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The use of wing shape indices: An evaluation

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The properties of five wing shape indices were evaluated using data on the wing morphology of 540 Dark-eyed Juncos *Junco hyemalis*. These indices differed in their ability to detect age and sex related differences in wing shape. Correlations among the indices revealed that some between-index comparisons are not valid. Wing symmetry and pointedness, as identified by these indices, are not independent dimensions of wing shape. Comparison of the indices with an independent assessment of wing shape (PCA of the original variables) showed that no two indices of wing pointedness measure the same components of wing shape variation. Wing shape indices do not provide an unequivocal method for the analysis of wing shape and we recommend the use of alternative techniques such as multivariate analysis.

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Analysis of avian wing shape is often based on simple numerical indices (Holyński 1965, Busse 1967, Hedenström and Pettersson 1986). Because these indices provide an easy way to quantify such normally subjective aspects of wing shape as pointedness and symmetry, they are increasingly used to compare wing shapes among age/sex classes (Tiainen and Hanski 1985, Hedenström and Pettersson 1986), to identify distinct populations within samples of migrating birds (Nitecki 1969, Lövei 1983, Tiainen and Hanski 1985, Scebba and Lövei 1986), and for ecomorphological comparisons among species (Tiainen 1982).

This increasing use of wing shape indices, as well as the variety of indices available, raises several questions. For example, are the results of different indices directly comparable? At least four indices of wing pointedness are available (Holyński 1965, Busse 1967, Hedenström and Pettersson 1986) and results obtained using one index have been compared with those from a different index (Tiainen and Hanski 1985, Hedenström and Pettersson 1986). The validity of such between-index comparisons is unknown, but there is some indication that these indices do not always produce similar results (Busse 1967). If not, what components of wing shape do these indices actually measure? Although all wing shape indices are based on the same general principles of wing morphology (Kipp 1958, Kokshaysky 1973, Gaston 1974), there has been no attempt to quantify the sensitivity of different indices to known components of wing shape variation. Lastly, are pointedness and symmetry (as identified by wing shape indices) independent dimensions of wing shape?

In light of these questions, we evaluated five commonly used wing shape indices by comparing them with one another and with an independent assessment of wing shape (revealed by principal components analysis). Wing shape indices were calculated from data on the wing morphology of Dark-eyed Juncos *Junco hyemalis*, a species that exhibits differential migration among populations and age/sex classes (Ketterson and Nolan 1976, Rabenold and Rabenold 1985, Chandler and Mulvihill, unpubl.). In these respects this species is similar to those in most previous studies using wing shape indices (Lövei 1983, Tiainen and Hanski 1985, Hedenström and Pettersson 1986).

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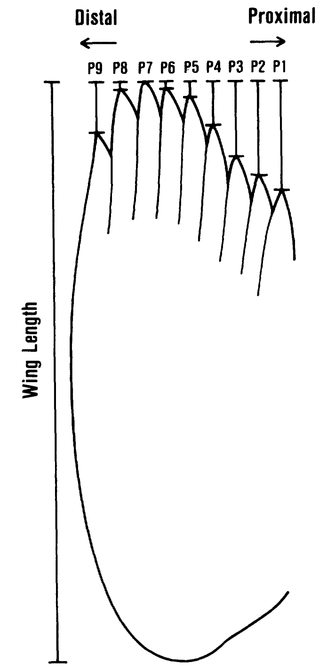
Fig. 1: Measurements used for the calculation of wing shape indices and multivariate analysis of wing shape in Dark-eyed Juncos.



We calculated five wing shape indices from these data (Tab. 1). Three indices (I9, I5, and WPT1) are designed to measure wing pointedness (i.e., a lengthening of distal primaries and shortening of proximal primaries that shifts the wingtip toward the leading edge of the wing). WPT2 has been described as measuring narrowness (Lövei 1983) or pointedness (Tiainen and Hanski 1985). We will consider WPT2 a fourth index of wing pointedness. The fifth index (WSYM) measures wing symmetry (i.e., symmetry of the primaries about the wingtip). Larger values of I9, WPT1, and WPT2, and smaller values of I5, indicate increasing wing pointedness. Asymmetry is indicated by increasing values of WSYM (see references in Tab. 1 for more details on the use and interpretation of these indices).

