The Condor 93:712–723

GEOGRAPHICAL MORPHOLOGY OF MALE YELLOW WARBLERS[1]

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Abstract. Morphological measurements were taken on study skins of breeding Yellow Warbler (*Dendroica petechia*) males collected from near the Arctic Circle to the Equator. The data were smoothed using LOESS (a non-linear, non-parametric scatterplot smoother), to elucidate patterns of geographic variation. Individuals are generally larger in the south than in the north, although birds from the Caribbean region show the reverse trend. Wing length follows the overall size trend poorly. Proportionate wing length is much shorter and more rounded in the non-migratory tropical populations, than in the far north. This finding supports the hypothesis that variation in wing length is related to migratory distance. Therefore, wing length is a poor choice for an overall size measure in this species. Comparison of morphological variation with climatic variation in this species provides counter-evidence to James's (1970) modification of Bergmann's Rule, that larger birds should occur in colder, drier climates; the largest Yellow Warblers are in warm, humid climates. In addition, no support for Bergmann's Rule can be detected analyzing the North American or tropical populations separately. Likewise, Allen's Rule (that appendages should be smaller or shorter in cold climates) also is unsupported by the Yellow Warbler.

Key words: Morphology; geographic variation; migration distance; Bergmann's Rule; Parulinae; Yellow Warbler.

INTRODUCTION

Describing patterns of morphological variation in bird species is a first step to formulating hypotheses that can open new, interesting avenues of research. Zink and Remsen (1986) noted that there have been few descriptions of morphological variation for widespread species over their entire breeding range. There have been even fewer studies of widespread species that have both temperate and tropical breeding populations. I describe here variation in morphology of the Yellow Warbler (*Dendroica petechia*), one of the most widespread of New World passerines. Using this morphological description, I then examine choice of a size measure, and some hypotheses that can be addressed from knowledge of morphological variation, such as Bergmann's Rule (body size in homeotherms tends to increase in colder climates), Allen's Rule (appendage length tends to decrease in homeotherms in colder climates), and the relationship between migratory distance and length and shape of birds' wings.

The Yellow Warbler has the largest breeding range of any wood-warbler (Parulinae). It breeds in all moist habitats across North America, south through the Caribbean islands and along the coasts of Middle America to the northern coasts of South America, even to the Galapagos Islands. Originally three groups of these populations, each with distinct differences in male plumage, were described as separate species. Although the three groups subsequently were lumped into *Dendroica petechia* (Lowery and Monroe 1968), the old species names make convenient labels for the plumage types. I will use the old names, therefore, to refer to these groups: "Yellow" Warbler (*D. p. aestiva* subspecies group; the migratory form breeding in the United States and Canada), "Golden" Warbler (*D. p. petechia* subspecies group; the non-migratory form of the Caribbean), and "Mangrove" Warbler (*D. p. erithachorides* subspecies group; the non-migratory form of the coasts of Middle America and northern South America).

METHODS AND MATERIALS

I used study skins only of adult male warblers. To restrict the analysis to breeding populations, I used only "Yellow" Warbler specimens obtained during the month of June. Because "Golden" and "Mangrove" Warblers are not known to migrate, and because the number of specimens available of these two forms is much smaller, I used "Golden" and "Mangrove" Warbler specimens collected at any time during the year.

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[1] Received 17 December 1990. Final acceptance 25 March 1991.

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On each of 617 specimens of warblers thus selected, I measured six characters: bill length (exposed culmen); bill width (at base); ninth primary measurement (= distance from bend of the wrist to tip of ninth primary; a measurement commonly referred to as "wing length"); sixth primary measurement (= distance from bend of the wrist to tip of sixth primary); tail length; and tarsus length. I also recorded body mass of the bird when available. The two wing measurements together can provide some information about wing pointedness for the hand-wing; if the ninth-primary measurement is longer than the sixth, the tip of the wing is more pointed than in the reverse case. That these wing measurements might be of interest on *Dendroica petechia* was suggested by Aldrich (1942). Because measurements such as these are usually log-normally distributed, I took the logarithm (base 10) of all of the measurements (Mosimann and James 1979). I chose as a size measurement the geometric mean of the six morphological measurements (hereinafter referred to as geometric mean), the measure of size used by Darroch and Mosimann (1985). This size measurement was available on all specimens. Body mass, while perhaps a more intuitive measure of size, was available on only a small fraction of the specimens I used. At the next step, I subtracted the geometric mean from each of the original (logged) measurements to produce proportionate measurements. This gave me a total of 13 characters: six measurements, six proportionate measurements, and the geometric mean. I then averaged the measurements for all individuals for each two-degree latitude-longitude block for which I had data, to obtain a set of measurements for each of 148 two-degree blocks.

I obtained information on long-term average June temperature and average June vapor pressure, a measure related to absolute humidity by the inclusion of barometric pressure. These data were collected from published sources (World Meteorological Organization 1971; Meteorological Office, London, 1958). I obtained climate data for 65 of the 148 two-degree blocks for which I had morphological data.

