Genetic Variability in

Larus argentatus and *Sterna hirundo*

by

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ABSTRACT

Blood serum and egg-white protein samples from individuals representing seven colonies of *Larus argentatus*, and four colonies of *Sterna hirundo* were electrophoretically analysed to determine levels of genetic variability and to assess the utility of polymorphic loci as genetic markers. Variability occurred at five co-dominant autosomal loci. *S. hirundo* protein polymorphism occurred at the *Est-5* and the *Oest-1* loci, while nineteen loci were monomorphic. *L. argentatus* samples were monomorphic at seventeen loci and polymorphic at the *Ldh-A* and the *Alb* loci. Intergeneric differences existed at the *Oalb* and the *Ldh-A* loci. Although LDH-A^{100} from both species possessed identical electrophoretic mobilities, the intergeneric differences were expressed as a difference in enzyme thermostabilities.

Geographical distribution of alleles and genetic divergence estimates suggest *S. hirundo* population panmixis, at least at the sampled locations. The *L. argentatus* gene pool appears relatively heterogeneous with a discreet Atlantic Coast population and a Great Lakes demic population. These observed population structures may be maintained by the relative amount of gene flow occurring within and among populations. Mass ringing data coupled to reproductive success information and analysis of dispersal trends appear to validate this assumption. Similar results may be generated by either selection or both small organism and low locus sample sizes. To clarify these results and to detect the major factor(s) affecting the surveyed portions of the genome, larger sample sizes in conjunction with precise eco-demographic data are required.

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Reason in itself confounded,
Saw division grow together;
To themselves yet either neither,
Simple were so well compounded,

W. Shakespeare.

To the memory of three people

Mr. and Mrs. H. H. Bastable

and

Mrs. Lucia Del Toro-Palumbo

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INTRODUCTION

The post 1945 industrial expansion of our society has precipitated a series of environmental problems. The widespread utilization of water systems as cheap, reliable and efficient sewage disposal sites, has introduced problematical quantities of relatively inert chemicals into the hydrosphere (Gerakis and Sficas, 1974; Haque and Freed, 1974; Harris and Miles, 1975). The bioconcentratable nature of these chemicals led to the political issue of government responsibility for public health and environmental quality. As part of the Canadian Wildlife Service's response to these questions, an indicator species has been sought to monitor toxic chemical problems in the Great Lakes ecosystem.

Fish-eating colonial nesting seabirds were selected as potential indicator species due to the well-documented correlative evidence of toxic chemicals on particular aspects of their reproductive biology (Cooke, 1973; 1975; Stickel, 1973; Foster, 1974; Peakall, 1975; Simkiss, 1975). Gilbertson (1974) suggested the following criteria for selecting an indicator species.

1. The species must be ubiquitous and numerous.

2. It should be relatively non-migratory and its local distribution be restricted to the Great Lakes watershed.

3. It should be a colonial nesting species, such that it will continue to nest in specific locations.

4. The species should be preferably euryphagic and at, or close to, the apex of its food chain.

Plate 1: *Sterna hirundo*

5. It should construct a substantial nest to reduce the influences of varying environmental factors.

6. The mean clutch size should be relatively invariable.

7. The species must show readily discernible signs of xenobiotic intoxication.

Initially it was proposed that Sterna hirundo (Plate 1) be used as an indicator species (G. A. Fox, pers. comm.). However, Gilbertson (1974) suggested that Larus argentatus (Plate 2) was more suitable as an indicator species, especially for the Great Lakes ecosystem, as this species fulfilled all of his criteria.

The suitability of L. argentatus as an indicator species depends upon the assessment of age-dependent dispersal, inter-colony movements, and the antagonistic interactions of these population parameters with the behavioural mechanisms associated with coloniality. Knowledge of dispersal trends is necessary to prevent ambiguous or erroneous conclusions, when attempting to establish correlations between toxic chemical loads and environmental chemo-dynamics. The evaluation of dispersal parameters in L. argentatus populations is complicated by the high rate of loss and deterioration of standard aluminum rings[1] (Kadlec and Drury, 1968; Kadlec, 1975).

An alternative method of assessing organismal movements or dispersal is the use of genetic markers (Tracey, 1974). Initially, the amount of genetic variability within and among populations must be determined, and if

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[1] Although the U.S. Fish and Wildlife Service Bird Bands are conventionally referred to as "bands" by North American workers, I will use the European terminology "ring" throughout this thesis. This choice of terminology is to avoid confusion between bird 'bands' and electrophoretic 'bands'.

Plate 2: *Larus argentatus*

possible, suitable markers chosen (see Maurer, 1968). Following selection of suitable loci and the determination of population gene frequencies, subsequent shifts in gene or genotypic frequencies may be attributed to either stochastic or directional events, such as selection, migration, mutation (Li, 1955; Falconer, 1964), or drift (Wright, 1970, 1977).

This thesis presents the results of a preliminary electrophoretic investigation into genetic variation at selected gene loci in S. hirundo and L. argentatus. Also polymorphic loci are assessed for suitability as population genetic markers, and mechanisms that are effecting or maintaining the variability will be examined.

LITERATURE REVIEW

The advent of supporting zone electrophoresis in 'molecular sieves' (Smithies, 1955; Raymond and Weintraub, 1959; Davis, 1964; Ornstein, 1964) allowed high resolution separation of proteins based on differences in molecular weight, net electrical charge and molecular configuration. Empirical data indicated that the same protein may exist in functionally equivalent forms, yet with different discrete electrophoretic mobilities (Smithies, 1959A). Concurrent advances in molecular biology allowed electrophoretic data to be extrapolated to the DNA level of an organism.

These methodologies have been increasingly applied in an attempt to quantitatively estimate the amount of genetic variability in both natural and laboratory populations (Powell, 1975A). The most striking result of these surveys has been the large amount of variability present in populations, although electrophoresis can detect only 20-30% of amino acid substitutions (Ayala, 1975; 1976; Nei, 1974; Powell, 1975A, 1975B; Scandialios, 1975; Johnson, 1977; Throchmorton, 1977). This level of detection may be raised to 80-90% by using combinations of gels with different acrylamide concentrations (Coyne, 1976; Johnson, 1977), and by further separating electrophoretic groups on the basis of different enzyme thermostabilities (Singh et al., 1975; 1976; Cochrane, 1976; Johnson, 1977), sensitivity to high urea concentrations (Lewontin, in Powell, 1975A), and investigations of enzyme catalytic properties (Johnson, 1977).

Investigations of allelic variants having the same electrophoretic mobilities (electromorphs) have revealed considerable variability within classes. Turner (1973) used thermostabilities to identify species specific

esterases in five species of the genus Cyprinodon. Thermolabile esterase variants at the Est-6 locus in Drosophila melanogaster were discovered, although the locus appeared to be monomorphic (Cochrane, 1976). Monomorphic octanol dehydrogenase in Drosophila virilis, could be defined into different thermolabile variants, that showed some gene pool differentiation (Singh et al., 1975). Similar results were obtained at the xanthine dehydrogenase locus in D. pseudoobscura (Singh et al., 1976; Prakash, 1977). Such changes in enzyme thermostabilities may result from the substitution of an amino acid with an acidic side group (e.g., aspartic acid, glutamic acid) in the interior of a tertiary/quaternary structured polypeptide/protein (Johnson, 1977). Internal amino acid residues are protected from the effects of external pH shifts by the buffered proteinaceous internal environment of the enzyme. Consequently, the ionization states of these residues cannot be altered as a means of further separating electromorphs.

These allelic variants may be the result of either simple amino acid substitutions, or complex regulatory events. Changes in regulatory gene-structural gene interactions may either accompany or be the major force in cladogenesis and speciation (Britten and Davidson, 1976; Valentine and Campbell, 1976; Wilson, 1976). Regulatory genes may allow the transcription of a structural gene, such that the properties of the structural gene product are affected (Pandey, 1977; McDonald and Ayala, 1978; Hendrick and McDonald, unpublished manuscript). Structural gene product alteration may be due to either the presence or absence or mutation of enzyme(s), that alter either the nascent mRNA or the nascent polypeptide (henceforth these mechanisms will be collectively referred to as post-transcriptional mechanisms) to confer different thermostabilities on initially identical

DNA base sequences. Recent findings from recombinant DNA plasmids indicate the presence of post-transcriptional mechanisms. Sacchromyces cerevisiae tRNA precursor cannot be activated until a nuclear enzyme(s) tailors the immediate gene product (O'Farrel et al., 1978). Gallus gallus ovo-albumin gene plasmids have shown the gene to be approximately 6×10^3 base pairs, or three times the length of the DNA required to directly encode the mRNA for this protein. Additionally six gene interruptions occur, which do not occur in ovo-albumin mRNA. The nascent mRNA is either tailored after transcription, or the DNA-RNA polymerase skips these segments. Furthermore, two ovo-albumin electromorphs differ in the number of interrupting segments in the gene; the major electromorph has six gene interruptions, while the minor form has five gene interruptions (Garpin et al., 1978; Mandel et al., 1978). If similar events have occurred at regulatory loci, and if regulatory loci function in the mechanisms documented above, the thermostabilities may indicate even greater genome divergence than just one mutational event at a structural locus.

These empirical results generated new theoretical interpretations, and two major hypotheses were developed. Although allelic variants are produced by mutation, their maintenance in the population was the point of contention. One theory suggested that genetic variability was a transient phenomenon, and most allelic states were maintained in the population by stochastic events (Kimura and Ohta, 1972). The other theory proposed that genetic polymorphisms, caused initially by mutation, were maintained in the population by selection (Powell, 1975B). A subsequent polarization of empirical tests and theoretical developments occurred and influenced both evolutionary and population genetics (Harris, 1976; Selander, 1976).

Invertebrates have the highest levels of genetic variability, followed by vertebrate poikilotherms. The lowest levels of genetic variability are found in the vertebrate homeotherms. Heterozygosity values reported for avian populations appear to be significantly smaller than any other taxa, although non-regulatory enzyme variability is considerably higher than any other vertebrate class (Powell, 1975A). The genetic variability pattern of the three enzyme classes (Johnson, 1973) is reversed compared to any other taxa, either vertebrate or invertebrate. However, interpretations of the preceding must be made with caution as relatively few avian species have been surveyed for heterozygosities at multiple loci. Similar observations were initially made on levels of heterozygosities in Crustacea and the low levels of genetic variability were hypothesized to result from the restricted mobility of this taxon (Tracey et al., 1975; Tracey, pers. comm.). However, Hedgecock and Nelson (unpublished manuscript) reported average heterozygosities from 60 decapod crustaceans; values range from 0.0% to 12.0%. These values are approximately the same as reported for other invertebrate taxa (Powell, 1975A). The degree of heterozygosity within a taxon may then be correlated with metabolic, physiological and environmental factors. Determination of the extent of heterozygosity within avian species requires an increased number of surveys of genetic variability.

Investigations of genetic variability in avian populations have generally been restricted to either domesticated species and breeds or to captive populations of wild birds (Common et al., 1953; Lush, 1961; Clark et al., 1963; Baker, 1968; Tamaki and Tanabe, 1970; Beck et al., 1975; Juneja and Wilhelmson, 1975; Meyerhoff and Haley, 1975; Tamaki, 1975;

Tamaki et al., 1975; Grunder and Hollands, 1977). Complications arise from such work as the investigations may specifically examine only one or two loci. Resultant conclusions may have little applicability to wild populations (see Manwell and Baker, 1975), as captive populations may have higher levels of variability than occur in natural populations (Corbin et al., 1974; Manwell and Baker, 1975). However, the transmission and inheritance patterns of a specific locus may have direct application in the understanding of the genetics of the same locus in wild populations.

Electrophoretic methodologies have been applied in avian systematics (Gysels, 1963; Brown and Fisher, 1966; Sibley and Brush, 1967; Sibley et al., 1969; Sibley and Hendrikson, 1970; Sibley and Frelin, 1972). Data acquired from phylogenetic assays may be useful in predicting potential polymorphic loci which may be used in intraspecific population surveys. Milne and Robertson (1965) investigated variability in the egg-white proteins from several avian species. In 200 eggs from L. argentatus colonies, no polymorphic loci were resolved. Populations of Somateria mollissima mollissima examined were polymorphic at the ovo-albumin locus, with three electromorphs. In the S. mollissima mollissima colonies surveyed, all but one conformed to Hardy-Weinberg equilibrium expectations. This colony was composed of two subgroups; one migratory, the other non-migratory and dispersing locally. During the reproductive season both subgroups nested in relative separation from each other.

Genic variability at loci encoding egg-white protein fractions were reported by other workers. Conalbumin (ovo-transferrin) was polymorphic in Phasianus colchius (Baker et al., 1966), Passer domesticus, Hirundo tahitica neoxena and Petrochelidon ariel (Manwell and Baker, 1975). In egg-white

samples from Coturnix coturnix six protein fractions, including lysozyme, were polymorphic (Baker and Manwell, 1967). Ovo-albumin was polymorphic in Lagopus scotius with an apparent two loci multi-allelic system generating the phenotype (Henderson, 1976).

A penta-allelic polymorphic ovo-esterase locus was resolved in Passer domesticus, Hirundo tahitica neoxena and Petrochelidon ariel. The variability at this locus allowed Manwell and Baker (1975) to survey populations of these three species to estimate the amount of intraspecific nest parasitism ("nest infidelity") occurring in the populations. Ten percent of P. domesticus and 2.5% of P. ariel nests contained at least one egg with different esterase electropherograms than the remainder of the clutch.

Vohs and Carr (1969) resolved four co-dominant alleles at the blood serum transferrin locus in Phasianus colchicus. When Montag and Dahlgren (1973) sampled wild populations from Pennsylvania and South Dakota, three common alleles were found. Allelic frequencies from the Pennsylvania populations were uniform over the sampling area, while gene pool heterogeneity occurred in three South Dakota populations.

The Ngase locus was polymorphic in Dendragapus obscurus (Redfield et al., 1972) and Hardy-Wienberg equilibrium expectation deviations occurred in three of the nine populations sampled. Selective pressures operative at this locus were invoked to explain the observed deviations. The authors suggested that this locus and its correlation to selective pressures may make the locus useful as a genetic marker in monitoring the behaviour cycle of this species.

