

THE RELATIONSHIP BETWEEN WING SHAPE AND DIFFERENTIAL MIGRATION IN THE DARK-EYED JUNCO

ROBERT S. MULVIHILL¹ AND C. RAY CHANDLER^{2,3}

¹The Carnegie Museum of Natural History, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677 USA, and

²Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403 USA

ABSTRACT.—We quantified wing shape in migrant and wintering Dark-eyed Juncos (*Junco hyemalis*) from southwestern Pennsylvania to assess the relationship between wing shape and differential migration (with respect to distance) among age/sex classes. There were significant differences in wing length and primary distances (distances from the wing tip to the tip of each of the nine primaries) among age/sex classes. Adult juncos had longer wings, larger proximal and distal primary distances, and a wing tip shifted proximally relative to immatures. Males had longer wings and larger proximal primary distances than females, but the sexes did not differ in distal primary distances or wing-tip placement. Wing-shape differences between males and females persisted even after accounting for differences in body mass between the sexes. With few exceptions, wing shape was not correlated with body mass within age/sex classes. The traits usually associated with a pointed wing (the wing shape generally considered adaptive for longer migrations) were really two independent dimensions of wing-shape variation in juncos that did not covary among age/sex classes. Overall, our results are inconsistent with the hypothesis that wing "pointedness" covaries positively with distance migrated in juncos. Received 14 April 1989, accepted 21 February 1990.

WING shape affects energy expenditure during a variety of flight-related activities (Pennycuik 1969, Feinsinger and Chaplin 1975, Norberg 1979, Rayner 1988). Migration, in particular, is an energetically demanding behavior (Berthold 1975, Blem 1980) that should exert strong selection for wing shapes that perform efficiently during migratory flights. Not surprisingly, an adaptive relationship between wing shape and migration is presumed in the generalization that migrants have longer, more pointed wings than nonmigrants (Chapman 1940; Kipp 1942, 1958; Dorst 1962; Stegmann 1962; Gaston 1974). This generalization is based both on broad interspecific comparisons (Meinertzhagen 1951, Griscom 1957, Dorst 1962, Gaston 1974) and intraspecific comparisons between migratory and nonmigratory populations (Palmer 1900, Chapman 1940).

If there is a strong adaptive relationship between wing shape and distance migrated, then the effects of natural selection also should be detectable across a gradient of migratory effort.

Comparisons among species that migrate varying distances, however, are inconclusive. Researchers have (Averill 1920, Kipp 1942, Gaston 1974) and have not (Keast 1980) found the expected correlation between wing length or wing pointedness and distance migrated. Comparisons among populations within species eliminate some of the confounding variables associated with interspecific comparisons (such as interspecific differences in foraging behavior and habitat selection; Gaston 1974); positive correlations between wing pointedness and distance migrated have been found more consistently in these cases (*Geothlypis trichas*, Palmer 1900; *Phylloscopus* spp., Gaston 1974; *Sylvia atricapilla*, Lo Valvo et al. 1988).

Differential migration (with respect to distance) among age/sex classes is another kind of intraspecific gradient that may correlate with wing shape. One of the best examples of this phenomenon is provided by the Dark-eyed Junco (*Junco hyemalis*) (Ketterson and Nolan 1976, 1979, 1983, 1985). Differential migration results in a pattern of latitudinal segregation among age/sex classes, the evolution of which has been the subject of considerable speculation. Speculation has focused on environmental (Ketter-

³ Present address: Department of Biology, Indiana University, Bloomington, Indiana 47405 USA.

son and Nolan 1976), behavioral (Gauthreaux 1978, 1982; Ketterson 1979; Myers 1981), and morphological/physiological (Ketterson and Nolan 1976, 1978, 1983; Dolbeer 1982; Stuebe and Ketterson 1982) correlates of differential migration. However, the relationship between wing shape and distance migrated among age/sex classes that exhibit differential migration remains unassessed. The possibility of differential migration effecting a divergence in wing shape among age/sex classes is plausible given recent documentation of wing-shape differences between ages and sexes (Tiainen and Hanski 1985, Busse 1986, Hedenström and Pettersson 1986).

In order to assess a possible relationship between differential migration and wing shape, we analyzed wing-shape differences among age/sex classes of the Dark-eyed Junco. The objectives of this analysis were to determine if wing shape differed significantly among the four distinguishable age/sex classes of Dark-eyed Juncos; if so, to identify the components of wing shape primarily responsible for these differences; lastly we wanted to see if differences were consistent with the effects of selection for increased migratory performance in the farther-migrating age and sex classes. In addition, we estimated the proportion of the variation in wing shape that is due to differences among and within age/sex classes, and explored the relationship between wing shape and body mass in juncos.

