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GEOGRAPHIC VARIATION IN YELLOW-HEADED BLACKBIRDS FROM THE NORTHERN GREAT PLAINS[1]

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Abstract. We assessed geographic variability in morphology among Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) collected from breeding populations in Minnesota, North Dakota, and South Dakota in the United States and Alberta, Manitoba, and Saskatchewan in Canada during spring. Both male and female Yellow-headed Blackbirds tended to be larger in the more northern breeding populations. Males collected in Manitoba and southeast Saskatchewan tended to be more like populations from the United States, whereas other populations in Saskatchewan and Alberta populations were morphologically similar to each other. For females, however, only the Manitoba population was similar to the U. S. populations, and the females from the southeastern Saskatchewan were similar to other Saskatchewan birds. Southeastern Saskatchewan appears to represent a transitional region between northwestern and southeastern breeding populations of Yellow-headed Blackbirds.

Key words: Yellow-headed Blackbirds; Xanthocephalus xanthocephalus; *morphology; northern Great Plains; geographic variation; breeding; sub-populations.*

INTRODUCTION

Geographic variation has been detected and clinal patterns of variation have been postulated for contiguous breeding species (Power 1970, Endler 1977, Aldrich and James 1993). Both environmental factors (James 1970, James 1983) and isolated breeding populations (Wright 1946) contribute to this geographic variation. Yellow-headed Blackbirds, although migratory (Royall et al. 1971), display philopatric tendencies (Searcy 1979) with adults returning to large, often isolated, prairie wetlands to breed. Although the extent to which natal site fidelity occurs is not known, the breeding-site fidelity of adults, combined with the isolated nature of large prairie wetlands used as breeding sites, may contribute to increased geographic variation among Yellow-headed Blackbird populations. We examined the geographic variation in morphology among male and female Yellow-headed Blackbirds, collected within the northern Great Plains, to determine the extent of morphometric variation and to detect discernable differences among populations.

STUDY AREA AND METHODS

We collected adult male and female Yellow-headed Blackbirds from active nesting localities within the northern Great Plains (Fig. 1). Before dissecting these birds, we obtained their total mass in grams (WT) and four external measurements (Baldwin et al. 1931): total body length (LENG), tail length (TAIL), wing chord (WING), and length of culmen (CULMEN). After dissection, we obtained eight skeletal measurements (Baumel et al. 1979): skull length (SKL) from tip of bill to the posterior supraoccipital, skull width (SKW) between opposing temporals, keel length (KEEL) from the posterior edge of the sternum to the acrinal apex, and the greatest linear lengths of the ulna (ULNA), humerus (HUMER), femur (FEMUR), tarsus (TARSUS), and tibiotarsus (TIBTAR).

We measured total length, wing chord, and tail length to the nearest millimeter and culmen length to the nearest 0.01 mm. All skeletal measurements were recorded to the nearest 0.01 mm after cleaning; dermestid beetles cleaned the skull and keel, but long bones were cleaned by heating (~76°C) in water and an enzymatic detergent