Nottebohm and Selander (1972) reported results from a multi-locus genetic variability survey in four populations of Zonotrichia capensis. Twenty-four loci were examined, but only fifteen loci could be scored consistently, five of which were polymorphic. The mean heterozygosity was 3.53% and percent polymorphic loci 31.3%. The authors indicated that an essentially panmictic breeding structure may exist in the populations studied. However, song dialect analysis and a non-significant trend in gene frequencies at three loci were suggestive of gene pool heterogeneity. No definite comments concerning the population structure could be advanced due to the small sample size. When the study was repeated (Handeford and Nottebohm, 1976) with a larger sample size over an altitudinal gradient, genetic variability was similar to the first study. Average heterozygosity was 8.10% with 37.5% polymorphic loci. Significant clinal patterns in allelic frequencies existed at three loci; glucose-6-phosphate dehydrogenase, 6-phospho-gluconate-1-dehydrogenase, and mannose-6-phosphate isomerase. Song dialect analysis and geographic patterns of allelic distributions were indicative of gene pool heterogeneity that corresponded to the altitude and a 'patchy' environment. The authors commented that the association of these factors structured the Z. capensis population into specific philopatric demes.

Baker (1975) attempted to assess the effect of female-male choice and the role of vocal dialects on population structure of Z. leucophrys. Nineteen loci were surveyed to determine if gene pool heterogeneity existed in populations from Colorado and California. Colorado populations were polymorphic at three loci (15.8% polymorphic loci), with an average heterozygosity of 4.18%. These results were indicative of gene pool

heterogeneity and a demic population structure. California populations were polymorphic at six loci (31.6% polymorphic loci), and had an average heterozygosity of 9.94%. Results again suggested a demic population structure. Such a population structure could be due to a founder effect in association with site tenacity (philopatry), and female choice for a male with the 'proper' song. A heterogeneous environment with differential selection pressures could also structure such a population.

The effect of extensive topographical barriers on genetic variability in colonial nesting (Aplonis metallica) and solitary nesting (A. cantoroides) birds was examined by Corbin et al. (1974). Three of eighteen loci were polymorphic, and a clinal pattern of variability was observed at two of these three loci. A. metallica had an extensive polymorphism at the Ldh loci which corresponded to gene pool heterogeneity at these loci. The Est-1 locus was also polymorphic, although no apparent pattern existed in the geographical distribution of allelic variants. A. cantoroides was polymorphic for two loci: Ldh and Est-1. The pattern of genetic variability was reversed in this species, Ldh allele frequencies had a uniform distribution, while gene pool heterogeneity existed at the Est-1 locus. Average heterozygosity was 4.7% (16.6% polymorphic loci) for A. metallica, and 0.8% (11.1% polymorphic loci) for A. cantoroides. The paucity of data describing age structure, mortality, reproductive success, dispersal, feeding habits, as well as heterospecific and conspecific interrelationships, prevented the authors from formulating any explanatory definitions of the observed results. (The aforementioned parameters will be collectively referred to as eco-demographic data).

Passer domesticus populations in Australia were marked by considerable variability, average heterozygosity was 9.8% and 40% of the loci surveyed were polymorphic. Manwell and Baker (1975) suggested that this level of genetic variability was high ; however, Z. leucophyrs from California were also marked by high values (Baker, 1975). This result may represent either the adaptability of P. domesticus, or else is a result of its being introduced into new environments. Hirundo tahitica neoxena (average heterozygosity 7.8%) and Petrochelidon ariel (average heterozygosity 6.5%) were believed to be more representative of variability estimates in birds . However, in comparison with other published values, the results of Manwell and Baker (1975) appear inflated. If these values are indeed respresentative of genetic variability estimates in avian populations, then similar results may be occurring with birds as Hedgecock and Nelson (unpublished manuscript) reported for decapod crustaceans.

Smith and Zimmerman (1976) investigated the biochemical phylogenetic relationships of seven species of the Agelaine and Quiscaline groups (Family: Icteridae). Fifteen loci were examined and five loci were monomorphic (P = 1.00). However, variability was restricted at the Mdh-1 locus. One individual out of 215 was heterozygous at this locus, all others were monomorphic. Calculated allele frequencies are p = 0.998 and $q = 2.0 \times 10^{-3}$, which suggests that actually six loci were monomorphic (Selander, 1976). Although genetic identities ($\bar{I} = 0.797 \pm 0.116$) and genetic distances ($\bar{D} = 0.237 \pm 0.142$) are reported, average heterozygosities are not. Using the published allele frequencies, average heterozygosity is 17.22% (H = 8.93% to H = 22.11%) with 45.7% polymorphic loci (33.3% to 60.0%).

Peden and Whitney (1976) examined populations of Anas platyrhynchos from Quebec, Manitoba and British Columbia. Blood serum when electrophoresed, showed variation in an esterase which indicated that very little gene flow existed between western and eastern populations.

Studies of genetic variability in wild avian populations have made use of plumage variations and colour phase frequencies. Jefferies and Parslow (1976) found that bridling in Uria aalge is controlled by a recessive allele at a single autosomal locus. The frequency of bridling in colonies increases on a south-north cline, although evidence of a west-east cline off the shores of Norway was evident. The authors suggested that bridling may be selected for in areas where surface water has a low temperature. How bridling confers this superior fitness is unknown. Alternatively, balancing selection may be maintaining the polymorphism in the areas of the reported clines.

Colour phase polymorphism is also found in Stercorarius parasiticus with three distinct genotypes: light, intermediate, dark-intermediate and dark. The polymorphism is controlled by two alleles at a semi-dominant locus (O'Donald and Davis, 1975) and studies of colonies on Fair and Foula Islands in the Shetlands appear to indicate that several selectional events may be presently maintaining the polymorphism (O'Donald, 1972; 1974; 1978; O'Donald and Davis, 1975; Davis and O'Donald, 1976A; 1976B).

Cooch and Beardsmore (1959) identified a colour phase polymorphism in Anser caerulescens and indicated that positive assortative mating was occurring in the population. Furthermore, the authors suggested that the reported increase of the blue phase in all locations was due either to blue males having an increased advantage as a result of mate choice, or to balancing selection maintaining the polymorphism. Genetic studies of the

colour phases indicated that plumage colour was controlled by two alleles at a single autosomal locus with the blue allele semi-dominant to white (Cooke and Cooch, 1968; Cooke and Mirsky, 1972). The increasing blue phase may be a function of male dispersal as most females return to their natal colony. However, the rate of increase may be slowed by assortative mating coupled with early imprinting and differential phase migration (Cooke et al., 1975). Considerable gene flow occurs between the Hudson Bay colonies due to mixing on the wintering grounds where initial mate choice occurs. Furthermore, such large amounts of gene flow would appear to negate any selection acting on the subpopulations (Rockwell and Cooke, 1977).

THEORETICAL REVIEW

Observed genotype frequencies obtained from electrophoretic methodologies are routinely compared to Hardy-Weinberg equilibrium expectations. Under equilibrium conditions, observed genotypes should be normally distributed. If two alleles, A, a, are present at a single co-dominant locus, then the resulting genotypes are: A//A, A//a, a//a. In a sample of N diploid organisms (2N gene sample size), the representative contribution of each genotype is D, (A//A); H, (A//a) and R, (a//a), where D + H + R = N. The observed genotypic frequencies are,

$$D/N + H/N + R/N = 1.0 \qquad (1)$$

The frequency of the A allele (p) in the sample is given by

$$p = \frac{2D + H}{2N}$$

and the frequency of the a allele (q) in the sample is given by

$$q = \frac{2R + H}{2N}$$

such that $p + q = 1.0$. Under equilibrium conditions, the two alleles assort to form the genotypes

$$(p + q)^2 = 1.0$$

$$p^2 + 2pq + q^2 = 1.0 \qquad (2)$$

This relationship (2) is the Hardy-Weinberg equilibrium expectation for the two alleles, A, a (Li, 1955; Falconer, 1964). Deviation from the expected values implies the presence of perturbing forces (migration, mutation, selection and population structure) affecting the sampled portion of the genome. In a demic population, either isolated random breeding subunits may exist or the population may be panmictic. If a population consists of i subunits, then p_h is the frequency of the A allele in the h-th subunit ($p_h + q_h = 1.0$). Assuming that each of the i subunits are in equilibrium, then the zygotic proportions of the two alleles in the h-th subunit are: p_h^2, $2p_hq_h$, q_h^2.

The mean frequency of p in the entire population is given by

$$\bar{p} = \sum_i p_h/i$$

and the variance of $\bar{p}$ is

$$\sigma^2_{\bar{p}} = \sum_i (p - \bar{p})^2/i$$

The zygotic proportions of the pooled subunits are:

$$A//A = \sum_i p_h^2/i = \bar{p}^2 + \sigma^2_{\bar{p}}$$

$$A//a = 2\sum_i p_h q_h/i = 2\bar{p}\bar{q} - 2\sigma^2_{\bar{p}}$$

$$a//a = \sum_i q_h^2/i = \bar{q}^2 + \sigma^2_{\bar{p}}$$

which become

$$(\bar{p}^2 + \sigma^2_{\bar{p}}) + (2\bar{p}\bar{q} - 2\sigma^2_{\bar{p}}) + (\bar{q}^2 + \sigma^2_{\bar{p}}) = 1.0 \qquad (3)$$

If the population subunits were from a panmictic breeding structure then the zygotic proportions would be:

$$\bar{p}^2 + 2\bar{p}\bar{q} + \bar{q}^2 = 1.0$$

which is similar to equation (2), and describes a Hardy-Weinberg population. In cases of isolated breeding pools, the heterozygote classes are reduced by the quantity $2\sigma^2_{\bar{p}}$, and each homozygote class is increased by $\sigma^2_{\bar{p}}$. The numerical value of $\sigma^2_{\bar{p}}$ is dependent upon the frequency distribution of p in the i subunits (Wahlund, 1928 in Li, 1955).

An increase in the homozygote class may arise from inbreeding occurring in the subunits. Furthermore, any process affecting the genome may be responsible for the establishment of gene pool heterogeneity. However, regardless of the mechanism generating the heterogeneity, gene flow must be reduced between subunits to maintain differentiation, otherwise p_h will approach $\bar{p}$. Sampling of subpopulations, that are separated by extremely small interdemic distances, may not detect gene pool heterogeneity. Allelic frequencies are not subunit frequencies, but rather mean allelic ($\bar{p}$) frequencies.

Deviation from Hardy-Weinberg equilibrium expectation may arise from small sample size. This experimental error arises from probabilistic considerations of the sampling regime. In one locus-two allele systems, there exists a greater probability of sampling a homozygote (either of the two classes), than sampling a heterozygote (Levene, 1949). On the other hand, with either multi-locus systems, or multi-allelic systems, or combinations of these two, there exists a greater chance of sampling heterozygotic classes than homozygotic classes (Li, 1955: Milkman, 1975).

These sampling-induced errors may be corrected by altering the Hardy-Weinberg equilibrium expectations to increase either heterozygotic or homozygotic deficiencies. Levene's (1949) small sample size correction compensates for the heterozygote deficiency in one locus systems, while Li (1969) and Milkman (1975) suggested corrections for homozygote deficiencies in multi-locus systems.

Selander (1976) defines a polymorphic locus, as a locus that has a common allele frequency equal to less than 0.99. This definition is an arbitrary, but commonly used standard. Small sample surveys do not allow determination of actual population allele frequencies, but rather generate estimates thereof. The process of estimation is dependent upon the probability of non-detection of rare alleles (Table 1). At intermediate allele frequencies ($p = 0.80$) the non-detection probability is low, even with an organismal sample size of three. However, when the common allele frequency is high ($p = 0.99$), the non-detection probability is low only when the organismal sample size approaches fifty. The non-detection probabilities indicate that only common alleles will be detected. As a result the genetic variability in the population will be underestimated. Conversely, if a rare allele is detected, the small sample size would inflate the estimate of population genetic variability. Such sampling errors may cause erroneous conclusions about either gene pool homogeneity or heterogeneity, if only genetic data are considered.

Selection may be responsible for the alteration of allelic frequencies, and levels of genetic variability due to phenotypic response to environmental factors (Wright, 1970; 1977; Powell, 1975A; 1975B; Lowther, 1977; Berry, 1978), cumulative differential viability and steady drift (Wright,

Table 1: Probabilities of Non-Detection[1] of Rare Alleles in Relationship to Number of Individuals Sampled and Population Frequency of the Common Allele

Number of Individuals Sampled	Frequency of the Common Allele						
	0.99	0.95	0.90	0.80	0.70	0.60	0.50
3	0.94	0.79	0.53	0.26	0.12	0.05	0.02
6	0.89	0.54	0.28	0.06	0.01	2.2×10^{-3}	2.4×10^{-4}
9	0.83	0.40	0.15	0.02	1.6×10^{-3}	1.0×10^{-4}	3.8×10^{-6}
12	0.79	0.29	0.08	4.7×10^{-3}	1.9×10^{-4}	4.7×10^{-6}	6.0×10^{-8}
15	0.79	0.21	0.04	1.2×10^{-3}	2.3×10^{-5}	2.2×10^{-7}	9.0×10^{-10}
18	0.70	0.16	0.02	3.2×10^{-4}	2.7×10^{-6}	1.0×10^{-8}	1.5×10^{-11}
50	0.37	0.01	2.7×10^{-5}	2.0×10^{-10}	3.2×10^{-16}	6.5×10^{-23}	7.9×10^{-23}

1. The probability that only common allele (p) homozygotes are drawn in a sample is equal to the frequency of this homozygote (p^2) raised to the power of the sample size (n). Thus the probability of non-detection is $(p^2)^n$

   e.g., p = 0.99; $p^2 = 0.9801$; therefore when n = 3, the probability of non-detection becomes $(p^2)^3 = 0.94148$.

1970). Populations established by either sampling drift (Cain and Curry, 1963 in Wright, 1970), or sampling processes (Li, 1955; Falconer, 1964), and then having undergone random drift, may have different genotypic expressions when directionalized by selection (Wright, 1969; 1970; 1977). Selection has its influence on the genotype (Waddington, 1976), or the "mean fitness ($F(w/\bar{w})$)" (Dobzhansky, 1966; Wright, 1970; 1977). Since the phenotype is the summation of genetic and environmental events, different genotypic phenotypes may respond differently to similar selective pressures. This process is related to the concept of multiple adaptive peaks in a fitness space (Wright, 1970; 1977). Populations may respond to equal selective pressures and the result may be gene pool heterogeneity, with population subunit fitnesses being equally maximized. This process of selection would, in the context of evolution, allow multiple routes to fitness maximization.

The presence or absence of selection affecting the zygotic proportions of a locus depends on variability at the locus under study. Since changes in gene frequency are used to quantify selection, there can be no selection if the locus is monomorphic ($p = 1.00$) (Wright, 1970; 1977). However, lack of electrophoretic variation does not necessarily indicate a lack of selection, due to the previously documented implications of hidden variability within electromorph classes. Yet electrophoretic monomorphism, by similar criteria, does not imply selection operating on the locus.