METHODS

Study area and sample.—All juncos used in this study were captured during the daily banding operations (see Leberman and Wood 1983 for details) at the Powdermill Nature Reserve of The Carnegie Museum of Natural History, Westmoreland County, Pennsylvania (40°10'N, 79°16'W). Powdermill (elevation 400 m) is located between the westernmost ridges of the Allegheny Mountains in southwestern Pennsylvania. The banding area is dominated by a variety of early successional habitats. At this site, Dark-eyed Juncos are abundant migrants and common winter residents (Leberman 1976). At Powdermill, >21,000 individuals were banded between 1961 and 1986.

Between October 1983 and December 1986, we measured the wing shape of 540 juncos. Most individuals were captured during October through December ($n = 476$) or March through April ($n = 51$). Because the juncos were caught during migration or as winter residents, their geographic origin is uncertain. However, all individuals in the sample were assignable to the nominate subspecies *J. h. hyemalis*. Juncos from a

local breeding population that is distinguishable as *J. h. carolinensis* (Mulvihill unpubl. data; cf. Miller 1941) were excluded. Essentially, *J. h. carolinensis* is a nonmigratory race (Rabenold and Rabenold 1985, Nolan et al. 1986) that breeds at high elevations (>600 m) near Powdermill.

Measurement of variables.—We measured the unflattened wing length and wing formula for each individual. *Wing formula*, as used in this study, is a measure of the distances (projected along the wing chord) from the wing tip (tip of the longest primary of the folded wing) to the tip of each of the other primaries (numbered descendantly; see Chandler and Mulvihill 1988 for details). Individually, these nine measurements are referred to as primary distances (P1–P9). The wing formula quantifies the position of the primaries relative to the wing tip and thus characterizes the overall shape of the wing (i.e. wing-tip placement, pointedness, allometric relationships). All measurements were to the nearest 0.5 mm. Individuals with worn, missing, or disarranged primaries were omitted from our analyses.

Juncos were sexed on the basis of size and plumage characters (summarized in Ketterson and Nolan 1976). Age was determined by the degree of skull pneumatization and the presence or absence of retained juvenal greater primary coverts (Yunick 1981, Mulvihill unpubl. data). Juncos were categorized as immatures (HY/SY in banding terminology) or adults (AHY/ASY). Because juncos have an incomplete first prebasic molt and only a partial prealternate molt (Dwight 1900), all immature birds had juvenal primaries. Prebasic molts subsequent to the first are complete in juncos (Dwight 1900), so all adults had nonjuvenal primaries. Body mass (to the nearest 0.1 g) and fat score (ranked from 0 to 3; Leberman 1967) were recorded (by the same person) for each individual. Fat-free (i.e. residual) body mass was estimated by a regression of the natural logarithm of body mass on fat score. Residual body mass was used in subsequent analyses. *Residual body mass* represents the variation in mass that is independent of differences in fat scores among individuals (Sokal and Rohlf 1981).

Statistical analyses.—The variables wing length, P1–P5, P8, and P9 were normally distributed within and showed homoscedasticity among (F -max test) age/sex classes of juncos. Differences between ages and sexes for these variables were assessed by two-way analysis of variance. Primaries six, seven, or both usually form the wing tip in juncos. They are the longest primaries and have a primary distance of zero. Therefore, we assessed differences in wing-tip placements between ages and sexes with G -tests for three-way (age \times sex \times wing-tip placement) frequency tables (Sokal and Rohlf 1981).

Wing length, P1–P5, P8, and P9 were used to characterize wing shape in a variety of multivariate analyses. Although these variables are traditionally used to calculate simple numerical indices of wing shape

TABLE 1. Wing length and primary distances (mm) for age/sex classes of Dark-eyed Juncos captured at Powdermill Nature Reserve, 1983-1986. Values are $\bar{x} \pm SE$.

Variable	Age/sex class				Age ^a	Sex ^a
	Adult males	Adult females	Immature males	Immature females		
Wing length	78.38 ± 0.11	73.69 ± 0.12	77.00 ± 0.15	72.60 ± 0.14	***	***
P1	16.60 ± 0.07	15.10 ± 0.10	15.86 ± 0.10	14.58 ± 0.09	***	***
P2	14.67 ± 0.07	13.28 ± 0.08	13.95 ± 0.09	12.87 ± 0.08	***	***
P3	12.27 ± 0.07	11.20 ± 0.08	11.42 ± 0.10	10.54 ± 0.08	***	***
P4	7.84 ± 0.07	7.30 ± 0.07	7.10 ± 0.09	6.78 ± 0.08	***	***
P5	2.32 ± 0.05	2.09 ± 0.05	2.01 ± 0.05	2.03 ± 0.05	***	*
P8	1.22 ± 0.04	1.24 ± 0.05	0.88 ± 0.05	0.90 ± 0.04	***	NS
P9	7.21 ± 0.07	7.19 ± 0.09	6.39 ± 0.09	6.41 ± 0.07	***	NS
n	198	137	85	120		

^a Two-way ANOVA: NS = $P > 0.05$, * = $P < 0.05$, *** = $P < 0.001$.

