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Thaddeus A. Grudzien
Oakland University

William S. Moore
Wayne State University, wmoore1415@gmail.com

J. Richard Cook
Wayne State University

Danilo Tagle
Oakland University

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GENIC POPULATION STRUCTURE AND GENE FLOW IN THE NORTHERN FLICKER (*COLAPTES AURATUS*) HYBRID ZONE

THADDEUS A. GRUDZIEN,[1] WILLIAM S. MOORE,[2]
J. RICHARD COOK,[2] AND DANILO TAGLE[1,3]

[1]*Department of Biological Sciences, Oakland University, Rochester, Michigan 48063 USA, and*
[2]*Department of Biological Sciences, Wayne State University, Detroit, Michigan 48202 USA*

ABSTRACT.—The Yellow-shafted Flicker (*Colaptes auratus auratus*) and Red-shafted Flicker (*C. a. cafer*) form a stable, narrow hybrid zone on the western Great Plains of North America. Allozyme data were obtained from 31 structural gene loci for 33 samples representing 246 Northern Flickers from throughout the Great Plains. Flickers were approximately equivalent to other birds in terms of proportion of polymorphic loci ($\bar{P}$ = 0.207) and average heterozygosity ($\bar{H}$ = 0.056). There was no concordant variation between plumage characters and allelic frequencies.

Gene-diversity analysis indicated that 92.5% of the genic variation occurred as within-deme heterozygosity (G_D = 0.925), approximately 7% occurred among individual demes (G_{DT} = 0.07), and only 0.9% occurred among major river drainages (G_{ST} = 0.009). Even less diversity was found among parental and hybrid groups (G_{ST} = 0.002). There is substantial allozymic structuring of the Northern Flicker species population, but the structuring is not associated with the hybrid zone, and there is, at most, very weak structuring into riparian zones of habitat.

The electrophoretic data support the inference that gene flow among Northern Flicker populations is high (Nm = 1.9–4.4/generation). If the high gene-flow estimates are correct, then geographical selection gradients would be the most likely mechanism maintaining the narrow hybrid zone of plumage and morphometric traits. *Received 21 July 1986, accepted 16 April 1987.*

THE Yellow- and Red-shafted subspecies of the Northern Flicker (*Colaptes auratus*) form a narrow hybrid zone in woodland areas of the North American Great Plains (Fig. 1). Extensive hybridization between these two forms (Allen 1892, Short 1965) has resulted in the assignment of Yellow-shafted (*C. a. auratus*) and Red-shafted (*C. a. cafer*) flickers to subspecific status (A.O.U. 1983). Hybrid individuals do not have lower fitness than the parental types (Moore and Koenig 1986), and there is no evidence of preferential mating between flickers with similar plumages (Moore 1987). The position and width of the hybrid zone have been stable in historical times (Moore and Buchanan 1985). The central and northern portions of the hybrid zone probably formed as secondary contacts during the retreat of the Pinedale (Wisconsin) cordilleran glaciers in the Rocky Mountains (Short 1965, Hubbard 1969, Barrowclough 1980a). This occurred 10,000–13,000 years before the present (YBP) in the central Rockies (Baker 1976, Madole 1976) and as recently as 7,500 YBP in the Canadian Rockies (Barrowclough 1980a). The hybrid zone south of Colorado may have a different history, and the possibility that divergence between the subspecies occurred primarily during interglacials, with the central prairies and deserts serving as a geographical barrier, cannot be excluded (Mengel 1970).

Electrophoretic analysis of birds sampled throughout a hybrid zone, coupled with statistical techniques for estimating genetic population structure and gene flow, could help clarify the nature of the hybrid zone and provide insight into the processes of speciation. Despite the potential of such studies, genetic analyses of avian hybrid zones are rare. Genetic differentiation has been examined among several avian taxa known to hybridize occasionally (e.g. Martin and Selander 1975, Johnson and Zink 1983). At present, however, there are only five allozymic studies that specifically address the question of genetic variation in avian hybrid zones: Northern Orioles, *Icterus galbula galbula* × *I. g. bullockii* (Corbin et al. 1979); Yellow-rumped Warblers, *Dendroica coronata coronata* ×

[3] Present address: Department of Anatomy, Wayne State University, Detroit, Michigan 48202 USA.

