SHORT COMMUNICATIONS

Allozyme Analysis of the California Gull (*Larus californicus*)

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Jehl (1987) analyzed morphological variation in the California Gull (*Larus californicus*) and identified two potential races: a small, dark-mantled form mainly from the Great Basin of the United States, and a larger, paler form that breeds in the Great Plains and prairie provinces of Canada. Size differences between these races averaged 5–12% in linear dimensions and 27% in body mass.

Zink and Winkler (1983) found no significant genetic differentiation between California Gulls from two colonies in the Great Basin (Mono Lake, California, and Great Salt Lake, Utah) that were morphologically similar but differed in average clutch size. We broadened the analysis to document genetic differentiation between the two proposed races, which, until very recently, retained highly disjunct ranges. We hypothesized, based on the morphological differences (Jehl 1987), that the genetic variation should be more pronounced between the Canadian and Great Basin birds than between the Great Basin colonies.

We obtained tissue samples from 23 adult California Gulls from colonies in Alberta (13) and Mono Lake, California (10), collected in the 1985 breeding season. The Alberta sample included 6 birds from Frog Lake (ca. 200 km east of Edmonton, Alberta) and 7 from Beaverhill Lake (ca. 100 km east of Edmonton). Each bird was frozen whole and shipped on dry ice to San Diego, where samples of liver, heart, kidney, and pectoral muscle were removed and immediately frozen at −70°C. Protein electrophoresis followed standard procedures specified by Harris and Hopkinson (1976), with specific modifications outlined by Johnson et al. (1984). Unused tissue was deposited in the Louisiana State University Museum of Zoology Frozen Tissue Collection. From each specimen, sex, standard body-size measurements, and mass were recorded (data given by Jehl 1987).

Of the 32 loci surveyed, 25 are monomorphic and fixed for the same allele in the Mono Lake, Beaverhill Lake, and Frog Lake groups. These loci are: mannose phosphate isomerase (Mpi; E.C. 3.2.1.24), glucose-6-phosphate dehydrogenase (6-Pgd; 1.1.1.49), glutamate oxaloacetate transaminase (Got-1, 2; 2.6.1.1), adenosine deaminase (Ada; 3.5.4.4), sorbitol dehydrogenase (Sdh; 1.1.1.14), malate dehydrogenase (Mdh-1; 1.1.1.37), lactate dehydrogenase (Ldh-1, 2; 1.1.1.27), glutathione reductase (Gsr; 1.6.4.2), peptidase B (Lgg; 3.4.11), acid phosphatase (Acp-1, 2; 3.1.3.2), leucine amino peptidase (Lap; 3.4.11), superoxide dismutase (Sod-1, 2; 1.15.1.1), guanine deaminase (Gda; 3.5.4.3), creatin kinase (Ck-1, 2; 2.7.3.2), isocitrate dehydrogenase (Icd-2; 1.1.1.42), fumarate hydratase (Fum; 4.2.1.2), alcohol dehydrogenase (Adh; 1.1.1.1), and three general proteins (using Amido Black). The remaining 7 loci (21.2%) are: glycerol-3-phosphate dehydrogenase (α-Gpd; 1.1.1.8), phosphoglucomutase (Pgm; 2.7.5.1), isocitrate dehydrogenase (Icd-1; 1.1.1.42), esterase (Estd; 3.1.1.1), peptidase A (La-1; 3.4.11), purine nucleoside phosphorylase (Np; 2.4.2.1), and glucose phosphate isomerase (Gpi; 5.3.1.9) and are polymorphic in at least one of the three samples (Table 1). The computer program BIOSYS-1 (Swofford and Selander 1981) was used for quantitative data analysis. Data analyzed with the Frog Lake and Beaverhill Lake groups combined or separate were nearly identical; therefore, only the results of the analysis with the groups separate are discussed.

