

## PLUMAGE AND SIZE VARIATION IN THE MOURNING WARBLER<sup>1</sup>

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**Abstract.** The Mourning Warbler (*Oporornis philadelphia*) is highly variable throughout its breeding range (Hall 1979, Pitocchelli 1990) but a thorough study of geographic variation in this species is lacking. Therefore, the nature of this variation is poorly understood. I studied macrogeographic variation in plumage and skeletal characters of 364 specimens from most of the breeding range in North America. There was no clear pattern of variation in external or skeletal measurements. Univariate analyses of external characters and skeletal characters revealed little variation between localities for most characters. Multivariate analyses also yielded little structure or subdivision among populations. Regression analyses failed to find significant north–south clines in several size measurements ( $P > 0.05$ ). The Mourning Warbler did not conform to predictions based on Bergmann's rule. Spatial Autocorrelation of plumage, external and size measurements only found one character—TAIL length—which conformed to the isolation by distance model. A significant Canonical Correlation ( $P < 0.05$ ) was found between external measurements and climatic data but only 36% of the external variation could be explained by the environmental variables.

There appears to be little geographic variation among populations from the breeding range of the Mourning Warbler. There was a weak relationship between some morphological measurements and climatic variables. Environmental selection does not appear to play a role in shaping the pattern of variation on the breeding grounds in North America.

**Key words:** Mourning Warbler; geographic variation; plumage; morphometrics; *Oporornis philadelphia*.

### INTRODUCTION

The Mourning Warbler (*Oporornis philadelphia*) and MacGillivray's Warbler (*Oporornis tolmiei*) form an east–west species pair that breed in North America (Mayr and Short 1970). Individuals of these taxa bear a striking morphological resemblance to each other making identification of some individuals very difficult. Extreme or intermediate adults, possessing plumage characters and/or external measurements of both taxa have been documented by several authors (Chapman 1917, Lanyon and Bull 1967, Cox 1973, Patti and Meyers 1976, Beimborn 1977, Hall 1979, Kowalski 1983, Pitocchelli 1990) but the frequency and distribution of these individuals is poorly understood. Neither taxon has undergone a thorough study of geographic variation (sensu Zink and Remsen 1986). Therefore, the range of variation within each taxon is unknown. Hall (1979)

suspected that most purported *hybrids* were actually extreme individuals within the normal range of variability of either taxon. He considered most of the extreme birds to be *O. philadelphia*. Pitocchelli's (1990) analyses of birds that were taped recorded before collection supported Hall's earlier conclusions. The sporadic contact and absence of large hybrid zones (Cox 1973, Pitocchelli 1990) like those found in other species pairs hybridizing in the Great Plains (for review see Rising 1983) also strongly suggest that extreme *Oporornis* specimens are not hybrids. *Oporornis philadelphia* plumage is more variable than *O. tolmiei* (Hall 1979, Pitocchelli 1990) and members of this taxon are more likely to give ornithologists problems with identification.

The primary goal of this study is to describe macrogeographic variation in plumage and size from throughout the breeding range of *O. philadelphia* in North America. I investigated variation in the external phenotype by analyzing the spatial distribution of plumage characters, external measurements and extreme specimens from the breeding range. I also analyzed varia-

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tion in the internal phenotype using skeletal dimensions.

Ornithologists have historically used wing length or weight as indicators of body size (Lanyon 1978) but some controversy exists over which measurements best describe body size (Baker 1985, Rising and Somers 1989, Piersma and Davidson 1991). Body weight and primary feather length are known to vary over the breeding season and therefore may not be robust indicators of body size (Baker 1985, Zink and Remsen 1986). Because skeletal characters are not susceptible to seasonal fluctuation they may provide a better indicator of body size (Ross and Baker 1982, Zink and Remsen 1986, Rising and Somers 1989). When the loadings of skeletal variables on the first Principal Component axis are all positive it is considered a "size" axis. In this study I analyzed and compared patterns of variation in size using external measurements, weight and Principal Component scores based on skeletal measurements.

Finally, I examined the correlation between observed patterns of morphological variation and environmental variables. Significant relationships between morphological variation and climatic data have been cited as evidence as for environmental selection and used to formulate Bergmann's, Allen's and Gloger's ecogeographic rules (James 1970, Aldrich and James 1991). I performed analyses to test for significant relationships between morphological and climatic variables. I also tested whether *O. philadelphia* conforms to Bergmann's rule.

## METHODS

From 1983 to 1988 I collected 364 adult males and females at 21 breeding localities from Newfoundland to British Columbia (Appendix 1). All collections were made between 6 June–15 July. I prepared specimens as flat skins and skeletons in the field for analyses of plumage and skeletal differences between populations. This technique provides an additional set of characters (skeletal dimensions) for size comparisons between populations (Barlow and Flood 1983) and for comparisons between variation in external and internal aspects of the phenotype (Troy 1985). All materials have been deposited at the American Museum of Natural History.

I performed two separate analyses of geographic variation. The first analysis examined spatial

variation in weight, external characters, and external measurements. In the second analysis I examined skeletal variation.

Ornithologists are also interested in the nature of the variation in each character. For instance, *F* statistics are commonly used in studies of electrophoretic variation to assess the amount of within versus among population variation in gene frequencies (Rockwell and Barrowclough 1987). In this study I analyzed the amount of *among population versus individual variation* for weight, external and skeletal measurements using a nested analysis of variance (ANOVA, PROC NESTED; SAS 1985). I graphed the percentage of variance attributed to these two variance components for each character.

