GENETIC DIFFERENTIATION OF PIPING PLOVERS ACROSS NORTH AMERICA

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ABSTRACT.—We studied the effect of a recent gap in the range of Piping Plovers (*Charadrius melodus*) on interpopulation variability and differentiation. Chicks from 79 broods (122 individuals) in Saskatchewan, North Dakota, Manitoba, Minnesota, and New Brunswick were examined by protein electrophoresis. Of 36 presumptive loci examined, 4 were polymorphic (99% criterion).

Genotypic distributions in each population conformed to Hardy-Weinberg predictions in 16 of 20 Chi-square tests performed ($P < 0.05$). Variability within populations was comparable to other avian species ($\bar{x}$ heterozygosity = 0.016 ± 0.014) and was slightly greater than reported for other species of *Charadrius*. Inbreeding was not a significant factor within any of the sampled populations ($\bar{x}\ F_{is} = 0.049$). Values for F_{st} ($\bar{x} = 0.02$) and results of genetic distance/identity calculations indicated little population differentiation has occurred. Hence, either the gap has not affected the genetics of the species, or changes were not detectable by electrophoresis. Furthermore, results from distribution data, dispersal patterns, and other life-history variables suggest that Piping Plover populations experience annual gene flow. Therefore, current subspecific classifications for the species appear unwarranted. *Received 5 June 1987, accepted 19 November 1987.*

THE ability to determine gene flow and assortative mating across a species' range is important in assessing potential changes during severe population declines (e.g. Denniston 1978, Seal 1978, Frankel and Soulé 1981, Soulé and Wilcox 1980, Barrett and Vyse 1982, Slatkin 1987). Unfortunately, few detailed genetic analyses of endangered avian populations have been reported, and the few available were conducted after the species was near extinction (Ralls and Ballou 1983, Mace 1986, Wayne et al. 1986).

The Piping Plover (*Charadrius melodus*) is a threatened (U.S. northern Great Plains and Atlantic coast) or endangered (Canada, and U.S. Great Lakes) North American shorebird that represents a taxonomic, genetic, and conservation dilemma to biologists. The species has a wide distribution, yet most birds are concentrated at extremes of the range (Fig. 1). Ord's designation of Piping Plovers as a species in 1824 began a taxonomic controversy that has continued to this day. Since then, the American Ornithologists' Union has fluctuated between accepting and rejecting designation of inland and Atlantic subspecies (*C. m. circumcinctus* and *C. m. melodus*, respectively; A.O.U. 1886, 1957). Breast-band patterns and geographic distributions were proposed as primary evidence for division of the species (Moser 1942, A.O.U. 1945, Wilcox 1959), although no definitive analyses were performed. Wilcox (1959) reported a variety of breast-band forms among Piping Plovers on Long Island, New York. Subsequent morphological measurements of Atlantic and inland birds did not indicate significant differences among individuals from different geographic regions (Wilcox 1959). Nevertheless, two subspecies still are recognized by the A.O.U. (1983).

Recently, evaluation of the species' taxonomic status became an important issue in resolving the status of Piping Plover populations. Since the early 1900's the number of Piping Plovers declined throughout the range. Currently only 2,100–2,300 pairs remain (e.g. Bent 1929; Cairns and McLaren 1980; Haig 1985, 1986a, b; Haig and Oring 1985; Haig et al. 1988). Although range boundaries have not declined substantially, breeding birds have all but disappeared from the Great Lakes region in the past 50 years (Fig. 1). Today, about 17 pairs are distributed across Lake Superior, Lake Michigan, and Lake Erie (Haig et al. 1988). This decline in breeding

