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Genetic Structure and Gene Flow in the Northern Bobwhite

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Electrophoretic studies have revealed that birds generally exhibit less interpopulational genetic differentiation than is typical of other vertebrates (Corbin 1977) and that genetic variation is usually partitioned within rather than among populations (Barrowclough 1980). Despite these observations, avian electrophoretic data have not been extensively utilized to estimate levels of gene flow among populations (Rockwell and Barrowclough 1987). Recently Slatkin (1985a, b) and Barton and Slatkin (1986) have shown that the conditional average frequencies of private alleles (alleles unique to a single population) provide a convenient estimate of the number of reproductively successful individuals exchanged among local populations each generation (Nm). Estimates of gene flow in combination with the standardized variance of allele frequency (F_{ST}) can determine the genetic structure of natural populations (Barton and Slatkin 1986).

Social organization in New World quail results in populations subdivided into coveys (Johnsgard 1973). In the Northern Bobwhite (*Colinus virginianus*), coveys normally occupy a limited geographic area (Murphy and Baskett 1952, Lewis 1954). A predisposition to a cohesive, gregarious social organization and low functional vagility produce a social structure distinctively different from the majority of avian species examined electrophoretically (Matson 1984).

We attempted to determine if the unique social system and sedentary nature of bobwhites alter the partitioning of genetic variance within and among local populations (i.e. promote genetic subdivision). We estimated from allozymic data components of genetic variance and levels of gene flow among three natural populations of Northern Bobwhites from southern Illinois.

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Bobwhites ($n = 122$) were live-trapped from three primarily agricultural areas in southern Illinois in autumn 1983. Two sites were on Crab Orchard National Wildlife Refuge (Area 3, $n = 85$, and Area 13, $n = 12$) in Williamson County; the third was on Southern Illinois University-Carbondale properties (SIU; $n = 25$) in Jackson County. Area 3 (85 ha) and Area 13 (263 ha) were 4.8 km apart and were effectively separated by Crab Orchard Lake. The lake's minimum intershore distance in this vicinity was ca. 1 km, and the minimum between-area distance around the lake's perimeter was 11.7 km. The SIU site (290 ha) was 17.3 km distant. The three areas were not hunted and supported estimated autumn densities of ≥80 birds/100 ha.

Captured quail were held at the Illinois Department of Conservation Game Farm, Mt. Vernon, Illinois. Blood (0.5–1.0 ml) was drawn from the brachial vein in 1-ml heparinized tuberculin syringes with 25-gauge, 15.9-mm needles. Blood samples were stored on ice in heparinized 3-ml evacuated containers and then processed according to Manlove et al. (1975). Undiluted plasma and erythrocyte hemolysate were stored at −70°C.

Horizontal starch-gel electrophoresis (Selander et al. 1971, Harris and Hopkinson 1976) was used to resolve 19 presumptive genetic loci. Buffer systems employed to visualize specific proteins (designated according to McAlpine et al. [1987] and followed by International Union of Biochemistry [1984] EC numbers) were as follows: (1) citrate-phosphate, pH 5.9 (Hopkinson and Harris 1969)—acid phosphatase 1 (ACP1;3.1.3.2), aldolase A, fructose-bisphosphate (ALDOA;4.1.2.13), and hemoglobin (HB); (2) continuous tris citrate II (Selander et al. 1971)—adenylate kinase 1 (AK1;2.7.4.3), creatine kinase (CK;2.7.3.2), glucose-6-phosphate dehydrogenase (G6PD;1.1.1.49), lactate dehydrogenase A,B (LDHA,LDHB;1.1.1.27), malate dehydrogenase, NAD (soluble) (MDH1;1.1.1.37), and phosphogluconate dehydrogenase (PGD;1.1.1.44); (3) lithium hydroxide (Selander et al. 1971)—esterase

TABLE 1. Allelic frequencies at the polymorphic loci among 3 Northern Bobwhite populations.

Locus	Allele	Allelic frequency		
		Area 3	Area 13	SIU[b]
ES	104	0.469	0.417	0.550
	100	0.531	0.583	0.450
GPI	−100	0.946	1.000	0.917
	−73	0.036	—	0.083
	−23	0.018	—	—
IDH1	100	0.912	0.889	0.935
	83	0.088	0.111	0.065
LDHA	170	—	—	0.040
	100	1.000	1.000	0.960
MDH1	126	0.029	—	—
	100	0.971	0.958	1.000
	74	—	0.042	—
PGD	121	0.060	0.167	0.060
	100	0.940	0.833	0.940
TF[a]	109	0.006	—	—
	100	0.988	1.000	1.000
	91	0.006	—	—

[a] TF homozygotes were 2-banded; heterozygotes 3-banded. The midpoint of the 2-banded TF homozygote was designated 100.