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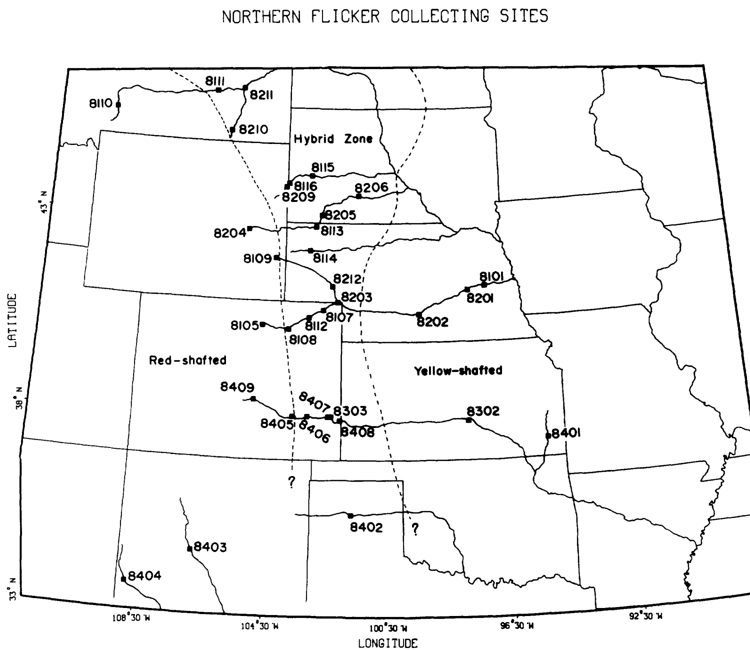

Fig. 1. Collecting sites of Northern Flickers in the central United States. Dashed lines indicate the position of the hybrid zone based on the 20th and 80th isopleths of the hybrid index.

D. c. auduboni (Barrowclough 1980a); Rufous-sided × Collared towhees, *Pipilo erythropthalmus* × *P. ocai* (Braun 1981); Tufted Titmice, *Parus bicolor bicolor* × *P. b. atricristatus* (Braun et al. 1984); and Black-capped × Carolina chickadees, *Parus atricapillus* × *P. carolinensis* (Braun and Robbins 1986). Each of these five studies was restricted to a few localities sampled along single transects across the respective hybrid zones.

The Northern Flicker hybrid zone could be viewed in terms of two differing population structures. First, the hybrid zone itself could be a barrier to gene flow (*sensu* Barton 1979b). If this is the case, there should be a structuring of the population from east to west across the hybrid zone. Second, in the United States hybrid populations are restricted to riparian woodlands along the generally west-to-east-flowing drainages of the western prairies (Fig. 1), and intervening grasslands may inhibit gene flow in a south-north direction along the length of the hybrid zone. Flickers are seasonally migratory and first breed at age 1 yr (Moore unpubl. banding recovery data). Both first-year and older adults are philopatric, but some dispersal does occur before first-year adults breed (Moore and Buchanan 1985). It is not known whether first-year birds return to their natal sites and then disperse along the length of their natal riparian woodland or whether there is significant between-drainage dispersal, perhaps as a consequence of seasonal south-north migration. If grasslands between riparian woodlands are barriers to gene flow, then a south-north structuring of populations would emerge. Documentation of gene-flow pattern and magnitude is critical for evaluating the plausibility of alternative hybrid-zone models.

We used allozymic data to investigate the genetic population structure of Northern Flickers and to infer dispersal rates and patterns among flickers sampled from throughout the hybrid zone.

Materials and Methods

Thirty-three samples of Northern Flickers comprising 246 specimens were collected during the breeding seasons of 1981–1984. Samples were collected throughout much of the Great Plains (Fig.1) and, based on plumage traits, ranged in average hybrid index ($\overline{HI}$, 0 = Yellow-shafted, 23 = Red-shafted; see Short 1965, Moore and Buchanan 1985) from essentially "pure" Yellow-shafted (e.g. sample 8101, Schuyler, Nebraska; $\overline{HI}$ = 1.0) to almost "pure" Red-shafted (e.g. sample 8110, Livingston, Montana, and 8404, Catron, New Mexico; $\overline{HI}$ = 20+). For grouping

and comparison, samples were classified according to average hybrid index: Yellow-shafted samples, $\overline{HI} \le 4.0$; hybrids, $4.1 \le \overline{HI} \le 19.9$; Red-shafted samples, $\overline{HI} \ge 20.0$.

Pectoral muscle and liver tissues were removed from the birds in the field, frozen on dry ice, and maintained at −80°C in the laboratory. Homogenates of each tissue were surveyed electrophoretically for the products of 31 presumptive gene loci by horizontal starch-gel electrophoresis. Electrophoretic conditions and enzyme staining procedures followed Turner (1983). Genotype counts were analyzed with the BIOSYS-1 computer program (Swofford and Selander 1981) to estimate the proportion of polymorphic loci, heterozygosity, and hierarchical F-statistics. The fixation index (F_{IT}; Wright 1969) was used to determine the status of the entire sample relative to panmixia. If the total sample is panmictic, $F_{IT} = 0$; positive values indicate heterozygote deficiencies, and negative values indicate heterozygote excesses (see Eanes and Koehn 1978). Gene-flow rates were estimated using the techniques of Slatkin (1981, 1985) and Barton and Slatkin (1986).