In order to obtain an independent assessment of wing shape with which to evaluate the wing shape indices, we conducted a principal components analysis (PCA) on the correlation matrix of the ten original variables (wing length and primary distances). PCA produces linear combinations of the original variables that represent the primary sources of variation in the data and provides an objective assessment of wing shape variation in juncos. The correlation matrix was analyzed so that each age/sex class would contribute equally to the analysis despite differences in sample sizes (Pielou 1984).

Differences in the distribution of wing shape indices among age classes and sex classes were evaluated using Wilcoxon's two-sample tests. Spearman's rank correlations were calculated among the five indices and for each index with the derived PCA axes. All statistical analyses were conducted using SAS (SAS Institute, Inc. 1985).

Materials and methods

Migrant and wintering juncos (n=540) used in this study were captured at Powdermill Nature Reserve, SW Pennsylvania, USA (40° 10′N, 79° 16′W) from autumn 1983 through autumn 1986 (see Leberman and Wood 1983 for a complete description of ringing operations at Powdermill). We recorded wing length (unflattened wing chord) and wing formula of the right wing of each individual. Wing formula was recorded by measuring the distance from the wingtip to the tip of each of the nine primaries on the folded wing (Fig. 1). These measurements are referred to as primary distances and abbreviated P1–P9, descendantly (Fig. 1). All measurements were to the nearest 0.5 mm. Birds were aged and sexed by degree of skull pneumatization, size, and plumage characters (Dow 1966, Grant and Quay 1970, Balph 1975, Ketterson and Nolan 1976, Yunick 1981). Individuals of uncertain age or sex, as well as those moulting or with missing, worn, or disarranged primaries, were omitted from our analyses.

Results

Age/sex classes of juncos differed significantly in wing shape as indicated by each of the five indices (Tab. 2). However, the four indices of wing pointedness are contradictory with respect to which age/sex classes have more pointed wings. Only two indices (I5 and WPT1) provide the same ranking of age/sex classes (Tab. 2).

In order to further assess between-index relationships, we calculated the pairwise correlations among all five indices (Tab. 3). Despite the fact that they are all designed to estimate pointedness, the four wing poin-

Tab. 1: Calculations for the wing shape indices used in this study. The formulas are based on the primary distances for P9 to P3, inclusive (these correspond to P2 through P8 in some literature). Σp is the sum of these distances proximal to the wingtip. Σd is the sum of these distances distal to the wingtip. See Fig. 1 for a complete description of the variables used in the wing shape indices. Wing shape characteristics are indicated by increasing (+) or decreasing (−) values of the index.

Index	Formula	Wing characteristic	References
I9	(wing length − P9)/wing length	pointedness (+)	Hedenström and Pettersson 1986
I5	(wing length − P5)/wing length	pointedness (−)	Hedenström and Pettersson 1986
WPT1	$(\Sigma p + \Sigma d)$/wing length	pointedness (+)	Busse 1967, Tiainen 1982
WPT2	$100(\Sigma p - \Sigma d)$/wing length	pointedness (+)	Holyński 1965, Lövei 1983
WSYM	$\Sigma p/\Sigma d$	symmetry (−)	Tiainen 1982, Tiainen and Hanski 1985

Tab. 2: Wing shape indices ($\bar{x} \pm SD$) for age/sex classes of Dark-eyed Juncos captured at Powdermill Nature Reserve. Superscripts represent the rankings of age/sex classes based on each wing pointedness index (1= most pointed). Significance levels for Wilcoxon's two-sample test: *= $p<0.05$, **= $p<0.01$, ***= $p<0.001$, ns= not significant.

