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POPULATION GENETICS AND GENE FLOW OF THE COMMON TERN[1]

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Abstract. Genetic analysis using isoelectric focusing of blood proteins indicated that Common Terns, *Sterna hirundo,* from four colonies in Minnesota and Wisconsin had an observed average heterozygosity (H_o) of 0.044 and had 12 polymorphic loci of the 34 loci examined ($P = 0.353$). These values suggest that Common Terns of Minnesota and Wisconsin have approximately average levels of genetic variation and diversity for avian species. Interpopulational F_{st} values, four genetic distance estimates and an overall F_{st} value of 0.0022 revealed that the four colonies (subpopulations) were not genetically differentiated. Indirect estimates of gene flow, using the method of conditional average allelic frequency, indicated high levels of gene flow. Using the method of private alleles (alleles found in only one subpopulation), the estimated number of immigrants per generation (Nm) into each subpopulation ranged from seven to 16, again demonstrating significant levels of movement of terns among colonies. Direct estimates of dispersal from band recovery data corroborated these findings. By extending these results, I suggest that other Common Tern colonies in North America have at least as much gene flow among regional breeding populations as do these disjunct inland colonies.

Key words: Sterna hirundo; *isoelectric focusing; population genetic structure; genetic variability; gene flow; dispersal.*

INTRODUCTION

Common Terns (*Sterna hirundo*) have undergone wide population fluctuations in North America during the last 100 years for several reasons. There has been the loss of suitable breeding habitat due to competition with other larids, water level fluctuation, and human disturbance, and populations have been reduced by predation and hunting by the millinery trade (Nisbet 1973, Morris and Hunter 1976, Kress et al. 1983, Richards and Morris 1984, Erwin and Smith 1985, Herbert 1985). Common Terns are currently endangered, threatened, or of special concern in all states in the Great Lakes region (McKearnan 1986; S. Matteson, 1988 Tern Management Report for the Wisconsin Department of Natural Resources), and the stable population of the northeastern United States is restricted primarily to a few highly successful colonies (DiCostanzo 1980, Kress et al. 1983). The tern colonies in Minnesota have had low or no reproductive success over the last several years (L. Pfannmuller, Minnesota Department of Natural Resources, pers. comm.; Guertin and Pfannmuller 1985; McKearnan 1986), while Wisconsin has only one colony that has been consistently successful (Matteson, pers. comm.). The present situation causes concern for the future of the species in the upper Midwest.

Although the population dynamics of the species has been well studied (Palmer 1941; Austin 1946, 1951; Ludwig 1962; Nisbet 1973, 1978; Haymes and Blokpoel 1978; DiCostanzo 1980; Courtney and Blokpoel 1983; Kress et al. 1983), along with site tenacity (Austin 1951, Haymes and Blokpoel 1978, DiCostanzo 1980, Blokpoel et al. 1987), and breeding biology (Coulson 1968, Nisbet and Drury 1972, Morris and Hunter 1976, Haymes 1978, Burger and Lesser 1978, Nisbet and Welton 1984, Erwin and Smith 1985, Herbert 1985, Burger and Gochfeld 1988, Safina and Burger 1988), little population genetic information is available for any tern species (but see Randi and Spina 1987, Hackett 1989). The population dynamics and dispersal among breeding colonies of Common Terns have been described for the Atlantic coast (Austin 1946, 1949, 1951; DiCostanzo 1980) and for the Great Lakes (Ludwig 1962, Haymes and Blokpoel 1978, Courtney and Blokpoel 1983, Blokpoel et al. 1987). Dispersal patterns among inland lake colonies, however, are not well-known. Dispersal, defined as

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movement of first-time breeders away from the natal colony (natal dispersal) or of adults between breeding attempts (breeding dispersal) (Greenwood and Harvey 1977), is not unusual among colonies along the contiguous shoreline of the Great Lakes or the Atlantic Ocean (Greenwood and Harvey 1977). Banding records from New England indicate that Common Terns frequently move between local colonies and infrequently move longer distances between the Great Lakes and Atlantic colonies (Austin 1946, 1951; Haymes and Blokpoel 1978; DiConstanzo 1980). The distance between colonies of Common Terns on the inland lakes is within the dispersal range known to occur in New England, but dispersal between active inland lake colonies has not been documented.