The effectiveness of selective pressures on genic variability depends on the frequency of the allele, regardless of the phenotypic effect of that allele (Li, 1955; Falconer, 1964; Kimura and Ohta, 1972). If allele frequencies are either high ($p >> 0.99$) or low ($p << 0.01$), the effectiveness

of selection is extremely small in altering them. Alleles in these frequency classes may behave in a neutral fashion as described by Kimura (Kimura and Ohta, 1972), and may be lost from a population due to the statistical implications of gametic sampling and founder effects.

Selection may alter population allele frequencies indirectly either through linkage effects, or through effects on regulatory loci. Genes are distributed in linkage groups in an organism's genome. Consequently, if two genes are closely linked, then both genes may appear to be responding to the same selective pressure. Actually selection may be operative at only one of the loci, while spatial and positional effects cause the second locus (not affected by the selective pressure) to respond with perturbed zygotic proportions (Kimura and Ohta, 1972; Powell, 1974; Hedrick, unpublished manuscript).

The large amount of genetic variability maintained in a population may be due to selection. However, the actual effect of selection is difficult to prove, and equally difficult to disprove (Tracey, pers. comm.). The invocation of selection may categorically explain observed variability. Yet due to the tautological relationship between selection and fitness, experimental proof in natural populations is difficult to obtain. Requirements of proof of selection usually entail postulations of functional-physiological enzyme effects or linkage disequilibrium.

Initially, selection coefficients, arising from the abiotic factors (especially climate), are very high and result in a rapid increase in population fitness to these selective pressures. Subsequently, as fitness increases, the selection coefficients decrease with respect to that population; that is the population becomes more fit to a specific locale

(Lowther, 1977). As selection coefficients decrease, increasingly larger sample sizes are required to detect deviations from Hardy-Weinberg equilibrium expectation due to selection (Hubby and Lewontin, 1966; Powell, 1974). Small sample surveys may generate expectation agreements, when larger sample sizes would show perturbations arising from selection.

Endler (1973) investigated the establishment of gene pool heterogeneity by selection even in the presence of gene flow. However, reproductive success of the migrants, with respect to the residents, was not determined. In instances of gene pool heterogeneity and migration, reproductive success of migrant individuals should be monitored. Differences in reproductive success may lead to the development of gene pool heterogeneity. This concept is essential when interactions between gene flow and selection happen simultaneously and gene pool heterogeneity results.

Genetic variability may be measured by several parameters; average heterozygosities, percentage polymorphic loci, and average number of alleles at a locus. The last two metrics are dependent upon large sample sizes, which detect rare alleles and increase variability estimates (Nei and Roychoudury, 1974; Nei et al., 1975; Nei, 1975; 1978; Selander, 1976; Fuerst et al., 1978). Average heterozygosity is dependent more on locus sample size than organismal sample size (Tracey et al., 1975; Nei, 1975; 1978). However, when average heterozygosity is large with a corresponding small genetic distance, a large sampling bias is associated with the average heterozygosity (Fuerst et al., 1978; Nei, 1978). Average heterozygosity ($\bar{H}$) is given by

$$\bar{H} = \sum_{i} H_{o_k}/i$$

where H_{o_k} is the observed heterozygosity at the k-th locus and i is the

total number of loci surveyed. Average heterozygosity may also be given by

$$\bar{H} = \sum_{i}(1 - \sum x_k^2)/i$$

where x_k is the frequency of the x-th allele at the k-th locus (Nei and Roychoudury, 1975; Nei, 1975; 1978; Selander, 1976).

Percentage polymorphic loci is equal to the number of polymorphic loci divided by the total number of loci surveyed, and multiplied by 10^2.

Average number of alleles at a locus ($\bar{A}$) is given by

$$\bar{A} = \sum_{i} a_k/i$$

where a_k is the number of alleles at the k-th locus and i is the total number of loci surveyed (Tracey et al., 1975; Tracey, pers. comm.).

Single locus inbreeding coefficients (F_i) are calculated by

$$F_k = (H_{E_k} - H_{O_k})/H_{E_k}$$

where H_{E_k} is the Hardy-Weinberg equilibrium expectation heterozygosity at the k-th locus and H_{O_k} is the observed heterozygosity at the k-th locus (Li, 1955; Nei, 1975). Nei (1975) has used this metric as another method for evaluating gene pool heterogeneity. Single locus inbreeding coefficients may indicate the presence of perturbing influences affecting a sample locus: -F values indicate a sampled population has a heterozygote excess, while +F values indicate a sample has a homozygote excess. This coefficient is a measure of population divergence rather than Malecot's (1948) metric which measures the degree of relatedness within the population.

Degrees of genetic variability maintained in two populations may be compared by statistical methods (Li, 1955; Falconer, 1964; Wright, 1968; 1969), or by the use of Nei's statistics (1974; 1975). These latter calculations are designed specifically for computation using electrophoretic allele frequency data. The frequency of the alleles may be used to compute

statistical measures of genetic similarity between two populations or taxa. Nei's statistics estimate the probability of drawing two electrophoretically identical alleles at the same locus from two populations. If two populations, X and Y, exist and K is a given locus , then the normalized probability that the two electromorphs from X and Y are identical is given by:

$$I_k = \sum_i x_i y_i \left(\sum_i x_i^2 \sum_i y_i^2\right)^{-\frac{1}{2}}$$

where x_i and y_i are the frequencies of the i-th allele at the K-th locus in populations X and Y, respectively. If I is calculated for all loci analysed, then the average genetic identity over all loci is

$$I = J_{xy}(J_x J_y)^{-\frac{1}{2}}$$

where J_{xy}, J_x and J_y are the arithmetic means over all loci assayed of $\sum_i x_i y_i$ $\sum_i x_i^2$ and $\sum_i y_i^2$ respectively. The mean genetic identity is the average identity over all loci common to both populations. Since the genetic identity is a probability, then I can assume any value from 0.0 to 1.0. If two populations are identical, then I = 1.0; if they share no common alleles, then I = 0.0.

Genetic distance is estimated as the natural log transformation of I

$$D_k = -\log_e I_K$$

where I is the genetic identity at the K-th locus. Mean genetic distance over all loci is

$$D = -\log_e I$$

D may assume any value from 0.0 to ∞; D = 0.0 when I = 1.0 and D = ∞ when I = 0.0.

Genetic distance is the measure of electrophoretically detectable amino acid substitutions between populations X and Y for a given protein.

Since proteins are gene products, amino acid substitutions reflect changes in the DNA nucleotide base sequence. Genetic distance therefore measures population differences at the DNA level.

In application of these statistics, Nei (1974; 1975) made the assumption that soluble proteinaceous gene products are a random representative sample of the entire genome. However, structural gene products may be effected either by different evolutionary events or by different magnitudes of the same events than either non-structural or regulatory genes (Wilson, 1975; McDonald and Ayala, 1978; McDonald and Hedrick, unpublished manuscript). Consequently, information obtained from analysis of structural gene products may apply only to the surveyed portion of the genome and conclusions should be cautiously drawn.

Dobzhansky (1976) indicated that a genetic distance of $D = 0.226 \pm 0.033$ between semi-species in Drosophila paulistorum correlates with divergence existent in separate reproductivity isolated populations. Avise (1976) reviewing the genetic differentiation that accompanies the speciating process showed that genetic identity values in the D. willistoni complex range from $\bar{I} = 0.970 \pm 0.06$ (geographic populations) to $\bar{I} = 0.352 \pm 0.23$ (non-sibling species). In sunfishes, particularly the species Lepomis macrochirus, the two subspecies produce fertile F_1 hybrids, yet the genetic divergence is large $D = 0.171$. Considering the entire genus, mean inter-specific genetic distance ($\bar{D} = 0.627 \pm 0.029$) is high, fertile F_1 hybrids are also produced by any combination. This large genetic distance and the distinct morphology are perplexing in the light of the ability to inter-breed. In the genus Taricha Hedgecock, (1974; 1978) genetic identity and distance approximate those observed in the D. willistoni complex. Smith

and Zimmerman (1976) published interspecific and intergeneric divergence estimates for the Icteridae that ranged from I = 0.989 to I = 0.637 ($\bar{I}$ = 0.797 ± 0.116; $\bar{D}$ = 0.237 ± 0.142).

Discussions of genetic variability within populations, either conspecific or heterospecific may estimate large genome divergence even when fertile F_1 progeny are produced. Genetic variability detected by electrophoresis may not indicate actual divergence, unless genome reorganization has occurred. Within a species, or subspecies, large divergence estimates may indicate the presence of mechanisms affecting the genome, while at generic levels they indicate only structural similarities or differences. If genome organization, particulary gene-chromosome arrangements, has been conservative, then information on regulatory loci is important. If genome reorganization has occurred, then regulatory gene differences may correlate with observed structural gene changes. In concepts of evolutionary processes total genome divergence may be driven by a single event (chromosomal rearrangements) or by a summation of mutational events.

In cladogenesis, whether speciating or non-speciating, the greater the degree of temporal-spatial isolation, the greater the genetic divergence. With non-speciating events, divergence is dependent upon gene flow and selection (Avise and Ayala, 1975). Population subdivision, whether due to intrinsic or extrinsic factors, is an evolutionary event that may lead to speciation.

The most important factors in the establishment of a new deme are the genotypes of the founder/colonizer(s), and the effective population size (Kimura and Ohta, 1972). The establishment of a new population is a sampling event and is governed by the same probablistic considerations as experimental sampling (Li, 1955; Cain and Curry, in Wright, 1970). It is

this mechanism that reduces genetic variability in new populations. Furthermore, loss of variability may arise from selection, increased inbreeding and drift correlated with initial sampling (Wright, 1970). This loss of genetic variability or bottleneck persists for several generations and is followed by a time period that is characterized by rapidly increasing genetic variability. The length of time for a population to enter this last stage is dependent upon the relative rate of population increase (Ayala, 1976; Nei et al., 1976). The effect of gene flow on an expanding new population dilutes this process, and does not allow the formation of gene pool heterogeneity (Ehrlich and Raven, 1969). Rather, new frequencies. allele frequencies rapidly conform to population mean allele frequencies.

Levels of genetic variability and geographic distributions of specific alleles in time and space are intrinsically dependent upon the eco-demographic parameters of species existence. The knowledge of the natural history of a species will aid in attempting to assess the effects of selection, gene flow and drift upon a population's genetic variability.

NATURAL HISTORY

Sterna hirundo and Larus argentatus (family Laridae) are colonial nesting seabirds that have circumpolar distributions (Godfrey, 1966; p. 178; p. 189). S. hirundo may be described as a medium sized migratory stenophagic bird (Austin, 1938; 1942; 1949; 1951; 1953; Palmer, 1941A, 1941B; Hunter, 1976), while L. argentatus is a large euryphagic bird that has an age dependent dispersal (Hickey and Allen, 1937; Gross, 1940; Paynter, 1949; Hofslund, 1959; Smith, 1959; Tinbergen, 1960; Kadlec and Drury, 1968; Moore, 1976; Threlfall, 1978). In the Great Lakes, colonies

of both species may nest in association with each other and with colonies of L. delawarensis (Ontario Nest Records Scheme (ONRS)).

The spring arrival of S. hirundo on colony sites is largely weather dependent, and may occur from mid-April to early June. When weather conditions are favourable, colony members may arrive in pairs or in small groups. In the presence of spring inclemency, colony members may arrive en masse with the onset of moderating weather (Austin, 1938; 1942; 1949; 1951; 1953; Palmer, 1941A; pers. obs.).

With the end of the reproductive period, pairs that have successfully nested may disperse locally as family groups (Palmer, 1941A; Austin, 1942; 1951). Ringing recoveries from newly fledged juveniles indicate that dispersal from the Cape Cod terneries occurs immediately after fledging (Austin, 1942; 1949; 1951). Palmer (1941A; 1941B) indicates that a similar pattern exists for the Sugar Loaf, Maine colony, with migration commencing as early as 10-15 August, although most of the migration occurs from 10-20 September. Migration from the Port Colborne Lighthouse colony (and possibly the adjacent Canada Furnace Colony) occurs around 1-8 October (J. Bonnisteele and A. Kendrick, pers. comm.).

Austin (1940; 1942; 1953), Palmer (1941A; 1941B) and recent ringing returns (Godfrey, 1966; p. 189; G. A. Fox, pers. comm.; Haymes, unpublished data; Haymes and Blokpoel, 1978) indicate that S. hirundo migrate through the Great Lakes, then south-east to the Finger Lakes, New York, to the Mohawk-Hudson River valleys and then to the Atlantic coast. At this point, the flyways of the Great Lakes and Atlantic Coast populations merge, and the migration continues along the Atlantic Coast to Florida. Eventually, the migration may continue as far south as Peru on the Pacific and Brazil on

the Atlantic coasts by approximately mid-January, at which time potential breeders begin to retrace their migratory route. The initial stages of courtship are expressed as an integral part of the northward migration (Austin, 1940; 1942; 1945; 1953; Palmer, 1941A; 1951B).

The distribution of S. hirundo juveniles, the majority of which do not mature sexually until their fourth year, is not well documented (Palmer, 1941B; Austin, 1949). Haymes (unpublished data), and Haymes and Blokpoel (1978) report ringing recoveries of Great Lakes juveniles from Ascension Island in the Atlantic to the Hawaiian Islands in the Pacific. Palmer (1941A; 1941B) suggested that the juveniles are pelagic wanderers over their winter range distribution during the years before their first nesting season. The sighting of "white-faced terns" reported from some colonies may be older birds nesting in eclipse plumage (Austin, 1938; Palmer, 1941B), although very rare occurrence of juveniles on colonies is documented (Palmer, 1941B).

L. argentatus pairs arrive on the gullery from mid-March to mid-May (Gross, 1940; Paynter, 1949; Hofslund, 1959; Smith, 1959; Tinbergen, 1960; Kadlec and Drury, 1968; Moore, 1976; Threlfall, 1978). The onset of courtship usually occurs before the pair return to the gullery, and may commence at loafing points or 'clubs' (Tinbergen, 1960). After fledging, parents and young may remain in the vicinity of the colony. First-year juveniles usually undergo a slight northward dispersal from October to mid-November (Moore, 1976; Threlfall, 1978), and from mid-November to December juveniles have an increasing tendency to move south. However, this southward dispersal is regionally specific. Juveniles from Newfoundland (Threlfall, 1978), and the Atlantic Coast (Kadlec and Drury, 1968) follow

the coast south to Florida and the coast of the Gulf of Mexico. Juveniles from Lakes Erie, Ontario and eastern Huron move south-east then follow either the St. Lawrence River, or the same route as S. hirundo (Gross, 1940; Kadlec and Drury, 1968; Moore, 1976). Flyways of both eastern Great Lakes and the Atlantic Coast populations merge and continue south. Hofslund (1959) and Smith (1959) indicate that juveniles from the western Great Lakes have a tendency to move south along the Mississippi River valley to the Gulf of Mexico. Occasionally, migrants from the upper Great Lakes may move south-east and join the flyway of the lower Great Lakes population. Moore (1976) and Kadlec and Drury (1968) imply that these flyways are unique enough that the Great Lakes' population may be divided into two groups, an eastern subunit and a western subunit, both of which are distinct from the Atlantic Coast population.