(e.g. Holyński 1965, Busse 1967, Lövei 1983, Tiainen and Hanski 1985, Hedenström and Pettersson 1986), such indices are difficult to compare and provide a less objective assessment of wing shape than multivariate methods (Chandler and Mulvihill 1988, Rayner 1988). We evaluated overall differences in wing shape between ages and sexes with two-way multivariate analysis of variance (MANOVA). To identify which dimensions of wing shape were primarily responsible for differences among the age/sex classes, we conducted a canonical discriminant analysis (DFA). Canonical discriminant analysis identified the linear combinations of original wing-shape variables that discriminated maximally among the four age/sex classes.

We calculated the proportion of variation in wing shape that was due to differences among and within age/sex classes (Straney 1978). To do this, we first reduced the number of wing-shape variables by using principal components analysis (PCA). Principal components analysis identified linear combinations of the original variables that allowed a more concise description of wing-shape variation. We then estimated the variance in PC scores due to wing-shape differences among and within age/sex classes (VARCOMP procedure; SAS Institute Inc. 1988). The estimated variance component was expressed as a proportion of the total variation (Sokal and Rohlf 1981). Straney (1978) provides a more complete description of estimating variance components.

We calculated a generalized variance measure (determinant of the variance-covariance matrix) for each age/sex class to compare the overall variability in wing shape among age/sex classes of juncos.

The relationship between wing shape and body mass was evaluated by calculating Pearson's correlations (both across and within age/sex classes) between residual body mass and wing shape (as described by PCA). The effect of residual body mass on the ability of DFA to discriminate wing-shape differences among age/sex classes was assessed by analysis of covariance (ANCOVA). All statistical analyses were conducted with SAS (SAS Institute Inc. 1988).

RESULTS

Univariate analyses.—Age/sex classes of juncos differed significantly in wing length and primary distances. Adults' wings and primary distances were significantly longer—both proximal (P1-P5) and distal (P8-P9) to the wing tip—than immatures' (Table 1). Males' wings and proximal primary distances were significantly longer than females' (Table 1). With the exception of P5 ($F = 5.89$, $df = 1, 537$, $P = 0.015$), there were no significant interactions between age and sex.

The location of the wing tip (i.e. the longest primaries) differed significantly between ages ($G = 48.18$, $df = 3$, $P < 0.001$), but not sexes ($G = 0.81$, $df = 3$, NS). Among immatures, primary 7 was the most common wing-tip location. Adults were more likely to include primary 6 in the wing tip (Fig. 1).

Multivariate analyses.—MANOVA indicated that there were significant overall differences in wing shape between ages (Wilks' lambda = 0.651, $P < 0.001$) and sexes (Wilks' lambda = 0.299, $P < 0.001$) of juncos.

Canonical discriminant analysis described two significant canonical axes (Table 2). These linear combinations of the original variables accounted for >99% of the between-group (i.e. among age/sex class) variation in wing shape (Table 2). The first axis (CAN1) was correlated highly with wing length and primary distances proximal to the wing tip. The second axis (CAN2) was correlated primarily with distal primary distances (P8-P9). Plotting the location of the four age/sex classes in the space defined by the discriminant axes (Fig. 2) provided a characterization of wing-shape differences among juncos. CAN1 discriminated primarily between

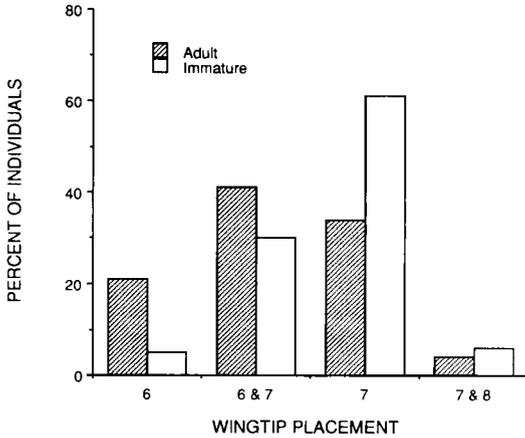


Fig. 1. Percent frequency of alternative wing-tip placements (position of the longest primary) in adult and immature Dark-eyed Juncos.

sexes, reflecting longer wings and greater proximal primary distances (P1–P5) in males. CAN2 discriminated primarily between ages, reflecting longer distal primary distances in adults. Nevertheless, ages and sexes differed significantly along both canonical axes (ANOVA, $P < 0.05$).

The first two PC components (Table 3) together accounted for 73.6% of the total variation in wing shape and expressed similar intervariable relationships to those described by DFA. PC1 (similar to CAN1) was an axis of increasing wing length and proximal primary distances. PC2 was highly correlated to distal primary distances (as was CAN2) but differed from CAN2 in its relationship to other variables. PC3 accounted for 10.3% of the variation in wing shape and represented something of an inverse relationship between wing length and P4–P5.

We estimated the variance in PC scores due to wing-shape differences among and within age/sex classes (Table 4). For each PC component, a large proportion of the variation was due to wing-shape differences within age/sex classes (42–87% of the variation in a given component; Table 4). Despite significant differences among age/sex classes, wing shape appeared to be variable among individuals of a given age and sex. The variation described by PC1 had a large among-group component, but PC2 and PC3 were dominated by within-group variation.