I studied the population structure and genetics of four Common Tern colonies in Minnesota and Wisconsin to compare the population structure and dynamics of Common Tern colonies on isolated inland lakes with that of the better studied colonies that share a contiguous shoreline in the Atlantic Ocean and the Great Lakes. Estimates of natal and breeding dispersal patterns were made directly from recoveries of previously banded birds and indirectly from statistical parameters of population genetics. The latter include measures of gene flow (the incorporation of immigrant genes into a population's gene pool) estimated by the distribution among subpopulations of private alleles (those alleles occurring in only one subpopulation) (Slatkin 1985a) and the conditional average frequency of alleles (Slatkin 1981). I also present estimates of genetic diversity and variation within the four colonies of Common Terns in Minnesota and Wisconsin.

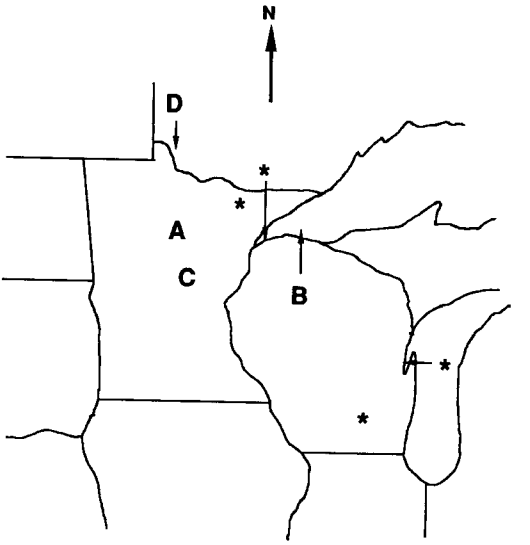

FIGURE 1. Locations of current Common Tern colonies in Minnesota and Wisconsin. A—Gull Island, Leech Lake, MN; B—Ashland Pier, Ashland, WI; C—Hennepin and Spirit Islands, Mille Lacs Lake, MN; D—Fourblock Island, and Pine and Curry Island, Lake of the Woods, MN; *—Colonies not studied.

MATERIALS AND METHODS

SAMPLE COLLECTION

I banded and collected blood samples from 83 adult Common Terns at three colonies in Minnesota and one in Wisconsin. The Minnesota colonies were: Gull Island (47°06′N, 94°23′W), Leech Lake, Cass County; Hennepin Island (46°11′ N, 93°32′W), Mille Lacs Lake, Mille Lacs County; and Fourblock Island (49°17′ N, 94°53′W), Lake of the Woods, Lake of the Woods County. I also sampled the Ashland Pier colony (46°36′N, 90°52′W) in Lake Superior, Ashland County, Wisconsin (Fig. 1).

Each colony was visited once between 7 June 1988 and 26 June 1988. At each site I trapped incubating adults on the nest using chicken-wire drop traps (I.C.T. Nisbet, pers. comm.). Only terns on two- or three-egg clutches were trapped to decrease the chance of desertion (Nisbet 1981), and I also usually caught only one bird of each pair to minimize nest disturbance. In Minnesota, I banded the right leg with a green/white plastic color band for year-class over a U.S.F.W.S. aluminum band and I placed one colored leg band on the left leg, coded for the colony; Leech Lake—light green, Mille Lacs Lake—white, Lake of the Woods—light blue. In Wisconsin, the birds were banded with a yellow metal band and a U.S.F.W.S. band on the right leg.

From each bird I collected approximately 0.5 ml of blood from a branchial vein in a heparinized syringe by direct venipuncture. This blood volume equals approximately 0.5% of a tern's body weight. Arctander (1988) found that a blood sample of up to 1% of a bird's body weight can be taken without compromising the bird's safety. After the needle was withdrawn, direct pressure was applied to the puncture wound using sterile gauze. Clotizol, a veterinary blood clotting liquid, was used to stop the bleeding in a number of individuals. After the wound was sealed, the

bird was released. The blood samples were transferred to cryogenic tubes and immediately frozen in liquid nitrogen. The first few birds of each colony were monitored after release to ensure their return to the colony. The duration of each visit to a colony varied between 3 and 6 hr.

PROTEIN ANALYSIS

Eighty-two individuals were used for the biochemical analysis. Each blood sample was thawed and centrifuged at 3,000 rpm for 15 min to separate the cellular debris from the plasma and red cell lysate. Horizontal thin-layer agarose gel isoelectric focusing (Corbin and Wilkie 1988) was used to analyze each sample for all gene loci screened. Enzyme assay methods of Shaw and Prasad (1970), Barrowclough and Corbin (1978), Werth (unpubl.), Hebert and Beaton (unpubl.), Evans (1987), and Zink (pers. comm.) were used or modified for optimal results.

