WING-SHAPE VARIATION AND DIFFERENTIAL TIMING OF MIGRATION IN DARK-EYED JUNCOS[1]

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Abstract. Wing shape among Dark-eyed Juncos, *Junco hyemalis,* (as described by principal components analysis of eight wing measurements) varied significantly with capture date during the fall migration in southwestern Pennsylvania. We assessed the relationship between this variation and the differential timing of migration among and within age/sex classes in a sample of 463 juncos. Differential timing of migration among morphologically distinct age/sex classes accounted for most of the temporal variation in wing shape. Adult juncos tended to migrate earlier than immatures and females tended to precede males. Significant variation remained, however, even after accounting for differential timing of age/ sex classes. Specifically, wing shape varied with capture date among adult males and among immature males. Although some components of wing shape were correlated with body mass in juncos, body mass did not vary with capture date. Temporal variation in wing shape among Dark-eyed Juncos caught during fall migration seems to be the complex result of differential timing of migration both among and within age/sex classes. Variation in the distance migrated and/or timing of prebasic molt may contribute to these differences in migratory timing.

Key words: Dark-eyed Junco; Junco hyemalis; *wing shape; differential migration; intraspecific variation; prebasic molt.*

INTRODUCTION

Intraspecific variation in the timing of migration has been documented in many species of birds (see reviews by Tordoff and Mengel 1956, Gauthreaux 1982). This differential timing may occur among age classes (Schifferli 1963; Johnson 1965, 1973; Hussell et al. 1967; Leberman and Clench 1969; Ely 1970; Hall 1981; Hussell 1981; Mueller et al. 1981), sexes (Annan 1962, Schifferli 1963, Johnson 1965, King et al. 1965, Nolan and Mumford 1965, Leberman and Clench 1971, Hussell 1981, Francis and Cooke 1986), or among individuals of different geographic origin (Mueller et al. 1981, Högstedt and Persson 1982, Lövei 1983, Hedenström and Pettersson 1986). To the degree that these groups differ in morphology, their differences in migratory timing will result in morphological variation among samples of migrants captured at the same locality

at different times. Thus, differential timing of migration at a given site is commonly inferred from patterns of temporal variation in wing length (Hussell 1981, Mueller et al. 1981, Hedenstrom and Pettersson 1984), wing shape (Lövei 1983, Tiainen and Hanski 1985, Scebba and Lövei 1986), or other morphological characters (Hedenström and Pettersson 1984).

Detecting and interpreting temporal patterns of morphological variation among migrants is hampered by the fact that different ages, sexes, and populations may all migrate at slightly different times within a given season. Thus, temporal variation in morphology may be the complex result of several underlying patterns (Tordoff and Mengel 1956, King et al. 1965, Johnson 1970). Furthermore, if age/sex classes or populations are difficult to distinguish, patterns of differential timing will be further obscured. For example, Lövei (1983) explained seasonal changes in the wing shape of Chiffchaffs (*Phylloscopus collybita*) as the result of differential timing of migration among subspecies. Tiainen and Hanski (1985) suggest, however, that undetected dif-

ferences in the migratory timing of age/sex classes may have contributed to the variation in wing shape. Consideration of all possible patterns of differential timing is crucial to understanding the nature and extent of the relationship between variation in morphology and variation in migratory timing.

In this paper we document wing-shape variation among fall-migrating Dark-eyed Juncos (*Junco hyemalis*) at a site in southwestern Pennsylvania and relate this variation to differential timing of migration among and within age/sex classes. Age/sex classes of juncos differ significantly in wing shape (Chandler and Mulvihill 1988; Mulvihill and Chandler, unpubl.) and are distinguishable by size and plumage characters throughout the fall. Thus, juncos provide an excellent opportunity to evaluate the relationship between morphological variation and differential timing of migration. In this paper, differential timing refers specifically to the differential temporal passage of juncos at a site along their migration route. However, assuming that age and sex classes are not latitudinally segregated on the breeding grounds, differential timing of passage should accurately reflect differences in the onset or rate of migration among age/sex classes (Ketterson and Nolan 1985, Chandler and Mulvihill 1990).