I used LOESS, a non-linear, non-parametric scatterplot smoother (Cleveland and Devlin 1988 and references therein) to analyze the data. LOESS is useful for description of patterns, and has the advantage for this purpose that no model is fitted. The amount of smoothing is controlled by the smoothing neighborhood, f. The f can vary between 0 and 1. The higher the value of f, the smoother the fitted curve. I used an M-plot to choose the f value (Cleveland and Devlin 1988; interpretation of M-plots is like that of C_p-plots described by Mallows 1973). The M-plot shows the trade-off between variance and bias for different levels of f. LOESS can smooth multivariate data. For the geographic data I used latitude and longitude as the independent variables X_1 and X_2, and the morphological character being analyzed as the dependent variable Y.

There are large lacunae in the geographical data set caused by the Caribbean Sea, Pacific Ocean, and other areas of non-occurrence of the warblers, over which I did not wish to smooth. Therefore, I smoothed the data in three units: North America; Caribbean Islands + South America east of Colombia; and Middle America + South America west of Venezuela. The smoothed surfaces for these three regions are presented together on single maps. Because the entire map was not smoothed as a unit, there can be discontinuities between the smoothed surfaces of the three regions.

I also used parametric multiple regression to make climate vs. morphology comparisons.

RESULTS

The correlation of geometric mean with body mass is $r = 0.42$ ($n = 19$, $P = 0.071$). This is higher than that of ninth primary measurement with body mass ($r = 0.15$, $n = 20$, $P > 0.500$). Body mass shows a significant negative correlation with latitude ($r = -0.47$, $n = 20$, $P < 0.050$).

From the M-plot (Fig. 1), I chose f = 0.45. Although this does not produce the minimum bias, smoothing at f = 0.45 has low bias, and should remove enough "noise" from the data to facilitate interpretation. All data smoothed using LOESS were smoothed at f = 0.45.

Inspection of the maps showed that there were no sharp discontinuities between the three regions that were smoothed separately. For example, on the map showing size variation (Fig. 2), birds are the same size from two-degree blocks that are adjacent but on opposite sides of the division between smoothing regions on the northern coast of South America, and the trend along that coast appears to be smooth. Birds in northern Mexico and Arizona in the Middle American and North American regions are not the same size, although

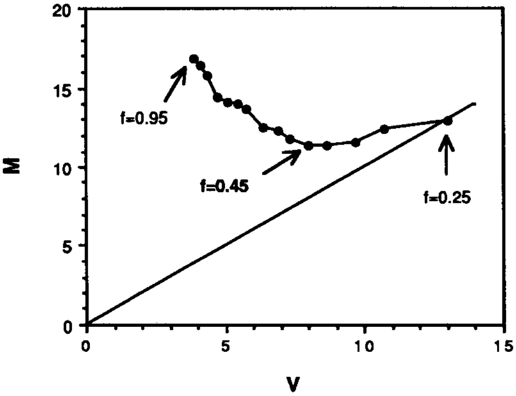

FIGURE 1. M-plot of data for geometric mean of all six characters from North America. The M-plot shows the trade-off between variance (V) and a measure of variance + bias (M). The points represent V and M at successively larger values of f (from *right to left*), beginning at f = 0.25 (that is, the smoothing neighborhood includes one-quarter of the data) and increasing in increments of f of 0.05 to f = 0.95 (the smoothing neighborhood includes 95 percent of the data). The value f = 0.45 was chosen for all further smoothing because it has low bias (although not the minimum) *and* low variance (although not the minimum).

they are close, and again the trend seems to be continuous from one smoothing region to the other. This indicates that trends between the regions probably were not seriously affected by smoothing the regions separately, and that the trends shown probably do reveal underlying morphology.

From the smoothed maps I categorized the variation of the 13 morphological characters into six types. I present one representative map for each of the six. I describe any differences between the representative map and the maps for the other characters with the same type, but for which maps are not shown.

Type 1. The geometric mean shows a fairly smooth increase from north to south (Fig. 2), although it is steeper along the southern border of the United States. Birds in northern Alaska and Canada are the smallest, whereas birds on the Equator are the largest. Within North America, relatively large birds are found in the southwest, of course, but also in the northeast (Newfoundland and New Brunswick) and southern Alaska (Kodiak Island). Birds from the Great Plains region are larger than birds from the southeast or northwest.

In the tropics in Middle America the trend of the "Mangrove" Warblers is fairly steadily larger to the south. In the Caribbean, however, the trend is reversed, with the largest birds occurring in the Florida Keys and the smallest in the southern Lesser Antilles and on the eastern coast of Venezuela. Birds from the Florida Keys, in fact, are among the largest in the species, as large as those from the Pacific coast of South America.

Two other morphological characters follow this general pattern of variation. Bill width shows almost exactly the same pattern. Bill length shows less variation but the same general trend (i.e., the surface is more flat) within North America and within the tropics. There is, however, a greater discontinuity between the tropical forms and North American birds in bill length than there is in the geometric mean.

Type 2. Tarsus length shows the same general trend to increase from north to south as do the Type 1 characters (Fig. 3). The longest tarsi, however, occur in birds from the northern Bahamas, and birds from near the Equator have nearer to average-length tarsi. Also, in North America all tarsi are short, but the shortest do not occur the farthest north. Through the Caribbean tarsus length increases from south to north, the smallest being on Barbados. In Middle America the shortest tarsi are from birds in the middle (Guatemala to Panama), with longer tarsi to the south and north. Tail length shows much the same pattern.

