Genetic variation in male Yellow-headed Blackbirds from the northern Great Plains

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Electrophoretic differences at 15 presumptive loci were used to assess allelic frequencies, heterozygosities, and polymorphism for male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) collected in east-central Alberta, north-central North Dakota, and east-central South Dakota. Five loci were polymorphic and mean heterozygosities ranged from 0.119 to 0.133. Significant differences were detected among these geographic populations of Yellow-headed Blackbirds, primarily due to differences in the allelic frequencies of isocitrate dehydrogenase and glucose-6-phosphate dehydrogenase. Differences detected were not sufficient to uniquely identify the geographic origin of Yellow-headed Blackbrids.

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L'électrophorèse à 15 locus présomptifs a servi à déterminer les fréquences alléliques, l'hétérozygotie et le polymorphisme chez des Carouges à tête jaune (*Xanthocephalus xanthocephalus*) du centre est de l'Alberta, du centre nord du Dakota du Nord et du centre est du Dakota du Sud. Cinq locus se sont avérés polymorphes et l'hétérozygotie moyenne se situait entre 0,119 et 0,133. Il y avait des différences significatives entre ces populations géographiques du Carouge à tête jaune, différences dues surtout à des variations dans les fréquences alléliques de l'isocitrate déshydrogénase et de la glucose-6-phosphate déshydrogénase. Les différences enregistrées n'étaient pas suffisantes pour permettre d'établir avec précision l'origine géographique des Carouges à tête jaune.

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Introduction

Although the average intraspecific genetic differentiation among avian populations is low (F_{ST} = 0.022; Barrowclough 1983, p. 237), some studies have revealed that genetic variability may be useful in distinguishing geographically distinct populations (Van Wagner and Baker 1986; Zink et al. 1987). Male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) exhibit breeding-site philopatry (Searcy 1979) and as a result, genetically distinct subpopulations of male Yellow-headed Blackbirds may exist in the migratory population that breeds on the northern Great Plains of North

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TABLE 1. Allelic frequencies for polymorphic loci of Yellow-headed Blackbirds from Alberta (AL; $n = 27$), North Dakota (ND; $n = 26$), and South Dakota (SD; $n = 20$)

Locus	Allele	Subpopulation AL	ND	SD	F_{ST}	χ^2	df	P
ME-2	A	0.611	0.615	0.700	0.007	0.948	2	0.622
	B	0.389	0.385	0.300				
IDH	A	0.500	0.481	0.842[a]	0.127	19.991	4	<0.001
	B	0.481	0.519	0.105[a]				
	C	0.019		0.053[a]				
G-6-PDH	A	0.722	0.700[b]	0.600	0.047	24.895	4	<0.001
	B	0.241	0.300[b]	0.125				
	C	0.037		0.275				
EST-1	A	0.980[b]	0.942	1.000	0.023	1.953	2	0.377
	B	0.020[b]	0.058					
EST-2	A	0.574	0.640[b]	0.500	0.013	1.786	2	0.409
	B	0.426	0.360[b]	0.500				

NOTE: *ME-2*, malic enzyme-2; *IDH*, isocitrate dehydrogenase; *G-6-PDH*, glucose-6-phosphate dehydrogenase; *EST-1*, esterase-1; *EST-2*, esterase-2.
[a] $n = 19$.
[b] $n = 25$.

America. Given sufficient differences in enzymatic proteins among subpopulations of Yellow-headed Blackbirds, electrophoretic analyses could be used to identify birds from specific subpopulations and subsequently assess the proportions of local and migrant birds in roosting or foraging flocks. Our objective was to estimate the extent of genetic variation, as expressed by enzyme electromorphs, among and within samples of male Yellow-headed Blackbirds from distinct geographic locations of the northern Great Plains; we hoped to use this genetic variation to aid in identification of migrants' geographic areas of origin.

Methods

We collected adult male territorial Yellow-headed Blackbirds from 3 geographic locations: east-central Alberta, north-central North Dakota, and east-central South Dakota (Twedt et al. 1991). Collected birds were either placed directly on dry ice or dissected in the field, and excised liver, heart, and muscle tissues were placed in cryogenic tubes on dry ice. Upon return to the laboratory, birds placed directly on dry ice were thawed; tissues were excised, placed in cryogenic tubes, and stored at −70°C.

