prior probabilities were computed from group sizes, and missing values were replaced with the mean for that character. The leave-one-out method was used to cross-validate the accuracy

TABLE 1. Numbers of male Yellow-throated Warblers examined across the continental U.S. Map numbers refer to numbers plotted on the map in Figure 1.

Map No.	Population	State	Subspecies	*n*	Locality
1	LA	Louisiana	*albilora*	4	Pointe Coupee Parish
2	MO	Missouri	*albilora*	11	Oregon, Ripley County
3	AL–West	Alabama	*albilora*	8	Lawrence County
4	AL–East	Alabama	*dominica*	12	Conecuh, Macon, Talladega County
5	FL–West	Florida	*stoddardi*	9	Wakulla County
6	OH	Ohio	*albilora*	12	Lawrence County
7	NC	North Carolina	*dominica*	9	Graham County
8	FL–East	Florida	*dominica*	9	Marion County
9	MD–West	Maryland	*dominica*	7	Charles, Prince George, St. Mary's County
10	MD–Delmarva	Maryland	*dominica*	8	Worcester County

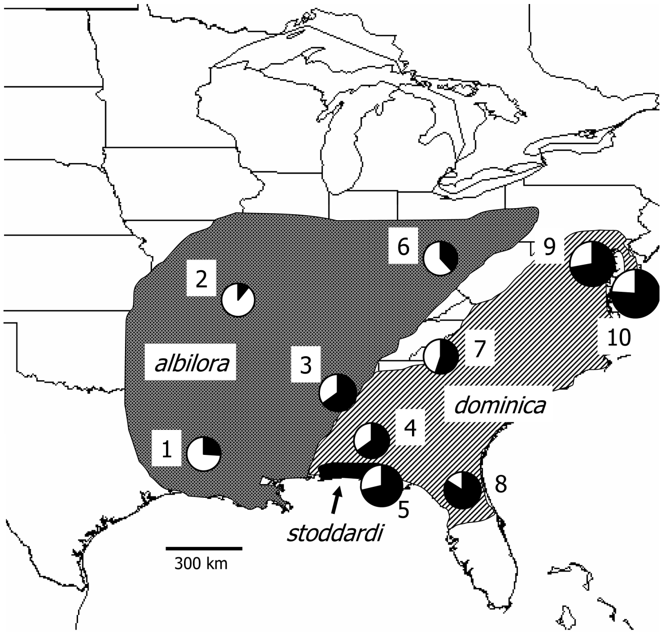

FIGURE 1. Map of the eastern United States showing the approximate breeding range of continental Yellow-throated Warbler subspecies (adapted from Dunn and Garrett 1997) and geographic locations of sampled populations in this study (circles). The pie chart represents the average proportion of yellow in the left lore (indicated in black) for that population. The size of the circles reflects the relative difference in average bill length. Numbers correspond to populations in Table 1.

of the group assignments. Finally, to check for patterns between characters and geography, I computed two-tailed Pearson correlation coefficients for all pairwise comparisons between both latitude and longitude for all characters. I used SPSS 12.0 for Windows^{TM} (SPSS Inc., Chicago, Illinois) for all statistical analyses, and considered $P \leq 0.05$ statistically significant.

RESULTS

All data conformed to normality. Adding data from museum specimens from different years did not affect results, so it is unlikely that interannual phenotypic variation was a confounding factor. Two pairs of size measurements, among the six size variables measured, were significantly correlated: bill width and bill depth ($r = -0.60$, $n = 133$, $P < 0.001$), and wing chord and tail length ($r = 0.36$, $n = 83$, $P < 0.001$). ANOVAs indicated that five characters differed significantly among populations (Table 2) and four differed significantly among subspecies. Three of these characters were the same: bill length (population: $F_{85} = 16.8$, $P < 0.001$; subspecies: $F_{137} = 12.9$, $P < 0.001$), bill width (population: $F_{85} = 12.9$, $P < 0.001$; subspecies: $F_{137} = 7.0$, $P < 0.001$), and the proportion of yellow in the lore (population: $F_{87} = 18.5$, $P < 0.001$; subspecies: $F_{87} = 25.7$, $P < 0.001$). In addition, bill depth ($F_{80} = 8.1$, $P < 0.001$) and tail length ($F_{87} = 2.1$, $P < 0.04$) differed significantly among populations, and wing chord ($F_{82} = 3.4$, $P < 0.04$) differed significantly among subspecies. Tukey's HSD test revealed overlap between all groups in all characters differing significantly among both populations and subspecies; thus, no exclusive groups were identified. Bill length plotted against the proportion of yellow in the lore resulted in overlap among all subspecies (Fig. 2).