[b] Southern Illinois University–Carbondale properties.

(ES;3.1.1.1), and glucose phosphate isomerase (GPI;5.3.1.9); (4) Poulik (Poulik 1957)—albumin (ALB), glutamic-oxaloacetic transaminase 1, soluble (GOT1;2.6.1.1), isocitrate dehydrogenase 1, soluble (IDH1;1.1.1.42), peptidase E (PEPE;3.4.11.1), and transferrin (TF); (5) tris-hydrochloric acid (Selander et al. 1971)—nucleoside phosphorylase (NP;2.4.2.1); and (6) tris-maleate (Brewer 1970)—phosphoglucomutase 1 (PGM1;5.4.2.2).

A locus was considered polymorphic if the frequency of the most common allele was ≤0.99 in any sample. The common allele at each locus was labeled 100 or −100 to denote its respective anodal or cathodal migration. Other alleles were designated numerically by expressing the electrophoretic mobility of their protein products relative to the common allele.

For each population, genotypic frequencies were tested for conformance to Hardy-Weinberg equilibrium by Chi-square goodness-of-fit. Average individual heterozygosity over all loci ($\bar{H}$) was determined by direct count. Coefficients of genetic distance among the populations were calculated according to Rogers (1972).

Fixation indices (F_{ST}; Nei and Chesser 1983, as modified by Van Den Bussche et al. 1986) were calculated to estimate the amount of genetic variance partitioned among populations. We inferred the extent of gene flow from the number of effective (reproductively successful) migrants exchanged between localities per generation (Nm). Estimates of Nm were obtained from the conditional average frequencies ($\bar{p}(1)$) of private

TABLE 2. Inbreeding coefficients (F_{IT} and F_{IS}) and fixation indices (F_{ST}) for the polymorphic loci among 3 Northern Bobwhite populations.

Locus	F-statistics		
	F_{IT}	F_{IS}	F_{ST}
ES	0.2536	0.2448	0.0116
GPI	−0.0239	−0.0523	0.0269
IDH1	−0.0681	−0.0727	0.0043
LDHA	0.0083	−0.0186	0.0264
MDH1	0.0039	−0.0151	0.0187
PGD	0.2387	0.2163	0.0286
TF	0.0198	0.0140	0.0059
$\bar{F}$	0.1557	0.1424	0.0155

alleles (Barton and Slatkin 1986). We calculated all Nm estimates for sample sizes of 50 then adjusted to accommodate differences in mean sample size of the populations under consideration. Nm was estimated among all populations sampled and, independently, for all pairwise comparisons of the three populations.

Twelve of the 19 loci were monomorphic for the same allele in all populations; 7 loci exhibited variation (Table 1). We observed no significant deviations ($P > 0.05$) from Hardy-Weinberg expectations, and estimates of average individual heterozygosity ($\bar{H}$) were similar for the three samples (0.053 in Area 3, 0.042 in Area 13, and 0.042 in SIU). Average heterozygosity over all populations ($\bar{H} = 0.046$) was similar to other odontophorine species but higher than heterozygosities reported for bobwhites from New Mexico ($\bar{H} = 0.027$, Gutiérrez et al. 1983).

We detected 6 private alleles among 4 of the 7 polymorphic loci. Single private alleles were detected at Area 13 and at SIU (MDH1[74] and LDHA[170], respectively). In Area 3 (the largest sample examined), we found 4 private alleles (GPI[−23], MDH1[126], TF[91, 109]). Frequencies of private alleles ranged from 0.006 (TF[91, 109]) to 0.042 (MDH1[74]).

The overall inbreeding coefficient (F_{IT}, Table 2) was positive, which suggests a deficiency of heterozygotes (Hedrick 1983). Nevertheless, only ES and PGD contributed substantially to this statistic. Heterozygote deficiencies at ES and PGD produced a positive estimate of inbreeding ($F_{IS} = 0.1424$) which indicated considerably greater intrapopulational variance than was apparent among the populations ($F_{ST} = 0.0155$).