The 18 presumptive loci coding for the 11 enzymes scored, their abbreviations and Enzyme Commission Numbers (Harris 1977, Webb 1988) are as follows: four esterases (Est), glucose-6-phosphate dehydrogenase (G-6-pdh, 1.1.1.49), glucose phosphate isomerase (Gpi, 5.3.1.9), two lactate dehydrogenases (Ldh, 1.1.1.27), two malate dehydrogenases (Mdh, 1.1.1.37), leucyl-glycyl-glycine dipeptidase (Pep-B, 3.4.11.4), leucyl-alanine dipeptidase (Pep-C, 3.4.11), phenyl-alanyl-proline dipeptidase (Pep-D, 3.4.11), 6-phosphogluconate dehydrogenase (6-pgdh, 1.1.1.44), glucose phosphomutase (Pgm-1 and Pgm-2, 5.4.2.2), and two superoxide dismutases (Sod, 1.15.1.1). Plasma proteins were stained with coomassie blue dye (Dykes et al. 1982) and hemoglobins were observed directly. A total of 34 presumptive gene loci were scored including 18 allozymes and the 16 nonenzymatic loci of four hemoglobins and 12 nonspecific plasma proteins. Either no enzymatic activity was found or genotypes could not be scored for acid phosphatase (Acp, 3.5.4.4), adenosine deaminase (Ada, 3.5.4.4), alcohol dehydrogenase (Adh, 1.1.1.1), aldolase dehydrogenase (Alddh, 1.2.3.1), adenylate kinase (Ak, 2.7.4.3), amylase (Amy, 3.2.1.1), catalase (Cat, 1.11.1.6), creatine kinase (Ck, 2.7.3.2), fructose-1-6-diphosphatase (F-1-6-dp, 3.1.3.11), glutamate dehydrogenase (Gdh, 1.4.1.3), glutamate oxalate transaminase (Got, 2.6.1.1), alpha-glycerol phosphate dehydrogenase (α-gpdh, 1.1.1.8), hexokinase (Hex, 2.7.1.1), isocitrate dehydrogenase (Idh, 1.1.1.42), malic enzyme (Me, 1.1.1.40), mannose phosphate isomerase (Mpi, 5.3.1.8), nucleoside phosphorylase (Np, 2.4.2.1), valyl-leucine dipeptidase (Pep-A, 3.4.11.11), peroxidase (Per, 1.11.1.7), sorbitol dehydrogenase (Sdh, 1.1.1.14), and xanthine dehydrogenase (Xdh, 1.2.1.37). Ak had good activity, but was not scorable because of unrecognizable banding patterns. Idh, Est-3, and Pep-A showed light, but inconsistent activity, and thus were not scorable. Starch gel electrophoresis was used to resolve problematic isoelectric focusing results for Mdh.

DATA ANALYSIS

The variation in banding pattern phenotypes was assumed to result from allelic differences, and thus, the genotypes of each individual could be inferred directly. Allelic frequencies, then, were estimated for each locus from the genotypic frequencies.

The proportion of polymorphic loci (P) was calculated as the ratio of polymorphic loci to total number of loci scored. Two heterozygosity values were calculated. $\bar{H}_e$, the expected mean heterozygosity value, was the average of h at each locus, each of which is (1 − the sum of the x_i squared), where x_i was the frequency of the ith allele at a locus (Nei 1978). The observed mean heterozygosity, $\bar{H}_o$, was calculated as the mean of h, where, in this case, h is the ratio of the number of heterozygous loci to the total number of loci scored for each individual sampled (Corbin 1981, 1983). The computer program GENESYS (Corbin and Wilkie 1988) was used to calculate allelic frequency and expected mean heterozygosity ($\bar{H}_e$).

Private alleles (Slatkin 1985a), those alleles occurring in only one subpopulation, were used to estimate Nm, the number of immigrants per generation using $\ln(\bar{p}[1]) = a \ln(Nm) + b$, where $\bar{p}(1)$ is the mean private allele frequency in each subpopulation, and a and b are the constants, −0.505 and −2.44, respectively. The estimates of Nm were corrected for sample sizes that deviated from Slatkin's model's sample size of 25 by dividing Nm_{est} by (N/25), where N = mean sample size of the tern subpopulations (20.5) (Slatkin 1985a).