Discriminant function analysis produced a final model with one function (eigenvalue = 0.64) and, of the seven characters, included only the proportion of yellow in the lore. The overall Wilk's lambda was significant ($\lambda = 0.61$, $\chi^2_{33} = 31.0$, $n = 89$, $P < 0.001$). Classification and cross-validation both indicated that 66% of all individuals were assigned to the correct subspecies (Table 3). Removing *stoddardi* did not affect the classification results of *dominica* or *albilora*. The majority (76%) of incorrectly assigned individuals were collected near the *dominica-albilora* border in Alabama, Ohio, and North Carolina.

Four characters were significantly correlated with geography. Bill length ($r = -0.41$, $n = 138$, $P < 0.001$; Fig. 3a) and the proportion of yellow in the lore ($r = -0.57$, $n = 87$, $P < 0.001$; Fig. 3b) were negatively correlated with longitude. Tail length ($r = 0.37$, $n = 88$, $P < 0.001$; Fig. 3c) and bill depth ($r = 0.22$, $n = 133$, $P < 0.01$; Fig. 3d) were positively correlated with latitude, whereas the proportion of yellow in the lore ($r = -0.32$, $n = 87$, $P < 0.005$) was negatively correlated with latitude.

DISCUSSION

My results indicated that there were significant differences in bill length, bill width, wing chord, and the proportion of yellow in the lore when samples were grouped by subspecies. There were also significant differences in several characters when samples were grouped by population. Post-hoc tests, however, did not place populations into exclusive groups that corresponded to subspecies, and instead indicated that populations were more similar to their nearest geographical neighbor than they were to their subspecies. The most common, albeit arbitrary, cutoff point used to define subspecies in ornithology is 75% diagnosability (Amadon 1949), and discriminant function analysis failed to assign at least 75% of either *albilora* or *stoddardi* individuals to the correct subspecies, suggesting that there is only one continental Yellow-throated Warbler subspecies. The discriminant function analysis correctly grouped individuals from extreme eastern or western populations into subspecies, but failed to correctly assign most *albilora* individuals from the more central Ohio and western Alabama populations and some *dominica* individuals from the more central North Carolina and eastern Alabama populations. Bill length and the proportion of yellow in the lore both gradually increased from west to east rather than showing a sharp break, as would be indicative of discrete groups. Plotting bill length against the proportion of yellow in the lore resulted in an undifferentiated cluster of points.

Although *stoddardi* individuals did have longer bills on average than *dominica* specimens, discriminant function analysis failed to distinguish *stoddardi* and assigned these individuals to *dominica*. The longer-billed birds on the Delmarva peninsula did not differ significantly from the nearby population on the western shore of Maryland. Thus, the three longest-billed populations that I sampled were also the three populations within 30 km of the coast. This supports a suggestion by Ficken et al. (1968) that shorter-billed Yellow-throated Warbler populations are more prevalent inland, where they may be more associated with deciduous forests, and longer-billed forms are prevalent in coastal areas, where they may be more associated with long-coned pine forests. This suggests that *stoddardi* may be an isolated example of what is a common form along the Atlantic coast. As suggested by Ficken et al. (1968), this could be an adaptive response to more

TABLE 2. Morphological and plumage character measurements (mean ± SD) and results of ANOVAs testing for significant differences among ten populations of the Yellow-throated Warbler in the continental U.S. See Table 1 for detailed population information.