*Morphology—external.* Baird (1858) first described *O. philadelphia* and *O. tolmiei* as separate species, noting critical plumage differences around the eye region. Most accounts of these species still point out that adult *philadelphia* males lack eye-arcs (broken eye-rings) and dark lores found in *tolmiei* males. Adult female *philadelphia* specimens typically lack eye-arcs found in *tolmiei* females. The WING minus TAIL (W-T) measurement was also considered an important character for separating specimens of *O. philadelphia* and *O. tolmiei* (Lanyon and Bull 1967) and subspecific taxa of *O. tolmiei* (Phillips 1947). Specimens with W-T less than or equal to 10 mm were considered *O. tolmiei* while W-T greater than or equal to 11 mm were *O. philadelphia*. However, several studies have shown overlap in these plumage characters (Hall 1979, Kowalski 1983, Pitocchelli 1990). Extreme *O. philadelphia* specimens that have been described in the literature or brought to my attention thus far include: males and females with eye-arcs but no lores, males with dark lores, males with W-T less than 10 mm, females with W-T less than 10 mm, males with eye-arcs and dark lores but W-T measurements greater than 11 mm, females with eye-arcs but W-T greater than 11 mm.

The evaluation of geographic variation in these external characters consisted of two different analyses. In the first analysis I summarized the patterns of variation in characters. I plotted the incidence (%) of males and females with eye-arcs versus those without eye-arcs on a map of North America. I did the same for males with dark lores versus males lacking dark lores. I also analyzed measurements of flattened WING and TAIL lengths and W-T (from Lanyon and Bull 1967).

For each locality I graphed the number of individuals with W-T measurements in each of the following intervals:  $W-T \geq 13$  mm,  $13 \text{ mm} > W-T \geq 12$  mm,  $12 \text{ mm} > W-T \geq 11$  mm,  $11 \text{ mm} > W-T \geq 10$  mm,  $10 \text{ mm} > W-T \geq 9$  mm,  $9 \text{ mm} > W-T$ . Analyses of external measurements were performed on males only. I tested for clinal patterns of variation in external measurements by regressing these measurements on latitude (LAT) and longitude (LON) (PROC REG, SAS 1985). If a significant relationship between character size and LAT or LON existed I noted the  $R^2$  value associated with the regression model. The  $R^2$  value or coefficient of determination expresses the amount of character variation that is related to the regression model versus residual error (Power 1970, SAS 1985).

The isolation by distance model has been offered as an alternative hypothesis which might explain patterns of variation in characters. Sokal and Wartenberg (1983) have shown that isolation by distance results in spatial autocorrelation. Spatial Autocorrelation analysis tests whether the value of a character at one locality is dependent on the values of the variables at neighboring localities. I used Spatial Autocorrelation to detect isolation by distance patterns in the following plumage characters: the frequency of birds with eye-arcs, frequency of birds with dark lores, WING, TAIL, W-T and WEIGHT. The Spatial Autocorrelation program was written in FORTRAN by G. F. Barrowclough. The program yielded Moran's  $I$  coefficient for each distance class (step) between localities. These data were then plotted on correlograms; abscissa—steps, ordinate—Moran's  $I$ . The shape of the correlogram surfaces for each character were then compared to isolation by distance surfaces from earlier publications of Sokal and Oden (1978a, 1978b) and Sokal and Wartenberg (1983).

Ornithologists are also interested in significant differences between population means for various characters. In the second analysis of plumage characters I tested for significant differences between populations for WEIGHT, WING, TAIL and W-T. I used the Simultaneous Sums of Squares Test Procedure (SS-STP) written in FORTRAN by G. F. Barrowclough. Only samples with 10 or more males were included in the ANOVA.

I used a canonical correlation analysis (CCA) (PROC CANCORR, SAS 1985) to determine whether variation in external skin characters was related to climatic variables. Zink (1986) used

CCA to determine whether patterns of morphological variation in Fox Sparrows (*Passerella iliaca*) could be explained by environmental data. This procedure tests the independence of patterns in two data sets—climatic variables and morphological measurements (Zink 1986). Results of CCA in this study were used to provide information on (1) whether there is a significant relationship between the two data sets, (2) how much of the variation in the morphological data is explained by the environmental variables, (3) the loadings of each variable on the CV axes, and (4) which variables are the best predictors of that variation. I performed a CCA on external measurements and climatic data. The OTUs were the localities and the external measurement data were the locality means for WING and TAIL. The climatic data were taken from publications by Environment Canada (1982a, 1982b, 1984a, 1984b) and the U.S. Department of Commerce (ESSA 1968). Environmental variables used in this study included LAT, LON, temperature—mean for June (MEJUNT), mean minimum for June (MIJUNT), mean maximum for June (MAJUNT), the same for July (MEJULT, MIJULT, MAJULT), and precipitation—mean June (MEJUNP) and mean July (MEJULP).

*Morphology—skeletal.* I examined geographic variation in 16 skeletal characters (from Pitocchi 1990): PRL—premaxillary length, NASW—nasal bone width, SKW—skull width, SKL—skull length, MANL—mandible length, HUML—humerus length, HRTL—humerus trochanter length, ULNL—ulna length, CARPL—carpometacarpus length, FEL—femur length, TIBL—tibiotarsus length, TARL—tarsometatarsus length, CORL—coracoid length, STERL—sternum length, KEED—keel depth, SYNW—synsacrum length. All measurements were made with Max-cal digital calipers to the nearest 0.1 mm. Measurements were entered directly into personal computers using Lessoft (Marcus 1982).