METHODS

All juncos were captured as part of the daily banding operations at Powdermill Nature Reserve, field station of the Carnegie Museum of Natural History, Westmoreland County, Pennsylvania (40°10'N, 79°16'W). For details of the banding procedures at the reserve see Leberman and Wood (1983). From 1983 through 1986 we quantified the wing shapes of 540 migrant and wintering Dark-eyed Juncos. All birds in this sample were assignable to the nominate race, *J. h. hyemalis*.

Wing shape was characterized by measuring wing length (unflattened wing chord) and wing formula for each individual. Wing formula, as used in this paper, is a measure of the distance (projected along the wing chord) from the wingtip to the tip of each of the nine primaries (for a more detailed description of measuring wing formula see Chandler and Mulvihill 1988). Individually, these nine measurements are referred to as primary distances (P1–P9, descendently). All measurements were to the nearest 0.5 mm.

Individuals with worn, missing, or disarranged primaries were omitted from our analyses. All birds were aged (AHY/ASY = adult; HY/SY = immature) based on skull pneumatization and/or the presence of retained juvenal wing feathers (Yunick 1981; R. S. Mulvihill, unpubl. data); individuals were sexed based on size and plumage characters (references in Ketterson and Nolan 1976). To ensure repeatability, all ageing, sexing, and measurements were conducted by the same individual (Mulvihill).

Body mass (to the nearest 0.1 g) and fat scores (ranked from 0 to 3; Leberman 1967) were also recorded for each individual. Fat-free body mass was estimated by regressing the natural logarithm of body mass on fat score and using residual body mass 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).

In order to identify the principal sources of variation in the wing shape of juncos we conducted a principal components analysis (PCA) on the correlation matrix of eight of the wing-shape variables (wing length, P1–P5, P8, and P9). The primary distances P6 and P7 were omitted from the analysis because they typically form the wingtip in juncos (i.e., have a primary distance of 0), are relatively invariant, and thus contribute little variation to overall wing shape. Variables entered into the PCA were not transformed because they were normally distributed within (*G*-test), and showed homoscedascity among (*F*-max test), age/sex classes.

The relationship between wing shape and capture date was assessed in the subset of juncos (*n* = 463) captured (first encounters only) during the fall migration (10 October–18 December) of 1983–1986. These birds were grouped by 10-day capture periods: (1) 10–19 October, (2) 20–29 October, (3) 30 October–8 November, (4) 9–18 November, (5) 19–28 November, (6) 29 November–8 December, and (7) 9–18 December. These dates span the period from the first appreciable arrival of juncos at Powdermill (where the species is not present during the breeding season) in October to just beyond the last detectable migrants in December. Ten-day capture periods were chosen as a compromise between small sample sizes (short sample periods) and loss of resolution (long capture periods). Because there was no a priori reason to suspect a linear relationship between morphology and capture date, differences in wing

TABLE 1. Results of the principal components analysis on the wing shape of Dark-eyed Juncos (n = 540).

Variable	Factor loadings		
	PC 1	PC 2	PC 3
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	4.40	1.56	0.82
% variance explained	54.07	19.48	10.27
Cumulative variance	54.07	73.55	83.82

shape (PCA scores) and body mass among capture periods were tested using analysis of variance (ANOVA). In order to assess the proportion of wing-shape variation attributable to differences among capture periods, intraclass correlation coefficients (r_i) were calculated (Sokal and Rohlf 1981).

Differences in timing of migration among age/sex classes were evaluated using all juncos of known age and sex captured at Powdermill during the fall migrations of 1985 (n = 528) and 1986 (n = 604). More birds were sexed and aged each year than were measured for this study because time constraints precluded measuring the wing shape of every junco handled at Powdermill. Nevertheless, the large sample of juncos of known age and sex allows a detailed examination of differential timing using G-tests of independence for three-way (age × sex × capture period) frequency tables (Sokal and Rohlf 1981). All statistical analyses were performed using SAS (SAS Institute 1985).