In spring juveniles retrace their migratory route returning to their natal lake, or more specifically their natal colony. Second and third year juveniles and sub-adults have a restricted winter dispersal that increases with increasing age. Individuals of these year classes either remain in their respective natal lakes, or move not more than 500 km during the winter (Moore, 1976). Adults, if food supply is sufficient, may remain in the vicinity of the colony and overwinter a few miles from the breeding grounds (Kadlec and Drury, 1968; Moore, 1976). Adults usually return to their natal colonies to nest (Gross, 1940), or have restricted distributions within their natal lake (Hofslund, 1959; Smith 1959; Kadlec and Drury, 1968; Threlfall, 1978). Adults who are not breeding, whether they are taken a year off from breeding or have not yet bred, loaf on the edges of their affiliated colony (Kadlec and Drury, 1968).

Implicit in the concept of larid coloniality are the twin phenomena of group adherence and site tenacity (philopatry). These three ethological mechanisms function to bind the individuals into a social aggregate and ensure the integrity of the colony as a self-perpetuating unit (Austin, 1948; 1953; Nelson, 1973; McNicholl, 1975). Group adherence is the mechanism which promotes colony integrity by the development of associations between individuals. Specific relationships or attachments may be formed by monogamy, family units (R. A. Hunter, pers. comm.), kin groups, interactions between nearest neighbours and possible social hierarchies (Austin, 1938; 1949; 1951; Palmer, 1941A). In S. hirundo, colony members may arrive or depart from the colony site as a unit, however no information concerning the maintenance of these associations on the wintering grounds is available. Individual L. argentatus colony members may remain together throughout the winter at loafing points, if sufficient food is available (Tinbergen, 1960).

Site tenacity (philopatry) is the attachment expressed by an individual for a specific geographic location for breeding purposes. This behavioural mechanism is enhanced by a pair's continued reproductive success, which ensures that the pair will continue to nest in the same location (Austin, 1949).

As a breeding pair ages, continued successful reproduction increases site tenacity and group adherence. When these factors are balanced and environmental conditions are optimal, maximum reproductive success may be realized. With age, the balance of these mechanisms may shift. Younger birds have a stronger group adherence trait, while older colony members have an increased site tenacity (Austin, 1949; 1951). Since colony integrity favours the maximization of reproductive success, a balance of

these factors in a colony is beneficial to colony well-being. If the colony site becomes unsuitable, then the colony members as a unit may desert and begin nesting in a more favourable location. However, if the old site improves, the individuals may return to the original site (Austin, 1949; 1951; McNicholl, 1975).

The concept of a colonial breeding system and how such a system would shape the genetic variability of a species was discussed by Shields (1977). Basically, the ethological mechanisms restrict variability by promoting inbreeding which would maximize relatedness among colony members. The effect with time, is that the breeding system may approach selfing; at least to the extent that mandatory outcrossing diploid individuals can achieve. The end effect is to maximize reproductive output and generate progeny that conform to maximum mean phenotypic fitness. The distribution of progeny fitness is altered from a normal distribution to a leptokurtotic distribution.

MATERIALS AND METHODS

Sampling Locations

Sterna hirundo

In late May to early June of 1975, eggs approximately one to four days of age were collected from four locations: Port Colborne on Lake Erie (n = 35), Presqu'île on Lake Ontario (n = 22), South Limestone Island (n = 9) and Little Courtlin Island, Malpèque Bay, Prince Edward Island (n = 39). On May 23, 1976, eggs (n = 10) were collected from Port Colborne (Map 1). Eggs taken from Port Colborne and Prince Edward Island were removed from numbered nests and egg ages were relatively well known. Eggs taken from Presqu'île and Limestone Island were aged by the technique of Hays and Le Croy (1971). The first egg of a clutch was removed for sampling, except in instances where the entire clutch was sampled. For clutch sampling, individual eggs were aged to establish laying order.

Larus argentatus

In mid-May 1975, eggs were collected from three locations, Port Colborne (n = 20), Presqu'île (n = 15) and South Limestone Island (n = 15). Fifteen, one day old chicks and two unincubated eggs from Little Courtlin Island, Prince Edward Island were provided by G. A. Fox (Canadian Wildlife Service). In mid-May to early June of 1976, eggs were collected from Port Colborne (n = 10), Little Courtlin Island (n = 12) and Mohawk Island (n = 3). The aging techniques and the method of nest sampling were identical with those described for S. hirundo. However, G. Haymes collected three unaged eggs from Mohawk Island. Ten, one day old chicks from Chantry Island, and

Table 2: Number of Eggs Incubated and Resulting Chick Sample Sizes from Four Nesting Locations of Sterna hirundo.

Colony Location	Date of Sampling	Number of Eggs Incubated	Chick Sample Size
Port Colborne	May 22, 1975	17	17
Port Colborne	May 20, 1976	15	10
Presqu'île	May 23-25, 1975	11	11
Limestone Island	June 1, 1975	5	1
Prince Edward Island	June 13, 1975	17	7

Table 3: Number of Eggs Incubated and Resulting Chick Sample Sizes from Five Nesting Locations of *Larus argentatus*.[1]

Colony Location	Date of Sampling	Number of Eggs Incubated	Chick Sample Size
Port Colborne	May 12, 1975	11	11
Port Colborne	May 20, 1976	10	2
Presqu'île	May 23-25, 1975	9	3
Limestone Island	June 1, 1975	9	4
Prince Edward Island	May 11, 1976	12	4
Mohawk Island	May 27, 1976	3	3

1. Chicks were obtained from C.W.S. for Prince Edward Island (1975) (n = 15); Chantry Island (1976) (n = 10); Scotch Bonnet Islands (n = 3)

Table 4. Egg-White Sample Sizes from Four Nesting Locations of *Sterna hirundo*, and Four Nesting Locations of *Larus argentatus*.[1]

Colony Location	Date of Sampling	Sample Sizes	
		Sterna hirundo	*Larus argentatus*
Port Colborne	May 12, 1975	--	9
Port Colborne	May 22, 1975	18	--
Presqu'île	May 23-24, 1975	11	6
Limestone Island	June 1, 1975	4	6
Prince Edward Island	June 13-23, 1975	22	2

1. Two eggs collected on June 8 from Prince Edward Island were provided by C.W.S.

Map 1: Locations of Sampling Sites of Larus argentatus and Sterna hirundo on the Great Lakes and Prince Edward Island (inset).

(0) Port Colborne

(1) Presqu'île

(2) S. Limestone Island

(3) Prince Edward Island

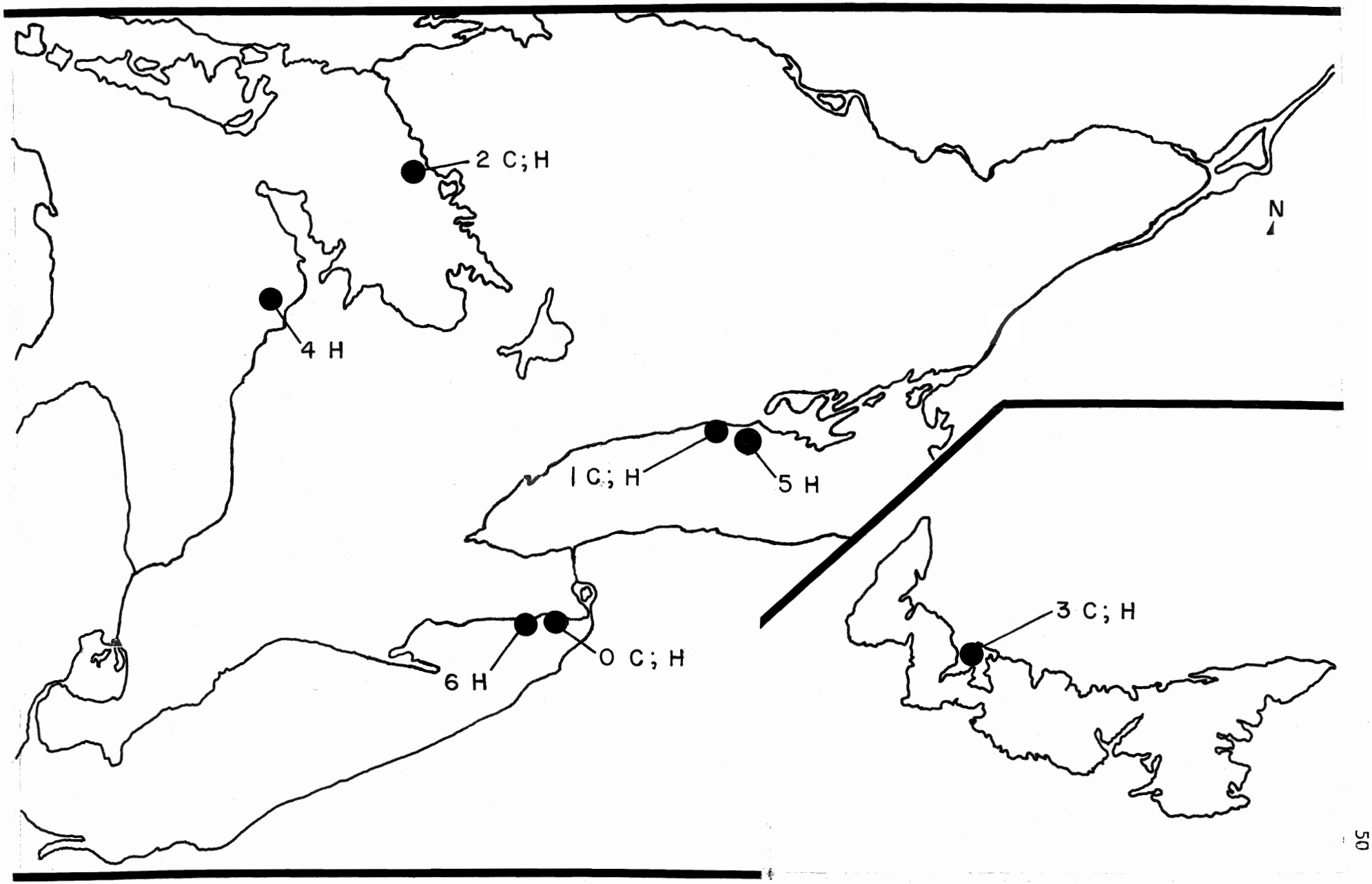
(4) Chantry Island

(5) Scotch Bonnet Island

(6) Mohawk Island

C Sterna hirundo colonies sampled

H Larus argentatus colonies sampled


2 C; H
4 H
1 C; H
5 H
6 H
0 C; H
3 C; H
N

three, one day old chicks from Scotch Bonnet Island were provided by G. A. Fox and A. P. Gilman (Canadian Wildlife Service) (Map 1).

Sample Preparation

Eggs collected from the sampling locations were portioned into two groups. One group (Table 2, Table 3) was incubated to term in a Robbins Hatchmatic Incubator (Model 1-A, Robbins Hatchamatic Co., Denver, Colorado) at 37.2 ± 0.3°C and a relative humidity (R.H.) of 60 ± 5.0% (Hunter et al. 1976). The second group of eggs (Table 4) were opened at the point of greatest shell diameter and the contents poured into a petri dish. Two ml samples of egg-white were pipetted into numbered glass vials and stored at -80°C in a Series HO Ultra-Cold Freezer (Kelvinator Co., Manitowac, Massachusetts).

L. argentatus and S. hirundo chicks aged 24 to 36 hours were decapitated, and bled into 15 ml centrifuge tubes containing 2 ml of chilled 0.9% sodium chloride (w/v). With the cessation of bleeding, additional saline was added to achieve a final 1:1 dilution of whole blood to saline. The resultant blood clot was broken up and extracted from the tube using wooden applicator sticks. The tubes and contents were then centrifuged at 5000 G for 10 min in a clinical desk top centrifuge (Danon/IEC, Needham Heights, Massachusetts). The supernatant was pipetted off, dispensed into numbered glass vials, and stored at -80°C. All separation procedures were performed at 4°C.

Samples from 1976 were placed in numbered cryogenic vials (Alman Cryogenics Inc. Oakland, California), frozen in liquid nitrogen (P. Nicholls, pers. comm.), and stored at -80°C. Samples from 1975, that were stored in

glass vials that had cracked due to the low storage temperatures, were transferred to similarly numbered cryogenic vials, and restored at -80°C.

For electrophoretic analysis, sample vials were removed from the freezer, and placed in an ice bath. Approximately 50 µl of the frozen sample was chipped out with a laboratory spatula, and placed in plastic sample holders. Egg-white samples were diluted 1:5 with distilled water immediately before electrophoresis.

Polyacrylamide Discontinuous Gel Electrophoresis[1]

Conventional polyacrylamide discontinuous gel electrophoresis (Davis, 1964; Ormstein, 1964) was initially used to attempt to separate protein components from egg-white from S. hirundo and L. argentatus. However, polymerization of the acrylamide monomer was prevented by the inclusion of egg-white in the sample-gel. The reduction of dilute egg-white concentration, even at 1% (v/v) of the large pore solution still had an inhibitory effect on polymerization. Doubling of polymerization time, or increasing the relative concentrations of riboflavin and TEMED (N,N,N',N'-tetramethylethylenediamine) or the combination of the two processes were ineffective in producing a polymerized sample-gel. To circumvent this problem, the gross structure of the gel matrix, and the pH of the gel buffer systems were altered. The main criteria in assessment of a successful modified system were ease of sample loading, and the maintenance of the excellent resolution typical of polyacrylamide discontinuous gel electrophoresis.

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[1] See Appendix 1 for a detailed listing of solutions and buffers used in this study.