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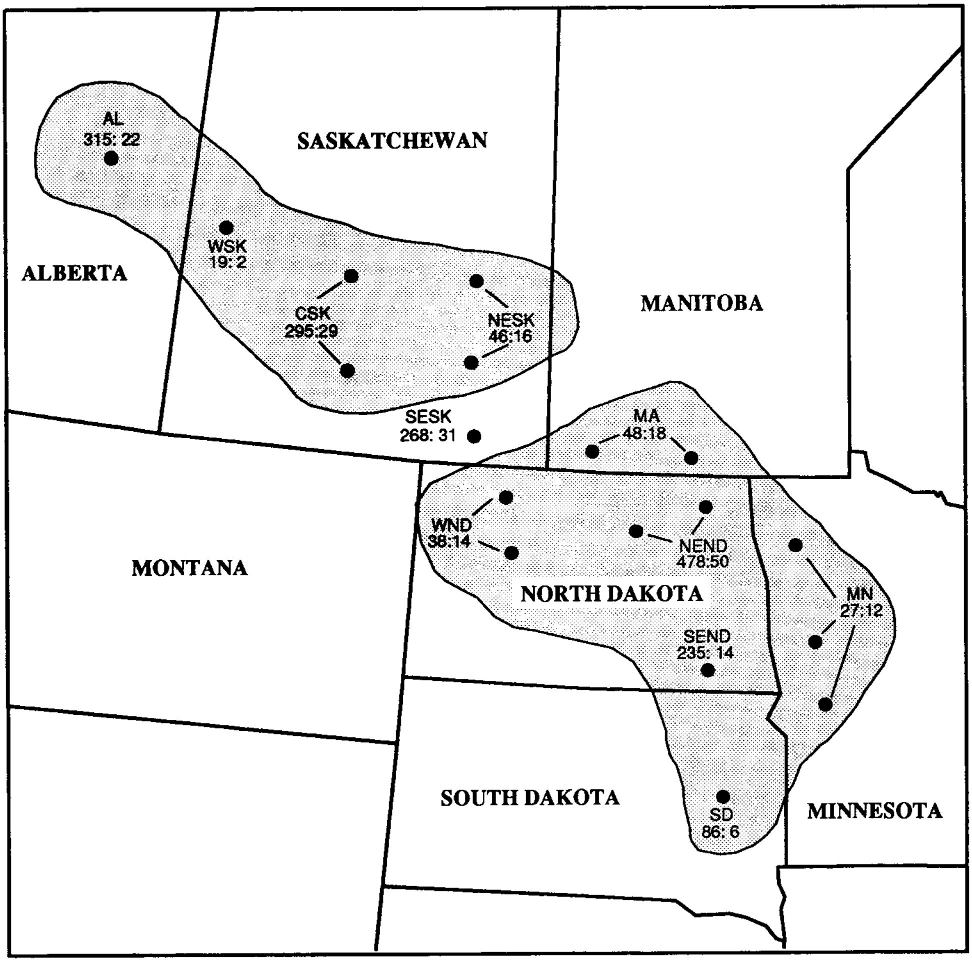

FIGURE 1. Total numbers of male and female (♂ : ♀) Yellow-headed Blackbirds collected in the northern Great Plains during the springs of 1987 and 1988. Circles indicate approximate center of 18 collection locations grouped by proximity and bio-political boundaries into 11 collection areas: South Dakota (SD), Minnesota (MN), southeast North Dakota (SEND), northeast North Dakota (NEND), west North Dakota (WND), Manitoba (MA), southeast Saskatchewan (SESK), northeast Saskatchewan (NESK), central Saskatchewan (CSK), west Saskatchewan (WSK), and Alberta (AL). Shaded areas represent geographic ranges of proposed sub-populations.

until flesh could be excised. We measured the right-hand member of bilaterally symmetric characteristics unless it was missing or damaged, in which case we substituted that from the left side. Measurement errors were obtained using the methods of Bailey and Byrnes (1990) for the nine skeletal mensurations from three repeated measurements on samples of 20 females and 20 males.

Univariate analyses. Before analyses we grouped birds into 11 discrete collection regions based on the proximity of collections and on bio-political boundaries (Fig. 1). Because Yellow-headed Blackbirds are sexually dimorphic, we calculated univariate statistics on each variable separately for each sex within each of these 11 regions. Using the mean measurements of the morphometric variables, we constructed phenograms using the UPGMA algorithm (Sneath and Sokal 1973) as applied by SAS (1985:286). We used analysis of variance (ANOVA) to compare regional differences in morphology. Using Bonferroni's criterion, we multiplied the resultant probability values by the number of simultaneous comparisons (Harris 1985). Pairwise comparisons between collection regions were ob-

TABLE 1. Means and standard deviations of selected weights and measurements from adult, female and male Yellow-headed Blackbirds collected during the springs of 1987 and 1988 within the northern Great Plains. Measurements in millimeters except weight is in grams. Maximum sample sizes within collection locations are given in Figure 1.