The conditional average frequency of alleles $\bar{p}(i)$ was calculated and plotted against i/d, where i is number of demes in which an allele is present, $\bar{p}(i)$ is the average allelic frequency of those al-

TABLE 1. Allelic frequencies of the 12 polymorphic loci from samples collected from four colonies of Common Terns in Minnesota and Wisconsin. n = the number of individuals sampled in each subpopulation and h = the subpopulation mean values of Nei's (1978) unbiased heterozygosity for each locus. The most anodal allele is denoted (a). Subpopulation abbreviations are as follows: Leech = Gull Island, Leech Lake; Ashland = Ashland Pier, Ashland, WI; Mille = Hennepin Island, Mille Lacs Lake; LOW = Fourblock Island, Lake of the Woods.

Locus and allele	Subpopulation			
	Leech	Ashland	Mille	LOW
n	20	21	20	21
Est-4				
a	1.0000	0.9762	1.0000	1.0000
b	—	0.0238	—	—
h	0.0	0.0476	0.0	0.0
Ldh-2				
a	0.8250	0.8095	0.8000	0.7619
b	0.1750	0.1905	0.2000	0.2381
h	0.2762	0.3159	0.3282	0.3717
Pep-C				
a	0.0250	—	—	—
b	0.9750	0.9524	1.0000	1.0000
c	—	0.0238	—	—
d	—	0.0238	—	—
h	0.0500	0.0940	0.0	0.0
Pep-D				
a	0.7500	0.7857	0.9000	0.7857
b	0.2500	0.2143	0.1000	0.2143
h	0.3846	0.3450	0.1846	0.3450
Gpi				
a	0.0500	—	0.0250	0.0476
b	0.9500	1.0000	0.9500	0.9524
c	—	—	0.0250	—
h	0.0974	0.0	0.0987	0.0929
Pgm-1				
a	0.8750	0.8333	0.9250	0.8095
b	0.1250	0.1667	0.0750	0.1905
h	0.2244	0.2846	0.1423	0.3159
Pgm-2				
a	0.0250	—	0.0250	—
b	0.0750	0.0238	0.0250	0.0476
c	0.9000	0.9762	0.9500	0.9524
h	0.1885	0.0476	0.0987	0.0929
Hb-2				
a	1.0000	1.0000	1.0000	0.9762
b	—	—	—	0.0238
h	0.0	0.0	0.0	0.0476
Hb-4				
a	—	—	—	0.0476
b	1.0000	1.0000	1.0000	0.9524
h	0.0	0.0	0.0	0.0929
PP-1				
a	0.9750	0.9524	0.9750	0.9762
b	0.0250	0.0476	0.0250	0.0238
h	0.0500	0.0929	0.0500	0.0476
PP-2				
a	0.8000	0.8571	0.8500	0.9762
b	0.2000	0.1429	0.1500	0.0238
h	0.3282	0.2509	0.2615	0.0476
PP-8				
a	—	0.0238	—	—
b	1.0000	0.9762	1.0000	1.0000
h	0.0	0.0476	0.0	0.0

leles, and d is the number of demes or subpopulations sampled (Slatkin 1981). This gives a qualitative estimate of gene flow by comparing the plotted results to Slatkin's (1981) simulations of high, medium, and low gene flow.

The coefficient of inbreeding, F_{is}, adjusted for sampling bias (Wright 1978a), was calculated for each subpopulation using the computer program GENESYS. Pairwise comparisons between subpopulations of F_{st}, the fixation index (Wright 1951, 1978a), were also calculated using GENESYS in addition to the total F_{st} value calculated over all loci and subpopulations.

Genetic distances were calculated for pairs of tern colonies using the methods of Cavalli-Sforza and Edwards (1967), Rogers (1972), and Nei (1978). These methods manipulate the similarity of subpopulation allelic frequencies in slightly different ways to estimate the genetic distance between the subpopulations.

The U.S.F.W.S. Bird Banding Laboratory provided data of band recoveries for Common Terns banded in Minnesota and Wisconsin since 1925. To obtain a direct estimate of gene flow among colonies I used these records and my own band recoveries to calculate the dispersal frequency of terns that were at least 4 years old.

RESULTS

POPULATION GENETIC STRUCTURE

Of the 40 enzymatic loci I attempted to score, I was able to score 18 coding for allozymes and I scored an additional 16 nonenzymatic gene loci.

TABLE 2. Subpopulation pairwise comparisons of F_{st} values corrected for sampling error (Wright 1978b) are listed below the diagonal, and the χ^2 values for each F_{st} are above the diagonal. No χ^2 values are significant at 0.05 level; the degrees of freedom are in parentheses. The F_{st} values are the mean values of the 12 polymorphic loci. See Table 1 for subpopulation abbreviations listed here.