Type 3. The ninth and sixth primary measurements show a different pattern from the previous two types (Fig. 4). Although the absolute longest wings occur in the south, the shortest also occur in the tropics, on Barbados. Birds from near the Equator and from the highlands of Mexico have the longest ninth primaries. Birds of the central Lesser Antilles have the shortest wings, with wing length increasing to the north and south.

Within North America, there is little pattern to ninth primary measurement variation, although, as in Type 1 characters, birds from the northeast and southern Alaska have the longest wings within the region.

Type 4. Four of the proportionate size characters all follow the same general pattern. They are proportionate ninth and sixth primary measurements, proportionate bill width, and proportionate tarsus length.

Birds with the proportionately longest wings occur in the far north, and the proportionately shortest in the far south, although birds in the northern Caribbean also have proportionately

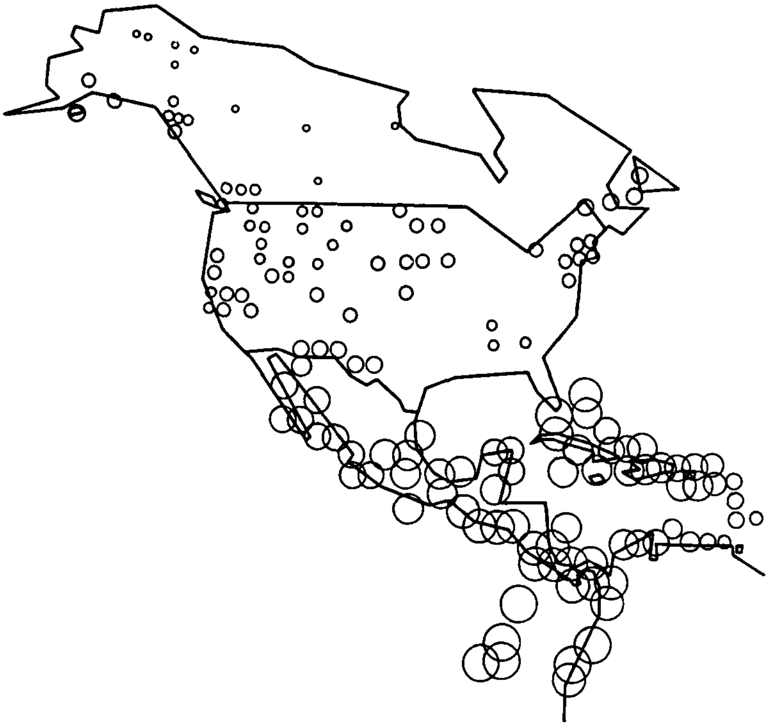

FIGURE 2. Variation in geometric mean of all six characters. Bill length and bill width follow the same pattern, so separate maps were not drawn for those characters. Points mark the centers of two-degree blocks; because of this, especially in the Caribbean and Middle America, some points are over water. All warblers, however, were collected on land. The points were smoothed across latitude and longitude simultaneously using LOESS (f = 0.45). The range of values of the geometric mean then was divided into ten equally-spaced categories, and diameters of the circles correspond to those categories.

short wings (Fig. 5). Except for the Caribbean, the trend is fairly even; within the Caribbean region the trend is from proportionately short in the north towards longer wings in the south. Note that all of the very smallest proportionate ninth primary measurements occur on islands.

The relative magnitudes of proportionate ninth and sixth primary measurements were smoothed vs. latitude only (Fig. 6). Although the general trend is the same in both, i.e., longer with increasing latitude, the rate of change is not the same at all latitudes.

Type 5. Proportionate tail length generally increases from south to north, but birds with the proportionately longest tails occur in the southern Caribbean on the coast of eastern Venezuela, and in California (Fig. 7). Through the Caribbean, in fact, the increasing proportionate tail length trend runs north to south. In North America, birds from near San Francisco have the proportionately longest tails, whereas birds from Kodiak Island have the proportionately smallest tails within the region.

Type 6. Proportionate bill length tends to increase from south to north, although the increase is not strong or even (Fig. 8). It is generally larger in North America than in the tropics. The proportionately longest bills, however, occur in the central Lesser Antilles. The proportionately shortest bills occur in "Mangrove" Warblers from Baja California Sur and along the west coast of Mexico, although they are also short on the Pacific coast of South America. Birds from the Mexican highlands (*D. p. dugesi*) and the Caribbean coast have proportionate bill lengths near average. Birds from the northern Bahamas also have proportionately short bills.