The natural logarithm of the generalized variance measure indicated slightly greater

TABLE 2. Canonical discriminant analysis of wing-shape differences among age/sex classes of the Dark-eyed Junco ($n = 540$).

Variable	Total canonical structure	
	CAN1	CAN2
Wing length	0.995	0.035
P1	0.719	0.191
P2	0.713	0.186
P3	0.651	0.406
P4	0.403	0.459
P5	0.208	0.228
P8	0.117	0.583
P9	0.180	0.731
Canonical correlation	0.861	0.501
Approximate F	48.97	12.39
P	<0.001	<0.001

overall variation in adult males (–48.11) and adult females (–50.96) than in immature males (–53.78) and immature females (–52.94).

Relationship between wing shape and body mass.—Residual body mass differed significantly between sexes ($F = 293.09$, $df = 1, 537$, $P < 0.001$), but not ages ($F = 0.04$, NS). Male juncos were significantly heavier than females. There were also significant correlations between wing shape (as described by PC scores) and residual body mass across age/sex classes (Table 5). However, with the exceptions of PC1 in adult and immature females and PC2 in immature males, there were no significant correlations between residual body mass and wing shape within age/sex classes. A regression of the canonical axis scores of the four age/sex classes on residual body mass produced homogeneous slopes (CAN1: $F = 2.11$, $df = 3, 528$, $P = 0.098$; CAN2: $F = 0.52$, $P = 0.667$). The common-slope regression lines for the four age/sex classes differed significantly in elevation (CAN1: $F = 284.93$, $df = 3, 531$, $P < 0.001$; CAN2: $F = 57.88$, $P < 0.001$). Thus, the discriminant axes still provided significant discrimination among age/sex classes (with no change in the relative position of group means along these axes) even after accounting for differences in residual body mass (ANCOVA).

DISCUSSION

Wing shape and differential migration.—Based on wing-shape comparisons among and within a variety of species, longer migration appears to favor relatively longer wings, a distal shift in

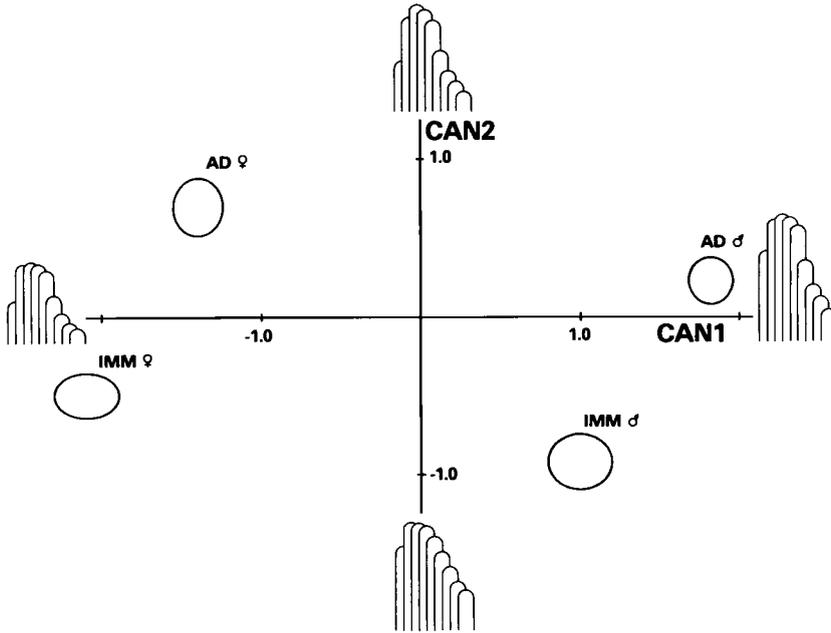


Fig. 2. Wing-shape differences among age/sex classes of Dark-eyed Juncos as described by 95% confidence ellipses for the two canonical axes. Wing-shape diagrams represent the relative position of the primaries for individuals at the extreme of each canonical axis.

the wing tip, increased primary distances proximal to the wing tip, and a reduction of primary distances distal to the wing tip (Palmer 1900; Chapman 1940; Kipp 1942, 1958; Dorst 1962; Stegmann 1962; Gaston 1974). These traits produce a wing shape that is thought to provide faster, more energy-efficient flight (Savile 1957, Norberg 1981, Hedenström and Pettersson 1986). The wing-shape differences among age/sex classes of Dark-eyed Juncos are not consistent with these generalizations.

Although female juncos migrate, on average, approximately 1,000 km farther each year than their male counterparts (Ketterson and Nolan 1976, 1983), they do not possess the wing shape usually associated with longer migrations. Compared with males, females have shorter wings and proximal primary distances, their wing tips are not shifted distally, and they do not have shorter distal primary distances (Table 1). These differences persist even after accounting for body-size differences. Differential migration between junco age classes is less pronounced than between the sexes (Ketterson and Nolan 1983, 1985), but adults (particularly females) appear to migrate farther than immatures. Adults' wings are longer and more

pointed in some respects (longer proximal primary distances) but not in others (wing-tip placement and distal primary distances).