	Leech	Ashland	Mille	LOW
Leech		0.0526 (10)	0.5974 (8)	2.3101 (10)
Ashland	0.0001		0.0423 (10)	1.0925 (12)
Mille	0.0019	0.0001		1.4055 (9)
LOW	0.0056	0.0022	0.0038	

Allelic frequencies of the 12 polymorphic loci are given in Table 1.

Twelve of the 34 scored loci were polymorphic over all subpopulations ($P = 0.3529$) (Table 1). A locus was considered polymorphic if the most common allele had a frequency of 0.99 or less in at least one subpopulation. Of the 12 polymorphic loci, seven were enzymes, two were hemoglobins, and three were nonidentified plasma proteins. The genotypic distributions for 11 of these 12 polymorphic loci, for all subpopulations, were in Hardy-Weinberg equilibrium, as indicated by χ^2 values. The one locus that deviated significantly from equilibrium values was a hemoglobin (Hb-4). All individuals were homozygous at this locus, although one individual was fixed for an alternative allele. The average number of alleles per locus over all loci = 1.471, whereas the average number of alleles per polymorphic locus = 2.333.

The expected mean heterozygosity, $\bar{H}_c$, was 0.042, ±0.016 SE, corrected for small sample sizes by the method of Nei (1978). $\bar{H}_o$, the observed mean heterozygosity, equaled 0.044, ±0.003 SE. Chi-squared analysis of the deviation between observed and expected heterozygosity values was not significant ($\chi^2 = 0.00004$, df = 1, $P > 0.05$).

Mean F_{is} values over all polymorphic loci for each subpopulation are as follows: Leech Lake = 0.0189, Ashland Pier = −0.0118, Mille Lacs Lake = −0.0442, and Lake of the Woods = 0.0396.

Wright's (1951) standardized variance in allelic frequency among subpopulations, or F_{st}, measures the extent of differentiation towards fixation of alleles in subpopulations over the total population (Wright 1978a). Subpopulations fixed for alternative alleles will have $F_{st} = 1$, whereas subpopulations fixed for identical alleles have $F_{st} = 0$. Individual locus F_{st} values, corrected for sampling bias (Wright 1978b), were zero with two exceptions, and the two nonzero F_{st} values were not significantly different from zero: PP-2, a nonspecific protein ($\chi^2 = 0.5545$ with df = 3, $P > 0.05$), and Hb-4, a hemoglobin ($\chi^2 = 0.5404$ with df = 3, $P > 0.05$). The overall F_{st} value of 0.0022 averaged over all loci was not significantly different from zero ($\chi^2 = 1.09$, df = 36, $P > 0.05$). Pairwise comparisons between subpopulations indicate very little among-population variance (Table 2).

Results from the analysis of the conditional average frequency of alleles (Slatkin 1981) closely match theoretical simulations of high levels of gene flow (Fig. 2). The graph indicates all subpopulations share most of the alleles for each locus. Quantitative estimates of the number of immigrants, Nm_{est}, per colony generation using the private alleles method of Slatkin (1985a) range from about seven to 16 individuals (Table 3). These values indicate high levels of gene flow into all subpopulations.

Genetic distance values of Cavalli-Sforza and Edwards (1967), Rogers (1972), and Nei (1978) are all close to zero, indicating near genetic identity for pairwise comparisons of subpopulations (Tables 4 and 5).

PHYSICAL POPULATION STRUCTURE

At least 12 tern colonies in the following five general locations in Minnesota have been active during the last century: Lake of the Woods, Duluth Harbor, Leech Lake, Voyageurs National Park, and Mille Lacs Lake (Fig. 1). Each of these general locations continues to have adults breeding or attempting to breed.

I analyzed U.S.F.W.S. band recovery data of Common Terns and found several records of dispersal between breeding colonies in Minnesota and Wisconsin. Because data from Austin (1942) and Nisbet (1978) indicate that Common Terns

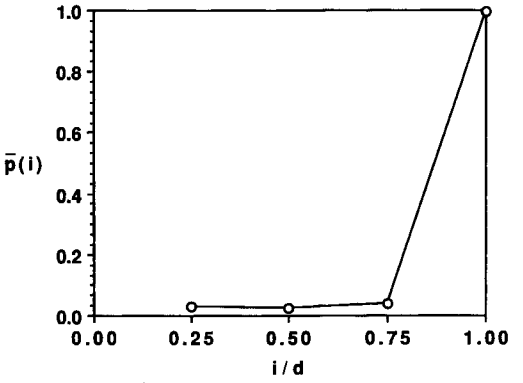

FIGURE 2. The ratio of the conditional average allele frequency, $p(i)$, and i/d, where $p(i)$ is the mean frequency of alleles found in i subpopulations, and d is the total number of subpopulations (Slatkin 1981). This graph closely resembles theoretical patterns of high gene flow among subpopulations.