Gene-diversity analysis (Nei 1975, 1977) partitions the total variation in the entire group of samples (H_T) into within-deme variation (G_D, equivalent to sample heterozygosity), variation among all demes relative to the total (G_{DT}), and variation among subdivisions relative to the total (G_{ST}) such that:

$$H_T = G_D + G_{DT} + G_{ST}.$$

Hierarchical F-values were converted to their equivalent gene-diversity G statistics (Swofford and Selander BIOSYS-1 manual).

Northern Flickers can be assigned to distinct groups based on plumage and morphometric characters: Yellow-shafted, hybrid, and Red-shafted. Alternatively, they can be grouped according to the riparian woodland (river drainage) where they were collected. G_{ST} estimates gene diversity among subdivisions, and the group scheme with the largest G_{ST} value would be most consistent with the genic population structure of the Northern Flicker hybrid zone. That is, if G_{ST} is large when the samples are grouped into Red-shafted, Yellow-shafted, and hybrid, then one could infer genetic divergence across the hybrid zone. Alternatively, if G_{ST} is large when samples are grouped by river drainages, then one could infer that intervening grasslands are barriers to gene flow.

RESULTS

General allozyme results.—Sixteen of the 31 loci were polymorphic in at least one of the samples (Appendix). The average proportion of polymorphic loci ($\bar{P}$; criterion for polymorphism: $q \ge 0.01$) was 0.207, and the average heterozygosity ($\bar{H}$) was 0.056. Northern Flickers are approximately equivalent to other birds in terms of polymorphism ($\bar{P} = 0.222$) and heterozygosity ($\bar{H} = 0.067$) based on 71 studies listed by Corbin (1983).

The "hybrid" allele phenomenon.—Allozymes present in hybrids but not in either of the parental types have been reported in some hybrid zones (e.g. Hunt and Selander 1973, Sage and Selander 1979, Greenbaum 1981). These "rare" hybrid-specific alleles probably result from intracistronic recombination of parental genomes (Sage and Selander 1979).

We found 4 hybrid-specific alleles in the Northern Flicker hybrid zone: LGG-D, sample 8406; IDH-1-B, sample 8107; and PGM-C and -D, sample 8210 (Appendix). Other rare alleles were found only in parental samples (e.g. ME-D, samples 8101 and 8201), and still others occurred in a few scattered samples of both hybrid and parental types, such as LDH-2-B found in samples 8111 and 8112 (hybrids) and in 8109 and 8110 (parental Red-shafted). Moreover, if the Northern Flicker hybrid zone has substantial numbers of these hybrid-specific alleles, one would expect heterozygosity to be greater in samples of hybrids in comparison with samples of the parental subspecies. Samples of hybrids did not have significantly greater heterozygosity than samples of parentals (Wilcoxon rank-sum test, $P > 0.05$). The occurrence of hybrid-specific alleles would also result in positive correlations between a folded hybrid index ($\overline{FHI}$) and either average heterozygosity or proportion of polymorphic loci. A folded hybrid index gives the maximum value to the most intermediate hybrid; both pure parental types have $\overline{FHI}$ of zero (see Dowling and Moore 1985). For the Northern Flicker hybrid zone the $\overline{FHI}$ maximum was 11.5, and there were no significant correlations between folded hybrid index and average heterozygosity ($r = 0.267$, $P > 0.05$) or proportion of polymorphic loci ($r = -0.419$, $P > 0.05$). Finally, samples of hybrids did not have more alleles per locus on average than did parental subspecies ($t = 0.502$, df $= 12$, $P > 0.50$). In sum, we found no evidence for the "rare" hybrid-specific allele phenomenon in the Northern Flicker hybrid zone.

Genetic differentiation.—There were no fixed allelic differences among the samples representing pure subspecies and hybrids, and there were no observable east-west clinal trends in allelic frequencies in any of the polymorphic loci (Appendix). Allozymic variation in the Northern Flicker hybrid zone was not concor-

dant with clinal variation in plumage traits (Short 1965, Moore and Buchanan 1985).

Despite the lack of clines in allelic frequencies, we detected substantial genic differentiation among the Northern Flicker demes (genic heterogeneity $\chi^2 = 1{,}264.9$, df = 864, $P < 0.00001$). Eight of the 16 polymorphic loci showed statistically significant intersample genic heterogeneity (Table 1). Chi-square tests for genic heterogeneity are extremely sensitive to small expected values, however. We performed a second genic-heterogeneity test on a condensed data set in which all "variant" ($q < 0.50$) alleles at a given locus were pooled into "pseudoalleles" (Eanes and Koehn 1978). This more conservative test was also significant ($\chi^2 = 815.7$, df = 512, $P < 0.00001$) and confirmed genic differentiation among some of the samples.