Age/sex	n	Index				
		I9	I5	WPT1	WPT2	WSYM
Adult male	198	0.908 (±0.012)[3]	0.970 (±0.008)[1]	0.399 (±0.032)[1]	18.07 (±3.73)[1]	2.73 (±0.565)
Adult female	137	0.903 (±0.014)[4]	0.972 (±0.007)[2]	0.398 (±0.032)[2]	16.63 (±3.68)[4]	2.51 (±0.530)
Immature male	85	0.917 (±0.010)[1]	0.974 (±0.006)[4]	0.367 (±0.027)[4]	17.70 (±3.21)[2]	2.93 (±0.533)
Immature female	120	0.912 (±0.011)[2]	0.973 (±0.007)[3]	0.373 (±0.029)[3]	17.04 (±3.22)[3]	2.75 (±0.500)
Age		***	ns	***	*	***
Sex		**	*	*	***	***

tedness indices are not in full agreement. For example, I9 is uncorrelated with I5 and negatively correlated with WPT1. Thus, in Dark-eyed Juncos, increasing wing pointedness as indicated by 19 is associated with decreasing wing pointedness as indicated by WPT1. The remaining correlations among wing pointedness indices are significant and in the expected direction.

The wing symmetry index is significantly correlated with all indices of wing pointedness (Tab. 3). These correlations indicate that increasing asymmetry of the wing (high WSYM) is always associated with increasing wing pointedness as indicated by these measures for Dark-eyed Juncos.

In order to independently assess wing shape variation in juncos, we conducted a PCA on the original wing variables. Three of the components produced by the PCA (explaining 74.7% of the variation in the original data) can be readily interpreted by examining the factor loadings (correlations) between the original variables and the derived components (Tab. 4). PC1 represents an axis of increasing wing length and its allometric effects on wing shape (disproportionate increase in proximal primary distances). PC2 is an axis of increasing distal primary distances (P7–P9). Finally, PC3 represents an inverse relationship between P7 and adjacent primary distances. Thus, PC3 can be interpreted as measuring the acuteness of the wingtip. These axes represent the three principal sources of variation in junco wing shape.

By comparing the five wing shape indices with the axes produced by the PCA, we can determine which components of wing shape these indices actually measure. Specifically, a significant correlation between an index and a PCA component indicates that the index is sensitive to that component of wing shape variation. Based on these correlations (Tab. 5), no two wing pointedness indices measure the same components of variation. I9 is insensitive to the variation represented by PC1 (wing length and its allometric effects). WPT1 fails to measure changes in distal primary distances (PC2). WPT2 is insensitive to variation in acuteness of the wingtip (PC3). Of the four wing pointedness indices, only I5 measures all three principal components of variation in junco wing shape. The index of wing symmetry is also correlated with these three components.

Discussion

The five indices that we evaluated differ in their ability to detect age and sex related differences in wing shape, are correlated in unpredictable ways, and differ in sensitivity to the principal components of wing shape in Dark-eyed Juncos. These results suggest that despite their widespread use wing shape indices may not provide an unequivocal method for quantifying wing shape in birds.

Previous studies that have used more than one index usually have found agreement between indices (Tiainen and Hanski 1985, Hedenström and Pettersson 1986), suggesting that comparisons among studies using different indices are justified (e.g., Hedenström and Pettersson 1986). However, the results of wing shape comparisons among age/sex classes of juncos are clearly depend-

Tab. 3: Spearman's rank correlations among the five wing shape indices used in this study (n=540). Significance levels: *= $p<0.05$, ***= $p<0.001$.

Index	I9	I5	WPT1	WPT2	WSYM
I9	–				
I5	−0.059	–			
WPT1	−0.457***	−0.589***	–		
WPT2	0.490***	−0.661***	0.427***	–	
WSYM	0.771***	−0.462***	0.096*	0.898***	–

Tab. 4: Results of the principal components analysis on the wing shape of Dark-eyed Juncos.