usually first breed successfully at 4 years of age, I did not use recoveries of terns less than 4 years old. There were 43 band recoveries of birds, four or more years of age, banded as nestlings at Leech Lake (the only colony that had an acceptable number of recoveries for analysis). Of these, two (4.6%) were recovered in nonnatal colonies during subsequent breeding seasons, with the remainder recovered at Leech Lake. The recovery records were incomplete because many station returns (birds recovered at the same location at which they were banded) may not have been included in the bird banding data base (D. Bystrak, pers. comm.). This factor may have inflated the dispersal frequency. Leech Lake, the natal colony, however, has been monitored more thoroughly than any other Minnesota or Wisconsin colony. With this bias, the actual dispersal rate is likely underestimated. Of 83 breeding adults I trapped during this study, four were previously banded and one was banded as a nestling at another Minnesota colony. It should be noted, however, that dispersal only provides evidence not proof of actual gene flow, because to have gene flow immigrant genes must be incorporated into the gene pool (Rockwell and Barrowclough 1987).

TABLE 3. Estimated number of immigrants, Nm_{est}, for each subpopulation, using Slatkin's (1985) method of private alleles. See Table 1 for subpopulation abbreviations listed here.

Deme	No. alleles	$p(1)$	Nm_{est}	Nm_{est} corrected[a]
Leech	1	0.0250	11.86	14.46
Ashland	4	0.0238	13.07	15.94
Mille	1	0.0250	11.86	14.46
LOW	2	0.0357	5.86	7.14
Mean		0.0273	10.66	13.00

[a] Nm_{est} corrected by dividing original Nm_{est} by (N/25), where N = the mean sample size of 20.5.

TABLE 4. Subpopulation comparison of Nei's (1978) unbiased genetic distance, D, below the diagonal, and Rogers' (1972) distance above the diagonal. All values indicate near genetic identity between subpopulations. See Table 1 for subpopulation abbreviations listed here.

	Leech	Ashland	Mille	LOW
Leech		0.0109	0.0110	0.0143
Ashland	−0.0007		0.0119	0.0131
Mille	−0.0001	−0.0002		0.0151
LOW	0.0003	−0.0003	0.0005	

DISCUSSION

By integrating the population genetics data with the distribution and abundance information of Common Terns in the Minnesota and Wisconsin region, the population structure and gene flow patterns of these Common Terns can be derived.

GENETIC VARIABILITY AND DIVERSITY

The observed level of polymorphism (0.353) was higher than the avian mean (0.222), but within the range of avian species included in Corbin's (1987) review. Observed mean heterozygosity ($\bar{H}_o$ = 0.044) equalled the avian mean for studies of 86 species with sample sizes greater than five individuals (Evans 1987). Observed heterozygosity averaged 0.030 in an allozyme study of 25 Forster's Terns, *Sterna forsteri* (Hackett 1989).

TABLE 5. Subpopulation comparison of Cavalli-Sforza and Edwards' (1967) chord distances below the diagonal and arc distances above the diagonal. All values indicate near genetic identity of allelic frequencies between subpopulations. See Table 1 for subpopulation abbreviations listed here.

	Leech	Ashland	Mille	LOW
Leech		0.0237	0.0156	0.0231
Ashland	0.0263		0.0243	0.0295
Mille	0.0173	0.0270		0.0251
LOW	0.0256	0.0327	0.0278	

In two allozyme studies of confamilial California Gulls (*Larus californicus*), Zink and Winkler (1983) and Karl et al. (1987) found slightly lower levels of observed mean heterozygosity ranging from 0.0267 to 0.0350.

I attempted to screen for enzymatic activity at 40 enzyme loci, all enzymes for which I had assay recipes. The 18 enzyme loci that provided unambiguous results were included in the analysis. In addition, the method used to detect nonenzymatic proteins stained all proteins that were present in high concentration. Because I did not assay only those systems most likely to be polymorphic, the estimates of P and $\bar{H}$ are as free from bias as is possible using electrophoretic analysis of blood proteins with small sample sizes. The observed level of polymorphism may be misleadingly high, however, due to the inclusion of three loci with the most common allele's frequency just below 0.99. In any case, these statistics indicate that the Common Terns of Minnesota and Wisconsin have typical avian levels of genetic variation and diversity.