		South Dakota	Minnesota	Southeast North Dakota	Northeast North Dakota	West North Dakota
Mass	F	59.58 ± 2.77	53.54 ± 5.38	56.93 ± 3.88	52.88 ± 3.94	58.31 ± 4.11
	M	92.91 ± 5.94	96.86 ± 5.78	94.49 ± 4.75	94.35 ± 5.67	95.04 ± 4.56
Length	F	218.27 ± 4.54	212.33 ± 7.00	216.07 ± 7.29	215.07 ± 6.76	218.71 ± 5.00
	M	259.99 ± 5.33	259.33 ± 9.47	266.24 ± 6.50	263.06 ± 7.30	265.26 ± 6.76
Wing chord	F	113.70 ± 3.20	112.58 ± 2.84	112.78 ± 2.96	112.59 ± 2.56	112.64 ± 2.47
	M	141.67 ± 3.05	141.23 ± 2.75	142.48 ± 3.26	143.49 ± 3.61	141.03 ± 2.12
Tail	F	82.28 ± 2.93	82.08 ± 2.58	81.28 ± 4.70	81.72 ± 3.82	82.50 ± 3.16
	M	103.83 ± 3.41	104.11 ± 4.31	104.61 ± 3.41	104.74 ± 3.93	104.10 ± 2.28
Skull length	F	40.77 ± 0.90	41.22 ± 0.58	40.76 ± 0.61	40.77 ± 0.61	40.86 ± 0.55
	M	47.43 ± 0.84	47.32 ± 0.80	47.24 ± 0.83	47.18 ± 0.85	47.65 ± 0.77
Skull Width	F	18.52 ± 0.23	18.41 ± 0.25	18.39 ± 0.24	18.40 ± 0.24	18.43 ± 0.28
	M	19.95 ± 0.38	19.90 ± 0.30	19.94 ± 0.34	20.01 ± 0.34	20.06 ± 0.32
Keel	F	27.82 ± 1.00	27.71 ± 0.97	27.47 ± 1.24	27.80 ± 0.85	27.59 ± 0.79
	M	35.07 ± 1.04	35.22 ± 1.06	35.43 ± 1.05	35.31 ± 1.01	35.70 ± 1.26
Ulna	F	31.54 ± 0.51	31.89 ± 0.72	31.46 ± 0.63	30.06 ± 2.01	31.51 ± 0.66
	M	38.39 ± 0.78	38.23 ± 1.07	38.33 ± 0.87	37.86 ± 1.62	38.52 ± 0.62
Humerus	F	26.12 ± 0.47	26.17 ± 0.44	26.10 ± 0.53	26.16 ± 0.54	26.12 ± 0.44
	M	31.63 ± 0.60	31.78 ± 0.60	31.74 ± 0.70	31.61 ± 1.57	31.87 ± 0.53
Tarsus	F	29.95 ± 0.66	30.21 ± 0.59	30.09 ± 0.73	29.97 ± 0.91	29.84 ± 0.77
	M	35.17 ± 0.81	35.22 ± 0.86	35.16 ± 0.89	35.19 ± 0.96	35.47 ± 0.82
Tibiotarsus	F	42.18 ± 0.98	42.47 ± 0.81	42.51 ± 0.57	42.39 ± 1.11	42.39 ± 0.89
	M	50.00 ± 0.98	50.12 ± 1.01	50.10 ± 1.12	49.98 ± 1.17	50.26 ± 1.10
Femur	F	24.24 ± 0.54	24.44 ± 0.47	24.26 ± 0.49	24.19 ± 0.56	24.28 ± 0.59
	M	29.02 ± 0.55	29.14 ± 0.71	29.02 ± 0.71	28.96 ± 0.64	28.08 ± 0.62
Culmen	F	18.46 ± 0.64	19.04 ± 0.47	18.44 ± 0.39	18.55 ± 0.52	18.72 ± 0.47
	M	22.90 ± 0.70	22.81 ± 0.65	22.79 ± 0.68	22.46 ± 0.76	23.06 ± 0.67

tained via Scheffe's *a posteriori* mean separation (Milliken and Johnson 1984:35–36) at alpha = 0.05.

Multivariate analyses. Before performing multivariate analyses, we replaced missing data (4.3% of total) using regressions against the most highly correlated variables (Chan et al. 1976). To reduce the morphological information in these data to a few succinct variables, we extracted principal components for each sex (Morrison 1976). Distributions along the principal components were used to express the phenetic and geographic relations among the collection regions.

RESULTS

We collected 1,855 male and 214 female Yellow-headed Blackbirds from 28 May to 16 June 1987 and from 14 May to 17 June 1988. Percent measurement error (%ME) for the skeletal variables ranged from 0.08 for skull length in males to 4.21 for humerus in males. Univariate statistics of morphological characteristics for each sex (Table 1) generally follow Bergmann's rule, exhibiting a trend toward larger birds in the more northern populations. Phenograms constructed from the mean measurements within each collection region revealed a southeast-northwest dichotomy in morphology for both males and females (Fig. 2). Males from southeast Saskatchewan and Manitoba had morphological characteristics similar to males from the states of Minnesota, North Dakota, and South Dakota; whereas, the remaining collection regions within Saskatchewan were morphologically similar to males from Alberta. Females exhibited similar groupings except that females from southeast Saskatchewan were morphometric siblings of the other Saskatchewan regions, and morphologically unique females were found in Alberta.