RESULTS

PCA produced three biologically interpretable axes which accounted for 83.8% of the variation in wing shape (Table 1). The first principal component (PC 1) represented an axis of increasing wing length and its allometric effects on wing shape (a disproportionate increase in proximal primary distances). PC 2 was an axis representing increasing distal primary distances. PC 3 was an inverse relationship between proximal and distal primary distances. It was also negatively correlated with wing length. These three axes represented the principal dimensions of wing shape
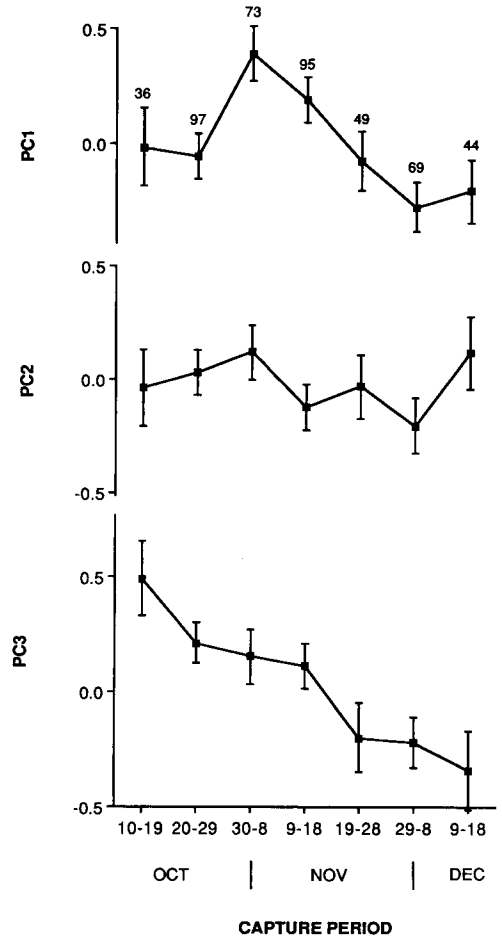

FIGURE 1. Principal component scores ($\bar{x}$ ± SE) for Dark-eyed Juncos captured during 10-day periods during fall migration at Powdermill Nature Reserve. Numbers at the top indicate sample sizes for each capture period.

in juncos and were used to quantify wing-shape variation.

There was significant variation in wing shape among capture periods as described by principal component scores (Fig. 1). Scores on PC 1 (F = 3.78, P < 0.01) and PC 3 (F = 4.44, P < 0.001) differed significantly among capture periods. Scores on PC 2 did not vary significantly with capture period (F = 0.94, ns).

