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Inability to Predict Geographic Origin of Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus*, During Migration

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Identification of the patterns, timing, and duration of migration for passerine birds has been hindered by an inability to identify the origin or destination of birds encountered during migration. Historically, encounters with banded birds have been used to ascertain migration routes and the timing of migration (e.g., Royall et al. 1971; Dolbeer 1982). However, encounters of banded birds are rare. Encounters at two locations within the same year, that may elucidate the timing of migration, are even rarer. Indeed, only 246 of 40,855 Yellow-headed Blackbirds banded between 1937 and 1968 were subsequently encountered, and only 36 of these were direct recoveries at separate locations during the same year (Royall et al. 1971). Encounters of banded birds, however, can be markedly increased if bands are accompanied by auxiliary markers that can be detected without the recapture of individuals (Bray et al. 1977).

Mass-marking of birds at en-route migration roosts using aerially applied micro-tags or dyes (Linz et al. 1991) has been successfully employed to mark large numbers of migratory birds (Otis et al. 1986) that were subsequently encountered at breeding or wintering localities (Knittle et al. 1987). Even with this vastly increased efficiency in marking birds, recovery rates of marked birds remained relatively low. For example, Knittle et al. (1987) found that only 770 of 8880 Red-winged Blackbirds (Agelaius phoeniceus) collected at breeding localities across the northern Great Plains had been marked during mass-marking of blackbirds at en-route roosts during spring.

An alternative to physically marking individual birds is to use their inherent morphometric or genetic variation to discern their geographic origin or destination. If geographically distinct subpopulations can be identified among breeding sites, these data could be used to identify the geographic origin of individuals encountered elsewhere. Indeed, morphometric data have been used to suggest breeding location of species encountered on wintering grounds (Ramos and Warner 1980) and during migration (James et al. 1984; Atwood 1989; Linz et al. 1993). Inability to assign individuals of widely distributed, panmictic species to subspecies or races — either through morphometric or genetic techniques — has hampered the development of these methods in the study of migration. However, both morphometric (Zink and Remsen 1986; Aldrich and James 1991) and genetic (Zink et al. 1987) techniques have been successfully employed in assessing geographic variation within otherwise monotypic species.

Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) breeding on the northern Great Plains of North America exhibit discernable clinal variation during migration.
in morphology: larger bodied birds with relatively shorter limbs breed at more northern and western locations (Twedt et al. 1994). We attempted to exploit these inherent morphological differences to infer the geographic origin of individuals that were encountered during migration. Our objective was to determine if and when Yellow-headed Blackbirds that breed within central North Dakota are displaced by migrants.

Methods
From 28 May to 16 June 1987 and from 14 May to 17 June 1988, we collected adult male and female Yellow-headed Blackbirds within breeding locales in Alberta, Saskatchewan, Manitoba, and North Dakota as part of a study on geographic variation (Twedt et al. 1993, 1994). Because after-second-year males can easily be distinguished from second-year males under normal field conditions and because few second-year males hold breeding territories, we only collected after-second-year males during May and June. Additionally, we collected adult male and female Yellow-headed Blackbirds within Benson, Ramsey, and Wells Counties in central North Dakota (48° 01’ N, 99° 40’ W) between 21 June and 18 September during 1987 and 1988 for studies on diet (Twedt et al. 1991) and molt (Twedt 1990). Because after-second-year males cannot be separated from second-year males by plumage characteristics after their pre-basic molt is completed in mid-summer, we collected both adult age classes after 1 July.

From collected Yellow-headed Blackbirds, we recorded 13 morphometric measurements (Twedt et al. 1994). Collection site locations, methods of skeletal preparation, and measurement procedures were described by Twedt (1990). Because pre-basic molt and pre-migratory fat deposition during late summer result in temporal changes in mass, wing chord, total length, and tail length, we dropped all morphometric variables that were temporally unstable (Twedt and Linz 2002). However, we derived one additional measurement — body length. Body length was the difference between total length and tail length. Both total length and tail length were temporally unstable due to loss and re-growth of the tail during molt. However, because their difference negated this temporal instability, body length was temporally stable.