The modified system was characterized by not including the protein sample into a sample gel. Rather 20 µl of the protein sample was mixed with 20 µl of 50% sucrose (w/v)-0.049 M Tris-HCl (pH 6.8), and 20 µl of the sucrose-sample solution was layered, with a micro-pipette, directly onto the stacking-gel interface. The pH of the stacking-gel buffer (0.049 M Tris-HCl) was lowered to 6.9, while the small pore (separation-gel) buffer 0.30 M Tris-HCl was maintained at pH 8.9 (Davis, 1964). Samples were layered after the gel tubes had been positioned, and both reservoirs filled with chilled electrophoresis buffer (Electrophoresis Stock Buffer 0.05 M Tris-glycine, pH 8.3 diluted 1:10 with distilled water). To minimize convectional disturbances, and resulting perturbations in electrophoretograms, during electrophoresis the current was reduced to 2.0-2.5 mA $tube^{-1}$. and the electromotive force maximized at 250 volts. Electrophoresis was performed at 4°C, until the marker front had migrated 7-10 mm from the anodal end of the gel. To reduce inter-run variation due to minute differences in the pore size of the gel matrix, gels were constructed in four sets of 12, and stored at 4°C in a water-saturated environment (A. J. S. Ball, pers. comm.).

Larus delawarensis serum protein electrophoretograms resulting from both polyacrylamide discontinuous gel electrophoresis systems were cross compared. No difference in either overall electrophoretic pattern or resolution were visually apparent. Similar results were obtained when electrophoretograms resulting from stored gels vs freshly constructed gels of both systems were cross compared. In light of these results, the modified system fulfilled all criteria and was subsequently used in all polyacrylamide discontinuous gel electrophoresis procedures.

The complexity of general protein and esterase electrophoretograms of both serum proteins and egg-white proteins from L. argentatus and S. hirundo prevented easy and unambiguous electromorph determination (Smith et al., 1973), and genotype assessment. The comparative relative ease of using starch-gel electrophoresis in this assessment was the principal reason for adopting this medium in the electrophoresis of proteins from the serum and egg-white of both species.

Upon completion of electrophoresis, gels were removed from the tubes, dark-stained for Lactate Dehydrogenase (LDH), scored, and dark stored in individual screw-capped glass tubes containing 10 ml of 30% ethanol (v/v).

Potential electromorph variants were identified by polyacrylamide discontinuous gel co-electrophoresis (Smith et al., 1973). Twenty µl of a sample containing one suspected electrophoretic variant were mixed with 20 µl of another sample containing either a suspected identical or suspected different electrophoretic variant. Twenty µl of this mixture was electrophoresed in parallel with pure samples containing the suspected electromorphs.

Starch Gel Electrophoresis[1]

Starch gel slabs (17.3 x 13.0 x 0.7 cm) composed of 40 g of Electrostarch and 330 ml of Poulik Gel Buffer (pH 8.65) (Poulik, 1957) in combination with 500 ml of Poulik Bridge Buffer (pH 8.1) (Poulik, 1957) were used in the separation of both egg-white and blood serum proteins (Milne and Roberston, 1965; M. L. Tracey, pers. comm). Samples were absorbed on paper wicks (7.0 x 10.0 mm) cut from Whatman No. 4 Filter Paper and inserted into the sample

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[1] See Appendix 1 for a detailed list of solutions, buffers and their chemical composition.

wells. Gels were electrophoresed for three hours at 4°C with a current of 80 mA, after which, slabs were removed from the plastic gel trays, sliced, stained, rinsed in distilled water, scored, fixed, dried, wrapped in plastic film and dark-stored.

Histochemical Techniques

General Protein

Starch-gel slices were stained overnight in a solution of 50 ml of 0.25% Coomassie Brilliant Blue R 250 C. I. 42660 (w/v) (Davis 1964; Wilson, 1973), 50 ml of methanol, and 10 ml of glacial acetic acid (Smithies, 1959B). After staining gels were rinsed in distilled water, and destained overnight in 60 ml of 95% ethanol and 40 ml of 7.5% acetic acid (v/v).

Oil Red "O"

Albumens in both blood serum and egg-white were identified using 50 ml of 20% trichloroacetic acid (w/v) and 50 ml of saturated solution of Oil Red "O" in methanol (Smithies, 1959B), and were stained overnight.

Esterases

Starch-gel slices were pre-soaked in 0.5 M boric acid for 30 min and were stained overnight. The staining solution was composed of 1 ml of 1% naphthyl ester (w/v) (Brewer and Singh, 1970), 50 mg of either Fast Red TR salt or Fast Blue RR salt, and 125 ml of 0.2 M sodium phosphate buffer (pH 6.8) (Oxford, 1973).

For routine analysis of blood serum esterases, Fast Red TR salt was used in conjunction with α-naphthyl acetate, β-naphthyl acetate, α-naphthyl caprylate and β-naphthyl stearate, while Fast Blue RR salt was used with α-naphthyl propionate and α-naphthyl butyrate. α-Naphthyl propionate dye coupled with Fast Red TR salt was used as the routine analysis for egg-white esterases. Substrate specificity of the egg-white esterases was determined using all substrates. Positive identification of esterases was determined by excluding substrates from the staining mixture.

Lactate Dehydrogenase

Polyacrylamide gels were individually dark-stained for 1 hour at room temperature. The staining mixture was composed of 5 mg of nicotinamide adenine dinucleotide (NAD), 7.5 mg of nitro-blue tetrazolium (NBT), 1 mg of phenosine methosulphate (PMS) and 10 ml of 0.2% sodium lactate (w/v) (Hebert, 1973). Positive identification of zones of enzyme was determined by the exclusion of the substrate from the staining mixture and using 10 ml of distilled water. Stepwise exclusions of NAD, NBT and PMS from the staining mixture were used to further define the enzyme as LDH.

Tetrameric subunit composition was defined using 10 ml of 0.05% α-hydroxybutyric acid (w/v) as the enzyme substrate (Market et al., 1975). Gels were dark stained for three hours at room temperature. Stepwise exclusions of chemicals from the staining mixture were used to clarify and specify activity zones.

Thermostabilities[1] of the electromorph were examined by heating 40 µl

[1] Results for the thermostabilities of LDH-A 100 are reported in Appendix 2.

aliquots of serum to 60 ± 0.5°C for 2, 5, 10, 15 and 20 minute intervals in a water bath (Heto, Model No. 623, Heto Co., Birkerod, Denmark). Subsequent electrophoretic and histochemical procedures were identical to the routine LDH assay. The effect on enzymatic activity of α-hydroxybutyric acid was also monitored. After staining gels were scored at 550 nm in a Gilford Photospectrometer (Model No. 2400, with a Model 2410-S Linear Transport, Gilford Instrument Co., Oberlin Ohio) Calibrated to 3.0 Absorbance units with a gel scan speed of 1.0 cm min^{-1} and a chart drive speed of 2.5 cm min^{-1}. Blood serum LDH from Larus delawarensis was used to determine the reproduc ability of the technique. Maximum peak height was used as the measure of enzyme activity (Singh et al., 1976).

Protein and Allelic Nomenclature[1]

Zones of either enzyme activity or protein bands in a starch-gel were numbered anodally from the origin. Within each zone, the most common variant was arbitrarily designated as the 100 electromorph. If a locus was polymorphic, then the electrophoretic variants were defined in relation to the electrophoretic mobility of the 100 variant. If an electromorph migrated 1 mm further into the gel than the 100 variant, then the faster electromorph was designated as the 101 variant. If the variant migrated 1 mm less than the 100 electromorph, the slower variant was designated as the 99 electromorph.

Due to the increased resolution of polyacrylamide discontinuous gel electrophoresis, the above nomenclature criteria were altered for this

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[1] All sample genotypes are recorded in Appendix 3.

system. To distinguish between electrophoretic variants 0.5 mm was used instead of 1 mm. The designation of electromorphs in relation to the most common variant was identical to the procedure outlined above.

Serum proteins were designated by a code of three upper case letters followed by the banding zone number (e.g., EST-2). The gene encoding that specific protein was designated by a three letter code (the first being an upper case letter, the last two being lower case) banding zone number italic code (e.g., Est-2). Egg-white proteins were similarly designated, only a four letter code beginning with 'O' was used (e.g., OPRO-1; Opro-1).

Blood Serum Proteins

Lactate dehydrogenase-A (Ldh-A) was polymorphic in samples from L. argentatus and monomorphic in S. hirundo. The 100 electromorph was located about 0.5 cm into the gel , the 99 about 0.45 cm, 102 about 0.6 cm and the 104 about 0.7 cm.

Tetrazolium oxidase 1 (To-1) was located about 3.5 cm into the gel and was monomorphic in both species.

Tetrazolium oxidase 2 (To-2) was located about 4.2 cm into the gel and was monomorphic in both species.

Protein 1 (Pro-1) was located about 1.4 cm into the gel and was monomorphic in both species.

Protein 2 (Pro-2) was located about 2.5 cm into the gel and was monomorphic in both species.

Protein 3 (Pro-3) was located about 2.8 cm into the gel and was monomorphic in both species.

Protein 4 (Pro-4) was located about 3.0 cm into the gel and was monomorphic in samples from S. hirundo. Samples from L. argentatus were

not able to be scored accurately or unambiguously.

Protein 5 (Pro-5) was located 5.6 cm into the gel and was monomorphic in samples from both species.

Albumin (Alb) is a polymorphic locus in L. argentatus. The 100 electromorph was located approximately 6.2 cm into the gel, while the 98 variant was located about 6.0 cm into the gel. Samples from S. hirundo were monomorphic for the 100 allele.

Esterase 1 (Est-1) was located about 1.7 cm into the gel, and was monomorphic in both species. This esterase showed little substrate specificity as all substrates were hydrolysed, except for α-naphthyl caprylate and β-naphthyl stearate.

Esterase 2 (Est-2) was located about 2.2 cm into the gel and was monomorphic in both species. A slight specificity for α-naphthyl acetate was observed, although all substrates, except α-naphthyl caprylate and β-naphthyl stearate were hydrolysed.

Esterase 3 (Est-3) was monomorphic in samples from both species, and was located about 3.0 cm into the gel. An increased substrate specificity for α-naphthyl acetate compared to Est-2 and a concommitant decrease in hydrolysis of other substrates, with no hydrolysis of α-napthyl caprylate or β-naphthyl stearate was observed.

Esterase 4 (Est-4) was located about 3.2 cm into the gel, was monomorphic and was found only in samples from L. argentatus. A high specificity for α-naphthyl propionate, no hydrolysis of either α-naphthyl caprylate or β-naphthyl stearate; and slight hydrolysis of the remaining substrates was observed.

Esterase 5 (Est-5) was not able to be scored in samples from L. argentatus, but was polymorphic in samples from S. hirundo. The 100 electromorph was located about 4.5 cm into the gel, and the 98 variant about 4.3 cm. No substrate specificity was apparent, although α-naphthyl caprylate or β-naphthyl stearate were not hydrolysed.

Esterase-6 (Est-6) located about 6.0 cm into the gel, was monomorphic and was found in samples from S. hirundo only. α-Naphthyl caprylate and β-naphthyl stearate were not hydrolysed, and no other substrate specificity was apparent.

Ngase (Ng) was located about 5.0 cm into the gel and was monomorphic in samples from both species.

Egg-White Proteins

Ovo-protein-1 (Opro-1) was located about 0.6 cm into the gel and was monomorphic in samples from both species.

Ovo-protein-2 (Opro-2) was located about 1.1 cm into the gel and was monomorphic in samples from both species.

Ovo-protein-3 (Opro-3) was located about 1.3 cm into the gel and was monomorphic in samples from both species.

Ovo-protein-4 (Opro-4) was located about 3.8 cm into the gel and was monomorphic in samples from both species.

Ovo-albumin (Oalb) was polymorphic in both species. However, the 99 allele, located at 6.6 cm, was monomorphic in samples from L. argentatus, while the 100 allele, located at 6.7 cm was monomorphic in samples from S. hirundo.

Ovoesterase (Oest-1) was polymorphic in samples from S. hirundo, but was not resolved in samples from L. argentatus. The 100 allele and the 106 allele were located at 0.1 cm and 0.7 cm, respectively.

Chemicals

Hydrolysed potato starch was obtained from Electro-Starch Company, Madison, Wisconsin.

All artificial enzyme substrates, dye-indicators, NAD and PMS were purchased from Sigma Chemical Company, St. Louis, Missouri. Oil Red "O" was donated by M. Kingery of the Greater Niagara General Hospital, Niagara Falls, Ontario.

TEMED, BIS (methylene bisacrylamide), were purchased from Kodak Distillation Products, Eastman Kodak, Rochester, New York, U. S. A.

All other chemicals were of the highest grade available and were purchased from BDH Chemical Company, Toronto, Ontario.

RESULTS

Intraspecific Genetic Variation

Sterna hirundo samples from four nesting locations were analysed electrophoretically for protein variation. Twenty-one loci were scored in samples from Port Colborne, Presqu'île, and Prince Edward Island, and nine loci were scored in samples from South Limestone Island ternery. Genetic variation was found at only two loci (Oest-1 and Est-5); the other nineteen loci (eight loci in the Limestone Island sample) were monomorphic (Opro-1, Opro-2, Opro-3, Opro-4, Oalb, Ldh-A, To-1, To-2, Est-1, Est-2, Est-3, Est-6, Ng, Pro-1, Pro-2, Pro-3, Pro-4, Pro-5, Alb). Blood serum from the single chick hatched from incubated eggs from the Limestone Island ternery was used primarily as an electrophoretical standard for LDH-A, TO-1 and TO-2. As a result, only these three blood serum proteins and the egg-white proteins were analysed. Allele frequencies,[1] sample sizes and heterozygosities are presented in Table 5. Sample sizes given for each location represent gene sample sizes, or twice the individual sample size.

The observed heterozygosities (H_O) were Chi-Square tested against Hardy-Weinberg equilibrium expectations (H_E),[2] and Levene's small sample size corrected expectations (H_L) (Levene, 1949). In addition, both expected heterozygosities were Chi-Square tested to determine if significant differences in expectation were evident. None of the Chi-Square probabilities (P) were significant for any of the comparisons at any of the nesting locations.

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1. See Appendix 5 for Hardy-Weinberg equilibrium expectations, and observed genotypic frequencies

2. See Appendix 6 for all results of Chi-Square analysis.

Table 5: Protein Variation in Sterna hirundo.[1] Gene sample sizes (twice the number of birds), allele frequencies, observed (H_0) and Hardy-Weinberg expected (H_E)[2] heterozygosities and Chi-square probabilities (P) are recorded for the four nesting locations. Means and standard deviations of allele frequencies are recorded in the total column for alleles; H_0, H_E and P are pooled values.