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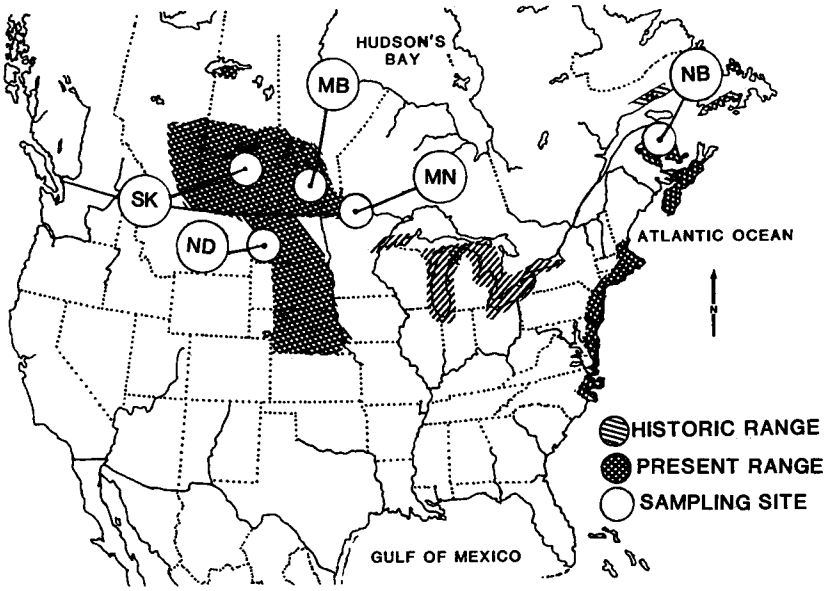

Fig. 1. Piping Plover breeding range before 1950 and in 1986. Locations of sampling sites are labeled with arrows (see Table 1 for details).

numbers creates a potential barrier for movement between Atlantic and inland breeding sites.

In 1981 we began investigating the effect of the numerical and distributional decline on the status of Piping Plovers. Initially, we determined life-history patterns, dispersal patterns, and the species' distribution (Haig and Oring 1985, Haig 1987). We found that breeding birds were site faithful but readily changed mates during and between breeding seasons. We also found that immigration of new breeding birds into local sites was a frequent annual event. Mixing of Atlantic and inland Piping Plovers, however, was not common during any phase of the annual cycle. In 1984 we began the present electrophoretic study to determine the extent of genetic variability within and among Piping Plover demes.

Materials and Methods

Tissue samples for electrophoresis were collected from fledgling Piping Plovers in five major breeding locations throughout the range (described by Haig 1987) (Table 1, Fig. 1). At all sites chicks were marked individually with color bands to facilitate identification of brood membership. In Manitoba and Minnesota adults were also marked individually for mate and family identification.

Feather pulp was collected by pulling 6 newly emerged feather shafts from each fledgling. Feathers were placed in cryogenic vials, transported on dry ice, and transferred to a liquid nitrogen flask for permanent storage. In 1984 preliminary sampling was

Table 1. Samples collected and population characteristics at 5 collection sites (1985).

Collection location[a]	Sites sampled	Chicks sampled	Broods sampled	Broods present	Adult population
Southern Manitoba (MB)	3	41	22	25	97
Lake of the Woods, Minnesota (MN)	1	6	5	5	28
Chain of Lakes, North Dakota (ND)[b]	5	24	20	36	182
Big Quill Lake, Saskatchewan (SK)	1	35	23	40	178
Gulf of St. Lawrence, New Brunswick (NB)	3	16	9	15	48
Total	13	122	79	121	533

[a] See Fig. 1 for locations.
[b] Population data from Prindiville 1986.

TABLE 2. Enzymes, buffer systems, and loci used in electrophoretic analysis of Piping Plover feather pulp.

Enzyme	Locus	E.C. no.	Buffer system[a]
Adenosine deaminase	ADA	3.5.4.4	C
Adenylate kinase	AK-1,2	2.7.4.3	C
Aldolase	ALD-1,2	4.1.2.13	C
Aspartate aminotransferase	AAT-1,2	2.6.1.1	C
Creatine kinase	CK-1,2	2.7.3.2	C
Esterase	EST-1,3	3.1.1.1	R
Glucosephosphate isomerase	GPI-2	5.3.1.9	4
Glucathione reductase	GR-1,2	1.6.4.2	M
Glyceraldehyde-3-phosphate dehydrogenase	GAPDH	1.2.1.12	C
Isocitrate dehydrogenase	IDH-1,2	1.1.1.42	C
Lactate dehydrogenase	LDH-1,2	1.1.1.27	4
Malate dehydrogenase	MDH-1,2	1.1.1.37	4
Malic enzyme	ME-1,2	1.1.1.40	C
Mannosephosphate isomerase	MPI	5.3.1.8	C
Methylumbelliferyl phosphatase	MUP	—	C
Peptidase w/glycyl-leucine	PEP-GL	3.4.11/13	C
Peptidase w/leucyl-leucyl-leucine	PEP-LLL	3.4.11/13	C
Peptidase w/phenyl-alanyl-proline	PEP-PAP-1,2	3.4.11/13	M
Phosphoglucomutase	PGM	2.7.5.1	M
Phosphogluconate dehydrogenase	PGD	1.1.1.44	4
Phosphoglycerate kinase	PGK	2.7.2.3	C
Protein	PRO-1,5	—	C
Superoxide dismutase	SOD	1.15.1.1	M
Triose phosphate isomerase	TPI	5.3.1.1	4