CORRELATIONS OF MORPHOLOGY AND CLIMATE

The correlations of morphological characters with each climate character separately, and multiple

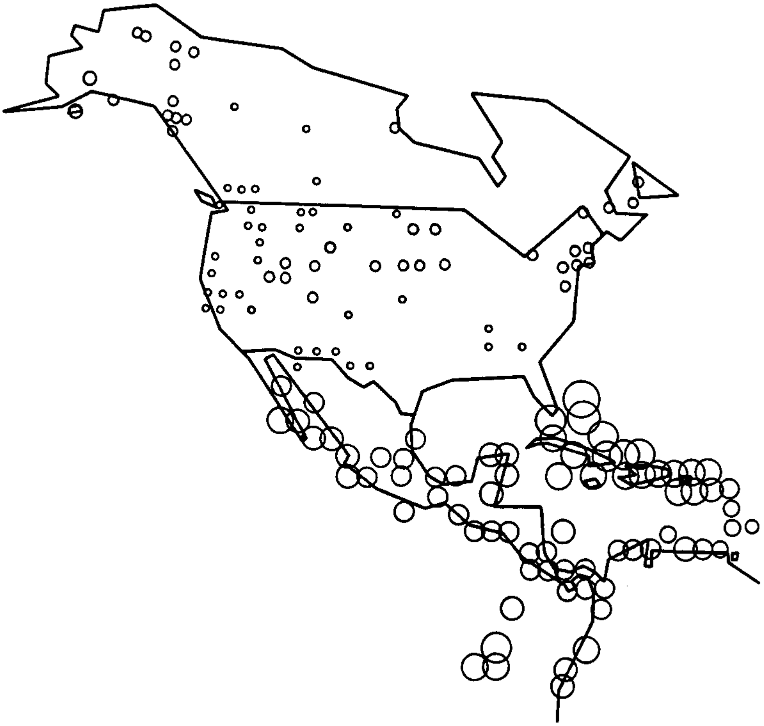

FIGURE 3. Variation in tarsus length. Tail length follows the same pattern. Symbols as in Figure 2.

correlation with both, are shown in the tables. The correlations have been calculated for all two-degree blocks, and for the North American blocks and tropical blocks separately.

The correlations for all blocks combined are almost all significant (Table 1). All are also positive except for the non-significant ones for ninth primary measurement and proportionate ninth and sixth primary measurements. The models with both temperature and vapor pressure do not improve much over one or the other single-parameter models for any morphological character.

Considering the North American region (north of 28° N latitude) alone (Table 2), no correlations are significant except proportionate tail length with vapor pressure. At a significance level of *P*

TABLE 1. Correlations between log morphological characters and climate. All sample sizes are 65. Entries marked with an asterisk are significant at $P < 0.05$; significances have not been corrected for multiple tests. Values for temperature and for vapor pressure are r, value for temperature × vapor pressure is multiple R.

Morphological characters	Temperature	Vapor pressure	Temperature × vapor pressure
Geometric mean of all six characters	0.59*	0.64*	0.64*
Bill length	0.59*	0.71*	0.72*
Bill width	0.32*	0.40*	0.41*
Ninth primary measurement	−0.13	−0.22	0.27
Sixth primary measurement	0.30*	0.25*	0.30
Tail length	0.61*	0.64*	0.65*
Tarsus length	0.66*	0.72*	0.72*
Proportionate bill length	0.20	0.30*	0.33*
Proportionate bill width	−0.26*	−0.30*	0.30
Proportionate ninth primary measurement	−0.70*	−0.83*	0.83*
Proportionate sixth primary measurement	−0.50*	−0.63*	0.65*
Proportionate tail length	0.37*	0.35*	0.37*
Proportionate tarsus length	0.34*	0.36*	0.37*

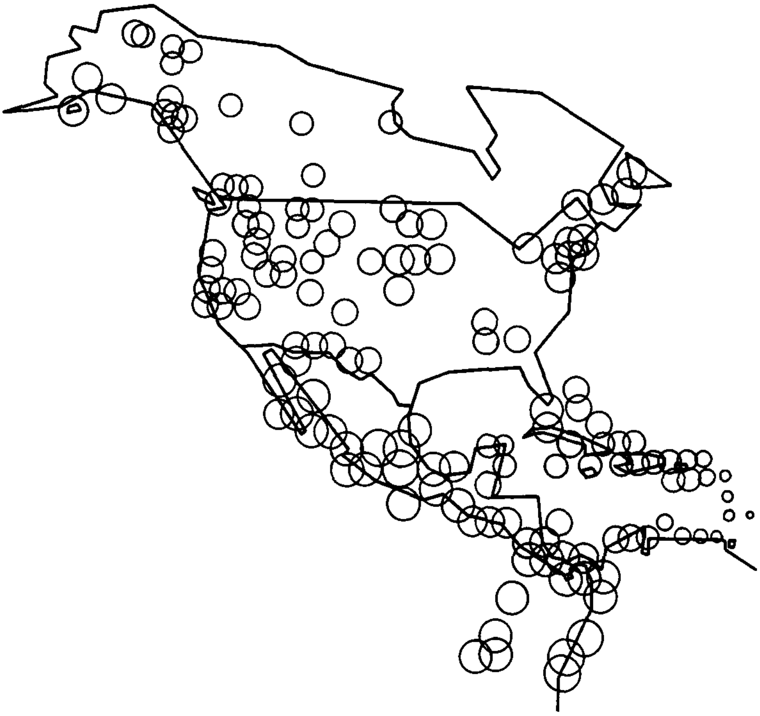

FIGURE 4. Variation in ninth primary measurement. Sixth primary measurement follows the same pattern. Symbols as in Figure 2.

= 0.05, with this many tests, one would have expected one or two correlations to be significant by chance alone.

In the tropics (Table 3), few correlations are significant, and most of these are related to wing measurements and proportionate bill width. Again, the models with both temperature and vapor pressure are not much improved over those with only temperature.