For males, 12 of the 13 simultaneous comparisons using ANOVA yielded significant ($F > 6.3$, $P < 0.01$) differences among collection regions—only TAIL did not differ ($F = 2.3$, $P = 0.13$). Within the 12 variables exhibiting significant differences, 48 significant ($F > 1.9$, $P <$

TABLE 1. Extended.

Manitoba	Southeast Saskatchewan	Northeast Saskatchewan	Central Saskatchewan	West Saskatchewan	Alberta
58.12 ± 3.44	59.01 ± 4.52	66.56 ± 7.65	61.41 ± 6.98	57.31 ± 0.06	50.70 ± 3.78
96.55 ± 5.39	96.69 ± 5.22	101.81 ± 9.29	97.97 ± 7.24	100.27 ± 7.12	96.64 ± 5.23
220.67 ± 3.83	222.57 ± 4.52	221.81 ± 7.56	221.76 ± 4.26	221.50 ± 2.12	221.58 ± 7.80
270.54 ± 4.40	269.24 ± 7.22	263.17 ± 6.56	267.06 ± 8.38	269.10 ± 9.01	267.13 ± 6.87
112.11 ± 2.08	112.70 ± 2.18	113.81 ± 3.14	113.56 ± 2.71	112.50 ± 3.54	111.25 ± 2.56
141.40 ± 3.52	142.62 ± 3.14	140.65 ± 2.27	141.82 ± 3.42	140.63 ± 3.17	143.46 ± 3.14
80.66 ± 3.25	82.67 ± 2.92	83.44 ± 3.16	82.93 ± 2.28	83.50 ± 3.54	80.41 ± 3.64
104.62 ± 3.54	104.64 ± 3.07	104.02 ± 2.82	103.66 ± 4.10	103.32 ± 4.31	104.21 ± 3.55
40.74 ± 0.59	40.99 ± 0.72	41.02 ± 0.74	41.12 ± 0.66	41.28 ± 1.36	41.41 ± 0.71
47.32 ± 0.81	47.36 ± 0.84	47.36 ± 0.90	47.75 ± 0.84	47.73 ± 0.90	48.05 ± 0.83
18.53 ± 0.29	18.46 ± 0.36	18.64 ± 0.26	18.53 ± 0.36	18.36 ± 0.19	18.45 ± 0.32
20.02 ± 0.29	20.08 ± 0.33	20.05 ± 0.36	20.11 ± 0.33	20.08 ± 0.24	20.11 ± 0.32
27.79 ± 0.58	27.91 ± 0.74	28.01 ± 0.70	27.96 ± 0.76	28.20 ± 0.23	27.95 ± 0.92
35.66 ± 1.07	35.52 ± 1.02	35.68 ± 1.04	35.81 ± 1.12	36.13 ± 0.93	35.84 ± 1.07
31.67 ± 0.32	31.29 ± 1.35	31.77 ± 0.49	31.59 ± 1.21	31.94 ± 0.93	27.90 ± 0.48
38.35 ± 0.75	38.54 ± 0.82	38.57 ± 0.69	38.80 ± 0.75	38.86 ± 0.83	38.71 ± 0.98
26.28 ± 0.23	26.30 ± 0.44	26.40 ± 0.40	26.36 ± 0.52	26.74 ± 0.66	26.09 ± 0.51
31.70 ± 0.68	32.87 ± 0.65	31.84 ± 0.49	32.05 ± 0.60	32.20 ± 0.65	32.08 ± 0.68
30.11 ± 0.48	30.24 ± 0.49	30.36 ± 0.84	30.38 ± 0.68	30.28 ± 1.34	29.90 ± 0.60
35.36 ± 0.80	35.39 ± 0.88	35.25 ± 1.11	35.64 ± 0.83	35.73 ± 0.86	35.65 ± 0.91
42.67 ± 0.65	42.84 ± 0.66	42.86 ± 1.05	42.95 ± 0.95	42.76 ± 1.18	42.64 ± 0.78
50.21 ± 1.04	50.26 ± 1.13	50.35 ± 1.18	50.66 ± 1.09	50.78 ± 0.76	50.65 ± 1.19
24.32 ± 0.31	24.41 ± 0.49	24.64 ± 0.37	24.51 ± 0.57	24.60 ± 0.93	24.15 ± 0.61
29.03 ± 0.57	29.13 ± 0.63	29.16 ± 0.55	29.32 ± 0.60	29.42 ± 0.74	29.31 ± 0.67
18.51 ± 0.49	18.67 ± 0.56	18.78 ± 0.44	18.83 ± 0.53	18.68 ± 1.48	18.78 ± 0.55
22.64 ± 0.73	22.55 ± 0.74	22.60 ± 0.70	22.90 ± 0.78	23.10 ± 0.78	22.99 ± 0.69