If wing shape is fine-tuned (i.e. linearly related; Fig. 3B) to distance migrated in Dark-eyed Juncos, the migratory differential among age/sex classes should have been sufficient to detect such a relationship (cf. Gaston 1974). It is possible that a more complicated "threshold" relationship exists between wing shape and dis-

TABLE 3. Principal components analysis of wing shape in Dark-eyed Juncos ($n = 540$).

Variable	Factor loadings		
	PC1	PC2	PC3
Wing length	0.739	0.180	-0.491
P1	0.910	-0.012	-0.218
P2	0.917	-0.008	-0.160
P3	0.947	-0.052	-0.016
P4	0.841	-0.170	0.333
P5	0.661	-0.316	0.567
P8	0.109	0.853	0.177
P9	0.238	0.816	0.207
Eigenvalue	4.41	1.56	0.82
% Variance explained	54.07	19.48	10.27
Cumulative variance	54.07	73.55	83.82

TABLE 4. Proportion of variation in wing shape (as described by PC scores) attributable to variation among and within age/sex classes.

	PC1	PC2	PC3
Among age/sex classes	0.579	0.127	0.344
Within age/sex classes	0.421	0.873	0.655

tance migrated in juncos. The wing shape of migrants may differ dramatically from nonmigrants (Fig. 3A) or wing-shape differences may be apparent only in juncos that migrate very long distances (Fig. 3C). In either case, there would be little correlation between wing "pointedness" and distance migrated among short-distance and medium-distance migrants. Juncos of known geographic origin and representing a wider gradient of migratory effort are needed to evaluate completely the possible alternative relationships between wing shape and distance migrated in this species. We are currently studying wing shape in a nonmigratory population of juncos.

Because longer migration can be accomplished by an increase in either distance per flight or the number of migratory flights, wing shape may be related to migration in unexpected ways. Ketterson and Nolan (1982) suggest that a greater number of stopovers at unfamiliar sites, not distance migrated per se, results in an increased risk of mortality (e.g. via predation) to juncos that migrate longer distances. If so, selection might act on wing shape primarily through differential mortality during stopovers. Females winter farther south than males and may spend a greater proportion of their time at unfamiliar stopover sites. Shorter, rounder wings give the highly maneuverable flight (Savile 1957, Alatalo et al. 1984) that may be advantageous to females under these circumstances.

Immature juncos migrate shorter distances on

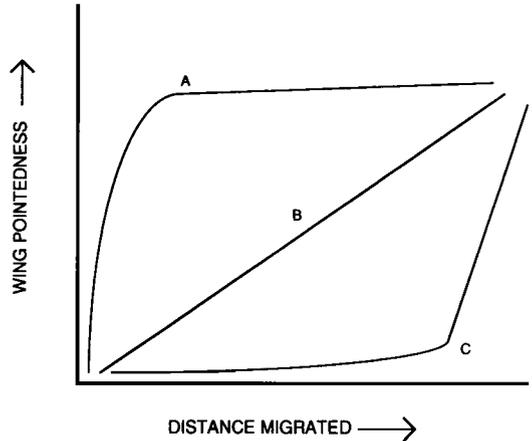


Fig. 3. Possible intraspecific relationships between wing "pointedness" and distance migrated.

average than adults, but, in general, young birds are thought to spend more time exploring unfamiliar migration corridors than adults (Baker 1978). Longer stopovers, together with inexperience (Sullivan 1988, 1989) and behavioral subordination to adults (Ketterson 1979), may make young juncos more susceptible to predation than adults. The maneuverability provided by short wings may be especially important in immatures, both during migratory stopovers and at other times (Alatalo et al. 1984). Alternatively, young birds may simply be constrained from growing wings that are as long as adults of the same sex by the necessary partitioning of resources among concurrently growing remiges (e.g. Slagsvold 1982). If so, then the wing-shape differences independent of wing length ("pointed" wing traits such as distally shifted wing tip and shorter distal primary distances) might be viewed as adaptive compensation for shorter, otherwise less-pointed wings.

Presumably, factors other than migration contribute substantially to wing-shape differ-

TABLE 5. Pearson's correlations between wing shape (as described by PC scores) and residual body mass across and within age/sex classes of Dark-eyed Juncos (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

	PC1	PC2	PC3
Across-groups	0.372***	0.087*	-0.377***
Within-groups			
Adult males	-0.024	-0.016	-0.060
Adult females	0.203*	0.057	-0.007
Immature males	-0.127	0.292**	-0.201
Immature females	0.209*	0.058	-0.170

ences among the age/sex classes of juncos. For example, the intersexual differences in wing shape described by CAN1 (increasing wing length and proximal primary distances; Fig. 2) could be the result of selection for larger body size in males. Longer wings in male juncos, achieved by disproportionate lengthening of the distal relative to the proximal primaries, would be a possible outcome of such selection because of allometric scaling between wing length and body mass (Pennycuick 1975, Norberg 1981, Rayner 1988). We found that higher scores for males on CAN1 persist, even after compensating for intersexual differences in residual body mass. In addition to a possible relationship to body mass, wing-shape differences between the sexes may be shaped by the need for early arrival on the breeding grounds by males (Ketterson and Nolan 1976, Myers 1981, Hedenström and Pettersson 1986), by social-dominance interactions (Ketterson and Nolan 1976, Ketterson 1979), or by sex-specific behavioral differences other than distance migrated (e.g. nest defense; Breitwisch 1988).