Locus	Allele	Nesting Locations: Port Colborne	Presqu'île	Limestone Island	Prince Edward Island	Total
Sample Size		24	14	6	44	88
Oest-1	100	0.54	0.29	0.33	0.68	0.46±0.18
	106	0.46	0.71	0.67	0.32	0.54±0.18
	H_0	0.75	0.29	0.00	0.36	0.43
	H_E	0.50	0.41	0.44	0.43	0.49
	P	0.14	--	--	0.65	0.50
Sample Size		48	22	0	14	84
Est-5	98	0.44	0.45		0.21	0.37±0.13
	100	0.56	0.56		0.79	0.63±0.13
	H_0	0.46	0.36		0.14	0.38
	H_E	0.49	0.50		0.34	0.48
	P	0.90	--		--	0.25

1. The following 19 loci were assayed and found to be monomorphic in samples taken from these four nesting locations: Opro-1, Opro-2, Opro-3, Opro-4, Oalb, Ldh-A, To-1, To-2, Ng, Est-1, Est-2, Est-3, Est-6, Pro-1, Pro-2, Pro-3, Pro-4, Pro-5, Alb.

2. Expected heterozygosities were also calculated using Levene's (1949) procedure to correct for small sample size, Chi-square probabilities were non-significant in all cases indicating agreement with the genetic model of co-dominant inheritance in Oest-1 and Est-5. See Appendix 6.

Note that the pooled sample suggests nesting location allele frequency homogeneity, as pooled populations are expected to yield heterozygote deficiencies (Wahlund, 1928 in Li, 1955).

Considerations of non-detection probabilities suggest that, the estimated frequency of polymorphic loci for S. hirundo may be a valid estimate of population polymorphic locus frequency. Furthermore, it is highly unlikely that any of the loci designated as polymorphic have a common allele frequency in excess of 0.99.

At all sampled nesting locations, with the exception of the Limestone Island ternery, the number of alleles per locus ranged from one for each of the monomorphic loci to two alleles at each of the polymorphic loci. The average number of alleles per locus was 1.09, while percent polymorphic loci was 9.5%. As three individual samples from Limestone Island were assayed for only the six egg-white protein loci, and only one individual provided information on Ldh-A, To-1 and To-2, the average number of alleles per locus (1.17) and percent polymorphic loci (16.7%), are higher than observed at the other three sampling locations. These values result from the reduction of locus sample size.

Average heterozygosities (Nei, 1975; 1978; Nei and Roychoudhury, 1974; Tracey et al., 1975) observed for the sampling locations are: Port Colborne, $H_A = 0.06$; Presqu'île, $H_A = 0.03$; Prince Edward Island, $H_A = 0.02$; Limestone Island, $H_A = 0.00$, and the pooled sample, $H_A = 0.04$. Average heterozygosity over all locations is $\bar{H}_A = 0.03 \pm 0.02$.

No single locus inbreeding coefficients (Table 6) are presented for samples from the Limestone Island ternery, as no heterozygotes were observed at the Oest-1 locus, and the Est-5 locus was not assayed. Oest-1 locus F

Table 6. Single Locus Inbreeding Coefficients (F)[1] for Samples from Six Nesting Locations of Larus argentatus, and Three Nesting Locations of Sterna hirundo. Totals represent pooled samples from all locations. Mean F values and standard deviations are over all sampling locations, and do not include the total (pooled) F values.

	Larus argentatus		Sterna hirundo	
Location	Ldh-A	Alb	Oest-1	Est-5
Port Colborne	0.29[2]	--[3]	-0.50[4]	0.06
Presqu'île	-0.18	-0.18	0.29	0.28
Limestone Island	--	--	--	n.s.[5]
Prince Edward Island	0.00	--	0.27	0.59
Chantry Island	0.08	--		
Scotch Bonnet Island	-0.18	-0.18		
Mohawk Island	-0.10	--		
Total	0.63	0.00	-0.14	0.21
Mean ± Std. Dev. ± Standard Deviation	-0.02 ±0.18	-0.18 ±0.00	0.02 ±0.45	0.31 ±0.27

1. $F = \frac{H_E - H_0}{H_E}$ (Li, 1955)

2. Positive F Values indicate a trend towards heterozygote deficiency.

3. Dashes indicate that $H_0 = 0.00$, i.e., the locus was monomorphic.

4. Negative F values indicate a trend towards homozygote deficiency.

5. Limestone Island ternery sample was not assayed for this locus.

values range from -0.50 for Port Colborne to 0.27 and 0.29 for samples from Prince Edward Island and Presqu'île, respectively. At the Est-5 locus calculated inbreeding coefficients are F = 0.59 for Prince Edward Island, F = 0.28 for samples from Presqu'île and F = 0.06 for samples from the Port Colborne ternery. Values for the pooled samples are: F = -0.14 at the Oest-1 locus and F = 0.21 at the Est-5 locus. Mean and standard deviation (Oest-1: 0.02 ± 0.45 and Est-5: 0.31 ± 0.27) do not include the pooled sample F values. Note that with the exception of the Oest-1 F value for samples from Port Colborne, all other F values are positive indicating a trend towards heterozygote deficiencies. The negative F value at the Oest-1 locus in samples from Port Colborne indicates a trend towards homozygote deficiency.

Larus argentatus samples from seven nesting locations were analysed for protein variation. Eighteen loci were scored in samples from the Port Colborne, Presqu'île, Limestone Island and Prince Edward Island colonies. Thirteen genetic loci were scored in samples from Chantry Island, Scotch Bonnet, and Mohawk Island gulleries. Locus sample size reduction was a result of not sampling egg-white proteins from these three colonies. Genetic variation occurs at two loci: Alb and Ldh-A. The remaining loci were monomorphic (Opro-1, Opro-2, Opro-3, Opro-4, Oalb, To-1, To-2, Est-1, Est-2, Est-3, Est-4, Ng, Pro-1, Pro-2, Pro-3, Pro-5). Sample sizes, allele frequencies,[1] and heterozygosities are presented in Table 7.

Where allelic variation occurs and sample size was statistically adequate the observed heterozygosities (H_O) were Chi-Square tested against Hardy-Weinberg equilibrium expectations (H_E), and against Levene's (1949)

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1. See Appendix 5 for Hardy-Weinberg expectations and observed genotypic frequencies.

Table 7. Protein Variation in Larus argentatus.[1] Gene sample sizes (twice the number of birds), allele frequencies, observed (H_0) and Hardy-Weinberg expected (H_E)[2] heterozygosities, and Chi-square probabilities (P) are recorded for seven nesting locations. Means and standard deviations of allele frequencies are recorded in the total column for alleles; H_0, H_E and P are pooled values.

		Nesting Locations							
Locus	Alleles	Port Colborne	Presqu'île	Limestone Island	Prince Edward Island	Chantry Island	Scotch Bonnet Island	Mohawk Island	Total
Sample Size		26	6	8	40	20	6	6	112
Ldh-A	99	0.04	0.00	0.00	0.00	0.30	0.83	0.50	0.13±0.32
	100B	0.04	0.17	0.00	0.98	0.45	0.17	0.33	0.47±0.34
	102	0.88	0.83	1.00	0.00	0.25	0.00	0.17	0.38±0.44
	104	0.04	0.00	0.00	0.03	0.00	0.00	0.00	0.018 $\pm 1.7\times10^{-2}$
	H_0	0.15	0.33	0.00	0.05	0.60	0.33	0.67	0.23
	H_E	0.21	0.28	0.00	0.05	0.65	0.28	0.61	0.62
	P	0.85	--		0.62	--	--		1.4×10^{-8}
Sample Size		26	6	8	40	20	6	6	112
Alb	98	0.00	0.17	0.00	0.00	0.00	0.17	0.00	0.02 $\pm 8.3\times10^{-2}$
	100	1.00	0.83	1.00	1.00	1.00	0.83	1.00	0.98 $\pm 8.3\times10^{-2}$
	H_0	0.00	0.33	0.00	0.00	0.00	0.33	0.00	0.04
	H_E	0.00	0.28	0.00	0.00	0.00	0.28	0.00	0.04
	P		--				--		0.73

1. The following 16 loci were assayed and found to monomorphic in samples taken from Port Colborne, Presqu'île, Limestone Island and Prince Edward Island: Opro-1, Opro-2, Opro-3, Opro-4, Oalb, To-1, To-2, Est-1, Est-2, Est-3, Est-4, Ng, Pro-1, Pro-2, Pro-3, Pro-5. Samples from Chantry Island, Scotch Bonnet Island and Mohawk Island were monomorphic for all serum proteins listed above, but no egg-white protein samples were assayed at these three nesting location.
2. Expected heterozygosities were also calculated using Levene's (1949) procedure to correct for small sample size; Chi-square values were non significant in all cases indicating agreement with the genetic model of co-dominant inheritance in Alb and Ldh-A. See Appendix 6.

small sample size corrected expectations (H_L). In addition both expected heterozygosities (H_E vs H_L) were analysed by Chi-Square to detect any significant discrepancies between the two expectation values.[1] Chi-Square probabilities (P) were not significant in any of the nesting locations. This lack of significance implies agreement with the Hardy-Weinberg distribution of genotypes.

The Ldh-A pooled sample Chi-Square probabilities are highly significant (H_E vs H_0: $P = 1.43 \times 10^{-8}$, H_L vs H_0: $P = 7.4 \times 10^{-9}$). The highly significant P values generated by the Chi-Square comparison of observed heterozygosity versus expected heterozygosity indicates a deviation from Hardy-Weinberg equilibrium expectation, in that a homozygote excess occurs in the pooled sample. This discrepancy implies that the nesting locations have dissimilar allele frequencies at the Ldh-A locus. In addition, an almost significant difference exists between the Hardy-Weinberg equilibrium expectation heterozygosity and Levene's (1949) small sample size corrected heterozygosity ($P = 5.9 \times 10^{-2}$). Levene's correction invariably reduces the homozygote expectation; the near significant difference between H_E and H_L stresses the extent to which the homozygosity has been reduced. The interesting point is however, that the observed discrepancy between H_0 and either H_L or H_E is not likely the result of small sample size, as the correction for small sample size yields an expectation with a lower probability than the uncorrected expectation. In an attempt to clarify the extent of gene pool heterogeneity at this locus, the data were re-grouped and re-analysed (Table 8). When L. argentatus sample genotypes were pooled according to the lakes in which the sampled colonies are located, resultant

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1. See Appendix 6 for all results of Chi-Square analysis.

Table 8: *Larus argentatus* LDH-A Gene Pool Summations.
Gene Pool Summations, gene sample sizes (twice the number of birds) (n), Allele Frequencies, Observed and Expected Heterozygosities (H_0, H_E) and Chi-square Probabilities (P).

Gene Pool Summation	Gene Sample Size (n)	Allele Frequency	H_0	H_E	P
Port Colborne-Mohawk Island	32	99: 0.13 100B: 0.09 102: 0.75 104: 0.04	0.25	0.41	0.30
Presqu'île	12	99: 0.42 100B: 0.17 102: 0.42 104: 0.00	0.33	0.63	0.27
Chantry Island-South Limestone	28	99: 0.21 100B: 0.32 102: 0.46 104: 0.00	0.43	0.64	0.17
Chantry-Scotch Bonnet-Mohawk	32	99: 0.94 100B: 0.38 102: 0.19 104: 0.00	0.56	0.63	0.75
Port Colborne-Presqu'île-Limestone-Prince Edward Island	80	99: 0.01 100B: 0.51 102: 0.45 104: 0.03	0.10	0.53	9.8×10^{-8}
Port Colborne-Presqu'île-South Limestone	40	99: 0.025 100B: 0.05 102: 0.90 104: 0.025	0.15	0.19	0.90
All colonies, Great Lakes	72	99: 0.21 100B: 0.19 102: 0.58 104: 0.014	0.33	0.58	1.9×10^{-5}
Great Lakes, except Chantry	52	99: 0.19 100B: 0.08 102: 0.71 104: 0.02	0.23	0.47	7.5×10^{-9}

Table 8, p. 2:

Gene Pool Summation	Gene Sample Size (n)	Allele Frequency	H_0	H_E	P
1975 Samples Port Colborne, Presqu'ile-Limestone-Prince Edward Island	68	99: 0.015 100B: 0.49 102: 0.50 104: 0.00	5.9 x 10^{-2}	0.51	3.6 x 10^{-7}
1976 Samples Port Colborne-Prince Edward Island-Chantry-Scotch Bonnet-Mohawk	44	99: 0.32 100B: 0.45 102: 0.18 104: 0.05	0.50	0.66	0.18
1975 Samples Port Colborne-Presqu'île-Limestone	36	99: 0.03 100B: 0.03 102: 0.94 104: 0.00	0.11	0.11	0.79
1976 Samples Port Colborne-Chantry-Scotch Bonnet-Mohawk	36	99: 0.39 100B: 0.36 102: 0.22 104: 0.03	0.55	0.67	0.42

zygotic proportions conformed to Hardy-Weinberg equilibrium expectations. This conformation implies gene pool homogeneity within lakes. Pooling data from all Great Lakes colonies deviation from expectation occurs ($P = 1.9 \times 10^{-5}$), even when Chantry Island (see Moore, 1976) data are excluded ($P = 7.5 \times 10^{-9}$). Pooling data by sampling year, a deviation from expectation occurs in the 1975 samples ($P = 3.6 \times 10^{-7}$), however when Prince Edward Island samples are excluded, gene pool homogeneity results ($P = 0.74$). A similar trend is also evident in the 1976 samples; exclusion of Prince Edward Island samples raises the probability from $P = 0.18$ to $P = 0.42$, the trend is however non-significant.

The number of alleles ranged from one for the monomorphic loci to four alleles at the Ldh-A locus. Samples from Port Colborne were polymorphic at the Ldh-A locus only, with four alleles present giving an average of 1.17 alleles per locus and 5.6% polymorphic loci. Samples from the Presqu'île gullery were polymorphic at the Ldh-A and Alb loci, with 10.5% polymorphic loci and 1.11 alleles per locus. Samples from South Limestone Island were monomorphic at all loci surveyed. Prince Edward Island samples were polymorphic at the Ldh-A locus with 1.06 alleles per locus, and 5.6% polymorphic loci. Samples from Chantry Island (1.15 alleles per locus and 7.7% polymorphic loci) and Mohawk Island (1.15 alleles per locus and 7.7% polymorphic loci) were polymorphic at the Ldh-A locus only. Scotch Bonnet gullery samples were polymorphic at the Ldh-A and the Alb loci, with 1.15 alleles per locus and 15.4% polymorphic loci. The last three colonies were assayed for only thirteen loci, rather than the eighteen loci for the first four colonies. The decreased locus sample size may explain the inflated values for the last three colonies.

Average heterozygosity for the sampled colonies are: Port Colborne, $H_A = 7.9 \times 10^{-3}$, Presqu'île, $H_A = 3.5 \times 10^{-2}$, Limestone Island $H_A = 0.00$, Prince Edward Island, $H_A = 2.6 \times 10^{-3}$, Chantry Island $H_A = 4.6 \times 10^{-2}$, Scotch Bonnet Island, $H_A = 5.1 \times 10^{-2}$, and Mohawk Island, $H_A = 5.2 \times 10^{-2}$. Mean and standard deviation of the average heterozygosities over all nesting locations is $H_A = 0.03 \pm 0.02$.