Variable	Factor loadings		
	PC 1	PC 2	PC 3
Wing length	0.724	0.269	−0.260
P1	0.911	0.056	−0.156
P2	0.946	0.057	−0.133
P3	0.946	0.029	−0.094
P4	0.845	−0.097	0.037
P5	0.685	−0.367	0.307
P6	0.291	−0.584	0.531
P7	−0.044	0.644	−0.259
P8	0.086	0.715	0.510
P9	0.208	0.695	0.456
% variance explained	44.64	19.73	10.30
Cumulative variance	44.64	64.38	74.68

ent on the index used (Tab. 2). Our results suggest that comparisons among indices may not always be justified and, in some cases, may actually be misleading. The lack of concordance among some indices is emphasized by their pairwise correlations (Tab. 3). I9 and I5 are uncorrelated despite the fact that they are supposed to be complementary measures of wing pointedness (Hedenström and Pettersson 1986). Busse (1967) has also reported a lack of correlation among wing pointedness indices. Other indices (WPT1 and I9) are correlated in the opposite direction from that expected. Any attempt to make comparisons among these various indices (under the assumption that they all measure the same thing) will produce misleading results.

Different indices do, in fact, measure different components of wing shape (Tab. 5). No two wing pointedness indices were able to measure the same components of wing shape variation. In addition to compromising comparisons among indices, this suggests that the usefulness of a wing shape index is dependent on which components of wing shape variation are important in the population of birds that the index will be applied to. Without knowledge of this variation, the choice of an index is arbitrary and possibly of limited value. For example, I9 may be inappropriate for juncos because it is insensitive to approximately 45% of the variation in wing shape (i.e., that variation represented by PC1). In this case, the focus on an index to measure a specific aspect of wing shape (pointedness) leads to an oversight of other biologically relevant sources of wing shape variation. Because wing shape indices are clearly not interchangeable measures of identical components of wing shape, future studies should justify their choice of an index for a given population.

Although symmetry has been considered a recognizable dimension of wing shape (Tiainen 1982, Tiainen and Hanski 1985), the index of wing symmetry is always significantly correlated with indices of wing pointedness in juncos. If symmetry and pointedness are, in fact, distinct dimensions of wing shape, our results suggest they are intimately related. It is more likely, however, that symmetry (as it is identified by WSYM) and pointedness are indistinguishable traits. Those characteristics which lead to increasing indices of wing pointedness almost invariably give increasing values of WSYM (Tab. 1). Other studies which have reported values for both symmetry and pointedness usually have found a positive relationship between WSYM and wing pointedness (Tiainen 1982, Tiainen and Hanski 1985). Thus, the designation of an index as a measure of pointedness or symmetry appears arbitrary and there is no evidence that the two can be considered independent dimensions of wing shape.

Wing shape indices have been applied to many species, in both intraspecific (Nitecki 1969, Lövei 1983, Tiainen and Hanski 1985, Scebba and Lövei 1986, Hedenström and Pettersson 1986) and interspecific (Busse 1967, Tiainen 1982, Tiainen and Hanski 1985) comparisons. Our results suggest, however, that these indices are inappropriate for characterizing wing shape variation within Dark-eyed Juncos. We suspect these shortcomings will be found in other intraspecific comparisons as well. It might be suggested that wing shape indices will still be useful in interspecific comparisons because all of these indices are likely to detect the gross morphological changes associated with the transformation of a blunt wing to a pointed wing across species (Kokshaysky 1973). Nevertheless, the fact that different indices measure different components of shape (and ignore other biologically relevant components) is a problem that is likely to remain. The general applicability of wing shape indices should be explored through additional studies such as ours as well as reexamination of data from earlier studies.

In conclusion, we have identified a number of problems with the use and interpretation of wing shape indices. We believe that these problems compromise the value of these indices as simple indicators of wing shape. Therefore, we recommend the use of alternative techniques for the analysis of wing shape. Multivariate methods (such as principal components analysis) provide an objective means of determining patterns of variation in wing shape and eliminate the interpretational problems associated with simple numerical indices.

Tab. 5: Spearman's rank correlations among the wing shape indices and the three derived principal component axes (n=540). Significance level: *= $p<0.001$.

Index	Principal component		
	1	2	3
I9	−0.021	−0.637*	−0.509*
I5	−0.454*	0.442*	−0.377*
WPT1	0.687*	0.075	0.445*
WPT2	0.621*	−0.659*	−0.083
WSYM	0.362*	−0.817*	−0.313*

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