Genetic population structure.—The inbreeding coefficient, F_i, for the ith deme in a population is a measure of the deficiency of heterozygotes resulting from inbreeding (Wright 1943, 1969). The expected frequency of heterozygotes in deme i is $2p_iq_i(1 - F_i)$. The parameter F_{IS} is the mean F_i averaged over all demes. F_{IT} is the correlation between uniting gametes relative to the gene pool of the entire population (all demes). With no geographical variation in allelic frequencies, $F_{IT} = F_{IS}$. The parameter F_{ST} has several interpretations. Fundamentally, it is the ratio of the actual variance in allelic frequency between demes to the maximum possible variance that would obtain if alternate alleles were fixed in all demes (Workman and Niswander 1970). Thus, F_{ST} is a measure of geographical variation in allelic frequency. When samples from demes in disparate Hardy-Weinberg equilibria are pooled, there is an apparent deficiency of heterozygotes (Wahlund effect) and F_{ST} is greater than 0. These three variables are related through the formula: $F_{IT} = F_{ST} + (1 - F_{ST})F_{IS}$ (Wright 1943, Swofford and Selander 1981).

Estimates of F_{IS}, F_{IT}, and F_{ST} for the 16 polymorphic loci and Chi-square statistics based on the multiple-allele heterogeneity test are given in Table 1. The F_{ST} values are averages weighted by allelic frequencies across all alleles (Swofford and Selander 1981). The largest F_{ST} values correspond to the significant Chi-square heterogeneity tests and confirmed the existence of geographical variation in some Northern Flicker allelic frequencies. For example, ADH had an F_{ST} of 0.251. This means 25.1% of the maximum possible between-deme variance in allelic frequency actually exists. The F_{ST} values for the Northern Flicker are high for the eight polymorphic loci that show significant geographic variation in comparison with other avian species (Barrowclough 1980a, Johnson and Zink 1983, Van Wagner and Baker 1986).

TABLE 1. Summary of F-statistics and Chi-square heterogeneity statistics for all polymorphic loci.

Locus	F_{IS}[a]	F_{IT}	F_{ST}	χ^2 (df)[b]
G3P	−0.123	−0.004	0.106	37.39 (32)
6PG	0.021	0.151	0.133	63.04 (32)***
AAT-1	−0.075	−0.005	0.064	29.28 (32)
ADH	0.543*	0.658	0.251	114.16 (32)***
GAPDH	−0.203	−0.036	0.139	66.86 (32)***
LGP-1	0.026	0.158	0.136	118.62 (64)***
LGP-2	−0.091	−0.007	0.077	32.25 (32)
LPP	0.061	0.248	0.198	167.17 (64)***
LGG	−0.018	0.081	0.097	95.15 (96)
EST-2	0.161	0.259	0.117	165.42 (128)*
IDH-1	−0.022	−0.001	0.021	9.71 (32)
IDH-2	−0.124	−0.029	0.084	34.85 (32)
LDH-1	−0.099	−0.020	0.072	30.38 (32)
LDH-2	−0.091	−0.009	0.075	32.61 (32)
ME	0.195	0.292	0.121	142.16 (96)**
PGM	−0.216	−0.029	0.154	125.84 (96)*
Mean	−0.003	0.107	0.115	
Total				1,264.89 (864)***

[a] Chi-square test based on Li (1955); H_o:$F_{IS} = 0$.

[b] Chi-square test for heterogeneity in allelic frequencies among demes based on the multiple-allele model. Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

The F_{IS} values (Table 1) can reveal deficiencies or excesses of heterozygotes within demes; positive values indicate heterozygote deficiencies. The squared estimate of F_i, multiplied by the sample size, for a single locus with two alleles in a single deme has a Chi-square distribution with 1 degree of freedom (Li 1955). The sum of these Chi-square values over all demes has a Chi-square distribution with n degrees of freedom, where n is the number of demes where the locus is polymorphic. The F_{IS} values (Table 1) were tested with this statistic (see Li 1955); only the F_{IS} for ADH was significant. Over all loci, however, there was no significant trend of either heterozygote deficiency or excess in the Northern Flicker hybrid zone.

Our results imply the existence of some genic differentiation among the samples of Northern Flickers. Gene-diversity analysis enabled us to investigate the pattern and magnitudes of this differentiation. The values obtained (Table 2) show that approximately 92% of the total allozymic variation was apportioned into the with-

TABLE 2. Gene-diversity estimates for the Northern Flicker hybrid zone.

Subdivision	G_D	G_{DT}	G_{ST}
Drainage	0.924	0.067	0.009
Parentals-hybrids	0.925	0.073	0.002

in-deme variance (G_D). Approximately 7% of the variance was accounted for by among-deme genetic diversity (G_{DT}), but only 0.9% of the variation occurred between drainage subdivisions (G_{ST}). The parental-hybrid subdivisions between subspecies (*cafer* and *auratus*) and hybrids accounted for only 0.2% of genic diversity (G_{ST}). The Northern Flickers do not have a genic population structure concordant with the hybrid zone. Division between drainages is only slightly more pronounced and may not be statistically significant. Most of the geographical subdivision appears to involve either random divergence of local demes or a trend other than differentiation across the hybrid zone or among river drainages.