Inbreeding coefficients (Table 6) at the Ldh-A locus are: Port Colborne, F = 0.29, Presqu'île, F = -0.18, Prince Edward Island, F = 0.00, Chantry Island, F = 0.08, Scotch Bonnet Island, F = -0.18, Mohawk Island, F = -0.10. Samples from the Limestone Island gullery were monomorphic for the Ldh-A 100B allele, and inbreeding coefficients were not calculated for these samples. The mean inbreeding coefficient and associated standard deviation at the Ldh-A locus is -0.02 ± 0.18. Inbreeding coefficients for both Presqu'île and Scotch Bonnet gulleries are F = -0.18, indicating a trend to heterozygote excess in both colonies.

Conspecific Genetic Identities and Genetic Distance

Sterna hirundo

The six pairwise combinations (Table 9) for the Oest-1 locus average to a genetic identity of $\bar{I} = 0.88 \pm 0.09$ and a genetic distance of $\bar{D}$ $\bar{D} = 0.13 \pm 0.11$. Genetic identity and genetic distance for the Est-5 locus (Table 10) have average values of $\bar{I} = 0.94 \pm 0.04$ and $\bar{D} = 0.06 \pm 0.04$. Total genetic identities over all loci surveyed for all pairwise combinations are recorded in Table 13. Average total genetic identities and genetic distance are $\bar{I} = 0.99 \pm 0.06$ and $\bar{D} = 0.01 \pm 0.01$.

Table 9. Single Locus Genetic Identities[1] and Genetic Distances[2] at the Oest-1 Locus in Samples from Four Nesting Locations of Sterna hirundo (genetic identities above the diagonal, genetic distances below the diagonal).

	Sterna hirundo			
	Port Colborne	Presqu'île	Limestone Island	Prince Edward Island
Port Colborne		0.88	0.92	0.96
Presqu'île	0.12		0.99	0.73
Limestone Island	0.08	0.00(3)		0.78
Prince Edward Island	0.04	0.31	0.24	

1. Genetic Identity = $I_k = \sum_i x_i y_i \left(\sum_i x_i^2 \sum_i y_i^2 \right)^{-\frac{1}{2}}$; where x_i and y_i are the frequencies of the i-th allele at the k-th locus in populations X and Y respectively (Nei, 1974, 1975).

2. Genetic Distance = $D_k = -(\log_e I_k)$ (Nei, 1974, 1975).

Table 10: Single Locus Genetic Identities[1] and Genetic Distances[2] at the Est-5 Locus in Samples from Three Nesting Locations of Sterna hirundo (genetic identities above the diagonal; genetic distances below the diagonal).

	Sterna hirundo		
	Port Colborne	Presqu'île	Prince Edward Island
Port Colborne		0.99	0.92
Presqu'île	0.001		0.91
Prince Edward Island	0.08	0.09	

1. Genetic Identity = $I_k = \sum_i x_i y_i \left(\sum_i x_i^2 \sum_i y_i^2 \right)^{-\frac{1}{2}}$, where x_i and y_i are the frequencies of the i-th allele at the k-th locus in populations X and Y respectively (Nei 1974, 1975).

2. Genetic Distance = $D_k = -(\log_e I_k)$ (Nei 1974, 1975).

Larus argentatus

Genetic identities and genetic distance at the Alb locus are recorded in Table 11. Average values over all nesting locations sampled are $\bar{I}$ = 0.98 ± 0.01 and $\bar{D}$ = 0.02 ± 0.01. ALB-98 alleles are found only in samples from Lake Ontario (Presqu'île and Scotch Bonnet Island, Table 6), which accounts for the slight differences observed among all pairwise combinations, and the uniform identity distributions.

Average genetic identities and genetic distances for the Ldh-A locus are $\bar{I}$ = 0.47 ± 0.36 and $\bar{D}$ = 1.04 ± 1.07. Pairwise combinations recorded in Table 12 show a considerable range in genetic identity and genetic distance. Comparisons of colonies separated by approximately 2000 km (Prince Edward Island - Presqu'île I = 0.20; Prince Edward Island - Port Colborne I = 0.05) with colonies 16 km apart (Port Colborne - Mohawk Island I = 0.33; Presqu'île - Scotch Bonnet Island I = 0.04) indicates that spatial separation of nesting locations is not an explanation of the genetic distance at this locus.

Genetic identities and genetic distances over all loci are $\bar{I}$ = 0.90 ± 0.15 and $\bar{D}$ = 0.12 ± 0.19. Surveying all pairwise combinations (Table 13), those combinations of Chantry Island with either Port Colborne, Presqu'île, Limestone Island and Prince Edward Island appear to exceed these means and associated standard deviations.

Interspecific Genetic Identities and Genetic Distances

Interspecific allelic variation was detected at three loci: Oalb, Alb and Ldh-A. Samples from all nesting locations of Larus argentatus are monomorphic for OALB-99, and colonies from Lake Ontario were polymorphic at the Alb locus with two allelic variants (ALB-98, ALB-100)

Table 11: Single Locus Genetic Identities[1] and Genetic Distances[2] at the Alb Locus in Samples from Seven Nesting Locations of Larus argentatus (genetic identities above the diagonal, genetic distances below the diagonal).

	Larus argentatus						
	Port Colborne	Presqu'île	Limestone Island	Prince Edward Island	Chantry Island	Scotch Bonnet Island	Mohawk Island
Port Colborne		0.98	1.00	1.00	1.00	0.98	1.00
Presqu'île	0.02		0.98	0.98	0.98	0.98	0.98
Limestone Island	0.00	0.02		1.00	1.00	0.98	1.00
Prince Edward Island	0.00	0.02	0.00		1.00	0.98	1.00
Chantry Island	0.00	0.02	0.00	0.00		0.98	1.00
Scotch Bonnet Island	0.02	0.00	0.02	0.02	0.02		0.98
Mohawk Island	0.00	0.02	0.00	0.00	0.00	0.02	

1. Genetic Identity = $I_k = \sum_i x_i y_i \left(\sum_i x_i^2 \sum_i y_i^2 \right)^{-\frac{1}{2}}$, where x_i and y_i are the frequencies of the i-th allele at the k-th locus in populations X and Y, respectively (Nei, 1974, 1975).

2. Genetic Distance = $D_k = -(\log_e I_k)$ (Nei, 1974, 1975).

Table 12: Single Locus Genetic Identities[1] and Genetic Distances[2] at the Ldh-A Locus in Samples from Seven Nesting Locations of Larus argentatus (genetic identities above the diagonal, genetic distances below the diagonal).

	Larus argentatus						
	Port Colborne	Presqu'île	Limestone Island	Prince Edward Island	Chantry Island	Scotch Bonnet Island	Mohawk Island
Port Colborne		0.99	0.99	0.05	0.75	0.05	0.33
Presqu'île	0.01		0.98	0.20	0.56	0.04	0.37
Limestone Island	0.00(3)	0.02		0.00	0.42	0.00	0.28
Prince Edward Island	0.11	1.00	?		0.72	0.20	0.53
Chantry Island	0.75	0.58	0.57	0.28		0.64	0.92
Scotch Bonnet Island	0.97	3.26	?	1.63	0.44		0.89
Mohawk Island	1.13	1.00	1.32	0.63	0.03	0.12	

1. Genetic Identity = $I_k = \sum_i x_i y_i \left(\sum_i x_i \sum_i y_i \right)^{-\frac{1}{2}}$, where x_i and y_i are the frequencies of the i-th allele at the k-th locus in populations X and Y, respectively (Nei, 1974, 1975).

2. Genetic Distance = $D_k = -(\log_e I_k)$ (Nei, 1974, 1975).

Table 13. Total Genetic Identities[1] and Genetic Distances[2] from Samples from Four Nesting Locations of Sterna hirundo, and Samples from Seven Nesting Locations of Larus argentatus (genetic identities above the diagonal, genetic distance below the diagonal).[3]

		Sterna hirundo				Larus argentatus						
		Port Colborne	Presqu'île	Limestone Island	Prince Edward Island	Port Colborne	Presqu'île	Limestone Island	Prince Edward Island	Chantry Island	Scotch Bonnet Island	Mohawk Island
Sterna hirundo	Port Colborne		0.99	0.99	0.99	0.89	0.89	0.88	0.88	0.60	0.92	0.94
	Presqu'île	0.003[4]		0.99	0.99	0.89	0.89	0.88	0.88	0.60	0.92	0.94
	Limestone Island	0.01	0.00		0.96	0.76	0.76	0.75	0.75	0.75	0.70	0.79
	Prince Edward Island	0.003	0.01	0.01		0.89	0.89	0.88	0.88	0.60	0.92	0.94
Larus argentatus	Port Colborne	0.12	0.12	0.27	0.12		0.99	0.99	0.95	0.60	0.94	0.98
	Presqu'île	0.12	0.12	0.27	0.12	0.02		0.99	0.96	0.61	0.94	0.97
	Limestone Island	0.13	0.13	0.29	0.13	0.004	0.003		0.95	0.60	0.93	0.96
	Prince Edward Island	0.12	0.12	0.27	0.12	0.05	0.04	0 .06		0.60	0.95	0.97
	Chantry Island	0.51	0.51	0.29	0.51	0.51	0.50	0.51	0.51		0.98	0.99
	Scotch Bonnet Island	0.08	0.08	0.36	0.06	0.06	0.06	0.07	0.06	0.02		0.99
	Mohawk Island	0.06	0.06	0.29	0.06	0.03	0.03	0.04	0.03	0.004	0.01	

1. Genetic Identity = $I = J_{xy}(J_x J_y)^{-\frac{1}{2}}$, where J_{xy}, J_x and J_y are the arithmetic means of $\sum_i x_i y_i$, $\sum_i x_i^2$ and $\sum_i y_i^2$ respectively over all loci (Nei, 1974;1975).

2. Genetic Distance = $D = -(\log_e I)$ (Nei, 1974;1975).

3. Although only two significant digits are routinely used in this work, the use of three digits in mandatory when two digits would indicate D = 0.00.

4. See Appendix 7 for loci included in pairwise combinations.

detected. Sterna hirundo samples were monomorphic for both OALB-100 and ALB-100. The Ldh-A locus has five allelic variants over both species. The 100 allele was found in all samples from all locations except the Limestone Island gullery. The Ldh-A locus is monomorphic for the 100 allele in S. hirundo. The identical electrophoretic mobility of the LDH-A 100 allele in both species does not allow distinction of the two variants. However, the 100A allele found in samples from S. hirundo has a different thermostability than does the 100B allele found in samples from L. argentatus. This observed alteration of a basic enzymatic trait implies a genetic difference between these two species at this locus.

The average interspecific genetic identities (I = 0.83 ± 0.11) and genetic distance (D = 0.20 ± 0.14) over all loci is calculated from 28 pairwise combinations (Table 11). Considering these structural loci, these two species appear to be as genetically similar as some of the populations of L. argentatus are to each other, at least at the loci compared.

The data show that co-dominant autosomal polymorphic loci exist in the sampled portion of both species' genomes. Due to their polymorphic nature, these loci may be exploited as genetic markers to monitor populations. The spatial arrangement of allele frequencies and the genetic divergence estimates imply both species have different population structures. S. hirundo populations appear to be panmictic, at least over the sampling range. The L. argentatus gene pool appears relatively heterogeneous with a discreet Atlantic Coast population and a Great Lakes demic population.

DISCUSSION

Non-Genetical Explanations

In assessing the results, artifacts arising from the methods used must be considered. Artifacts may arise from the alteration of the *in vivo* environment to the electrophoretic environment. These changes may result in shifts of protein structure, which will result in concommitant changes of the electrophoretograms. This type of artifact should be uniform for specific proteins assayed from all samples. However, deciphering this problem is beyond the scope of this work. Changes in protein electrophoretic mobilities, and total electrophoretograms may arise from altered physiological states, and pathological conditions (Smithies, 1959B). Storage conditions may affect both enzyme activity and electrophoretic mobilities (M.L. Tracey, pers. comm.). However, eighteen months of storage caused no changes in either electrophoretic mobilities, or enzyme action in comparison to the same fresh sera-saline mixture electrophoretic pattern.

Depending on the definition of artifacts, they may arise from statistical analysis. The use of Nei's Statistics (Nei, 1974; 1975) for intraspecific and intergeneric comparisons relise on the dogmatic assumption that electromorphs are genetically identical. However, the hypothesis of the 'wandering electrophoretic profile' (Kimura and Ohta, 1974; Wright, 1978), and hidden variability in electromorph classes (Singh *et al.*, 1976; Prakash, 1977) suggest that the aforementioned assumption may not be valid in intergeneric comparisons. As a result, genetic distances may be underestimated, and the high genetic identity may be an artifact due to the use of this statistic.

Genetic Variability

Sterna hirundo: Variability was detected at only two loci in this species; blood serum esterase (*Est-5*) and ovo-esterase (*Oest-1*). OEST-1 is a product of the maternal genotype and female birds are heterogametic; therefore *Oest-1* is a co-dominant autosomal locus (see Mandel *et al.*, 1978). If this locus were sex linked, only single banded electrophoretograms would be expected. Double and single banded electrophoretograms were observed and their frequencies did not depart from Hardy-Weinberg equilibrium expectations. Both ovo-transferrin (conalbumin) and ovo-albumin are secreted by the magnum of the oviduct and their synthesis and subsequent secretion are under hormonal control (Sharma *et al.*, 1976; Breathnach *et al.*, 1977) OEST-1 may also be synthesized by cells in the oviductal wall and may be similarly controlled (see Grunder and Hollands, 1977; Mandel *et al.*, 1978). Furthermore, this enzyme is not synonymous with blood serum esterases due to electrophoretic mobilities and substrate specificities. Manwell and Baker (1975) reported ovo-esterase polymorphisms in *Passer domesticus*, *Hirundo tahitica neoxena* and *Petrochelidon ariel*.

Although five zones of esterase activity were resolved from the blood serum, only EST-5 was polymorphic. The remaining four zones of activity may possess allelic variants not resolved by the electrophoretic system used (Singh *et al.*, 1975; Coyne, 1976; Singh *et al.*, 1976; Prakash, 1977). Avian esterase polymorphisms have been previously reported (Corbin *et al.*, 1974; Manwell and Baker, 1975; Smith and Zimmerman, 1976; Peden and Whitney, 1976).