Differential timing of migration among morphologically distinct age/sex classes could account for these differences. To explore this possibility we calculated the frequency of individuals from the four age/sex classes among the seven capture periods (Fig. 2) for 1985 and 1986. In
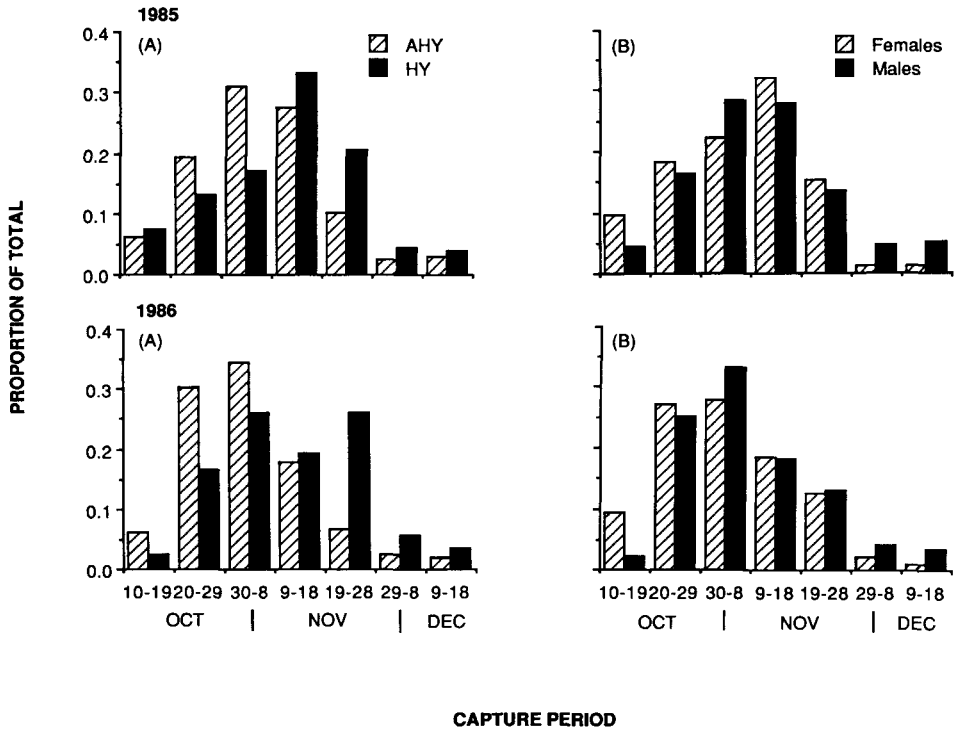
FIGURE 2.   Timing of fall migration of ages (A) and sexes (B) of Dark-eyed Juncos in 1985 and 1986 at Powdermill Nature Reserve. Calculations are based on all juncos of known age and sex captured at Powdermill during fall 1985 (n = 528) and fall 1986 (n = 604).

both years there were significant differences in the timing of migration among both ages (1985: G = 25.24, P < 0.001; 1986: G = 56.35, P < 0.001) and sexes (1985: G = 19.66, P < 0.001; 1986: G = 20.53, P < 0.001). There were no significant interactions among age, sex, and capture period. Adult juncos tended to precede immatures and females tended to precede males (Fig. 2).

The effect of differential migration among age/sex classes on variation in wing shape is confirmed by adding age/sex class as a treatment effect in the original ANOVA. Variation due to age/sex class is significant for all components and the effect of capture period disappears for PC 3 (Table 2). There were no significant interaction effects between age/sex class and capture period.

Differential timing among age/sex classes is not sufficient, however, to account for all the temporal variation in wing shape. For example, a significant effect due to capture period remains for PC 1 (Table 2). Analysis of variance within age/sex classes reveals that PC 1 differs among capture periods within both adult males (F =

2.36; df = 6, 154; P < 0.05; r_i = 0.057) and immature males (F = 2.97; df = 6, 65; P < 0.05; r_i = 0.171). Values for PC 1 (i.e., wing length and proximal primary lengths) in males peak in late October and decrease significantly through the remainder of the migration (Fig. 3). PC 2 also varies with capture date among adult males (F = 2.31; P < 0.05; r_i = 0.056). Thus, there is detectable variation in wing shape among capture periods (ranging from 5–17% of the total variation in a given component within a particular age/sex class) that is attributable to the differential migration of morphologically distinct individuals within male age classes.

Patterns of wing-shape variation within age/sex classes could be related to body-size differences between early and late migrants. However, with the exception of PC 1 in adult females (r = 0.203, P < 0.05), PC 2 in immature males (r = 0.292, P < 0.01), and PC 1 in immature females (r = 0.209, P < 0.05), there is no correlation between dimensions of wing shape (PC scores) and residual body mass. Furthermore, residual body mass did not differ significantly among cap-

TABLE 2.   Two-way analysis of variance of wing-shape differences (as indicated by PC scores) among age/sex classes and capture periods.

	Source of variation	Mean square	df	F	P
PC 1	Age/sex class	54.29	3	97.84	<0.001
	Capture period	2.36	6	4.25	<0.001
	Error	0.55	435		
PC 2	Age/sex class	14.19	3	16.30	<0.001
	Capture period	1.18	6	1.36	ns
	Error	0.87	435		
PC 3	Age/sex class	28.29	3	40.81	<0.001
	Capture period	1.03	6	1.49	ns
	Error	0.69	435		

ture periods for any age/sex class (ANOVA, P's > 0.05).