[a] C = Clayton and Tretiak 1972, M = Markert and Faulhaber 1965, 4 = Selander et al. 1971, R = Ridgeway et al. 1970.

carried out at West Shoal Lake, Manitoba, to evaluate the effects of feather sampling on fledgling success. Samples were taken from 2 chicks in each of 5 broods. The remaining 2 chicks in each brood were handled but not sampled. There was no difference in fledging time or success between sampled, control, or unbanded chicks.

Horizontal starch-gel electrophoresis was performed at the Cornell Laboratory for Ecological and Evolutionary Genetics (CLEEG). Buffer systems were adapted from Clayton and Tretiak (1972), Markert and Faulhaber (1965), Selander et al. (1971), and Ridgeway et al. (1970). Staining procedures were adapted from Harris and Hopkinson (1976). Details of the electrophoretic procedure were summarized by May et al. (1979) and Marsden and May (1984).

Initial screening of 52 enzyme systems resulted in 24 pulp enzymes that were sufficiently clear for inclusion in the study (Table 2). Of the 36 presumptive loci resolved, 4 were polymorphic (i.e. frequency of most common allele did not exceed 0.99): EST-1, SOD, PRO-5, and PGM. Nucleoside phosphorylase (NP) was resolved but was eliminated from further analyses because of inconsistent banding patterns.

We sampled 60–100% of all broods present at the study sites in 1985 (Table 1). In many cases multiple members of a brood were included in sampling; hence, population data were analyzed in two ways. One data set contained one randomly chosen member from each brood sampled (ensuring that degree of relatedness was less than 0.5), and the second contained all chicks sampled (increasing the sample size by 65%). Both data sets were similarly analyzed, and no significant difference was found between them. Nevertheless, the results of each are presented for comparison. All data were analyzed using the BIOSYS-1 statistical program for analysis of electrophoretic data in population genetics (Swofford and Selander 1981).

RESULTS

Within-population genetic variability.—Observed allelic frequencies were calculated for all 36 presumptive loci and analyzed by population. All populations shared a common allele among all loci surveyed. EST-1 was the most variable locus within all populations (Table 3). The remaining three polymorphic loci exhibited little variability; the frequency of the commonest allele exceeded 0.90 in all cases, and exceeded 0.95 in 67% of the cases.

For each polymorphic locus in each population, observed and expected genotypic frequencies were compared by a Chi-square test to evaluate departure from Hardy-Weinberg equilibrium. Levene's (1949) correction for small sample size was used to calculate expected values. In this test a P-value of 1.00 indicates a perfect fit to expected values, and a P-value of 0.00 indicates lack of fit. Across all samples 20%

TABLE 3. Allelic frequencies of polymorphic loci for each population and for the species, using samples from all Piping Plover chicks sampled in North America.