SS-STP analyses were performed on all the skeletal characters to determine whether population means were significantly different from each other. I plotted the results on maps to illustrate the pattern and degree of variation among population means for each character.

I used Principal Components Analysis (PCA) to examine the amount of overlap between populations in multivariate space (PROC PRINCOMP, SAS 1985). I focused the analysis on among population variation. Therefore I used sampling localities as the OTUs and the means

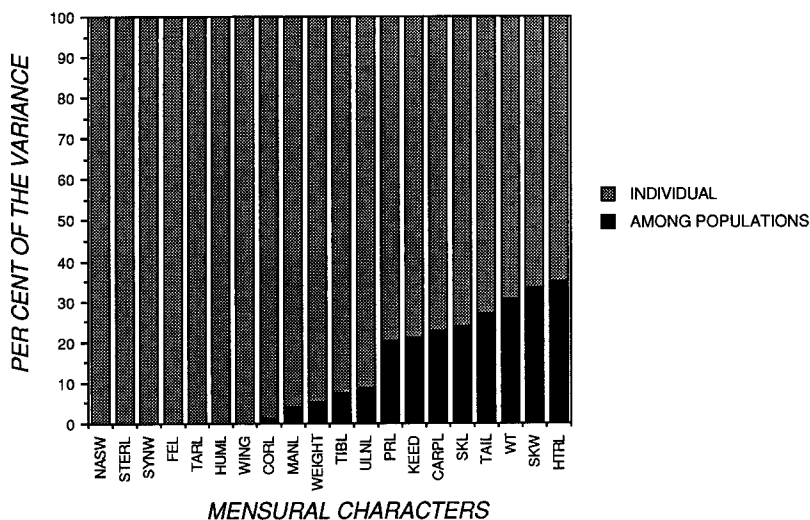


FIGURE 1. Stacked graph illustrating results of NESTED ANOVA. Gray portion represents percent of the variance component attributed to the *individual variation* component while black portion represents the amount attributed to the *among population* component.

for skeletal characters as the data for each OTU. All data were  $\log_{10}$ -transformed prior to the PCA. The principal components were extracted from a covariance matrix. I plotted PC1 and PC2 scores for each locality to document the structure of geographic variation based on skeletal characters.

I explored the relationship between morphometric and geographic variation. PC1 scores were interpreted as size scores and regressed on LAT and LON to test for clinal variation in size (PROC REG, SAS 1985). I also performed Spatial Autocorrelation to determine whether size, as indicated by PC1, fit the isolation by distance model.

I used a canonical correlation analysis (PROC CANCORR, SAS 1985) to assess covariation in skeletal and environmental variables. The climatic variables in this analysis were the same as those used in the canonical correlation analysis of external measurements and climatic data. The OTUs in this canonical correlation were the localities and the morphological data for each OTU were the locality means for each skeletal character.

## RESULTS

### NESTED ANOVA

The percentage of the variance attributed to among population versus individual variation varied in each character (Fig. 1). Ten of the 16

skeletal characters and two of the external measurements (WING, WEIGHT) had relatively low levels of among population variation (e.g., 0.0%–10.0% in Fig. 1). These results are comparable to  $F_{st}$  values of gene frequencies for birds summarized in Barrowclough (1983). The remaining mensural characters had among population variance components ranging from 11%–36% (Fig. 1).

*Morphology—external.* The number of birds with eye-arcs varied across the breeding range. Percentages of birds with eye-arcs ranged from 0% in parts of British Columbia, Quebec, Ontario and Maine to 19% and 35% in New York and western Saskatchewan respectively (Fig. 2). Birds with eye-arcs made up less than 10% of the population for 13 of 21 samples. There were no clinal patterns in the distribution of birds with eye-arcs. Regression analyses of birds with eye-arcs and LAT or LON were not significant ( $P > 0.05$ ).

In contrast to the eye-arcs results, males with dark lores were much more common. Only six of the 21 samples lacked birds with dark lores (Fig. 3). Thirteen localities had incidences of 20% or more of males with dark lores. The highest percentages occurred in Newfoundland—80%, Saskatchewan—54%, 50% and Nova Scotia—50%. Regression analyses testing for east-west or north-south clines of males with dark lores were not significant ( $P > 0.05$ ).

*O. philadelphia* specimens with W-T mea-

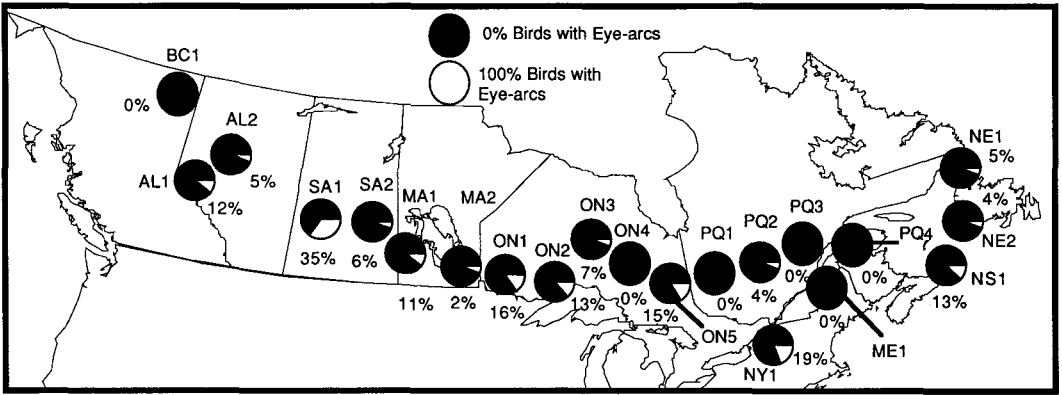


FIGURE 2. Geographic distribution of males and females with eye-arcs. Percentages are birds with eye-arcs at each locality. Sample sizes per locality range from eight (NS1) to 26 (PQ2) specimens.