In the absence of a detailed understanding of how specific wing-shape changes affect the aerodynamic performance of a small passerine wing, our suggestions remain tentative. However, the fact that age/sex classes of juncos differ in wing shape highlights the importance of distinguishing these groups in studies of wing-shape variation (Tiainen and Hanski 1985, Chandler and Mulvihill 1990).

Wing-shape variability.—Despite significant differences among age/sex classes, components of wing shape in juncos were variable among individuals of given age and sex (Table 4). The high within-group variation may indicate that the migrant juncos we sampled arose from a wide geographic area. There is evidence, at least for male juncos, that some of the variation in wing shape among birds in our sample is due to the presence of juncos from different geographic areas (Chandler and Mulvihill 1990). This evidence was largely for variation in PC1 (Table 3). The patterns of migration by juncos through southwestern Pennsylvania (Chandler and Mulvihill 1990) provide little (PC2) or no (PC3) evidence for geographic variation in other components of wing shape.

Until we have information about wing shape from several populations across the breeding range, it will remain unclear why wing shape varies substantially within age/sex classes. At

one extreme, this may be selectively mediated variation that is adaptive for juncos from any given geographic area. Alternatively, wing shape may be subject to wide variation due to the variable seasonal and environmental conditions experienced by individuals at relatively little selective cost. This would imply a range of evolutionarily acceptable wing shapes in Dark-eyed Juncos (Norberg 1981, Rayner 1988).

Generalized variance estimates indicate that adults are more variable in wing shape than are immatures. This probably is due to the fact that all juncos beyond their first year were included in our adult sample. If there is any tendency for wing shape to continue to change with age (as is sometimes true for wing length; Francis and Wood 1989), then adults will be more variable.

Intervariable relationships.—In addition to describing wing-shape variation between and within age/sex classes, canonical discriminant analysis and principal components analysis revealed similar patterns of covariation among the wing-shape variables. Wing length covaries positively with the length of the proximal primaries. Perhaps wing-length changes are the result of a lengthening of distal (6–9) relative to proximal (1–5) primaries. As the distal primaries lengthen disproportionately, wing length increases and the proximal primaries are left progressively farther from the wing tip. Variation in distal primary distances, including position of the wing tip, were relatively independent of the changes in wing length and proximal primary distances. Thus, a set of traits usually associated with longer migration is really two independent dimensions of shape that do not covary among age/sex classes of juncos. Attempts to measure a characteristic such as “pointedness” along a single dimension, when it is really the result of two or more independent dimensions of shape, will be misleading and result in a loss of information about patterns of wing-shape variation (Chandler and Mulvihill 1988).

Wing shape and body mass.—Components of wing shape are correlated significantly with residual body mass across age/sex classes of juncos (Table 5). However, within an age/sex class, significant correlations between wing shape and body mass are rare (Table 5). The most notable exception was that wing length and proximal primary distances (PC1) covaried positively with residual body mass in female juncos. Wing

length (a correlate of PC1) is usually assumed to be related to lean body mass within age/sex classes of juncos (Ketterson and Nolan 1983, Nolan and Ketterson 1983). Apparently this is true only within female age classes that migrate through Powdermill. Not surprisingly, given the general lack of within-class correlation between wing shape and mass, wing-shape differences among age/sex classes persist even after compensating for residual body mass.

The lack of significant differences in residual body mass between ages suggests that the wing-shape differences between ages will be aerodynamically important (cf. Nolan and Ketterson 1983). The differences in wing length, wing-tip placement, and distal primary distances between adult and immature juncos should translate into different flight performance, given the similarity in body mass between these groups. However, the specific aerodynamic consequences of these significant, but small, wing-shape differences are unknown for a small passerine wing.

Overall, our results are inconsistent with the hypothesis that wing "pointedness" covaries positively with distance migrated among age/sex classes of the Dark-eyed Junco. This, together with the possibility that a counterintuitive (negative) relationship may exist, should serve as a caution in framing generalizations about the wing-shape traits that are favored by longer migrations. We agree with Norberg (1981) and Rayner (1988) that in studies of wing-shape variation, the relative importance of many flight-dependent activities needs to be considered, as do potential constraints on wing-shape adaptation (Winkler and Leisler 1985, Rayner 1988). Finally, there is a need for laboratory studies (e.g. via experimental manipulation of wing shape) of how specific changes in wing shape affect the aerodynamic properties of a small passerine wing.