DISCUSSION

MORPHOLOGICAL VARIATION

Morphological variation in *Dendroica petechia* is very complex, as one would expect of a species

TABLE 2. Correlations between log morphological characters and climate, for the North American (north of 29°N latitude) two-degree blocks only. All sample sizes are 38. Significances as in Table 1. Values for temperature and for vapor pressure are *r*, value for temperature × vapor pressure is multiple *R*.

Morphological characters	Temperature	Vapor pressure	Temperature × vapor pressure
Geometric mean of all six characters	0.10	0.09	0.11
Bill length	−0.03	0.15	0.22
Bill width	0.06	0.16	0.18
Ninth primary measurement	0.19	0.24	0.24
Sixth primary measurement	0.10	−0.05	0.18
Tail length	0.04	−0.18	0.28
Tarsus length	0.07	−0.07	0.19
Proportionate bill length	−0.14	0.01	0.20
Proportionate bill width	0.15	0.28	0.28
Proportionate ninth primary measurement	−0.02	−0.03	−0.03
Proportionate sixth primary measurement	−0.08	−0.29	0.31
Proportionate tail length	−0.07	−0.34*	0.39
Proportionate tarsus length	−0.09	−0.28	0.31

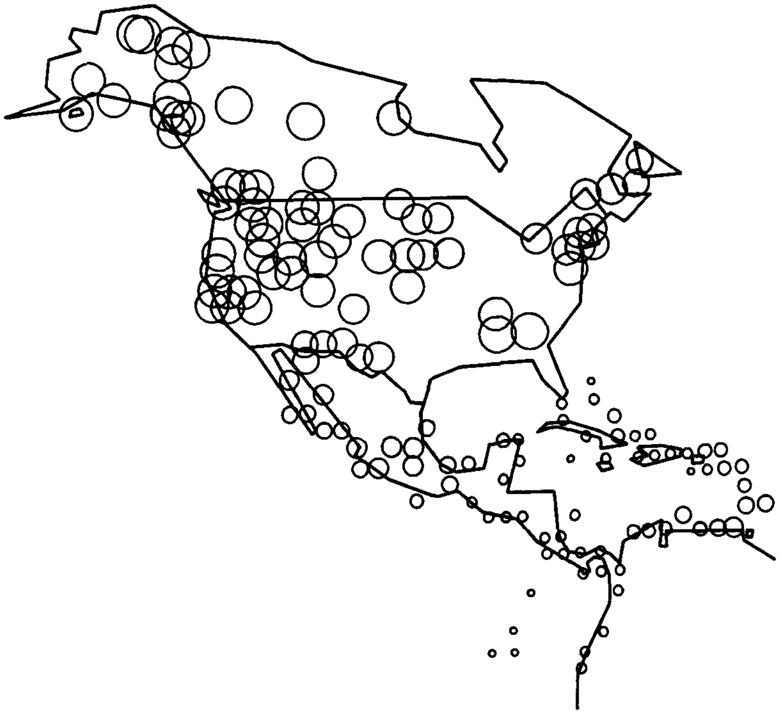

FIGURE 5. Variation in proportionate ninth primary measurement. Proportionate sixth primary measurement, proportionate bill width, and proportionate tarsus length follow the same pattern. Symbols as in Figure 2.

with such a large breeding range. A few patterns stand out, however. The Caribbean region differs from the general trend for all characters except bill length, which shows no trend in the region. In having long tarsi and tail and proportionately short wing and bill, birds from the northern Caribbean are more like birds occurring on the Pacific coast of Middle America or on the Galapagos Islands.

The Caribbean stands out even more for an-

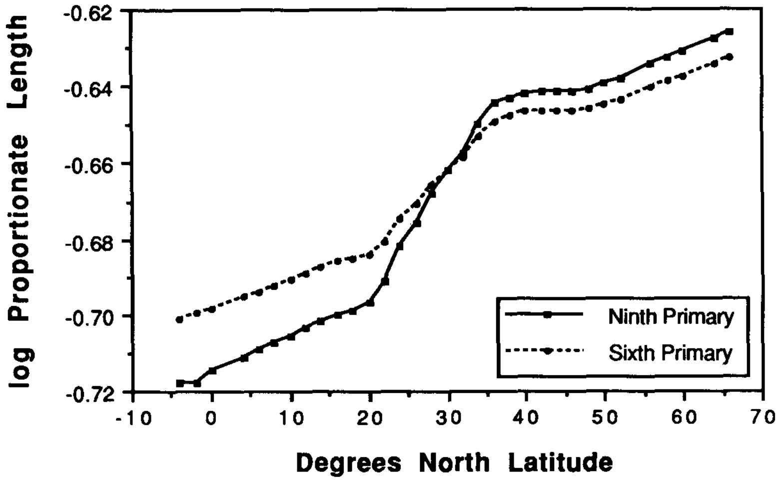

FIGURE 6. Proportionate ninth and sixth primary measurements smoothed (f = 0.45) against latitude only. The 296 data points used to produce the lines have been omitted for clarity.