0.05) pairwise comparisons were detected with 33 (69%) representing differences between the two dichotomous groups previously suggested. For females, however, only three morphometric variables (LENG, WT, and ULNA) differed significantly ($F > 6.8$, $P < 0.01$) among collection regions; whereas, the remaining 10 variables did not differ ($F < 1.9$, $P > 0.52$). The dichotomous grouping of populations is again supported by Scheffe's pairwise comparisons because none of

TABLE 2. Principal component (PC) loadings on morphometric variables for Yellow-headed Blackbirds from the northern Great Plains and the proportion of the variability accounted for by each principal component.

	Principal component I		Principal component II		Principal component III	
	Female	Male	Female	Male	Female	Male
Proportion of variability	0.37	0.36	0.15	0.14	0.11	0.10
Mass	0.24	0.24	0.14	0.05	−0.30	0.05
Length	0.21	0.20	0.41	0.39	−0.08	−0.05
Wing chord	0.19	0.14	0.48	0.52	−0.13	−0.29
Tail	0.17	0.11	0.56	0.60	−0.13	−0.27
Skull length	0.26	0.30	0.09	0.15	0.59	0.55
Skull width	0.20	0.17	0.14	0.04	0.03	0.03
Keel	0.24	0.24	−0.10	−0.06	0.14	0.03
Ulna	0.22	0.34	−0.14	−0.14	−0.34	−0.18
Humerus	0.38	0.30	−0.21	−0.15	−0.10	−0.17
Tarsus	0.37	0.38	−0.22	−0.19	−0.05	−0.12
Tibiotarsus	0.38	0.40	−0.24	−0.19	−0.03	−0.12
Femur	0.38	0.38	−0.20	−0.18	−0.09	−0.11
Culmen	0.20	0.21	0.12	0.20	0.60	0.65