Character	Population										F
	LA	MO	AL–West	AL–East	FL–West	OH	NC	FL–East	MD–West	MD–Delmarva	
Bill length (mm)	9.16 ± 0.40	9.04 ± 0.56	9.57 ± 0.31	9.35 ± 0.35	10.07 ± 0.44	9.17 ± 0.41	9.26 ± 0.30	9.45 ± 0.32	10.45 ± 0.68	10.91 ± 0.49	16.8^{**}
Bill width (mm)	2.82 ± 0.13	3.47 ± 0.12	2.86 ± 0.13	3.44 ± 0.54	3.35 ± 0.27	2.84 ± 0.14	2.86 ± 0.11	2.78 ± 0.22	2.82 ± 0.15	2.82 ± 0.01	12.9^{**}
Bill depth (mm)	3.15 ± 0.09	3.57 ± 0.16	3.23 ± 0.11	3.36 ± 0.19	3.39 ± 0.14	3.18 ± 0.15	3.20 ± 0.01	3.16 ± 0.11	3.24 ± 0.08	3.27 ± 0.15	8.1^{**}
Tarsus length (mm)	17.3 ± 0.4	16.7 ± 0.6	16.8 ± 0.3	16.9 ± 0.8	16.7 ± 0.3	16.6 ± 0.3	16.6 ± 0.5	16.8 ± 0.4	16.9 ± 0.6	17.2 ± 0.4	1.7
Wing chord (mm)	67.4 ± 2.3	67.8 ± 2.1	67.1 ± 1.2	68.2 ± 0.6	66.2 ± 1.4	67.0 ± 1.8	67.4 ± 1.5	66.8 ± 1.2	67.7 ± 0.8	67.8 ± 1.9	1.4
Tail length (mm)	48.4 ± 1.8	49.9 ± 1.5	50.0 ± 1.9	48.9 ± 1.1	48.4 ± 1.7	49.8 ± 1.5	49.1 ± 0.8	48.8 ± 1.1	49.7 ± 0.5	50.4 ± 1.3	2.1^{*}
Proportion of yellow in the lore	0.26 ± 0.45	0.11 ± 0.05	0.65 ± 0.12	0.65 ± 0.18	0.71 ± 0.07	0.38 ± 0.27	0.55 ± 0.10	0.84 ± 0.09	0.72 ± 0.10	0.76 ± 0.12	18.5^{**}

$^{*}P < 0.05$, $^{**}P < 0.001$.

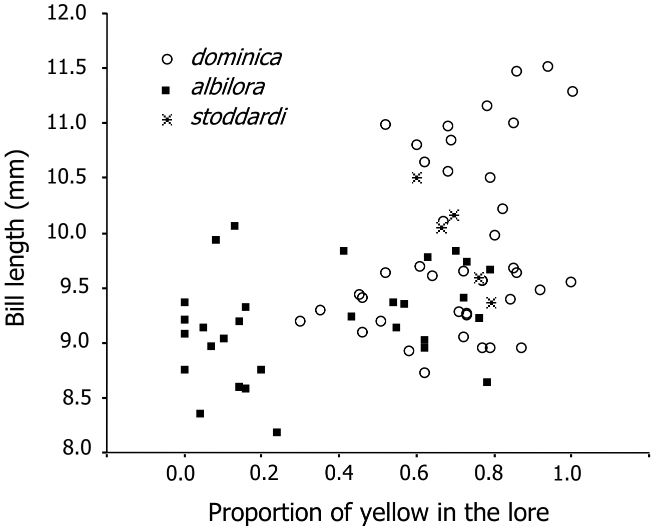

FIGURE 2. A scatterplot of the two most discriminating characters of Yellow-throated Warbler subspecies: bill length and the proportion of yellow in the lore. The overlapping points suggest a single interbreeding population, which is inconsistent with two or more independently evolving subspecies.

specific coastal habitat, perhaps due in part to competition with Pine Warblers (*Dendroica pinus*).

Differences in bill shape among avian subspecies can be highly heritable (Schluter and Smith 1986) or greatly influenced by the rearing environment (James 1983). Therefore, the clinality in bill lengths observed here in the Yellow-throated Warbler may: 1) have a completely genetic basis, 2) be largely the result of phenotypic plasticity, or 3) result from an interaction between genetic and environmental components. Transplant experiments with the Yellow-throated Warbler, such as those performed by James (1983) with Red-winged Blackbirds (*Agelaius phoeniceus*), could detect phenotypic plasticity in Yellow-throated Warbler bill shape. Lore color would likely have a genetic component, although it too could be heavily influenced by the environment. Carotenoids are probably responsible for the Yellow-throated Warbler's yellow throat and lores, and increased carotenoid consumption can cause yellows and reds to extend into other parts of a bird's plumage (Hill 2002). Because eastern and western Yellow-throated Warblers differ in their primary breeding habitat, it is likely they ingest different levels of carotenoids. A diet higher in carotenoids in *dominica* may make it more likely to allocate carotenoids to

TABLE 3. Predicted classification of Yellow-throated Warbler subspecies based on stepwise discriminant function analysis of seven morphological characters.