surements less than 11 mm fell into the range given for *O. tolmiei* by Lanyon and Bull (1967). These individuals were scattered throughout the breeding range (Fig. 4). Specimens with W-T less than 10 mm were found primarily in the western part of the breeding range but some birds in this measurement range were also collected in Ontario and New York. Specimens with W-T from 9 mm–11 mm were found throughout the breeding range in low frequencies. Most birds with W-T greater than 13 mm were found in the eastern provinces and Maine.

I performed separate ANOVAs (SS-STP) on WING, TAIL, W-T and WEIGHT characters. There were no significant differences between samples for WING ( $P > 0.05$ ). Although there were significant differences between localities for TAIL, W-T and WEIGHT, the subsets were large and few localities actually differed from each other.

Figure 5 illustrates the pattern of variation in W-T among localities. The number of subsets and pattern of differences between localities for TAIL and WEIGHT (not shown) were similar to W-T.

I used regression analyses to detect significant patterns of variation in external characters. Some external characters varied significantly with LAT and LON while others did not. WING was not significantly related to LAT or LON ( $P > 0.05$ ). However, there was a highly significant positive relationship between TAIL and LAT ( $P < 0.001$ ) and TAIL and LON ( $P < 0.001$ ). TAIL increased from south to north and from east to west. However, only 9.3% ( $R^2 = 0.093$ ) of the variation in TAIL was attributed to the regression model for LAT and only 5.9% ( $R^2 = 0.059$ ) for the model with LON. The relationship between W-T and LAT was also highly significant and negative but

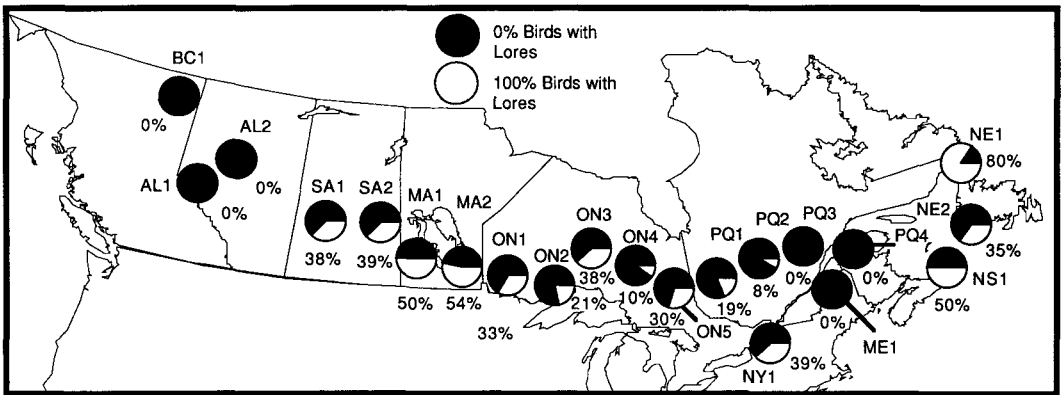


FIGURE 3. Geographic distribution of males with dark lores. Percentages are males with dark lores at each locality. Sample sizes per locality range from seven (NS1) to 25 (PQ2) specimens.

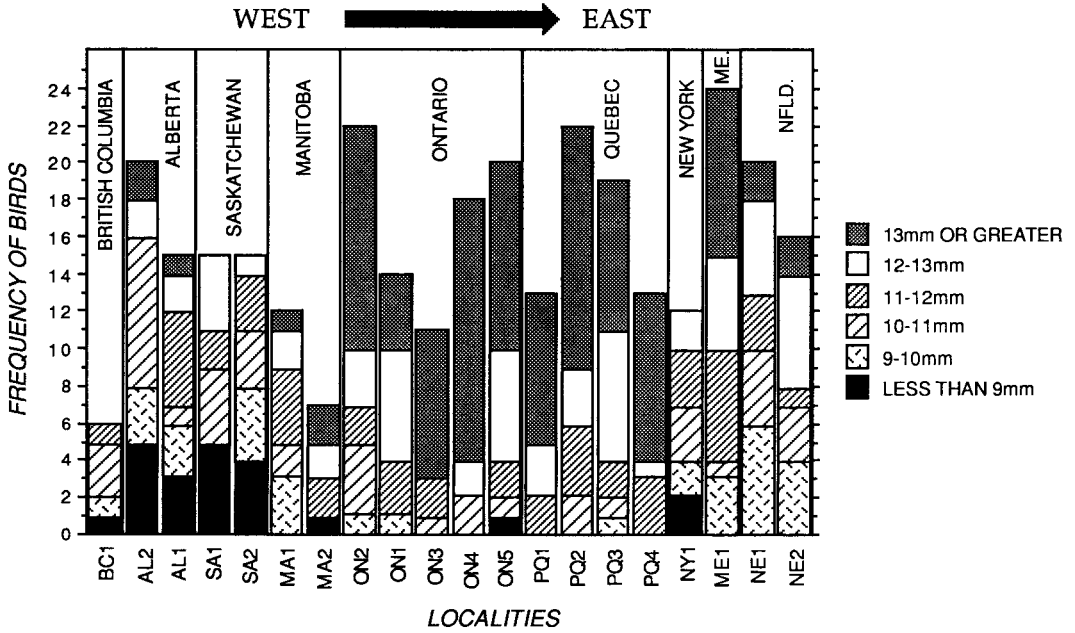


FIGURE 4. Stacked graph of frequency of males with W-T measurements falling into designated intervals. Western localities are located on the left side of the graph while eastern localities are on the right.