Heterozygosity values, *G*-values for the fit of the observed to the expected genotype proportions, and Wright's (1978) fixation indices (F_{st}) for each locus are summarized in Table 1. Considering each locus and all loci simultaneously, insignificant *G*-values (Table 1) suggest conformance with Hardy-Weinberg expected genotypic proportions within populations. Heterozygosity values per locus varied from 0 at most loci to 83% at the Icd-1 locus in the Frog Lake group. The observed mean (±SE) values for population heterozygosity were 2.7 ± 1.3% for Mono Lake, 3.0 ± 1.4% for Beaverhill Lake, and 3.5 ± 2.6% for Frog Lake, and were very similar to those expected at Hardy-Weinberg equilibrium. The values were typical of those reported elsewhere for *L. californicus* (Zink and Winkler 1983) (2.67 ± 0.39% for Mono Lake, 2.95 ± 0.48% for Great Salt Lake) but somewhat lower than those reported for avian species in general (Corbin 1983). The mean number of alleles (±SE) was 1.15 ± 0.06 for Mono Lake, 1.15 ± 0.06 for Beaverhill Lake, and 1.09 ± 0.05 for Frog Lake. Zink and Winkler (1983) found 1.2 ± 0.1 at both Mono Lake and Great Salt Lake.

At several loci, one allele existed at a frequency greater than 5% in one group but was absent in the

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TABLE 1. Allelic frequencies and statistics for variable loci in the California Gull. Samples were taken from Mono Lake, California (ML; $n = 10$); Beaverhill Lake, Alberta (BL; $n = 7$); and Frog Lake, Alberta (FL; $n = 6$). h = observed (direct count) heterozygosity. *G*-tests are for observed vs. expected genotypic proportions within samples, per locus.

Locus	Allele	Location			F_{st}[a]
		ML	BL	FL	
α-Gpd	A	0.900	0.929	1.000	
	B	0.100	—	—	
	C	—	0.071	—	0.047
h		0.200	0.143	0.000	
G (df)		0.123 (1)	0.041 (1)	—	
Pgm	A	0.850	0.929	1.000	
	B	0.150	0.071	—	0.055
h		0.300	0.143	0.000	
G (df)		0.311 (1)	0.041 (1)	—	
Icd-1	A	0.900	0.714	0.417	
	B	0.100	0.286	0.583	0.181
h		0.200	0.286	0.833	
G (df)		0.123 (1)	0.105 (1)	3.061 (1)	
Estd	A	0.950	1.000	1.000	
	B	0.050	—	—	0.034
h		0.100	0.000	0.000	
G (df)		0.028 (1)	—	—	
La-1	A	1.000	0.929	1.000	
	B	—	0.071	—	0.048
h		0.000	0.143	0.000	
G (df)		—	0.041 (1)	—	
Np	A	0.850	1.000	0.917	
	B	0.150	—	0.083	0.053
h		0.100	0.000	0.167	
G (df)		0.030 (1)	—	0.050 (1)	
Gpi	A	1.000	0.857	0.917	
	B	—	0.143	0.083	0.049
h		0.000	0.286	0.167	
G (df)		—	0.194 (1)	0.050 (1)	
Overall *G* (df)		0.855 (1)	0.422 (5)	3.161 (3)	
H_{obs} (SE)		0.027 (0.013)	0.030 (0.014)	0.035 (0.026)	
H_{exp} (SE)		0.029 (0.013)	0.032 (0.015)	0.024 (0.016)	
Mean no. of alleles (SE)		1.15 (0.06)	1.15 (0.06)	1.09 (0.05)	
% loci polymorphic		15.15	15.15	9.09	

[a] Mean $F_{st} = 0.067$.

other groups. Chi-square tests for homogeneity of genotypic values demonstrated statistically significant differences among the groups at only the Icd-1 locus ($\chi^2 = 8.643$, df = 2, $P = 0.013$). The frequency of Icd-1^A at Beaverhill Lake (0.714) was nearer to that from Mono Lake (0.900), which is inconsistent with geographical considerations and with morphological evidence showing that the Frog Lake and Beaverhill Lake birds are indistinguishable. Nei's (1978) unbiased genetic distance and Rogers' (1972) genetic distance (*D*) values (Table 2) both suggested that Mono Lake and Beaverhill Lake gulls are more similar to each other than the former is to gulls from Frog Lake, even though the Canadian samples are from localities less than 100 km apart. A phenogram (not shown) based on Rogers' *D* values, however, showed Beaverhill Lake and Frog Lake birds clustering more closely with each other than with Mono Lake. Also, although we used adult gulls, the large number of heterozygotes at Icd-1 in the Frog Lake sample could be attributable to sampling close relatives, thereby biasing estimates of gene frequency. Presumably, small sample sizes preclude conclusions about genotypic patterns of genetic variation. The genetic distances are all of a level comparable to those documented between other conspecific avian populations (Barrowclough 1980). These