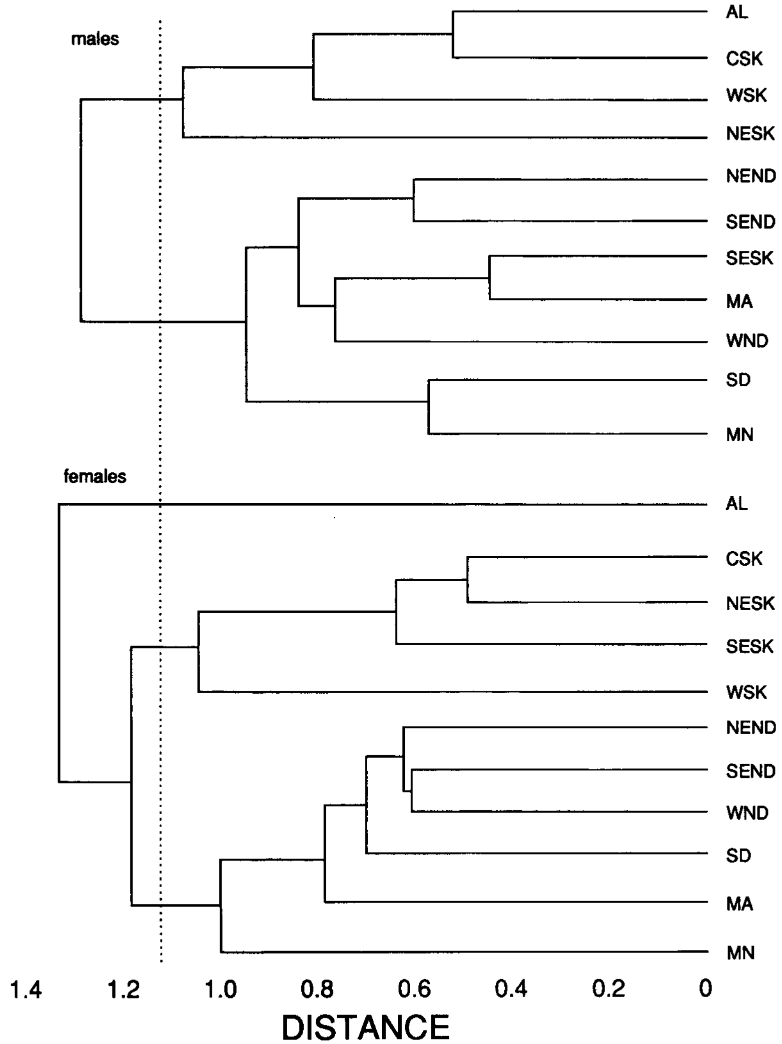

FIGURE 2. Phenograms of male and female Yellow-headed Blackbirds constructed from mean morphometric measurements using UPGMA algorithm. Collection location codes are listed in Figure 1. Populations joined to the right of the dotted line are morphometrically similar to each other.

the five significant ($F > 1.9$, $P = 0.05$) pairwise comparisons for females were within either of the two dichotomous groups, although the "aberrant" female population from Alberta differed from other populations in two instances.

The first three principal components extracted from 13 measured variables (Table 2) accounted for 63% and 61% of the variability within females and males, respectively. Principal component loadings were consistent across sexes. For both sexes, the positive loadings on the first principal component represent a general size character. The second principal component represents a contrast between positive loadings on the feathered measurements and negative loadings on the long bone measurements. Finally, the third principal component contrasts a positive skull length loading with a negative ulna loading. Spatial diagrams of the first principal component against latitude and longitude of collection (Fig. 3) suggest a separation into two groups; the more northern and western populations having greater first principal component scores than the more southern and eastern populations.

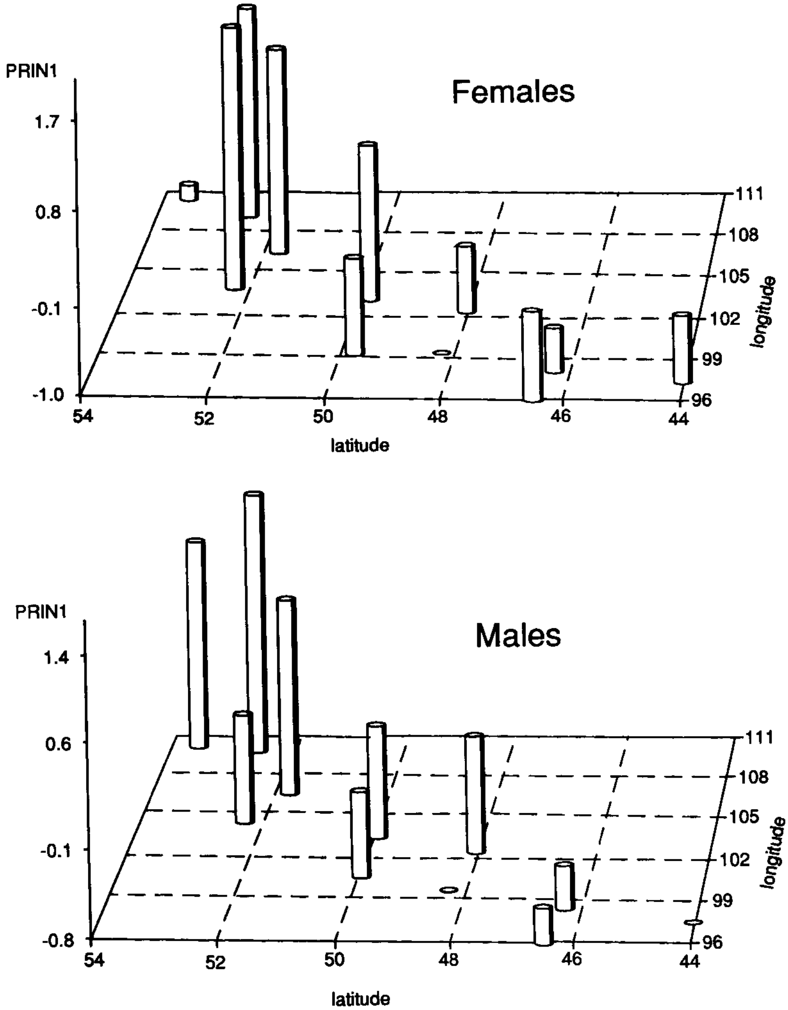

FIGURE 3. Relation of mean first principal component score, computed from morphometric data on Yellow-headed Blackbirds collected within discrete collection locations in Canada and USA, to latitude and longitude of collection location.