Genetic distances among the populations (Table 3) were within the range of values observed among local populations of other odontophorine species (Gutiérrez et al. 1983). The estimated number of effective migrants exchanged between localities per generation ($Nm = 5.95$; Table 3) suggests moderate levels of gene flow among the populations. Estimates of Nm for all pairwise comparisons of the populations were not consistent with interlocality distances.

Bobwhite populations exhibit greater behavioral

TABLE 3. Estimated numbers of effective migrants exchanged each generation (Nm) and coefficients of genetic distance (Rogers 1972) among 3 Northern Bobwhite populations. The conditional average frequencies of private alleles ($\bar{p}(1)$) were used to calculate Nm (Barton and Slatkin 1986).

Comparison	$\bar{n}$	No. private alleles	$\bar{p}(1)$	Nm	Rogers' D
All localities	40.7	6	0.024	5.95	
Area 3—13	48.5	6	0.023	5.24	0.015
Area 3—SIU[a]	55.0	5	0.020	5.82	0.012
Area 13—SIU	18.5	3	0.055	3.26	0.024

[a] Southern Illinois University–Carbondale properties.

subdivision than most avian species. Individuals are organized socially into coveys which are essentially sedentary during the nonbreeding season. Covey ranges seldom exceed 0.4 km in greatest dimension and individual movements are usually <0.8 km (Murphy and Baskett 1952, Lewis 1954). Exchange among neighboring coveys may occur between covey breakup and the breeding season and before covey formation in the fall (Stoddard 1931, Rosene 1969).

The unique social system and sedentary nature of bobwhites may promote genetic differentiation by predisposing local populations to reduced gene flow. Coveys in southern Illinois approach a continuous distribution which creates the potential for genetic exchange among neighboring social units. Estimates of genetic structure inferred from dispersal parameters indicate that among-population components of genetic variance (F_{ST}) range from 0.001 to 0.041 in continuously distributed avian species (Barrowclough 1980). Thus, the majority of avian species are not subdivided genetically. The amount of genetic variance partitioned among the bobwhite populations ($F_{ST} = 0.0155$) and the genetic distance measures did not indicate significant populational subdivision. A substantial portion of the total genetic variance ($F_{IT} = 0.1557$) was concentrated among individuals within populations ($F_{IS} = 0.1424$).

Notwithstanding, the presence of 6 private alleles at frequencies up to 0.042 suggest the absence of panmixia among the populations. Quantitative estimates of the extent of gene flow among the study areas (Nm statistic) indicated levels of gene flow comparable to that observed in California Quail (*Callipepla californica*) (Zink et al. 1987). Presumably, the demographic features of bobwhites do not inhibit the exchange of genetic information among neighboring populations, at least not to the extent that they promote significant genetic subdivision.

Estimates of gene flow inferred from extant patterns of allele frequency distributions are more indicative of historical than current levels of gene flow (Slatkin 1987). Effective gene flow can result from immigration of individuals into areas left vacant by extinction (Slatkin 1977, 1985a). Bobwhite populations in southern Illinois are subject to marked fluctuations in density (Roseberry and Klimstra 1984)

which can contribute to genetic homogenization by inducing gene flow. The population dynamics of midwestern bobwhites thus present the opportunity for periodic episodes of homogenizing gene flow which may inhibit the accumulation of biochemical differentiation.

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Gull Predation on Cassin's Auklet Varies with the Lunar Cycle

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Many species of small burrow-nesting seabirds visit their breeding colonies only at night. Nocturnal activity has usually been thought to be a defense against predation (Lack 1966, Cody 1973, Ainley et al. 1975), although diel-cycle variation in the availability of food may also play a role in determining the timing of

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colony visits (Grubb 1974, Imber 1975). Activity in seabird colonies is reduced on moonlit nights (Cassin's Auklet, *Ptychoramphus aleuticus*, Manuwal 1974a, Ainley and Boekelheide 1989; Manx Shearwater, *Puffinus puffinus*, Harris 1966, Storey and Grimmer 1986; Leach's Storm-Petrel, *Oceanodroma leucorhoa*, Watanuki 1986; Ashy Storm-Petrel, *O. homochroa*, Ainley and Boekelheide 1989; Madeiran Storm-Petrel, *O. castro*, Harris 1969), but it has not been shown that predation risk is a correlate of the lunar cycle. I found that Cassin's Auklets on Southeast Farallon Island