TABLE 2. Summary of Nei's (1978; above diagonal) and Rogers' (1972; below diagonal) genetic distances.

	ML	BL	FL
Mono Lake	—	0.001	0.007
Beaverhill Lake	0.023	—	0.001
Frog Lake	0.028	0.020	—

genetic distance values are slightly greater than those reported by Zink and Winker (1983) for Great Salt Lake vs. Mono Lake (morphologically uniform; Nei's $D = 0.001$, Rogers' $D = 0.013$). F_{st} values (Table 1) ranged from 0.047 (α-Gpd) to 0.181 (Icd-1). The mean F_{st} (0.067) was higher than those generally reported for birds (Barrowclough 1983), and was probably inflated by a single locus, Icd-1 ($F_{st} = 0.181$). Without Icd-1, the mean F_{st} would have been 0.048. Although indicative of higher than usual population subdivison, we believe our relatively small samples prevent further interpretation of the overall F_{st}.

Despite marked morphological differences between populations of California Gulls in Alberta and California, which, if the differences are genetic, suggest a long separation, the genetic data showed few differences. The only exceptions were the α-Gpd and Icd-1 loci. As noted by Zink (1986), allozymic homogeneity suggests that morphological diversification can arise in a relatively short span of time. The lack of correspondence between morphological and genetic evidence is not unique to our study (Lewontin 1984, Zink and Remsen 1986), and its elucidation poses a continuing challenge to evolutionary biologists.

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LITERATURE CITED

BARROWCLOUGH, G. F. 1980. Genetic and phenotypic differentiation in a wood warbler (genus *Dendroica*) hybrid zone. Auk 97: 655–668.

———. 1983. Biochemical studies of microevolutionary processes. Pp. 223–261 *in* Perspectives in ornithology (A. H. Brush and G. A. Clark, Jr., Eds.). New York, Cambridge Univ. Press.

CORBIN, K. W. 1983. Genetic structure and avian systematics. Pp. 211–244 *in* Current ornithology 1 (R. F. Johnston, Ed.). New York, Plenum Press.

HARRIS, H., & D. A. HOPKINSON. 1976. Handbook of enzyme electrophoresis in human genetics. Amsterdam, Netherlands, North-Holland Publ. Co.

JEHL, J. R., JR. 1987. Geographic variation and evolution in the California Gull. Auk 104: 421–428.

JOHNSON, N. K., R. M. ZINK, G. F. BARROWCLOUGH, & J. A. MARTEN. 1984. Suggested techniques for modern avian systematics. Wilson Bull. 96: 543–560.

LEWONTIN, R. C. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. Amer. Natur. 123: 115–124.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Stud. Genetics 7: 145–153.

SWOFFORD, D. L., & R. K. SELANDER. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72: 281–283.

WRIGHT, S. 1978. Evolution and the genetics of populations. Vol. 4, Variability within and among natural populations. Chicago, Univ. Chicago Press.

ZINK, R. M. 1986. Patterns and evolutionary significance of geographic variation in the *schistacea* group of the Fox Sparrow (*Passerella iliaca*). Ornithol. Monogr. No. 40.

———, & J. V. REMSEN, JR. 1986. Evolutionary processes and patterns of geographic variation in birds. Pp. 1–69 *in* Current ornithology 4 (R. F. Johnston, Ed.). New York, Plenum Press.

———, & D. W. WINKLER. 1983. Genetic and morphological similarity of two California Gull populations with different life history traits. Biochem. Syst. Ecol. 11: 397–403.

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