Using principal components analysis in SAS (SAS Institute 1989) we reduced body length and eight temporally stable skeletal measurements (skull width, and lengths of skull, keel, ulna, humerus, femur, tarsus, and tibiotarsus) to their principal components. Sex-specific principal components were obtained separately for birds collected at breeding locations and for birds collected in central North Dakota during summer and fall. Before deriving principal components, we replaced missing data that resulted from broken or deformed bones (4% of total data) using regressions against the most highly correlated variables (Chan et al. 1976). To assess the relationship between these morphometric mensurations and date of collection, we plotted principal component scores against date of collection. We reduced the variation among collection dates by constructing 5-day running averages. These 5-day running averages were subjected to regression analysis to relate collection date to principal component scores. Finally, we discriminated between hypothesized subpopulations in Canada and the USA using discriminant analysis.

Results
We collected 176 female and 1481 male Yellow-headed Blackbirds from breeding locations across the northern Great Plains (Twedt et al. 1994). An additional 624 females and 865 males were collected after 21 June from central North Dakota. The first two principal components derived from morphometric measurements were consistently, biologically interpretable among sexes and seasons. The first principal component (PC 1) represented generalized size whereas PC 2 represented the birds' shape by contrasting axial dimensions with appendicular dimensions (Table 1). Generally, PC 3 contrasted skull and body measurements but varied slightly in interpretation among sexes and seasons. Because of similarity in interpretation between seasons, we present sex-specific principal component scores for combined data from all collected birds. We restricted further analyses to PC 1 and PC 2 within each sex. These first two principal components accounted for 68% and 61% of the variability in females and males, respectively (Table 1).

Multivariate analysis of variance of principal component scores detected significant differences among breeding locations (F6,240 = 7.04, P < 0.01 female; F6,250 = 46.2, P < 0.01 male). Principal component scores from central North Dakota were negative but became increasingly positive at more northern and western locations as larger bodied birds with relatively shorter appendages were encountered (Table 2). Thus we hypothesized that migrants encountered in central North Dakota, that had originated in more northernmost breeding locations, would have greater PC scores than did Yellow-headed Blackbirds that bred in North Dakota.

To examine the hypothesis of increasing PC scores over time, we plotted 5-day running averages of PC scores against dates of collection (Figure 1). Although average PC scores derived from female measurements slightly increased over time, the slope of neither PC 1 nor PC 2 differed significantly from zero (t > 1.19, P > 0.21). Similarly, PC scores for males exhibited no significant trend over time (t > 1.58, P > 0.12).
TABLE 1. Principal component (PC) loadings on nine temporally stable variables for Yellow-headed Blackbirds.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Female PC 1</th>
<th>Male PC 1</th>
<th>Female PC 2</th>
<th>Male PC 2</th>
<th>Female PC 3</th>
<th>Male PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length</td>
<td>0.105</td>
<td>0.157</td>
<td>0.441</td>
<td>0.617</td>
<td>0.831</td>
<td>-0.577</td>
</tr>
<tr>
<td>Skull length</td>
<td>0.236</td>
<td>0.261</td>
<td>0.480</td>
<td>0.392</td>
<td>-0.475</td>
<td>0.009</td>
</tr>
<tr>
<td>Skull width</td>
<td>0.214</td>
<td>0.164</td>
<td>0.670</td>
<td>0.542</td>
<td>-0.202</td>
<td>0.767</td>
</tr>
<tr>
<td>Keel length</td>
<td>0.357</td>
<td>0.244</td>
<td>-0.153</td>
<td>0.184</td>
<td>-0.038</td>
<td>-0.273</td>
</tr>
<tr>
<td>Femur length</td>
<td>0.381</td>
<td>0.424</td>
<td>-0.074</td>
<td>-0.155</td>
<td>-0.032</td>
<td>0.009</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>0.415</td>
<td>0.419</td>
<td>-0.175</td>
<td>-0.160</td>
<td>0.028</td>
<td>0.007</td>
</tr>
<tr>
<td>Tibiotarsus length</td>
<td>0.413</td>
<td>0.436</td>
<td>-0.186</td>
<td>-0.158</td>
<td>0.023</td>
<td>-0.012</td>
</tr>
<tr>
<td>Humerus length</td>
<td>0.421</td>
<td>0.370</td>
<td>-0.180</td>
<td>-0.178</td>
<td>0.029</td>
<td>0.019</td>
</tr>
<tr>
<td>Ulna length</td>
<td>0.509</td>
<td>0.371</td>
<td>0.015</td>
<td>-0.177</td>
<td>0.196</td>
<td>0.055</td>
</tr>
</tbody>
</table>