ACKNOWLEDGMENTS

We are indebted to Robert C. Leberman for his key role in the origination and continuation of the Powdermill bird-banding program. Mulvihill, in particular, has benefited greatly from his advice and instruction over the past 10 years. D. S. Wood, director of the Powdermill banding program, facilitated our efforts and provided helpful comments on the manuscript. We also thank M. H. Balph, J. M. Cawthorn, Y. Cohen, M. Kesner, E. D. Ketterson, V. Nolan Jr., R. Panza, K. C. Parkes, J. T. Rotenberry, and M. Zuk

for their constructive comments. Mulvihill dedicates this paper to the memory of Mead J. Mulvihill III, who was fascinated by science and flight.

LITERATURE CITED

- ALATALO, R. V., L. GUSTAFSSON, & A. LUNDBERG. 1984. Why do young passerine birds have shorter wings than older birds? *Ibis* 126: 410-415.
- AVERILL, C. K. 1920. Migration and physical proportions. A preliminary study. *Auk* 37: 572-579.
- BAKER, R. R. 1978. The evolutionary ecology of animal migration. New York, Holmes and Meier.
- BERTHOLD, P. 1975. Migration: control and metabolic physiology. Pp. 77-128 in *Avian biology*, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- BLEM, C. R. 1980. The energetics of migration. Pp. 175-224 in *Animal migration, orientation, and navigation* (S. A. Gauthreaux Jr., Ed.). New York, Academic Press.
- BREITWISCH, R. 1988. Sex differences in defence of eggs and nestlings by Northern Mockingbirds, *Mimus polyglottos*. *Anim. Behav.* 36: 62-72.
- BUSSE, P. 1967. Application of the numerical indexes of the wing shape. *Notatki Ornitol.* 8: 1-8.
- . 1986. Wing-shape indices and the problems with their interpretation. *Notatki Ornitol.* 27: 139-155.
- CHANDLER, C. R., & R. S. MULVIHILL. 1988. The use of wing shape indices: an evaluation. *Ornis Scandinavica* 19: 212-216.
- , & ———. 1990. Wing-shape variation and differential timing of migration in Dark-eyed Juncos. *Condor* 92: 54-61.
- CHAPMAN, F. C. 1940. The post-glacial history of *Zonotrichia capensis*. *Bull. Am. Mus. Nat. Hist.* 77: 381-438.
- DOLBEER, R. A. 1982. Migration patterns for age and sex classes of blackbirds and starlings. *J. Field Ornithol.* 53: 28-46.
- DORST, J. 1962. *The migrations of birds*. Boston, Houghton Mifflin Co.
- DWIGHT, J., JR. 1900. The sequences of plumages and moults of the passerine birds of New York. *Ann. N.Y. Acad. Sci.* 13: 73-360.
- FEINSINGER, P., & S. B. CHAPLIN. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. *Am. Nat.* 109: 217-224.
- FRANCIS, C. M., & D. S. WOOD. 1989. The effects of age and wear on wing length of warblers. *J. Field Ornithol.* 60: 495-503.
- GASTON, A. J. 1974. Adaptation in the genus *Phylloscopus*. *Ibis* 116: 432-450.
- GAUTHREAUX, S. A., JR. 1978. The ecological significance of behavioral dominance. Pp. 17-54 in *Perspectives in ethology*, vol. 3 (P. P. G. Bateson and P. H. Klopfer, Eds.). New York, Plenum Press.