Estimates of gene flow.—The amount of gene flow can be inferred from statistics that reflect population structure. Slatkin (1981) defined the *occupancy number* (i) of an allele as the number of demes in which it is present and the *conditional average frequency* [$p(i)$] as the average frequency of alleles occurring in i demes. When $p(i)$ is plotted against i, the shapes of the curves for low, medium, and high gene flow are diagnostic. We plotted values for the Northern Flicker based on 58 alleles from 31 loci sampled from 33 demes (Fig. 2). The concave curve, where alleles with low to intermediate occupancy numbers have low average conditional frequencies, is characteristic of a species with high gene flow.

Expanding on the earlier work, Slatkin (1985) and Barton and Slatkin (1986) found that *private alleles*—alleles that occur in only one deme (i = 1)—can provide an estimate of Nm, the actual number of migrants between demes per generation (N = deme size, m = rate of migration between demes). From computer simulations Slatkin (1985) found a linear relationship between the logarithm of $p(1)$ and the logarithm of Nm for $0.01 < Nm < 10$; thus, Nm can be estimated from $p(1)$. The analysis was refined by Barton and Slatkin (1986). The most appropriate estimator from these two papers for our data derives from the equation $\log_{10}[p(1)] = a \log_{10}(Nm) + b$, where $a = -0.489$ and $b = -0.951$ (Barton and Slatkin 1986: 413). The values of a and b were determined by least-squares criteria from simulations with sample sizes of 10 (Barton and Slatkin 1986); our average sample size was 7.45 birds. We found 4 private alleles in 33 samples (Appendix; IDH-1-B, LGG-D, PGM-C, PGM-D) with an average conditional frequency of $\bar{p}(1) = 0.054$; thus, the estimate of Nm for the Northern Flicker is 4.44.

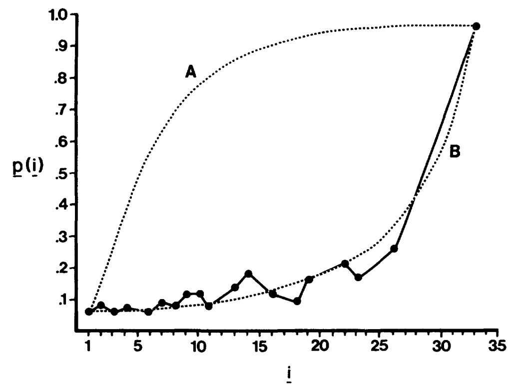

Fig. 2. Conditional allelic frequency [$p(i)$] vs. occupancy number (i) for Northern Flicker samples (solid line). The shape of the curve indicates high levels of gene flow. The dotted lines represent theoretical expected curves for low (A) and high (B) levels of gene flow (Slatkin 1981).

An alternative estimate of Nm, based on F-statistics, was suggested by Wright (1943): $F_{ST} = 1/(4Nm + 1)$. For our samples $F_{ST} = 0.115$, which yields a value of $Nm = 1.92$.

A literal interpretation of these results is that approximately 1.92–4.44 flickers/generation, on average, are exchanged between the demes we sampled. Obviously, this is a crude estimate, but it does imply that gene flow is substantial in the Northern Flicker and that it is an important determinant of the genetic structure of the species.

DISCUSSION

Of the few avian hybrid zones studied, only the Rufous-sided and Collared towhees in Mexico showed clinal variation in allelic frequencies through the hybrid zone (Braun 1981). Parental subspecies involved in the hybrid zone between the Tufted and Black-crested titmice implied clinal variation in five loci, although hybrid specimens were not sampled to verify this implication (Braun et al. 1984). Three other

studies of allozymes in avian hybrid zones (Yellow-rumped Warblers, Barrowclough 1980a; Northern Orioles, Corbin et al. 1979; and Black-capped and Carolina chickadees, Braun and Robbins 1986) were similar to the Northern Flicker study; subspecies-specific alleles were not found, and clinal variation in allelic frequencies was not observed.

Northern Flickers have a narrow, stable hybrid zone based on plumage and morphometric characters but show no genic diversity among Red-shafted, hybrid, and Yellow-shafted groups. We believe allozymic variation in flickers is selectively neutral, whereas plumage and morphometric variation is under selection. Comparisons of allelic-frequency distributions from 24 avian species showed that bird allozyme data are consistent with the neutrality hypothesis (Barrowclough et al. 1985). This does not imply all avian allozymic variation is independent of natural selection, but that the statistical evidence supports the neutral theory over a natural-selection hypothesis. Our allozyme data and analysis are consistent with this view. At the same time, the high level of dispersal implied by the homogeneous distribution of electromorphs implies that selection maintains the position and width of the plumage and morphological clines.