Locus	Allele	Population[a]					Total[b]
		MB	MN	ND	SK	NB	
EST-1	A	0.451	0.417	0.341	0.429	0.250	0.396 (0.416)
	B	0.549	0.583	0.659	0.571	0.750	0.604 (0.584)
	n	41	6	22	35	16	120 (77)
SOD	A	0.927	0.917	0.917	0.914	1.00	0.930 (0.937)
	B	0.073	0.083	0.083	0.086	0.00	0.070 (0.063)
	n	41	6	24	35	16	122 (79)
PRO-5	A	0.976	1.00	0.978	0.986	1.00	0.983 (0.987)
	B	0.024	0.00	0.022	0.014	0.00	0.017 (0.013)
	n	41	6	23	35	16	121 (78)
PGM	A	0.939	1.00	0.979	0.986	1.00	0.970 (0.975)
	B	0.061	0.00	0.021	0.014	0.00	0.030 (0.025)
	n	41	6	24	35	16	122 (79)

[a] MB = Manitoba, MN = Minnesota, ND = North Dakota, SK = Saskatchewan, NB = New Brunswick.
[b] Numbers in parentheses represent results of sampling 1 chick/brood.

(4/20) of the tests deviated significantly from Hardy-Weinberg equilibrium (Manitoba and New Brunswick populations at EST-1, North Dakota samples at SOD, Manitoba population at PGM), while 15% (3/20) deviated when one sample per brood was analyzed (Manitoba samples at EST-1 and PGM, North Dakota population at SOD). Calculation of coefficients for heterozygote deficiency or excess showed that all allelic frequencies that deviated significantly from Hardy-Weinberg were deficient of heterozygotes at that locus.

To illustrate the distribution of genetic variation among populations, we calculated the proportion of polymorphic loci (99% criterion) and estimates of mean heterozygosity (Table 4). The number of alleles per locus varied little among populations. The percentage of polymorphic loci varied from 2.8 in New Brunswick to 11.1 in Manitoba, North Dakota, and Saskatchewan. Results from both sampling methods indicate observed heterozygosity did not differ significantly from Hardy-Weinberg predictions.

Among-population genetic variability.—Variance in allelic frequencies among populations was examined using *F*-statistics (Wright 1951, 1965, 1978; Crow and Kimura 1970; Nei 1973, 1977) (Table 5). These statistics compare variability at the individual, subpopulation, and population levels. Each Piping Plover population (i.e. Manitoba, Minnesota, etc.) was considered a subpopulation of the total population sampled. Expected frequencies were derived from a Hardy-Weinberg equation; hence, *F*-statistics measured deviation from Hardy-Weinberg equilibrium.

F_{is} measures departure from equilibrium

TABLE 4. Genetic variability at 36 loci among all chicks sampled in all populations.

Population	*n*	Alleles/locus ($\bar{x}$ ± SE)	% polymorphic loci[a]	Heterozygosity/locus ($\bar{x}$ ± SE)	
				Direct count	Hardy-Weinberg expected[b]
Manitoba	41	1.1 ± 0.05	11.1	0.015 ± 0.009	0.022 ± 0.015
Minnesota	6	1.1 ± 0.04	5.6	0.028 ± 0.023	0.019 ± 0.015
North Dakota	24	1.1 ± 0.05	11.1	0.016 ± 0.012	0.019 ± 0.013
Saskatchewan	35	1.1 ± 0.05	11.1	0.022 ± 0.016	0.020 ± 0.016
New Brunswick	16	1.0 ± 0.03	2.8	0.003 ± 0.003	0.011 ± 0.011
Total					
All chicks	122	1.1 ± 0.04	8.3	0.016 ± 0.011	0.019 ± 0.014
1 chick/brood	79	1.1 ± 0.04	7.2	0.016 ± 0.012	0.019 ± 0.014

[a] Locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99.
[b] Unbiased estimate (Nei 1978).

TABLE 5. Summary of *F*-statistics at all polymorphic loci in Piping Plover chicks.

Locus	F_{is}	F_{it}	F_{st}
EST-1	0.039	0.061	0.023
SOD	0.050	0.067	0.018
PRO-5	−0.022	−0.012	0.009
PGM	0.218	0.239	0.027
Mean			
All	0.049	0.070	0.022
1/brood	0.081	0.099	0.020

TABLE 6. Matrix of genetic similarity coefficients for Piping Plover populations. Nei's (1978) unbiased genetic identity is above diagonal; Rogers' (1972) genetic similarity is below.[a]

Population	1	2	3	4	5
1. Manitoba	—	1.000	1.000	1.000	0.999
2. Minnesota	0.996	—	1.000	1.000	1.000
3. North Dakota	0.995	0.997	—	1.000	0.994
4. Saskatchewan	0.997	0.999	0.997	—	0.992
5. New Brunswick	0.990	0.993	1.000	0.999	—

[a] Used all chicks sampled.

among individuals in each subpopulation and is used as an inbreeding coefficient. Values range from −1 to 1; 0 indicates that allelic frequencies among all subpopulations, or the total population, are in Hardy-Weinberg equilibrium. For all loci, F_{is} values were close to 0.