DISCUSSION

WING SHAPE AND THE TIMING OF MIGRATION

Significant variation in wing shape among fall migrants captured at different times has been reported in several species (*Prunella modularis*, Nitecki 1969; *Phylloscopus collybita*, Lövei 1983; *Regulus ignicapillus*, Scebba and Lövei 1986). Because wing shape is presumed to vary adaptively in relation to migratory distance (Chapman 1940, Stegmann, 1962, Gaston 1974), variation in wing shape among migrants has been interpreted as indicating the passage of birds of

FIGURE 3.   Scores on PC 1 ($\bar{x} \pm$ SE) for adult (AHY) and immature (HY) male Dark-eyed Juncos captured during 10-day periods during fall migration at Powdermill Nature Reserve.

different geographic origin (Nitecki 1969, Lövei 1983, Scebba and Lövei 1986). However, increasing documentation of wing-shape differences among age and sex classes within species (Tiainen 1982, Tiainen and Hanski 1985, Hedenström and Pettersson 1986, Chandler and Mulvihill 1988) has led to caution concerning the interpretation of wing-shape variation among migrants (Tiainen and Hanski 1985).

Our results indicate that wing-shape variation among migrant juncos can be attributed to differential timing both among and within age/sex classes. Differences in migratory timing among morphologically distinct age/sex classes were sufficient to account for most of the temporal variation in junco wing shape. This supports Tiainen and Hanski's (1985) caution that age- and sex-specific variation in wing shape must be assessed before attributing further significance to temporal patterns. However, for some components of wing shape (particularly PC 1), significant differences among capture periods remain even after accounting for differential timing among age/sex classes (Table 2). This variation can be attributed to differential timing among morphologically distinct individuals within male age classes. Males captured at Powdermill late in migration have shorter wings and proximal primary distances than mid-season migrants (Fig. 3).

Wing-shape variation within age/sex classes may reflect the movement of birds of different geographic origin (Mueller et al. 1981, Tiainen and Hanski 1985). If so, it is not obvious why such variation is detectable within male, but not female, juncos. One possibility is that geographic variation in wing shape (specifically, PC 1) is sex-specific. In other words, only males show the geographic variability in wing shape that would
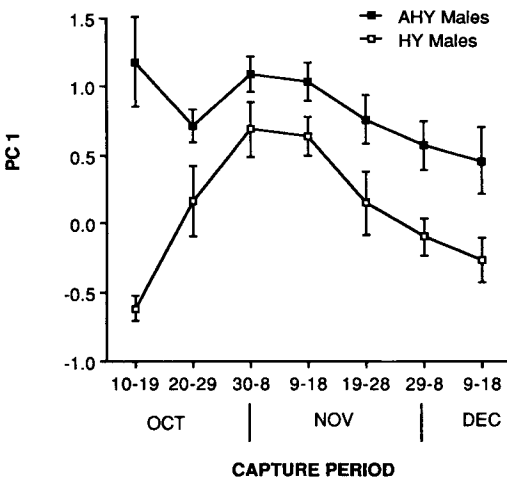
appear as temporal variation in wing shape at Powdermill. Wing shape in male juncos may be geographically fine-tuned because of intrasexual selection for early spring arrival and territory establishment (Myers 1981, Francis and Cooke 1986, Hedenström and Pettersson 1986). A second possibility is that both sexes show geographic variation in wing shape, but something about the way individuals sort themselves during migration preserves this variation within males and obscures it in females. Without knowledge of geographic variation in wing shape across the breeding grounds it is difficult to evaluate either of these possibilities for Dark-eyed Juncos. Finally, seasonal variation in males may reflect the fact that larger (or smaller) males migrate earlier irrespective of their geographic origin and that size is related to wing shape. However, with few exceptions, wing shape was not correlated to body mass in juncos captured at Powdermill. Furthermore, seasonal variation in body mass was not detectable within any age/sex class.