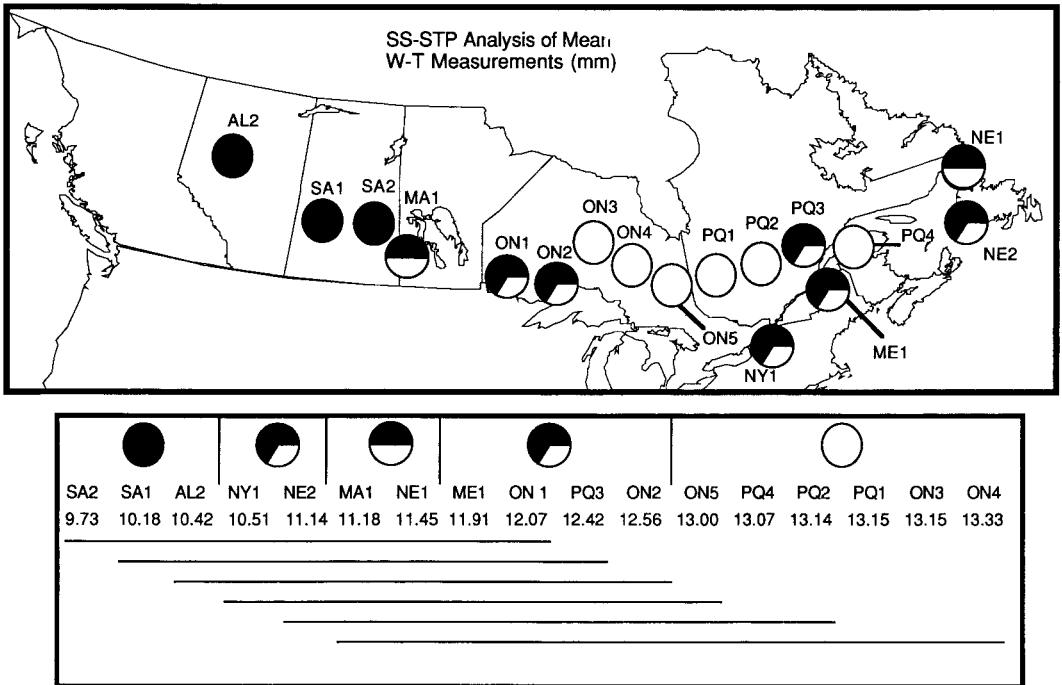


FIGURE 5. SS-STP analyses of significant differences between locality means for W-T measurement ( $P < 0.05$ ). Sample sizes per locality range from 12 (MA1) to 24 (ME1).

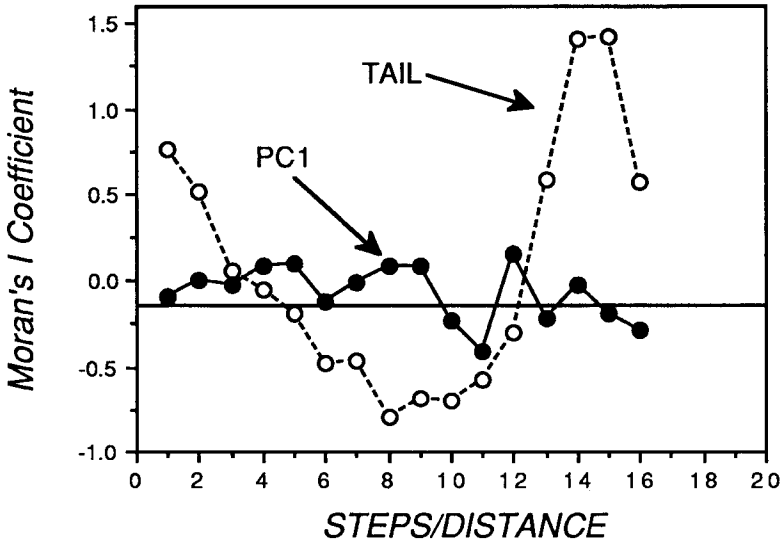


FIGURE 6. Correlograms for TAIL and PC1.

only 10.8% of the variation in W-T could be attributed to the regression model. I obtained similar results for W-T and LON. Only 10.1% of the variation in W-T was explained by the regression model for LON. Even though these characters varied significantly with LAT and LON the small  $R^2$  values suggest that there is no pronounced clinal variation in the external characters.

The linear relationship between WEIGHT and LAT was significant ( $P < 0.05$ ). WEIGHT increased with increasing LAT. However, only 1.2% of the variation in WEIGHT is explained by variation in LAT. The relationship between WEIGHT and LON was also significant ( $P < 0.01$ ) and positive but only 2.6% of the total variation in WEIGHT could be explained by variation in LON. The small  $R^2$  values also suggest the lack of pronounced clinal variation in WEIGHT.