INDIRECT ESTIMATES OF POPULATION DYNAMICS

The indirect methods for estimating gene flow and the genetic structure of the subpopulations make several assumptions. The gene flow models aim to measure the effects of gene flow while compensating for the confounding factors of genetic drift, natural selection, and mutation (Slatkin 1987). Slatkin's (1981) method of estimating the conditional average frequency of alleles uses the similarity in allelic frequency among subpopulations to estimate relative amounts of gene flow. The model also uses the infinite-alleles-mutation model of Kimura and Crow (1964). My results from this model (Fig. 2) closely resemble theoretical patterns of high levels of gene flow (Slatkin 1981).

Slatkin's more recent, and probably more useful, private alleles model (1985a) assumes nonoverlapping generations and an island model of dispersal. Slatkin, however, states that the use of other dispersal pattern models, including the two-dimensional stepping stone model (Kimura and Weiss 1964), a more realistic model for my study, result in similar estimates. Quantitative estimates of the number of immigrants to Common Tern colonies in Minnesota and Wisconsin using the private alleles model indicate high levels of gene flow per generation (Table 3). An important assumption is that the population must be stable and in genetic equilibrium for the model to give the most accurate estimates (Slatkin 1981). The χ^2 values indicate that 11 of the 12 polymorphic loci are in Hardy-Weinberg equilibrium.

The genetic distance estimates of Nei (1978), Rogers (1972), and Cavalli-Sforza and Edwards (1967) (Tables 4 and 5) are very close to zero, also indicating that the subpopulations are not genetically distinct. Subpopulation pairwise comparisons of F_{st} (Wright 1951) as well as the overall F_{st} indicate that the observed genetic variance is not explained by among-subpopulation genetic structure. Using data from the very large Common Tern colonies on Cape Cod from about 1920–1950, Barrowclough (1980) also estimated a small F_{st} of 0.0177. He used the stepping stone model of dispersal (Kimura and Weiss 1964) to calculate F_{st} from estimates of the effective population size and gene flow rates into this population.

The two indirect estimates of gene flow and the associated population structure parameters demonstrate that there is a significant level of gene flow and little if any genetic substructuring among the four Common Tern colonies studied. This prediction is further corroborated by the direct evidence of dispersal among the subpopulations.

DIRECT ESTIMATES OF POPULATION DYNAMICS

Dispersal patterns in colonial nesting seabirds could hypothetically range from complete natal site tenacity to complete natal dispersal. Most species fall within the extremes of this range. Seabirds are highly site tenacious (Austin 1946, 1949, 1951; Wooler and Coulson 1977; Brooke 1978; Greenwood and Harvey 1982). Familiarity with habitat, maintaining coadapted gene complexes by optimal inbreeding (Shields 1982), as well as greater probabilities of retaining a mate, are all possible functions of this site tenacity. If a reproductive effort is successful it could be beneficial to remain at the same colony for subsequent seasons (Brooke 1978; Cuthbert 1985, 1988). McNicholl (1975) postulates that site tenacity is correlated with breeding habitat stability. Colonial birds that nest in highly stable environments tend to return to the same locations annually, while colonial species that breed in unstable habitats are less site tenacious. Shugart and Scharf (1983) maintain that the Common Terns

on the Great Lakes seem adapted to the use of unstable breeding locations and will readily move between colonies.

All else being equal, natural selection should favor natal dispersal if the natal colony were saturated and suitable alternative colony sites were available. It is not uncommon for first-time breeding colonial seabirds to disperse (Greenwood and Harvey 1982). In a paper demonstrating high site tenacity in Common Terns on Cape Cod, Massachusetts, Austin (1949) presented data that indicated there was over 15% natal dispersal. Austin considered that the colonies of Cape Cod were an isolated breeding population that had considerable but unmeasured intercolony dispersal within the population of Cape Cod. This same population had less than 1% immigration from non-Cape Cod colonies (Austin 1949, 1951). Nisbet (1978) also calculated an immigration rate of less than 1% for terns of Cape Cod, but analyzing more recent data, Nisbet (pers. comm.) roughly estimates 5–10% annual immigration into the tern colonies on Cape Cod from the tern colonies on Long Island, New York. DiCostanzo (1980) reported at least 1–2% natal dispersal (emigration) from a Common Tern colony on Long Island. Using live recoveries, Haymes and Blokpoel (1978) documented over 75% natal dispersal between colonies within any one Great Lake, and found about 17% for natal and breeding dispersal among the Great Lakes.