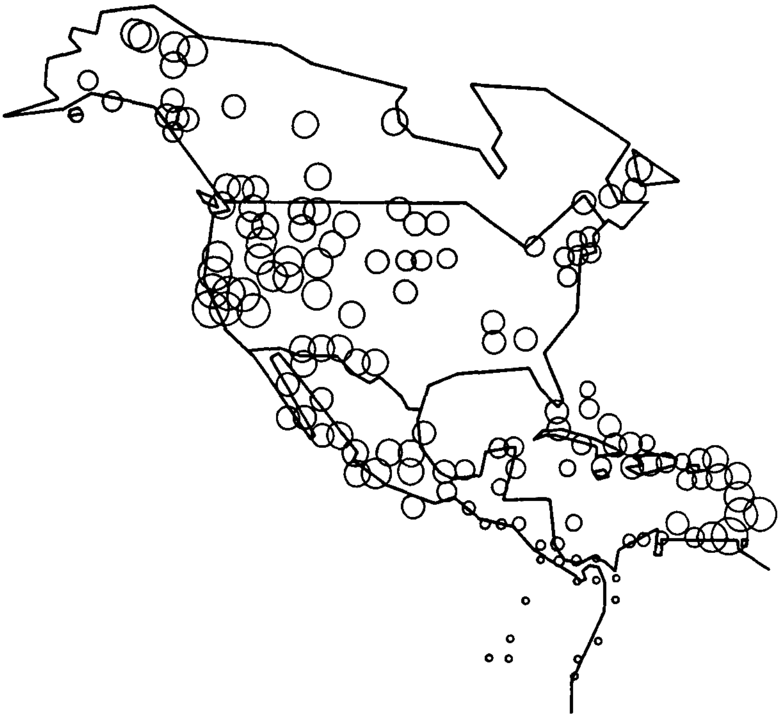

FIGURE 7. Variation in proportionate tail length. Symbols as in Figure 2.

other reason. Birds on Barbados and its neighbors Martinique and St. Lucia, in the central part of the Lesser Antilles, are unusual for tropical *Dendroica petechia* in almost all characteristics. They are quite small, with short wings, and birds to the south and to the north (within the tropics) are increasingly larger. They have long bills, however. Birds on Martinique are of the "Mangrove" Warbler plumage type, although birds on the adjacent islands of Guadeloupe, St. Lucia, and Barbados, are all of the "Golden" plumage type (Hellmayr 1935). That both unusual morphology and plumage distribution co-occur in the central Lesser Antilles is interesting. There

TABLE 3. Correlations between log morphological characters and climate, for the tropical (south of 29°N latitude) two-degree blocks only. All sample sizes are 27. Significances as in Table 1. Values for temperature and for vapor pressure are *r*, value for temperature × vapor pressure is multiple *R*.

Morphological characters	Temperature	Vapor pressure	Temperature × vapor pressure
Geometric mean of all six characters	−0.07	−0.24	0.31
Bill length	0.30	0.12	0.36
Bill width	0.10	0.00	0.16
Ninth primary measurement	−0.41*	−0.46*	0.46
Sixth primary measurement	−0.36	−0.43*	0.43
Tail length	0.23	0.09	0.27
Tarsus length	0.23	0.09	0.36
Proportionate bill length	0.37*	0.29	0.37
Proportionate bill width	−0.54*	−0.39*	0.54*
Proportionate ninth primary measurement	−0.64*	−0.57*	0.65*
Proportionate sixth primary measurement	−0.60*	−0.55*	0.61*
Proportionate tail length	−0.15	−0.25	0.26
Proportionate tarsus length	0.29	0.28	0.30

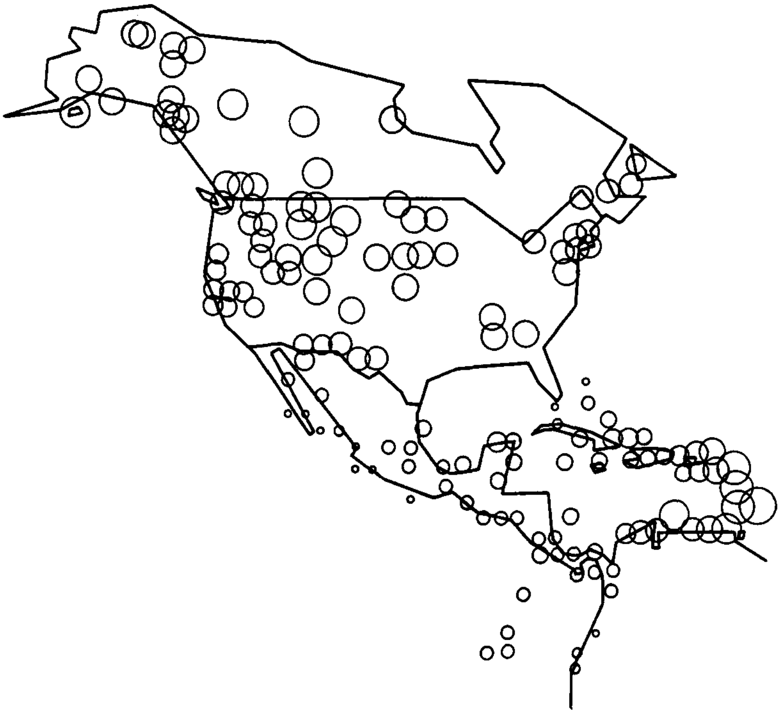

FIGURE 8. Variation in proportionate bill width. Symbols as in Figure 2.

are many possible explanations for this pattern; it deserves further study.