The only external character that appeared to conform to the isolation by distance model was TAIL (Fig. 6). The correlogram for TAIL shows a steadily decreasing Moran's  $I$  coefficient which later approaches zero. This pattern is similar to isolation by distance surfaces found in earlier publications of Sokal and Oden (1978a) and Sokal and Wartenberg (1983).

There was a significant canonical correlation (0.96399,  $P < 0.05$ ) between the external measurements and the climatic variables for the first pair of Canonical Variate (CV) axes. The first CV

axis accounted for 85.5% of the total variance but only 36.0% of the variance in the external measurements could be explained by the climatic data. MEJUNP and TAIL had the highest loadings on the CV-morphology and CV-environmental axes (Table 1). The negative loadings of MEJUNP indicate that TAIL increases while WING decreases with decreasing June rainfall. LAT, MEJULP, MEJULT, MIJULT had the next highest loadings. This suggests that as LAT, MEJULT, MIJULT increase and MEJULP decreases, WING tends to decrease while TAIL tends to increase. The canonical redundancy analysis revealed the first CV axis for environmental vari-

TABLE 1. Loadings of external and weather variables on the first Canonical Variate (CV) axes.\*

Character	Loadings on CV1-MORPH	Loadings on CV1-ENVIRON
WING	-0.5008	-0.4828
TAIL	0.7232	0.6972
LAT	0.4161	0.4316
LON	-0.0658	-0.0683
MEJUNT	0.1732	0.1796
MIJUNT	0.0854	0.0886
MAJUNT	0.2071	0.2148
MEJULT	0.3512	0.3643
MIJULT	0.3306	0.3429
MAJULT	-0.0103	-0.0106
MEJUNP	-0.5763	-0.5978
MEJULP	-0.3867	-0.4011

\* Canonical correlation was 0.96399,  $P = 0.044$ , 85.5% of the total variance was explained by the first pair of CV, 36.0% of the standardized variance in external variables was explained by the weather data.

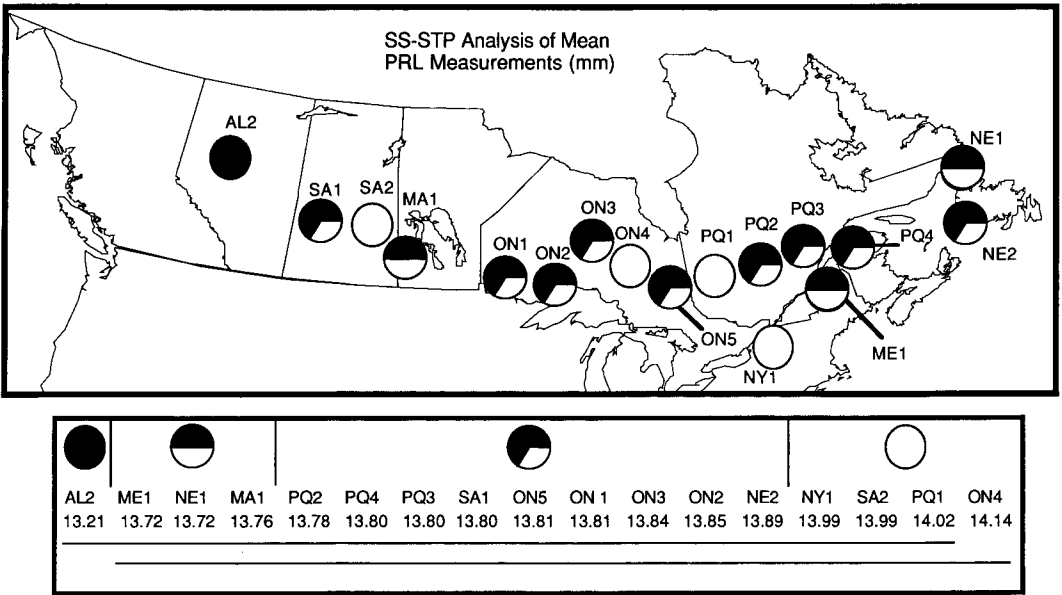


FIGURE 7. SS-STP analyses of significant differences between locality means for PRL measurement ( $P < 0.05$ ). Sample sizes per locality range from 12 (NY1) to 26 (ME1).

ables was a fair predictor of TAIL (squared multiple correlation = 0.4861) and a poorer predictor of WING (squared multiple correlation = 0.2331).

*Morphology—skeletal.* The results of SS-STP analyses indicated that there was little significant variation among population means for skeletal characters. Eleven of the sixteen skeletal characters did not show any significant differences between locality means (NASW, SKW, MANL, STERL, KEED, SYNW, TIBL, TARL, HTRL, HUML, CARPL). The remaining characters (PRL, SKL, CORL, FEL, ULNL) had three or fewer subsets where only one or two locality means were significantly different ( $P < 0.05$ ) from the other samples. The patterns of variation for these characters were similar to the pattern for PRL illustrated in Figure 7.

I used PCA to explore the relationships of different populations to one another. The first three PC axes accounted for 67.2% of the variance in the skeletal data (Table 2). PC1 was the largest, accounting for 38.6% of the total variance. All sixteen skeletal characters had positive loadings on PC1. When the loadings of the skeletal characters on the first PC are positive, the PC1 axis is regarded as a size axis (Zink 1988). NASW from the skull had the highest loading on PC1 followed by KEED and STERL from the girdle.