A contradiction is apparent in the avian literature regarding dispersal measures. Studies based on small finite areas yield estimates of RMS (root-mean-square) dispersal of about 1 km/generation (Barrowclough 1980b), whereas studies based on banding-recovery data yield estimates of 60–100 km/generation (Dolbeer 1982, Moore and Buchanan 1985). If RMS dispersal of 1 km/generation is more nearly correct, then the Northern Flicker hybrid zone could be explained readily by an ephemeral hybrid-zone model where the hybrid zone appears stable to a short-lived observer but is, in fact, slowly growing broader through introgressive hybridization. On the other hand, if RMS dispersal is more nearly 100 km, the introgression model would be inadequate because broadening in historical time would be detectable and the Red-shafted and Yellow-shafted flickers would have fused across the breadth of North America long ago (Moore and Buchanan 1985).

Although gene-flow rates inferred from genetic population structure are fraught with imprecision and potential biases (Slatkin 1981, 1985; Larson et al. 1984; Barton and Slatkin 1986), our calculations are consistent with earlier inferences (Moore and Buchanan 1985) that gene flow is substantial in flickers, closer to 100 than 1 km/generation. If this is true, dispersal of neutral alleles could account for the lack of allozymic structure associated with the hybrid zone. Such dispersal rates, however, imply strongly that natural or sexual selection acts on plumage and morphometric traits and maintains the width and position of the Northern Flicker hybrid zone.

There is a potential bias to gene-flow estimates that may be particularly acute when samples are taken from a hybrid zone. Severely detrimental alleles bias the average frequencies of private alleles [$\bar{p}(1)$] toward the low side, and this in turn results in an overestimate of Nm (Slatkin 1985: 86). The bias is negligible except when selection is severe and gene flow small. Many of the rare alleles peculiar to hybrid zones could be detrimental because they result from intracistronic recombination or hybrid dysgenesis. Therefore, an estimate of gene flow based on samples from a hybrid zone could be biased on the high side. This argument may not be applicable to the Northern Flicker because there is not an exceptional number of rare alleles in the hybrid zone (see Results).

Of the alternative explanations of hybrid zones (Moore 1977; Barton 1979a; Barton and Hewitt 1981, 1985) the bounded hybrid-superiority model best describes the Northern Flicker hybrid zone, but the nature of the geographical selection gradients that maintain the plumage and morphometric clines is presently unknown.

Northern Flickers of the Great Plains do not have a genic population structure concordant with the plumage and morphometric variation observed throughout the hybrid zone. Rather, they are subdivided very weakly into demes that occur along riparian zones of habitat. This is probably the result of high dispersal and the flow of selectively neutral genes. The plumage and morphometric characters diagnostic of the subspecies are subject to selection, however, and geographical selection gradients apparently determine the width and position of the hybrid zone.

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APPENDIX. Allelic frequencies of polymorphic loci in 33 samples of Northern Flickers.[a]