The situation on Martinique points out that plumage and morphology are not necessarily linked. The Martinique birds' morphology fits into clines beginning in the Bahamas to the north or in South America to the south. This suggests that there is some gene flow through the islands of the Caribbean, allowing the morphologies of different islands to intergrade into one another. Of course, there are other possible explanations for this morphological pattern. However, because the plumage pattern does not follow the same clines, it is apparent that plumage pattern and morphology may be at least partially independent. This can be corroborated with the example of birds from the Galapagos Islands. Birds from these Pacific islands have plumage much like those from some Caribbean islands (Hellmayr 1935). The Pacific island birds, however, have as their nearest neighbors "Mangrove" Warblers, and are morphologically similar to the "Mangrove" Warblers. This again suggests the independence of plumage and morphological patterns.

MEASUREMENT OF SIZE

The choice of measurement to represent overall size in a morphological study such as this usually presents a difficult problem. Intuitively, body mass appears the best choice, but as has been pointed out by Baldwin and Kendeigh (1938), body mass is highly variable depending on season, time of day when it is measured, whether a female had an egg in the oviduct, etc. In addition, body mass is a measurement that was rarely recorded on labels of earlier specimens, and is unavailable for those specimens even if the researcher wished to use it. In this study, body mass was available only for 20 of the 148 two-degree blocks with morphological data.

Traditional "wing length," in this paper called ninth primary measurement, has been used by many as a size measure, because it is less variable day-to-day or between seasons. The ninth primary measurement, however, is a poor size measure in *Dendroica petechia,* because it shows little correlation with body size. That wing length can be a poor measure of size also has been pointed our for other species by Freeman and Jackson (1990).

Body mass shows a significant negative correlation with latitude. The geometric mean of all six measurements is correlated with body mass, and shows the declining trend to the north also shown by body mass. The geometric mean has the advantage over body mass in being less temporally variable, and being available on all specimens. The geometric mean also has the advantage over ninth primary measurement in being a combination of characters. Because six characters contributed to the size measure, a local increase or decrease in one or two of the constituent measurements will have little effect on the estimate of size. If one were using wing length by itself as the size estimator, local variation in wing length alone would affect the estimate of size. (For further discussion of other factors that may be affecting wing length, see *Wing Length and Migratory Distance,* below.)

This analysis demonstrates that the choice of a size measure is complex, and should be based on thorough knowledge of variation within the species and careful choice of what one would like to represent size. This follows the recommendations of Mosimann and James (1979) and Freeman and Jackson (1990).

BERGMANN'S RULE

Bergmann's original ecogeographic rule states that body size in homeotherms should be larger in cooler climates. The rationale for this is that larger organisms have a smaller surface-to-volume ratio, and should therefore be more able to conserve body warmth.

From even a cursory look at the map of geometric mean (= size; Fig. 2), it is evident that *Dendroica petechia* does not show any large-scale congruence with Bergmann's Rule. On the contrary, geometric mean shows a remarkably steady decline from the largest birds near the Equator to the smallest ones in northern Alaska. Because average breeding season temperature also declines with increasing latitude, this trend is in direct contradiction to the idea that size should increase where temperature decreases.

James (1970) and Aldrich and James (in press) show that Bergmann's Rule should be considered to describe not only the effects of temperature, but also should include a humidity component. James's (1970) formulation of Bergmann's Rule states that larger individuals should be associated with cooler, drier conditions. The correlations of geometric mean which ignore latitude and only consider the climate conditions actually prevailing in each two-degree block (Table 1) again clearly contradict this. The geometric mean is positively correlated with both temperature and vapor pressure, showing that the largest birds are in the hottest, most humid climates.

Johnston and Selander (1964) found that House Sparrows (*Passer domesticus*) conform to the original formulation of Bergmann's Rule only as far south as 28° N latitude, but that tropical populations do not. Correlations with the geometric mean in Table 2 (North America only) are all non-significant, but even their general trend is again counter-Bergmannian and in disagreement with Johnston and Selander's (1964) findings. Within the tropical region (Table 3) the correlations are in the Bergmann's Rule direction, but are non-significant, and the correlation with temperature is so low as to likely be spurious.

Dendroica petechia may not be a species which should be expected to follow Bergmann's Rule, because the "Yellow" Warblers are migratory and never suffer winter cold-temperature stress. Their body size may be adapted instead to conditions which occur on their wintering grounds, or to other factors such as food availability or prey size, etc. In addition, even in comparisons using only the "Mangrove" and "Golden" Warblers, I used only climate data from a single month, June, which may not be in the critical period to cause adaptation in size for those warblers. If size in *Dendroica petechia* follows Bergmann's Rule, then the pattern is subtle, or it may be related only to climate conditions not examined in this study, such as winter climate. Zink and Remsen (1986) found that migratory species generally do not follow Bergmann's Rule as it was originally stated, although James (1970) and Aldrich and James (in press) showed that migratory species, but ones which winter in the southern part of the temperate zone and not in the tropics, do follow the rule. Perhaps Bergmann's Rule should be modified to cover only species without tropical wintering populations.