The skull measurement and two girdle measurements contributed most to the separation of localities along the PC1 axis. PC2 and PC3 had mixtures of positive and negative loadings from the skeletal characters indicating that they are shape components. PC2 accounted for 16.3% of the variance. PRL, KEED and FEL had the highest loadings on PC2. They contributed the most

TABLE 2. Eigenvectors of PCA of skeletal characters.

Character	PC1	PC2	PC3
PRL	0.203	0.414	-0.685
NASW	0.503	-0.281	-0.318
SKW	0.155	-0.281	-0.208
SKL	0.203	0.136	-0.106
MANL	0.134	0.022	0.081
CORL	0.245	-0.241	0.148
STERL	0.325	-0.270	0.091
KEED	0.368	0.429	0.218
SYNW	0.262	-0.203	0.020
FEL	0.145	0.342	0.184
TIBL	0.120	-0.064	0.308
TARL	0.232	0.303	0.190
HTRL	0.248	-0.279	-0.086
HUML	0.146	0.086	0.102
ULNL	0.218	0.162	0.026
CARPL	0.171	0.057	0.375
% of the total variance	38.6%	16.3%	12.2%



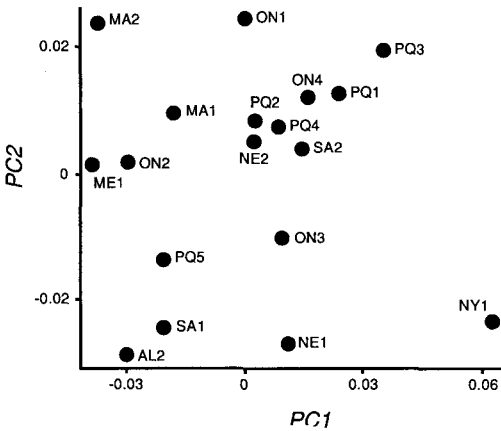


FIGURE 8. PCA plots of localities based on skeletal dimensions. The X, Y axes correspond to PC1 and PC2 axes, respectively.

to the separation of localities along this axis. PRL, CARPL and NASW had the highest loadings on PC3 which accounted for 12.2% of the variance.

Plots of the PC scores for each locality based on skeletal measurements did not reveal geographic structure or subdivision among populations (Fig. 8). Localities from throughout the breeding range were scattered amongst each other on the two dimensional graph of PC scores. I regressed PC1 scores on LAT and LON to determine whether this indicator of size varied clinally from east to west or south to north. There was a significant negative relationship between PC1 and LAT ( $P < 0.05$ ). PC1 decreased from south to north. However, only 23.8% of the variation ( $R^2 = 0.238$ ) in PC1 was attributed to the regression model. The relationship between PC1 and LON was not significant ( $P > 0.05$ ). The results of Spatial Autocorrelation for skeletal characters did not yield a pattern typical of the isolation by distance model (Fig. 6). All the skeletal characters (not shown here) exhibited a surface similar to PC1 when graphed on the correlogram, fluctuating above and below the zero mark.

Skeletal variation does not covary with environmental variation. There was no significant canonical correlation between the skeletal characters and the environmental variables ( $P > 0.05$ ).

## DISCUSSION

The goals of this analysis were to (1) describe and compare spatial patterns of variation in

plumage characters, external measurements and skeletal dimensions, (2) compare patterns of variation of three indicators of body size that have been used by ornithologists—WING, WEIGHT and PC1, (3) describe degree of correlation between morphological and environmental variables, and (4) perform analyses that reveal whether *O. philadelphia* conforms to Bergmann's rule.

Baker (1985) noted several possible patterns of character variation which have been revealed by studies of intraspecific differentiation. They range from continuous clinal variation in one direction (e.g., east–west or south–north) to haphazard variation. The pattern of plumage variation in *O. philadelphia* seems to fit the latter category. Extreme birds do not appear to be concentrated in any single region of the breeding range or vary clinally from east to west or north to south. The incidence of birds with eye-arcs or lores does not vary clinally from east to west or north to south. Nor are localities with similar percentages of extreme individuals necessarily within close geographic proximity of one another. Extreme birds with eye-arcs or dark lores are randomly distributed throughout the breeding range.

The patterns of geographic variation in WING, TAIL, W-T and WEIGHT were not concordant, nor did they fit any significant clinal patterns very strongly. Only one character, TAIL, appeared to fit the isolation by distance model. Ornithologists using measurements to identify extreme birds or specimens should be aware that individuals with extreme measurements are scattered throughout the breeding range. Birds with W-T less than 9 mm appear to be concentrated in the western parts of the breeding range (Figs. 4, 5). In contrast, birds with W-T from 9 mm–11 mm were distributed throughout the breeding range (Figs. 4, 5).

Univariate and multivariate analyses of skeletal variation did not reveal significant patterns of geographic variation. Most mensural characters had low levels of among population variation comparable to  $F_{st}$  values found for gene frequencies. There was also a lack of significant differences between locality means for most characters which also suggests little geographic variation on the breeding range of the Mourning Warbler. Patterns of skeletal measurement variation also appear to be haphazard. Plots of localities along the first two PC axes illustrate hap-

hazard distribution in multivariate space (Fig. 8). Localities with similar scores on these axes are not necessarily in close geographic proximity to one another.