	Predicted: *dominica*	Predicted: *albilora*	Predicted: *stoddardi*	Correct classification (%)
dominica	40	5	0	89
albilora	16	19	0	54
stoddardi	9	0	0	0

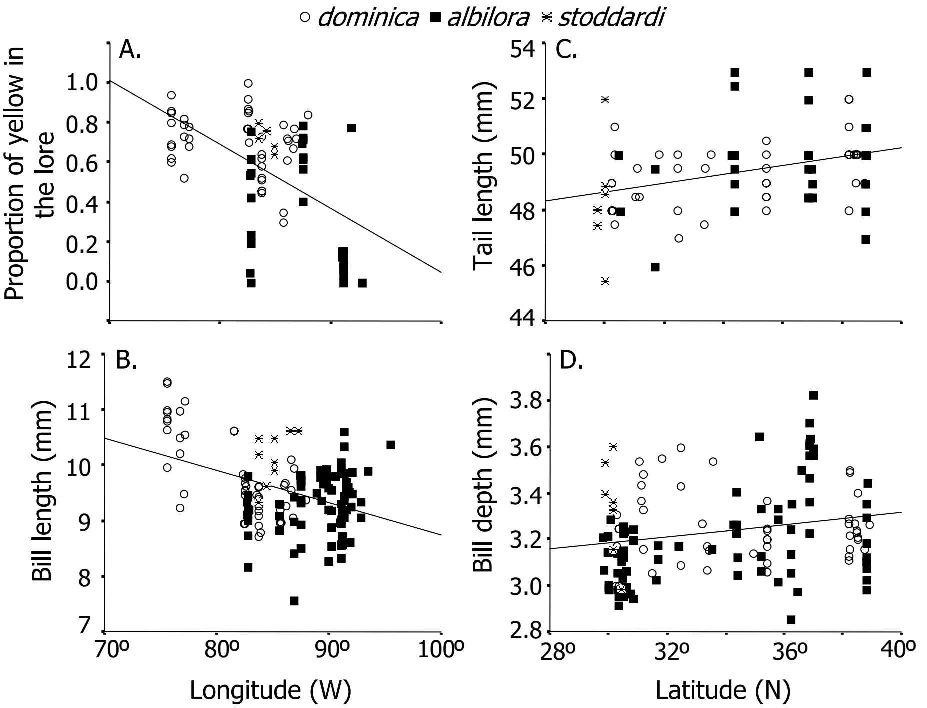

FIGURE 3. All morphological characters of the Yellow-throated Warbler, coded by subspecies, that significantly correlate with geography. The proportion of yellow in the lore and bill length decrease from west to east. The gradual transition without discontinuous breaks is inconsistent with discrete subspecies. Tail length and bill depth increase from south to north. This pattern is consistent with Bergmann's rule.

the lores. Blue tits (*Cyanistes caeruleus*) obtained more carotenoids in a deciduous than a coniferous forest (Partali et al. 1987). This is the opposite of what would be expected for the Yellow-throated Warbler, but because it is unknown exactly how the Yellow-throated Warbler's diet differs between eastern and western subspecies, it remains possible that the observed variation in lore color results from different diets. Ultimately, the underlying cause of the clinal patterns observed here cannot be resolved with these data. However, the relative amount of genetic versus environmental contribution to phenotypic variation in the Yellow-throated Warbler is probably irrelevant for deciding whether subspecies accurately reflect evolution within this taxon, and, therefore, whether or not they should be retained.

Overall, my observations indicated that there was much overlap in the morphological characters used to distinguish Yellow-throated Warbler subspecies. Average differences could distinguish subspecies when individuals from across the subspecies' range were included, but average differences have been argued to be insufficient for diagnosing subspecies (Patten and Unitt 2002). The failure of these analyses to identify discrete groups within the Yellow-throated Warbler corroborates the results of mtDNA surveys (McKay, in press), which indicated that Yellow-throated Warbler subspecies are not evolutionarily significant units (Moritz 1994). While there is an interesting pattern of phenotypic variation within the Yellow-throated Warbler, there appears to be little value in subdividing this clinal continuum into different subspecies (Rising 2007). Therefore, I recommend eliminating the *albilora* subspecies. It is clear that some avian subspecies have been described with insufficient evidence and do not correspond to evolutionary lineages (Pruett et al. 2004). This seems to be the case with *stoddardi*, as it cannot be reliably diagnosed and there is no evidence that it is different from other long-billed forms common along the Atlantic coast. Therefore, I also recommend eliminating the subspecies *stoddardi*.

G. Brewer, B. Hitch, M. Hoffman, G. Jett, and K. Rambo provided field assistance. I thank Steve Cardiff and the Louisiana State University Museum of Natural Science for access to their collection. This research was funded by grants from the Frank M. Chapman Memorial Fund, the American Museum of Natural History, and the Walter F. Coxe Research Fund, Birmingham Audubon Society. L. Carter helped with data digitization, and I. Lovette, J. Hudon, D. Dobkin, G. Hill, S. Santos, C. Guyer, and the Hill laboratory made significant improvements to the manuscript.

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