ALLEN'S RULE

Allen's Rule states that the appendages of homeotherms should be shorter or smaller in colder climates. The rationale is very similar to that for Bergmann's Rule. That is, appendages provide a large surface from which heat can be lost, and therefore should be reduced in birds living in colder climates. The feathers that form most of the wing length and tail length are non-vascularized, and Allen's Rule probably should not be expected to apply to them. Therefore I have not considered the wing and tail elements in the examination of these warblers' agreement with Allen's Rule.

Correlations in Table 1 follow Allen's Rule (which predicts positive correlation with temperature) for all four of the non-proportionate measurements (geometric mean, bill and tarsus length, bill width). Because the "Mangrove" and "Golden" Warblers already are known to be larger birds, however, this result may be unimportant; that is, larger birds have longer bills and tarsi just because they are larger and not because of Allen's Rule. Disregarding feather measures, the proportionate tarsus and bill lengths do follow Allen's Rule, although proportionate bill length's correlation is non-significant. The third measure, proportionate bill width, runs counter to the rule. Therefore, there is little corroboration of Allen's Rule disregarding the effects of overall size.

Logically, if vapor pressure is a causal factor for Bergmann's Rule, it should also be one for Allen's Rule. However, the correlation of the characters with vapor pressure and both factors together in Table 1 do not alter any conclusions based on the pattern from temperature alone.

Within North America (Table 2) all correlations between climate and morphological characters are so low as to give no support to Allen's Rule. The morphological characters do not vary in concordance with climate characters. Within the tropics (Table 3), the pattern of correlations between climate and morphological characters is very similar to that for all two-degree blocks, although the correlations are lower. These do not warrant separate discussion.

Dendroica petechia does not provide any support for Allen's Rule. Once again, the species perhaps should not be expected to follow Allen's Rule, because of its migratory habits. The other caveats accompanying the discussion of Bergmann's Rule also apply here.

WING LENGTH AND MIGRATORY DISTANCE

Studies of the aerodynamics of bird wings indicate that a longer and more pointed wing is more efficient for prolonged, direct flight (Savile 1957), as occurs during long-distance migration. Several authors have shown that the wings of migratory species are generally longer or more pointed than non-migratory ones (Averill 1925, Dilger 1956, Leisler and Winkler 1985, but see Keast 1980). This relationship is expected to hold also within species, with the expectation that wing length and pointedness should be correlated with migratory distance. The relationship has been demonstrated in some species (Averill 1920, Gaston 1974). It is not always evident, however (Mulvihill and Chandler 1990), or wing pointedness and length may offer contradictory evidence (Mulvihill and Chandler 1991).

"Mangrove" and "Golden" Warblers are not known to migrate. To where the different populations of "Yellow" Warblers do migrate is not known, although they all winter south of the United States. It is therefore not possible to calculate a migration distance for this species directly. Considering latitude as a rough index of migration distance, the proportionate ninth and sixth primary measurements show increasing length to the north, from where birds would have to migrate farther to winter (Fig. 6). The pattern is evident for both wing measures. It is also evident within the tropics (south of 28° N latitude), although the "Golden" and "Mangrove" Warblers are non-migratory.

Although both proportionate ninth and sixth primary measurements show a general increase from south to north, their lengths relative to one another and their rate of increase are not always the same. Within the tropics, the proportionate sixth primary measurement is longer than the ninth, making the wing-tip more rounded, whereas in North America the ninth is longer than the sixth, making the tip more pointed. This supports the conclusion of Gaston (1974) that the wings of migratory forms should be more pointed than those of non-migratory forms. However, because the *difference* between proportionate ninth and sixth primary measurements does not change north of about 36° N latitude (although both increase), the "Yellow" Warblers do not support the idea that increased wing *pointedness* is related to increased migratory distance. This is in agreement with the conclusions of Mulvihill and Chandler (1990).

Most change in wing shape is caused by changes in proportionate ninth primary measurement. With increasing latitude, the proportionate sixth primary measurement increases fairly evenly (that is, the line on Fig. 6 is nearly straight). Between about 20° and 36° N latitude, however, proportionate ninth primary measurement increases rapidly, to overtake and surpass proportionate sixth primary measurement.

Latitude is a crude measure of migratory distance, and the true relationship of wing length and migratory distance in this species is likely to be more complex. Warblers from northern Alaska may migrate only as far south as Mexico, although Wetmore et al. (1984) stated that "Yellow" Warbers belonging to the subspecies *Dendroica petechia amnicola,* which breeds in the far north including northern Alaska, winters from northern Mexico south to French Guiana, Colombia, and Peru. Therefore, the actual distance migrated by the North American birds may or may not be very strongly related to the latitude at which they breed. Nonetheless, the birds living the farthest north do have the proportionately longest wings, and the migratory birds have more pointed wings than non-migratory tropical ones.

CONCLUSIONS

Morphological variation in *Dendroica petechia* does support the idea that wing length increases with migratory distance, but does not support Bergmann's or Allen's ecogeographic rules. The description of morphological variation in this species from the Equator to the Arctic Circle shows many interesting patterns, and should open many avenues for further research.

ACKNOWLEDGMENTS

This work was supported by a grant from the Frank M. Chapman Memorial Fund. F. C. James, N. Klein, J. V. Remsen, and R. M. Zink have read and made many improvements on the manuscript.

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