Overall, these results support the suggestion that differential timing of migration is likely to be complex (Tordoff and Mengel 1956, Johnson 1970). Patterns of variation in morphology that result from this differential timing will also be complex and should be interpreted carefully (Tiainen and Hanski 1985). Of particular interest is the fact that wing-shape variation among capture periods was attributable to timing differences both among and within age/sex classes. This implies differential timing among ages, sexes, and populations within a single season.

FACTORS AFFECTING DIFFERENTIAL
TIMING OF MIGRATION

Although much attention has been given to differential timing of spring migration (Ketterson and Nolan 1976, 1983; Gauthreaux 1978, 1982; Francis and Cooke 1986), less consideration has been given to why age/sex classes follow different schedules of fall migration. Some of the explanations for the differential timing of spring migration may be applicable to fall patterns (such as dominance on the wintering grounds; Gauthreaux 1978, 1982) while others are clearly inadequate (sexual selection for early arrival; Myers 1981). Tordoff and Mengel (1956) suggest that patterns of differential timing are related to life-history differences among various species. For juncos these may include the well-known differences in the winter distribution of the age/sex classes (Ketterson and Nolan 1976, 1983) and/or intraspecific variation in the timing of the prebasic molt.

The age and sex classes of juncos that migrate through Powdermill earliest (adults and females) are also those that winter farthest south (Ketterson and Nolan 1983). This suggests a direct relationship between distance migrated and timing of migration in juncos with individuals undertaking longer migrations migrating earlier, migrating at faster rates, or both. Such a relationship, however, is not entirely consistent with likely causal factors such as endogenous rhythms (Ketterson and Nolan 1985) or dominance interactions (Nolan and Ketterson, in press).

The timing of fall migration in juncos may also be related to intraspecific differences in the timing, rate, and/or extent of the prebasic molt. For the most part, north temperate and arctic-nesting passerines accomplish the prebasic molt on the breeding grounds, following nesting and prior to migration (Dwight 1900, Stresemann and Stresemann 1966). The migration of many species immediately succeeds, or only slightly overlaps, the prebasic molt (Evans 1966, Morton et al. 1969, Meanley and Bond 1970, Mewaldt and King 1978, Sealy 1979, Cannell et al. 1983, Rimmer 1988). This raises the possibility that age and/or sex differences in the timing of molt may give rise to differential timing of departure from the breeding grounds (e.g., Tordoff and Mengel 1956, Niles 1972, Ketterson and Nolan 1985). Furthermore, geographic variation in the timing of molt could give rise to within age/sex class variation in migratory timing. For the timing of the prebasic molt among age/sex classes to be complementary to the observed pattern of migration in Dark-eyed Juncos, males and immatures should begin and/or complete their molts later than females and adults, respectively.

There are few data on the timing of molt in Dark-eyed Juncos. Ketterson and Nolan (1985) suggest that because immature juncos undergo an incomplete first prebasic molt they should complete their molts prior to adults. If so, the results of this study suggest that this difference does not result in an earlier migration by immatures. Furthermore, it is possible for the incomplete first prebasic molt of immatures to succeed the complete molt of adults (e.g., *Vermivora celata*, Foster 1967). Immature male Dark-eyed Juncos have a more extensive first prebasic molt, on average, than females (Mulvihill and Win-

stead, unpubl.); this could account for a slight difference in the timing of completion of molt (and thus the onset of migration) with females preceding males. Finally, immature juncos of northern subspecies molt significantly fewer wing coverts than southern birds (Mulvihill and Winstead, unpubl.). This suggests a shorter molt period for northern juncos that probably affects adults as well. Such geographic variation in the timing of molt could affect the timing of migration and might account for the within-class (within males of both age classes) variation reported here. In at least one species, geographic variation in the duration of molt was found for males but not females (*Carduelis flammea*, Evans et al. 1967). A full evaluation of the role of intraspecific variation in the timing of molt in imposing differential timing of migration in Dark-eyed Juncos awaits a detailed study of molt within and between breeding populations.

ACKNOWLEDGMENTS

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