DISCUSSION

Measurement errors for all skeletal mensurations of both sexes were small (<5%). However, measurement error was not consistent between sexes. Whereas, for males, skull length had the smallest measurement error, among females, skull length had the largest measurement error (%ME = 3.08). Conversely, measurements of humeri had the largest measurement error among males but among females, humerus exhibited a %ME of only 0.27. Nevertheless, for both sexes, measurement variability among individuals far exceeded variability within individuals.

Both female and male Yellow-headed Blackbirds breeding on the northern Great Plains exhibit increasing body size from the southeast to the northwest. These discernable morphometric differences among Yellow-headed Blackbirds breeding at different geographic locations contrast sharply with the lack of genetic differentiation detected among these populations (Twedt et al. 1992). Although there is an overall clinal trend, there appears to be a dichotomy within the Great Plains population of Yellow-headed Blackbirds. In general, the two groups of Yellow-headed Blackbirds indicated by phenograms were those breeding north and west of southeast Saskatchewan as opposed to those breeding south and east of this pivotal area. This finding was supported by analysis of variance (ANOVA) results in which most significant pairwise comparisons were between these two groups. Also, distances among principal component scores were greater between members of these two groups than within members of either group.

Based on the morphometric differences between these geographic populations, we propose division of the northern Great Plains population of Yellow-headed Blackbirds into two sub-population groups: the *Canadensis* group ranging north and west of southeast Saskatchewan and the *Dakotai* group ranging south and east of southeast Saskatchewan (Fig. 1). Further, we propose that these morphometric differences among Yellow-headed Blackbird populations may be a mechanism through which their gross migratory movements may be assessed similar to that conducted for Red-winged Blackbirds (James et al. 1984).

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LITERATURE CITED

ALDRICH, J. W., AND F. C. JAMES. 1991. Ecogeographic variation in the American Robin (*Turdus migratorious*). Auk 108:230–249.

BAILEY, R. C., AND J. BYRNES. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Syst. Zool. 39:124–130.

BALDWIN, S. P., H. C. OBERHOLSER, AND L. G. WORLEY. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Nat. Hist., Vol. 2.

BAUMEL, J. J., A. S. KING, A. M. LUCAS, J. E. BREAZILE, AND H. E. EVANS. 1979. Nomina anatomica avium. Academic Press, New York.

CHAN, L. S., J. A. GILMAN, AND O. J. DUNN. 1976. Alternative approaches to missing values in discriminant analysis. J. Am. Stat. Assoc. 71:842–844.

ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.

HARRIS, R. J. 1985. A primer of multivariate statistics, 2nd ed. Academic Press, New York.

JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51:365–390.

JAMES, F. C. 1983. Environmental component of morphological differences in birds. Science 221: 184–186.

JAMES, F. C., R. T. ENGSTROM, C. NESMITH, AND R. LAYBOURNE. 1984. Inferences about population movements of Red-winged Blackbirds from morphological data. Am. Midl. Nat. 111:319–331.

MILLIKEN, G. A., AND D. E. JOHNSON. 1984. Analysis of messy data. Van Nostrand Reinhold, New York.

MORRISON, D. F. 1976. Multivariate statistical methods. McGraw-Hill, New York.

POWER, D. M. 1970. Geographic variation of Red-winged Blackbirds in central North America. Publ. Univ. Kansas Mus. Nat. Hist. 90.

ROYALL, W. C., JR., J. W. DEGRAZIO, J. L. GUARINO, AND A. GAMMELL. 1971. Migration of banded Yellow-headed Blackbirds. Condor 73:100–106.

SAS INSTITUTE. 1985. SAS user's guide statistics. Statistical analysis system. SAS Institute, Raleigh, NC.

SEARCY, W. A. 1979. Size and mortality in male Yellow-headed Blackbirds. Condor 81:304–305.

SNEATH, P.H.A., AND SOKAL, R. R. 1973. Numerical taxonomy. W. H. Freeman, San Francisco.

TWEDT, D. J., BLEIER, AND G. M. LINZ. 1992. Genetic variation in male Yellow-headed Blackbirds from the northern Great Plains. Can. J. Zool. 70:2280–2282.

WRIGHT, S. 1946. Isolation by distance under diverse mating systems. Genetics 31:39–59.