Enzyme / Presumptive locus (E.C. no.) / Allele	Sample (*n*)															
	Red-shafted								**Hybrid**							
	8105 (11)	8204 (14)	8110 (5)	8403 (4)	8404 (5)	8405 (5)	8409 (6)	8109 (5)	8107 (23)	8108 (16)	8111 (11)	8112 (10)	8113 (5)	8114 (9)	8115 (7)	8116 (2)
Alcohol dehydrogenase																
ADH (1.1.1.1)																
A	0.955	1.00	1.00	0.750	0.600	1.00	0.917	0.600	0.978	1.00	1.00	0.800	1.00	1.00	1.00	1.00
B	0.045			0.250	0.400		0.083	0.400	0.022			0.200				
Glycerol-3-phosphate dehydrogenase																
G3P (1.1.1.8)																
A	0.864	0.786	1.00	1.00	0.800	1.00	0.917	1.00	0.826	0.688	0.909	0.750	0.900	0.778	1.00	1.00
B	0.136	0.214			0.200		0.083		0.174	0.312	0.091	0.250	0.100	0.222		
Lactate dehydrogenase																
LDH-1 (1.1.1.27)																
A	0.955	0.964	0.900	1.00	1.00	1.00	1.00	0.900	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B	0.045	0.036	0.100					0.100								
LDH-2																
A	1.00	1.00	0.900	1.00	1.00	1.00	1.00	0.900	1.00	1.00	0.955	0.950	1.00	1.00	1.00	1.00
B			0.100					0.100			0.045	0.050				
Malic enzyme																
ME (1.1.1.40)																
A	0.910	0.929	1.00	1.00	1.00	1.00	0.917	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B	0.045	0.071					0.083									
C	0.045															
D																
Isocitrate dehydrogenase																
IDH-1 (1.1.1.42)																
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.978	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B									0.022							
IDH-2																
A	0.955	1.00	0.900	1.00	1.00	1.00	1.00	0.800	0.978	1.00	1.00	0.950	0.900	1.00	0.929	1.00
B	0.045		0.100					0.200	0.022			0.050	0.100		0.071	
Phosphogluconate dehydrogenase																
PGD (1.1.1.44)																
A	0.818	0.750	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.844	0.818	1.00	1.00	1.00	1.00	1.00
B	0.182	0.250								0.156	0.182					
Glyceraldehyde-3-phosphate dehydrogenase																
GAPDH (1.2.1.12)																
A	1.00	0.964	1.00	0.875	0.900	1.00	1.00	0.700	1.00	1.00	0.955	1.00	1.00	1.00	1.00	1.00
B		0.036		0.125	0.100			0.300			0.045					
Aspartate aminotransferase																
AAT-1 (2.6.1.1)																
A	0.909	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.969	1.00	1.00	1.00	1.00	1.00	1.00
B	0.091									0.031						
Esterase (carboxylesterase)																
EST-2 (3.1.1.1)																
A	0.600	0.714	0.900	1.00	0.800	0.700	1.00	0.900	0.891	0.821	0.727	0.600	0.800	0.888	0.643	1.00
B	0.200	0.036			0.200	0.100			0.022	0.071	0.045					
C	0.100	0.071	0.100						0.065	0.071	0.136	0.200	0.200	0.056	0.143	
D		0.143						0.100	0.022	0.037	0.092	0.150		0.056	0.143	
E	0.100	0.036				0.200						0.050			0.071	
Leucyl-glycine peptidase																
LGP-1 (3.4.13.11)																
A	0.682	0.875	0.700	1.00	0.800	1.00	1.00	0.800	0.715	0.406	0.545	0.700	0.700	0.611	0.643	0.750
B	0.318	0.125	0.200		0.100				0.214	0.594	0.455	0.300	0.300	0.389	0.357	0.250
C			0.100		0.100			0.200	0.071							
LGP-2																
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.969	1.00	1.00	1.00	1.00	1.00	1.00
B										0.031						
Leucyl-glycyl-glycine peptidase																
LGG (3.4.13.11)																
A	0.955	0.821	1.00	1.00	1.00	0.800	1.00	1.00	0.935	0.875	0.955	0.900	1.00	0.889	1.00	0.750
B	0.045	0.071								0.031						
C		0.108				0.200			0.065	0.094	0.045	0.100		0.111		0.250
D																

APPENDIX. Continued.

Enzyme Presumptive locus (E.C. no.) Allele	Sample (*n*) Red-shafted								Hybrid							
	8105 (11)	8204 (14)	8110 (5)	8403 (4)	8404 (5)	8405 (5)	8409 (6)	8109 (5)	8107 (23)	8108 (16)	8111 (11)	8112 (10)	8113 (5)	8114 (9)	8115 (7)	8116 (2)
Leucyl-proline peptidase																
LPP (3.4.13.9)																
A	0.682	0.429	1.00	1.00	0.900	1.00	0.667	0.900	0.739	0.750	0.773	0.667	0.700	0.833	0.143	1.00
B	0.182	0.536			0.100		0.333		0.043	0.125	0.045	0.222	0.100	0.111	0.857	
C	0.136	0.035						0.100	0.218	0.125	0.182	0.111	0.200	0.056		
Phosphoglucomutase																
PGM (5.4.2.2)																
A	1.00	1.00	1.00	0.625	0.800	0.900	0.917	1.00	0.978	1.00	1.00	1.00	1.00	1.00	0.929	1.00
B				0.375	0.200	0.100	0.083		0.022						0.071	
C																
D																