We homogenized tissue samples in a Tris−glycine−sucrose buffer (pH 8.3). After centrifugation (1300 × *g*, 20 min, 4°C), supernatants were subjected to polyacrylamide-gel electrophoresis on either 5 or 6.5% polyacrylamide gels with Tris or phosphate buffers and stained with enzyme-specific stains. The electrophoretic apparatus, procedures, buffers, and stains were described by McDonald et al. (1978) and Johnson et al. (1984).

We used letters to designate different electromorphs and assumed that electromorphs represented alleles. From these data, we determined allelic frequencies, heterozygosity, and percentage polymorphism in each locality. We used allelic frequencies to estimate Nei's genetic distances (Nei 1978). Wright's *F*-statistics (Wright 1978) were calculated as measures of genetic differentiation within and among the localities. We used BIOSYS-1 (Swofford and Selander 1981, 1989) to perform statistical analyses.

Results and discussion

We scored 15 presumptive loci from 73 adult male Yellow-headed Blackbirds; only 5 were polymorphic in at least one of the localities (Table 1). The other 10 loci, which were monomorphic for a single allele in all localities, were alcohol dehydrogenase (*ADH*), adolase (*ALD*), sorbitol dehydrogenase (*SDH*), lactate dehydrogenase-1 (*LDH-1*), lactate dehydrogenase-2 (*LDH-2*), malate dehydrogenase (*MDH*), malic enzyme-1 (*ME-1*), 6-phosphogluconate dehydrogenase (*6-PGDH*), aspartate aminotransferase (*AAT*), and fumarase (*FUM*).

Observed mean heterozygosities and their associated standard errors were 0.119 ± 0.055 in South Dakota, 0.133 ± 0.055 in North Dakota, and 0.132 ± 0.057 in Alberta. Heterozygosities for Yellow-headed Blackbirds were greater than the average heterozygosity for birds (0.053; Barrowclough 1983, p. 228), but within the range of reported heterozygosities (0.00−0.31; Evans 1987, pp. 113−119).

Polymorphic loci of subpopulations were 33.3% in Alberta, 26.7% in South Dakota, and 33.3% in North Dakota. The percentage of polymorphic loci for Yellow-headed Blackbirds was similar to that for many other birds (Evans 1987). Although Smith and Zimmerman (1976) found that Red-winged Blackbirds (*Agelaius phoeniceus*) had 60% polymorphic loci, they observed a different set of loci than we observed in this study. All loci within each locality conformed to Hardy−Weinberg proportions ($P \geq 0.05$), except *EST-2* within the Alberta subpopulation ($\chi^2 = 11.99$; 1 df; $P < 0.001$), which had an excess of heterozygotes ($F_{IS} = -0.742$).

Wright's *F*-statistics (Table 1) revealed significant differences ($F_{ST} = 0.049$; $\chi^2 = 49.57$; 14 df; $P < 0.001$) among the three geographic subpopulations. These values indicate that the Yellow-headed Blackbirds were not from a single panmictic population. Geographic differences were largely attributable to only two loci, *IDH* and *G-6-PDH*. Alleles A and B of *IDH* were represented about equally in Alberta and North Dakota subpopulations, but in the South Dakota subpopulation we found a higher incidence of allele A. The South Dakota subpopulation was also differentiated at *G-6-PDH*, where the frequency of the C allele was 28%; this allele constituted only 4% of the *G-6-PDH* alleles in the Alberta subpopulation and was not detected in the North Dakota subpopulation. Nei's genetic distances were small between all populations: <0.001 between Alberta and North Dakota subpopulations, 0.015 between North Dakota and South Dakota subpopulations, and 0.011 between Alberta and South Dakota subpopulations.

The mean genetic differentiation (F_{ST}) for Yellow-headed Blackbirds was over twice that found among Red-winged Blackbird subpopulations (Brush 1968, 1970). In our study,

however, only males were considered, whereas in the studies on Red-winged Blackbirds, both males and females were considered. Philopatric differences between males and females may influence observed genetic differentiation. Although we detected genetic differences among geographic subpopulations, these differences were not sufficient to uniquely identify the geographic origin of male Yellow-headed Blackbirds.

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