Similar to F_{is}, F_{it} measures deviation of allelic frequencies from Hardy-Weinberg, but combines all individuals from all subpopulations sampled. Therefore, it examines the effects of nonrandom mating and subpopulation differentiation. All F_{it} values for Piping Plovers were close to 0.

Genetic variance among populations was determined by calculating values for F_{st}. An F_{st} value of 0 indicates that all subpopulations were identical in genetic structure; a value of 1 indicates complete subpopulation differentiation. In both sampling regimes, F_{st} values were almost identical and very close to 0. An F_{st} value of 0.02 indicates that 2% of all genetic variance or deviation from Hardy-Weinberg equilibrium was due to differentiation among subpopulations, while 98% of the variance occurred within subpopulations. These results suggest very little differentiation has occurred among the Piping Plover populations sampled.

A second method to assess population differentiation examines among-population heterogeneity at all polymorphic loci using Chi-square contingency analyses. *P*-values ranged from 0.29 (PGM) to 0.89 (PRO-5). These results indicate little differentiation has occurred among populations and further support conclusions from *F*-statistic analyses.

Finally, similarity among populations was calculated using Rogers' (1972) and Nei's (1978) indices of genetic similarity (Table 6). These results also showed little difference among any of the populations sampled. The closeness in identity among populations prevented further analysis of population or regional clustering.

DISCUSSION

Genetic comparison of Piping Plovers with other taxa.—Electrophoretic surveys across a range of taxonomic levels imply that avian taxa are less genetically differentiated than are equivalent taxa of other vertebrates, although they have similar levels of intraspecific genetic variation (Barrowclough and Corbin 1978, Avise and Aquadro 1982, Barrowclough 1983). Populations of North American Temperate Zone birds, however, are characterized by a relatively low degree of intraspecific differentiation (Barrowclough and Baker 1988).

Among North American birds, Piping Plover values of F_{st} are in the middle to high range of values for differentiation within a species. Low F_{st} values range from 0.0008 to 0.004 in Dark-eyed Juncos (*Junco hyemalis*; Barrowclough 1983), Trumpeter Swans (*Cygnus buccinator*; Barrett and Vyse 1982), and Short-billed Dowitchers (*Limnodromus griseus*; Baker and Strauch 1988). High F_{st} values range from 0.032 in White-crowned Sparrows (*Zonotrichia leucophrys*; Corbin 1981) and California Quail (*Callipepla californica*; Zink et al. 1987) to 0.041 in Red Knots (*Calidris canutus*; Baker and Strauch 1988). Among shorebirds, Piping Plover population differentiation (F_{st}) most closely resembles species with geographically restricted populations: Willets (*Catoptrophorus semipalmatus*; 0.020), Purple Sandpipers (*Calidris maritima*; 0.023), and Western Sandpipers (*Calidris mauri*; 0.020) (Baker and Strauch 1988).

Comparison of genetic variability within the genus *Charadrius* indicates that Piping Plovers have a greater number of alleles per locus, per-

TABLE 7. Comparison of genetic variability among North American plovers. All data except *C. melodus* are from Baker and Strauch (1988).

Species	*n*	*n* loci	Alleles/locus	Percentage polymorphic loci	Average heterozygosity (± SE)[a]
Pluvialis dominica	10	40	1.15	10.0	0.021 ± 0.011
P. squatarola	13	40	1.07	7.5	0.011 ± 0.006
Charadrius alexandrinus	7	40	1.02	2.5	0.011 ± 0.011
C. wilsonia	7	40	1.02	2.5	0.009 ± 0.009
C. semipalmatus	15	40	1.00	0.0	0.000 ± 0.000
C. melodus	122	36	1.07	8.3	0.019 ± 0.014
C. vociferus	12	40	1.02	2.5	0.004 ± 0.004
C. montanus	10	40	1.00	0.0	0.000 ± 0.000