Austin (1949, 1951), Nisbet (1973), Haymes and Blokpoel (1978), DiCostanzo (1980), and Blokpoel et al. (1987) demonstrated that although breeding dispersal of Common Terns was less likely than natal dispersal, it still regularly occurred. Most reports of Common Tern dispersal patterns have been from colonies on the Atlantic coast or Great Lakes, where movement among colonies on the same body of water may be more likely than between disjunct inland populations separated by many miles of land. Common Terns from Minnesota and Wisconsin, therefore, might be expected to be more site tenacious due to the distance over land between colonies.

Band recoveries of Common Terns indicate that natal or breeding dispersal can cover the hundreds of miles between the northeastern U.S. and the Great Lakes colonies (Austin 1951, Haymes and Blokpoel 1978, DiCostanzo 1980), and potential for much further gene flow is evident from the distances covered during migration and from the observation that Common Terns of the U.S. Midwest have been recovered in locations as far away as the Azores, Hawaii, and Newfoundland (Bird Banding Laboratory records) (Fig. 3). Although there is relatively little dispersal data from Minnesota and Wisconsin, the available band recovery data demonstrate that terns move between the colonies and attempt to breed as indicated by: (1) the Bird Banding Laboratory records of adults trapped in nonnatal colonies during the breeding season, (2) the adult tern I trapped on its nest in a nonnatal colony, and (3) observations of inland colony terns colonizing previously vacant sites, and conversely, the desertion of former colony sites.

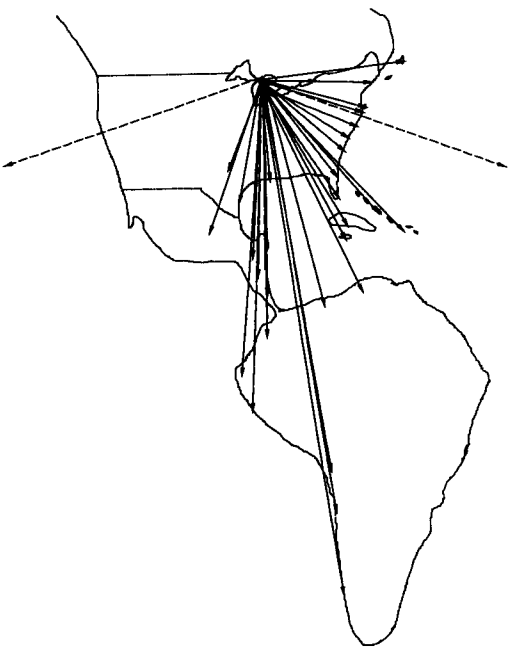

FIGURE 3. A partial summary of band recoveries of Common Terns banded in Ontario, Canada since 1922. This map illustrates the large geographical range these Common Terns have travelled and thus, the potential for long distance dispersal and gene flow.

The direct evidence of dispersal confirms that individuals do disperse, but it does not allow the quantification of rates or frequency of dispersal nor the estimation of actual levels of gene flow. Indirect methods using genetic models of population structure and gene flow do allow estimates of rates of gene flow as well as numbers of immigrants per generation.

Although only a small fraction of Common

Tern colonies have been studied, Common Tern site tenacity appears to be well developed, but dispersal is common. Specific dispersal patterns, however, depend on local conditions and intercolony distances. With the amount of gene flow necessary to prevent subpopulation differentiation being estimated as between only one individual per generation (Wright 1951) to one immigrant per two generations (Slatkin 1985b, 1987), natal and breeding dispersal among Common Tern colonies of Minnesota and Wisconsin, as well as among all others studied in North America, appears high enough to result in moderate to high levels of gene flow among regional subpopulations.

Fluctuating environmental conditions, intra- and interspecific competition, disturbance by humans, and vegetative succession cause colony sites to fluctuate in suitability for successful breeding, and therefore could be reasons for individuals to move among colonies. This study indicates that Common Terns of Minnesota and Wisconsin frequently disperse to nonnatal colonies at rates that cause the population to be virtually panmictic.

One management implication of these results is that no Common Tern colony in Minnesota or Wisconsin is genetically isolated from the others. This suggests that little to no genetic variation or diversity would be lost by the temporary failure of any specific colony. Given the limited resources available for conservation and management, efforts should be directed at colonies where the application of that effort has the highest probability of success.

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