- . 1982. The ecology and evolution of avian migration systems. Pp. 93-168 in *Avian biology*, vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- GRISCOM, L. 1957. The classification of warblers. Pp. 8-13 in *The warblers of America* (L. Griscom and A. Sprunt, Eds.). New York, Devin-Adair Co.
- HEDENSTRÖM, A., & J. PETERSSON. 1986. Differences in fat deposits and wing pointedness between male and female Willow Warblers caught on spring migration at Ottenby, SE Sweden. *Ornis Scandinavica* 17: 182-185.
- HOLYŃSKI, R. 1965. The methods of analysis of wing-formula variability. *Notatki Ornitol.* 6: 21-25.
- KEAST, A. 1980. Spatial relationships between migratory parulid warblers and their ecological counterparts in the Neotropics. Pp. 109-130 in *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (A. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst.
- KETTERSON, E. D. 1979. Aggressive behavior in wintering Dark-eyed Juncos: determinants of dominance and their possible relation to geographic variation in sex ratio. *Wilson Bull.* 91: 371-383.
- , & V. NOLAN JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis*). *Ecology* 57: 679-693.
- , & ———. 1978. Overnight weight loss in Dark-eyed Juncos (*Junco hyemalis*). *Auk* 95: 755-758.
- , & ———. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-eyed Juncos (*Junco hyemalis*). *Auk* 96: 532-536.
- , & ———. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analyses of winter populations. *Auk* 99: 243-259.
- , & ———. 1983. The evolution of differential bird migration. Pp. 357-402 in *Current ornithology*, vol. 1 (R. F. Johnston, Ed.). New York, Plenum Press.
- , & ———. 1985. Intraspecific variation in avian migration: evolutionary and regulatory aspects. Pp. 553-579 in *Migration: mechanisms and adaptive significance* (M. A. Rankin, Ed.). Univ. Texas Contrib. Marine Sci., Suppl. 27.
- KIPP, F. A. 1942. Über Flügelbau und Wanderzug der Vögel. *Biol. Zentralbl.* 62: 289-299.
- . 1958. Zur Geschichte des Vogelzuges auf der Grundlage der Flügelpassungen. *Vogelwarte* 19: 233-242.
- LEBERMAN, R. C. 1967. The influence of fat on bird weight. *EBBA News* 30: 181-184.
- . 1976. The birds of the Ligonier Valley. Carnegie Mus. Nat. Hist. Spec. Publ. 3.
- , & D. S. WOOD. 1983. Bird-banding at Powdermill: twenty years reviewed. Powdermill Nature Reserve Res. Rep. 42, Carnegie Mus. Nat. Hist.
- LO VALVO, F., G. LO VERDE, & M. LO VALVO. 1988. Relationships among wing length, wing shape and migration in Blackcap *Sylvia atricapilla* populations. *Ringing & Migrat.* 9: 51-54.
- LÖVEI, G. L. 1983. Wing shape variations of Chiffchaffs on autumn migration in Hungary. *Ringing & Migrat.* 4: 231-236.
- MEINERTZHAGEN, R. 1951. Review of the Alaudidae. *Proc. Zool. Soc. London* 121: 81-132.
- MILLER, A. H. 1941. Speciation in the avian genus *Junco*. *Univ. Calif. Publ. Zool.* 44: 173-434.
- MYERS, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* 59: 1527-1534.
- NOLAN, V., JR., & E. D. KETTERSON. 1983. An analysis of body mass, wing length, and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. *Wilson Bull.* 95: 603-620.
- , ———, & L. WOLF. 1986. Long-distance homing by nonmigratory Dark-eyed Juncos. *Condor* 88: 539-542.
- NORBERG, U. M. 1979. Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. *Phil. Trans. R. Soc. London (B)* 287: 131-165.
- . 1981. Flight, morphology and the ecological niche in some birds and bats. *Symp. Zool. Soc. London* 48: 173-197.
- PALMER, W. 1900. Ecology of the Maryland Yellowthroat and its relatives. *Auk* 17: 216-242.
- PENNYCUICK, C. J. 1969. The mechanics of bird migration. *Ibis* 111: 525-556.
- . 1975. Mechanics of flight. Pp. 1-73 in *Avian biology*, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- RABENOLD, K. N., & P. P. RABENOLD. 1985. Variation in altitudinal migration, winter segregation, and site tenacity in two subspecies of Dark-eyed Juncos in the southern Appalachians. *Auk* 102: 805-819.
- RAYNER, J. M. V. 1988. Form and function in avian flight. Pp. 1-66 in *Current ornithology*, vol. 5 (R. F. Johnston, Ed.). New York, Plenum Press.
- SAS INSTITUTE INC. 1988. SAS/STAT user's guide. Cary, North Carolina, SAS Institute Inc.
- SAVILE, D. B. O. 1957. Adaptive evolution in the avian wing. *Evolution* 11: 212-224.
- SLAGSVOLD, T. 1982. Sex, size, and natural selection in the Hooded Crow *Corvus corone cornix*. *Ornis Scandinavica* 13: 165-175.
- SOKAL, R. R., & F. J. ROHLF. 1981. *Biometry*. San Francisco, W. H. Freeman and Co.
- STEGMANN, B. 1962. Die verkümmerte distale

- Handschwinge des Vogelflügels. *J. Ornithol.* 103: 50-85.
- STRANEY, D. O. 1978. Variance partitioning and non-geographic variation. *J. Mamm.* 59: 1-11.
- STUEBE, M. M., & E. D. KETTERSON. 1982. A study of fasting in Tree Sparrows (*Spizella arborea*) and Dark-eyed Juncos (*Junco hyemalis*): ecological implications. *Auk* 99: 299-308.
- SULLIVAN, K. A. 1988. Ontogeny of time budgets in Yellow-eyed Juncos: adaptation to ecological constraints. *Ecology* 69: 118-124.
- . 1989. Starvation and predation: age-specific mortality in juvenile juncos. *J. Anim. Ecol.* 58: 275-286.
- TIAINEN, J., & I. K. HANSKI. 1985. Wing shape variation of Finnish and central European Willow Warblers *Phylloscopus trochilus* and Chiffchaffs *P. collybita*. *Ibis* 127: 365-371.
- WINKLER, H., & B. LEISLER. 1985. Morphological aspects of habitat selection in birds. Pp. 415-434 in *Habitat selection in birds* (M. L. Cody, Ed.). New York, Academic Press.
- YUNICK, R. P. 1981. Age determination of wintering and spring Dark-eyed Juncos. *N. Am. Bird Band-er* 6: 97.