[a] Average heterozygosity expected under Hardy-Weinberg equilibrium.

centage of polymorphic loci, and average heterozygosity than five other North American congeners sampled (Table 7). Conversely, Piping Plover genetic variability is lower than other charadriids and scolopacids sampled by Baker and Strauch (1988). In general, it is risky to make multispecies comparisons when sampling regimes vary in the number of populations, individuals, tissues, polymorphic loci, or enzymes examined. In the future, cooperative sampling among researchers will allow for more rigorous interspecific comparisons (Baker et al. 1985).

Differentiation among Piping Plover populations.—Currently, little detectable genetic differentiation has occurred among local populations or between Piping Plovers from distant geographic regions (i.e. Atlantic coast and northern Great Plains). This information is contrary to recent distribution patterns for the species. A number of factors may explain the discrepancy. First, severe decline of birds in the midportion of the species range is very recent. Therefore, these genetic data may serve as baseline information for future comparisons when the gap has existed for a longer time.

Second, gene flow among populations is a primary factor offsetting the diversifying effect of genetic drift within subpopulations, and may act as a cohesive factor that genetically unites geographically isolated populations (Wright 1951, Mayr 1963). Estimates of the amount of gene flow needed to offset the effect of genetic drift range from 1 individual·1,000^{-1}·generation^{-1} (Lewontin 1974) to 1 individual·population^{-1}·generation^{-1} (Wright 1931).

Among Piping Plover populations *annual* gene flow is commonly known to occur at least in Manitoba, Minnesota, and New York, and probably occurs in most other major breeding areas (Haig 1987). Dispersal data for Piping Plovers showed that while most breeding birds were site faithful, natal philopatry was low (Haig 1987). Simultaneous observation of marked birds in a number of local breeding sites indicated that chicks dispersed great distances, so gene flow occurred even if breeding areas were far apart (Haig 1987). Dispersal data also showed that during winter, Piping Plovers from inland breeding sites readily mixed, and there was at least some mixing between inland and Atlantic birds. This contact between local and regional populations, occurring at least on an annual basis, further explains the low F_{st} value.

Available evidence suggests that Piping Plovers are not genetically, behaviorally, or, perhaps, morphologically differentiated into two distinguishable subspecies. Greater resolution of population differences may result from increased sampling of individuals from throughout the range. A cluster analysis using Rogers' (1972) genetic similarity indices indicated a slight separation of New Brunswick birds from other populations, although standard errors were too high to place confidence in the results.

Demographic considerations.—Additional factors may affect Piping Plovers. The overall population size for Piping Plovers is low (less than 4,700 individuals), and their breeding distribution is characterized by small local populations that occur in highly variable and ephemeral habitat. Significant, permanent destruction of habitat continues throughout their range, and annual catastrophic destruction of local breeding sites (and perhaps winter sites) results in wide fluctuations in local population size. Finally, birds on the Atlantic coast and other lo-

cations suffer from intense predation. These characters point to the fact that even though gene flow occurs currently, other factors may soon prevent frequent population mixing.

ACKNOWLEDGMENTS

We gratefully acknowledge the technical advice provided by A. Baker, J. LaDuke, and B. May. A. H. Brush, R. Crawford, D. Lieberman, and two anonymous reviewers made helpful suggestions on the manuscript. Collection of electrophoretic samples was facilitated through the assistance of H. Beach, M. Colwell, C. Gratto, W. Harris, B. Johnson, P. Kehoe, E. Prindiville, D. Rave, Webster Fellows from Delta Waterfowl and Wetlands Research Station, the Canadian Wildlife Service, and Parks-Canada. Financial support was provided by Delta Waterfowl and Wetlands Research Station, University of North Dakota, World Wildlife Fund (Canada), Minnesota Department of Natural Resources, and National Science Foundation grant DCB 8608162 to L. Oring and A. Fivizanni. The National Zoo provided resources to S. Haig during manuscript preparation.

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ERRATUM

The correct dates for the **XX International Ornithological Congress** are **2–9 December 1990.** The month was incorrectly printed in the July 1987 issue of *The Auk*.