Because a previous analysis (Twedt et al. 1994) detected two discernable subpopulations within the overall morphometric cline exhibited by Yellow-headed Blackbirds, we attempted to predict membership in these subpopulations using discriminant analysis. We first used stepwise discriminant analysis to reduce the number of morphometric variables to four for females (body length, skull length, humerus, and femur) and five for males (body length, skull length, skull width, keel, and tibiotarsus). Using birds collected at breeding locations and discriminating between birds breeding in Canada and those breeding in the USA, the four variable discriminant model for females had a 0.70 (CI95% = 0.65–0.75) probability of correctly classifying birds (i.e., 70% of birds were correctly classified to their collection location). Similarly, the five variable model we used for males had a 0.68 (CI95% = 0.66–0.70) probability of correct classification. Kappa statistics (Titus et al. 1984) for both female and male models were significantly greater than zero (κ > 0.35, SEκ < 0.11, z > 3.37, P < 0.01) which indicated that both models predicted significantly better than chance.

When we applied these discriminant models to Yellow-headed Blackbirds collected in central North Dakota during summer and fall, we classified 232 of 601 females and 190 of 936 males as migrants (i.e., birds with geographic origins to the northwest of the collection location). The proportion of migrants within 5-day collection periods ranged from 0.09 to 0.59 for females and from 0.04 to 0.39 for males (Figure 2). However, regression slopes of the proportion of migrants against time did not differ from zero (t = 1.376, P = 0.17) for females and had a significant negative slope (t = -4.857, P < 0.01) for males.

**Discussion**

We were unable to detect our hypothesized increase in principal component scores over time within central North Dakota. Indeed, average PC scores tended to decrease slightly from June through September. Discriminant models constructed to distinguish birds breeding in Canada from those breeding in the USA similarly were unable to detect trends in the migratory status of Yellow-headed Blackbirds in central North Dakota. Failure of these models was likely, in part, due to their relatively poor ability to discriminate between local breeding birds and birds breeding at more northwestern locations — only 70% of birds could be correctly classified. In fact, the inferred proportion of migrants that resulted from application of our discriminant models remained constant or declined during summer and fall. Neither of these


<table>
<thead>
<tr>
<th>Location</th>
<th>Female PC 1</th>
<th>Male PC 1</th>
<th>Female PC 2</th>
<th>Male PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alberta and western Saskatchewan</td>
<td>0.546</td>
<td>0.751</td>
<td>0.365</td>
<td>0.205</td>
</tr>
<tr>
<td>Central Saskatchewan</td>
<td>0.143*</td>
<td>0.573</td>
<td>-0.078*</td>
<td>0.065</td>
</tr>
<tr>
<td>Southern Saskatchewan and Manitoba</td>
<td>-0.015</td>
<td>0.206</td>
<td>-0.341</td>
<td>-0.339</td>
</tr>
<tr>
<td>Central North Dakota</td>
<td>-0.822</td>
<td>-0.909</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*aIncludes all females collected in Saskatchewan and Manitoba.*
scenarios conformed with our hypothesis of an increase in the proportion of migrants over time. Several possible explanations could account for our inability to detect late-summer migrants passing through central North Dakota. Most likely, our principal component and discriminant function models had insufficient power to discriminate along the morphometric cline exhibited by Yellow-headed Blackbirds. Our ability to detect migrants may have also been hindered by a failure of migrants to displace locally breeding birds but instead congregating in heterogeneous populations within central North Dakota throughout late summer.

Alternatively, despite data from returns of banded birds that indicate a southeasterly migration route is used by Yellow-headed Blackbirds, it is possible that most migrants passing through our central North Dakota study area may have originated in more proximate locations in southern Manitoba and eastern Saskatchewan. Populations within these relatively nearby breeding locations share greater morphometric similarity with birds breeding in central
Females

FIGURE 2. Proportion of male and female Yellow-headed Blackbirds classified as migrants in central North Dakota during 1987 and 1988. Plotted proportions are running averages based on 5-collection-day samples. Mean sample sizes were 54 (range 15–134) for females and 78 (range 29–166) for males.

North Dakota (Twedt et al. 1994), thereby increasing the difficulty of distinguishing differences between these populations using either principal components analysis or discriminant function analysis.

In summary, although distinct morphometric differences exist between Yellow-headed Blackbirds breeding in central North Dakota and those breeding at more northwestern locations in Canada, we were unable to exploit these differences to elucidate either the duration or magnitude of migration through central North Dakota. Unless refinement of these morphometric techniques can be achieved, it appears that elucidating migratory movements of this species will continue to rely on physically marking individual birds or the development of improved genetic markers.

Acknowledgments

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Literature Cited


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