	Hybrid												Yellow-shafted				
	8203 (9)	8205 (6)	8206 (5)	8209 (5)	8210 (9)	8211 (12)	8212 (5)	8303 (4)	8402 (7)	8406 (6)	8407 (4)	8408 (5)	8101 (9)	8201 (6)	8202 (4)	8302 (9)	8401 (3)
Alcohol dehydrogenase																	
ADH (1.1.1.1)																	
A	1.00	1.00	1.00	1.00	1.00	0.875	0.700	0.625	0.929	0.500	1.00	0.900	1.00	1.00	1.00	0.833	1.00
B						0.125	0.300	0.375	0.071	0.500		0.100				0.167	
Glycerol-3-phosphate dehydrogenase																	
G3P (1.1.1.8)																	
A	0.833	0.833	0.800	0.800	0.722	0.833	1.00	0.875	0.786	1.00	1.00	1.00	0.778	0.917	0.625	0.722	0.677
B	0.167	0.167	0.200	0.200	0.278	0.167		0.125	0.214				0.222	0.083	0.375	0.278	0.333
Lactate dehydrogenase																	
LDH-1 (1.1.1.27)																	
A	1.00	1.00	1.00	1.00	1.00	0.929	1.00	1.00	1.00	1.00	1.00	0.900	0.944	1.00	0.875	1.00	1.00
B						0.071						0.100	0.056		0.125		
LDH-2																	
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B																	
Malic enzyme																	
ME (1.1.1.40)																	
A	0.833	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.929	1.00	1.00	1.00	0.777	0.750	1.00	1.00	1.00
B	0.167								0.071				0.056	0.083			
C													0.111				
D													0.056	0.167			
Isocitrate dehydrogenase																	
IDH-1 (1.1.1.42)																	
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
B																	
IDH-2																	
A	1.00	0.917	1.00	1.00	1.00	0.958	1.00	1.00	1.00	1.00	0.875	1.00	1.00	0.917	1.00	1.00	1.00
B		0.083				0.042					0.125			0.083			
Phosphogluconate dehydrogenase																	
PGD (1.1.1.44)																	
A	0.889	1.00	0.800	0.800	0.889	1.00	1.00	1.00	1.00	0.917	1.00	1.00	1.00	1.00	0.875	1.00	1.00
B	0.111		0.200	0.200	0.111					0.083					0.125		
Glyceraldehyde-3-phosphate dehydrogenase																	
GAPDH (1.2.1.12)																	
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.857	1.00	0.875	0.900	1.00	1.00	1.00	1.00	0.833
B									0.143		0.125	0.100					0.167
Aspartate aminotransferase																	
AAT-1 (2.6.1.1)																	
A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.944	1.00	1.00	1.00	1.00
B													0.056				
Estrase (carboxylesterase)																	
EST-2 (3.1.1.1)																	
A	0.722	0.416	0.900	0.700	0.888	0.917	0.700	0.625	0.858	0.500	0.750	0.700	0.687	0.750	0.750	0.389	1.00
B		0.168	0.100	0.100				0.375		0.167		0.100				0.111	
C	0.167	0.250		0.200	0.056	0.083	0.100		0.071	0.333		0.100	0.188	0.167	0.250	0.333	

APPENDIX. Continued.

	Hybrid												Yellow-shafted				
	8203 (9)	8205 (6)	8206 (5)	8209 (5)	8210 (9)	8211 (12)	8212 (5)	8303 (4)	8402 (7)	8406 (6)	8407 (4)	8408 (5)	8101 (9)	8201 (6)	8202 (4)	8302 (9)	8401 (3)
D	0.111	0.083			0.056		0.100		0.071		0.125	0.100	0.125	0.083		0.111	
E		0.083					0.100				0.125					0.056	
Leucyl-glycine peptidase																	
LGP-1 (3.4.13.11)																	
A	0.611	0.917	0.800	0.800	0.833	0.583	0.800	1.00	0.571	0.834	0.750	0.900	0.778	0.666	1.00	0.944	0.833
B	0.389	0.083	0.200	0.200	0.167	0.417	0.200		0.429	0.083	0.250		0.222	0.167		0.056	0.167
C										0.083		0.100		0.167			
LGP-2																	
A	1.00	1.00	1.00	0.900	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.917	1.00	1.00	1.00
B				0.100										0.083			
Leucyl-glycyl-glycine peptidase																	
LGG (3.4.13.11)																	
A	0.944	0.917	0.900	0.900	0.944	0.955	1.00	1.00	1.00	0.917	0.875	1.00	0.944	1.00	0.875	0.889	0.667
B					0.056								0.056				
C	0.056	0.083	0.100	0.100		0.045					0.125				0.125	0.111	0.333
D										0.083							
Leucyl-proline peptidase																	
LPP (3.4.13.9)																	
A	0.556	0.584	0.800	0.900	0.750	0.773	0.600	0.875	0.929	0.917	0.750	0.700	0.666	0.750	0.625	0.944	1.00
B	0.222	0.083	0.100	0.100		0.227	0.100			0.083	0.250	0.300	0.167		0.375		
C	0.222	0.333	0.100		0.250		0.300	0.125	0.071				0.167	0.250		0.056	
Phosphoglucomutase																	
PGM (5.4.2.2)																	
A	0.833	1.00	1.00	1.00	0.832	1.00	1.00	0.875	0.714	1.00	1.00	1.00	1.00	0.917	1.00	0.889	0.833
B	0.167				0.056			0.125	0.286					0.083		0.111	0.167
C					0.056												
D					0.056												

[a] The following loci (E.C. number) were monomorphic in all samples: malate dehydrogenase-1, -2 (1.1.1.37), glucose-6-phosphate dehydrogenase (1.1.1.49), dihydrolipoamide dehydrogenase (1.8.1.4), superoxide dismutase (1.15.1.1), aspartate aminotransferase-2 (2.6.1.1), pyruvate kinase (2.7.1.40), creatine kinase (2.7.3.2), esterase-1, -3 (3.1.1.1), acid phosphatase (3.1.3.2), aconitate hydratase-1, -2 (4.2.1.3), mannose-6-phosphate isomerase (5.3.1.8), glucose-6-phosphate isomerase (5.3.1.9).