Plumage variation and external measurements have been used traditionally to delineate subspecies or evolutionary units. The haphazard variation in plumage characters and external measurements points to a lack of subdivision on the breeding grounds of *O. philadelphia*. Analyses of skeletal variation among populations also suggest a lack of subdivision among populations. Thus, evolutionary units or races/subspecies are not apparent in this taxon.

*Environmental selection and geographic variation.* Biologists not only observe patterns of variation but seek to explain the observed pattern. Significant association between variation in morphological characters and environmental variables have been considered evidence of environmental selection (Gould and Johnston 1972). Although strong correlations between morphological characters and environmental variables may suggest evidence for environmental selection on morphology, Rensch (1960) and others (Gould and Lewontin 1979, Baker 1985) have cautioned the generality of this explanation because similar results could be obtained from other selective pressures such as isolation by distance, predator-prey relationships, energetics of foraging, competition, etc. . . . Significant correlations between morphological and environmental data only *infer* evidence for environmental selection.

There appears to be no relationship between climatic and skeletal variables and only a weak one between external measurements and climatic data. Only 36.0% of the variation in WING and TAIL measurements could be explained by temperature and precipitation variables. However, I must urge the same caution alluded to by Zink (1986) when interpreting climatic data analyses. Most weather stations do not include important climatic variables such as *evapotranspiration, humidity and wet bulb temperature* which are considered to be more important than the *rain-fall and temperature* data which were used in this analysis.

*Body size and Bergmann's rule.* The robustness of Bergmann's rule has been a matter of constant controversy (Baker 1985, Zink and Remsen 1986). A recent reevaluation by Zink and Remsen (1986) for North American birds

showed that many species do not conform to the rule which predicts an inverse relationship between body size and climate variables such as LAT, temperature and humidity. *O. philadelphia* is another nonconforming exception to Bergmann's rule. Several indices of size—WING, WEIGHT, and PC1 did not fit regression models with LAT very strongly, if at all. WING, the most important size indicator in earlier studies of geographic variation using study skins, did not vary significantly from south to north in *O. philadelphia*. The significant relationship between increasing WEIGHT and increasing LAT was a weak one with over 98% of the variation in WEIGHT explained by residual error versus the regression model. PC1 also exhibited a significant south to north cline but the results were contrary to the prediction from Bergmann's rule. According to the regression model of PC1 and LAT, body size decreased from south to north instead of increased. However, 76.2% of the variation in PC1 was due to residual error, suggesting a weak relationship between skeletal body size and LAT.

The lack of clinal variation observed for some species (James 1970), as well as the absence of relationships between skeletal data and climatic variables or geographic distance coupled with weak or no relationships between external measurements and climatic data or geographic distances suggests selection or isolation by distance models. These do not explain current patterns of morphological variation in *O. philadelphia*.

The results of the above analyses suggest extensive gene flow between populations. Preliminary analyses of electrophoretic data (Pitocchelli and Barrowclough, unpubl. data) also support this. Habitat selection may encourage gene flow between populations of *O. philadelphia*. *Oporornis philadelphia* prefers second growth habitat, especially where clearcut logging or mining has been practiced. In the northern portion of the breeding range *O. philadelphia* prefers clearcuts 10–15 years old but in the Appalachian Mountains they may be found in second growth areas less than 10 years old (Hall, pers. comm.). Soon after, the habitat changes and forces birds into younger stands of second growth. Constant movement into fresh breeding habitat may enhance gene flow between populations. Much of Canada and the northern United States is currently being logged, creating new breeding habitat for colonization by these birds and simul-

taneously enhancing the probability of gene flow between populations. This also suggests that observed patterns of geographic variation are probably unstable over a five to 20 year time frame. Zink (1983) found that patterns of geographic variation in *Passerella iliaca* are subject to change over time. This may be especially true for species like *O. philadelphia* which prefer second growth habitat whose location is constantly changing due in part to natural disturbances such as avalanches and forest fires or artificial disturbances such as current logging or mining practices in North America.

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APPENDIX 1. Latitudes and longitudes for Mourning Warbler localities.

Province/state Locality	Code	Latitude	Longitude
British Columbia			
Ft. Nelson	BC1	58°49'N	122°31'W
Alberta			
Obed	AL1	53°33'N	117°13'W
Whitecourt	AL1	54°10'N	115°37'W
Lodgepole	AL1	53°10'N	115°10'W
Slave Lake	AL2	55°16'N	114°43'W
Saskatchewan			
Candle Lake	SA1	54°3'N	105°48'W
Hudson Bay	SA2	52°51'N	102°38'W
Manitoba			
Duck Mountain	MA1	51°15'N	101°19'W
Pine Falls	MA2	50°33'N	96°37'W
Ontario			
Minitaki	ON1	49°48'N	92°48'W
Dorion	ON2	49°49'N	88°33'W
Geraldton	ON3	49°43'N	86°58'W
Hearst	ON4	49°42'N	83°40'W
Cochrane	ON5	49°4'N	81°1'W
Quebec			
Val Paradis	PQ1	48°48'N	78°28'W
Lebel-sur-Que-			
villion	PQ2	48°55'N	77°10'W
Girardville	PQ3	48°3'N	72°16'W
St. Paule	PQ4	47°58'N	69°10'W
New York			
Chazy	NY1	44°52'N	73°28'W
Maine			
St. Francis	ME1	47°15'N	68°33'W
Nova Scotia			
Wreck Cove	NS1	46°45'N	60°45'W
Newfoundland			
Burgeo	NE2	47°36'N	57°30'W
Roddickton	NE1	50°22'N	56°7'W