Larus argentatus: Variability was detected at two loci in this species; blood serum albumin (Alb) and lactate dehydrogenase (Ldh-A). Baker (1975) reported an albumin polymorphism in Zonotrichia leucophrys populations from Colorado. Albumin polymorphisms were also reported from samples from Icteridae. Five alleles at a single autosomal locus generated double-banded homozygotes and triple-banded heterozygotes (Smith and Zimmerman, 1976). These observations vary from my results. This discrepancy may be explained by considering that the faster (light) band, which Smith and Zimmerman assumed to be under the genetic control of the albumin locus, is in fact a definite pre-albumin and controlled by a separate locus. This would generate single-banded homozygotes and double-banded heterozygotes, which would be comparable to the electrophoretic phenotypes that I observed.

Allelic variability at the Ldh-A locus is more pronounced with four allelic variants; the 100B allelic product from L. argentatus samples exhibits a greater thermostability than the 100A allelic product from S. hirundo samples. The blood serum LDH in both species appears to be the transcriptional product of one locus for the following reasons:

(1) This enzyme has a pronounced substrate affinity for lactate and not α-hydroxybutyric acid,

(2) B and C forms of LDH are known to hydrolyse both substrates, but the C form has a restricted tissue specificity (Market, 1975), and

(3) Due to the lack of substrate specificity of LDH-B, the resolved form of LDH has been tentatively identified as LDH-A (Market et al., 1973; Whitt et al., 1975).

The LDH-A electrophoretic phenotypes observed in my study vary from those descriptions previously published (Market et al., 1973; Corbin et al.,

1974; Market, 1974; Smith and Zimmerman, 1976). The typical five-banded electrophoretogram was not observed in either S. hirundo (one band only), or L. argentatus (maximum of two bands), or L. delawarensis (maximum of three bands). These results may be explained by considerations of hidden variability in electromorph classes. The charge differentials between the tetramers may be slight and preclude their resolution. The largest charge differentials would be expected between the two homotetramers, and consequently the LDH-A bands may be composed of mixtures of the five tetramers (Singh et al., 1975; 1976; Coyne, 1976; Prakash, 1976; Johnson, 1977).

LDH genic variability is generally thought to be uncommon in birds (Powell, 1975A), as most investigations of wild avian populations have found LDH to be monomorphic (Nottebohm and Selander, 1972; Baker, 1975; Handford and Nottebohm, 1975; Manwell and Baker, 1975). However, Corbin et al. (1974) and Smith and Zimmerman (1976) reported LDH polymorphisms in the populations that they surveyed. Heat sensitive allelic variants have been reported to occur (Turner, 1973; Cockburn, 1974; Singh et al., 1975; 1976; Prakash, 1977), although not in birds. The nature of the intergeneric LDH thermostability allelic variants I observed, appears to be a DNA encoded amino acid substitutional change due to the magnitude of the inactivation. However, these results may be artifactual as only crude enzyme preparations were used. Also, heat-sensitivity may be conferred by either regulatory events (Pandey, 1977; McDonald and Ayala, 1978; Hedrick and McDonald, unpublished manuscript), or by post-transcriptional events (Garapin et al.. 1978; Mandel et al., 1978; O'Farrell et al., 1978).

The degree of gene pool heterogeneity at the Ldh-A locus in the L. argentatus colonies samples appears quite pronounced for a large mobile

vertebrate. However, Ehrlich and Raven (1969) indicate gene pool heterogeneity may not be unusual in wild avian populations, which has been shown using electrophoresis (Corbin et al., 1974), electrophoretic and vocal dialect analysis (Nottebohm and Selander, 1972; Baker, 1975; Handeford and Nottebohm, 1975), and colour morph frequency (Cooch and Beardsmore, 1958; O'Donald, 1972; 1973; 1974; O'Donald et al., 1974A, 1974B; Cooke et al., 1975; O'Donald and Davis, 1975; Davis and O'Donald, 1976A; 1976B; Jefferies and Parslow, 1976; Rockwell and Cooke, 1977).

Average heterozygosities for both L. argentatus and S. hirundo are lower than most published estimates of avian genetic variability (Corbin et al., 1974; Baker, 1974; Handeford and Nottebohm, 1975; Manwell and Baker, 1975; Smith and Zimmerman, 1976), except for Zonotrichia capensis (Nottebohm and Selander, 1972) and Aplonis cantoroides (Corbin et al., 1974). This range of average heterozygosities appears to contradict the argument of Powell (1975A). Levels of genetic variability in birds appear to be consistent with other surveyed taxa, a result similar to that reported by Hedgecock and Nelson (unpublished manuscript) for decapod crustaceans. However, if experimenters are selecting loci that are polymorphic to principally investigate population structure (Tracey, 1974), then these surveys may represent non-random genome sampling. Estimates of genetic variability may be inflated, although the results may generate descriptions of population structure.

Genetic Identity and Genetic Distance

Interspecific genetic identities and genetic distances in Drosophila (Ayala, 1975; Avise, 1976; Dobzhansky, 1976), Taricha (Hedgecock, 1974; 1975), and Lepomis (Avise and Ayala, 1975; Avise, 1976; Avise and Smith, 1977), are greater than observed in my study. The high genetic identity ($\bar{I}$ = 0.83 ± 0.11) and low genetic distance ($\bar{D}$ = 0.20 ± 0.14) observed may be a reflection of species sample size. However, values reported for the Icteridae ($\bar{I}$ = 0.797 ± 0.116; $\bar{D}$ = 0.237 ± 0.142) (Smith and Zimmerman, 1976) appear similar to my results. These low values may reflect processes, or the lack of processes affecting the avian genome. Wilson (1976) argues that there has been slow chromosomal evolution and slow loss of hydridization potential in birds, which may indicate a slow rate of genetic divergence in this taxon. The low genetic distance values are consistent with Wilson's tentative conclusion.

The intraspecific genetic identity and genetic distance estimates for S. hirundo ($\bar{I}$ = 0.99 ± 0.01; $\bar{D}$ = 0.01 ± 0.01) appear to agree with published results of population divergence values (Ayala, 1975; Tracey et al., 1975; Avise, 1976; Dobzhansky, 1976; Avise and Smith, 1977). The values reported for L. argentatus ($\bar{I}$ = 0.90 ± 0.15; $\bar{D}$ = 0.12 ± 0.19) exceed most published results for intraspecific genetic identity and genetic distance estimates. It is possible that the considerable genome divergence detected by electrophoretic methodologies may not reflect total genome divergence and correlated reproductive isolation (Avise, 1976), although the converse has also been observed (Ayala, 1975).

Genetic distance measures the amount of electrophoretically detectable amino acid substitutions per 100 codons, that has occurred between the two gene pools at the surveyed loci (Nei, 1975). Between L. argentatus and S. hirundo two base changes per 10^3 codons have occurred, since the clado-genetic event that resulted in the formation of the two genera. This statement must be qualified, since only two species have been examined. Intraspecific genetic distances indicate the existence of considerable differences between these two species in terms of gene pool sturcture. Sampled colonies of S. hirundo have an average of six base substitutions per 10^5 codons, while L. argentatus colonies have an average difference of twelve base changes per 10^4 codons. These estimates of mutational events indicate that different processes or different magnitudes of these processes may be differentially affecting the surveyed portions of the genomes.

Mechanisms Affecting Genetic Variability

The genetic structure of a population can be altered by either random (mutation or drift) or directional (selection or migration) events (Li, 1955; Flaconer, 1964; Wright, 1968; 1969; 1970; 1976; Ehrlich and Raven, 1969; Richardson, 1970; Endler, 1973; Nei, 1974; Ayala, 1975; 1976, Avise and Ayala, 1977). If a mutational event is rare ($q = 10^{-5}$) then non-detection probabilities ($n = 3$; $p = 0.99999$; $n = 50$; $p = 0.999$) indicate that this mechanism may be relatively inconsequential in small sample surveys, and will not be considered further. The classical effect of gene flow is to shift diverging gene pool allele frequencies towards the mean population allele frequencies (Li, 1955; Falconer, 1964; Wright, 1970). Both genetic drift and selection can cause gene pool heterogeneity. Possibly one or all of these mechanisms are operative in S. hirundo and L. argentatus.

Gene Flow

Migration as gene flow is dependent on the eco-demographic and ethological parameters describing the donor and the recipient population subunits. Mass ringing data cannot be used uncritically as a gene flow estimator as the majority of ringing returns are from dead individuals (see Paynter, 1949). Consequently individual or pair migration into a new colony may not be *a priori* evidence of gene flow, unless coupled with pair reproductive success. In cases of colony mergence, driven by nest-site habitat deterioration (Austin, 1949; 1951; McNicholl, 1975), gene flow may be accelerated. The results of the gametic sampling will then be dispersed with the return of colony members, if original nest-site amelioration occurs.

S. hirundo: Austin (1938; 1940; 1941; 1949; 1951; 1953) indicated that established pair nesting is restricted to a specific social and geographical location unless nest-site deterioration or death of one of the pair occurs. This combination of site tenacity and group adherence, in conjunction with mate fidelity (Palmer, 1941A) constrains individuals in time and space, subsequently promoting reproductive success.

Colony members from the Great Lakes and the Atlantic coast converge on migration and on the wintering grounds (Austin, 1953; Haymes and Blokpoel, 1978). However, the question of social group integrity throughout this period of the life cycle is unknown, although Haymes (unpublished data) suggests that considerable mixing of juveniles does occur. Palmer's (1941A) observation on time and location of mate choice in *S. hirundo* suggests that this phase of courtship occurs on the wintering areas and on the vernal

migration. These data suggest that an individual mating for the first time may have an equal chance of choosing a mate from any colony on either the Great Lakes or the Atlantic coast. This drawing of immigrants from the same pool would produce genetic uniformity or panmixia in the population (Williams et al., 1974). Austin's (1951) data can be used to calculate estimates of gene flow within the Cape Cod terneries (Table 14). However, the relationship between the effective population size (n_{eff}) and the censused population sizes are unknown (see Kimura and Ohta, 1972). Effective population size was estimated by using the censused population size, and increasing and decreasing this value. Calculated migration rates ($m = 1.4 \times 10^{-2}$; $N_{eff} = 2.5 \times 10^{4}$) are indicative of large amounts of gene flow occurring in the population even when the population size is increased to four times the censused population size. The reduction of S. hirundo colonies and population numbers (Hunter, 1976) may further decrease the effective population size, especially if population numbers cycle (Kimura and Ohta, 1972; Nei, 1975), and subsequently increase gene flow ($m = 0.72$; $n_{eff} = 500$). Austin (1951) realized the importance of these migrants in affecting the genetic structure of S. hirundo, however, the low occurrence frequency of migrants did not negate his theories of group adherence and site tenacity.

The observed gene pool homogeneity at the Oest-1 locus can be explained by gene flow. Considering that OEST-1 is a product of a co-dominant autosomal locus implies that the regulatory gene(s) affecting expression is sex-linked; that is the gene product is found only in reproductively active females. Consequently this locus is included in both male and female genomes, which are subject to the averaging effect of gene flow. Gene pool uniformity

Table 14: Estimated Genetic Migration Rates for the Sterna hirundo Colonies at Cape Cod, Massachusetts (From Austin, 1951).

Effective Population Size (n_{eff})[1]	Number of Migrants/year	Number of Migrants/generation	M^2
5.0×10^2	90	360	7.2×10^{-1}
10^3	90	360	3.6×10^{-1}
5.0×10^3	90	360	7.2×10^{-2}
10^4	90	360	3.6×10^{-2}
1.5×10^4	90	360	2.4×10^{-2}
2.0×10^4	90	360	1.8×10^{-2}
2.5×10^4	90	360	1.4×10^{-2}
5.0×10^4	90	360	7.2×10^{-3}
10^5	90	360	3.6×10^{-3}
10^6	90	360	3.6×10^{-4}
10^9	90	360	3.6×10^{-4}

Origin of Migrants into the Cape Cod Terneries (n_{eff} = 10,000)

Location of Initial Migrant Banding	Number of Migrants/Generation	M
South	25	2.5×10^{-3}
North	6	6.0×10^{-4}
West	20	2.0×10^{-3}
Vineyard	410	4.1×10^{-2}

1. Effective population size (n_{eff}) was not available, so step increments of the censused population size were used in estimating values of migration rates.
2. Genetic Migration Rates = $M = \left(\frac{\text{Number of Migrants}}{\text{Generation}}\right) \cdot \frac{1}{n_{eff}}$ (Kimura and Ohta, 1972)

at the Est-5 locus requires no subtle interpretation of genetic mechanisms, except that the extent of genetic migration present in the population is sufficient to generate the observed results. The migratory movements of adults, the location of initial mate selection, in conjunction with juvenile pelagic wandering can negate any obvious gene pool heterogeneity, and produce uniform allele frequencies across the sampling range.

L. argentatus: The aforementioned concepts of larid coloniality apply equally to L. argentatus as these concepts apply to S. hirundo, yet they appear to affect different genetic responses in both species. If gene flow is assumed to be producing the observed gene pool heterogeneity in the L. argentatus colonies, then this reduction may arise from basic ethological mechanisms differing between the two species (Ehrlich and Raven, 1969; Richardson, 1970). Intuitively, the intensity of ethological mechanisms affecting the breeding cycle, and generating the genetic structure of a population may be modified by behaviour expressed during the non-reproductive portion of the life cycle.

The relatively sedentary habits of L. argentatus may accentuate the coloniality expressed during the reproductive season. Both reproductive and non-reproductive periods of the life cycle appear to be keyed to specific geographical locations (Tinbergen, 1960; Kadlec and Drury, 1968). Information on general dispersal trends indicate that the Atlantic coast and the Great Lakes populations are separate (Kadlec and Dryry, 1968; Moore, 1976; Threlfall, 1978). Furthermore, data also suggest that the Great Lakes population is subdivided into eastern and western subunits (Hofslund, 1959; Smith, 1959; Moore, 1976). LDH-A gene pool summations (Table 8) are in apparent agreement with these observations as removal of Prince Edward

Island samples from the pooled data drastically reduced the deviation from Hardy-Weinberg equilibrium expectation, indicating gene pool homogeneity. The residual gene pool heterogeneity from all Great Lakes/both years may be the result of two subgroups, or the existence of subgroup boundary mixing. The geographical distributions of the ALB-98 allele corresponds to general movement patterns. Moore's (1976) statement on dispersal trends of eastern Lake Ontario L. argentatus, implies gene flow from this area may be primarily eastwards. This restriction would not allow the spread of this allele into colonies of the other Great Lakes.

The gene pool heterogeneity observed in sampled colonies may be ascribed to differential selection, which is masking a similar process to that described for S. hirundo.

Selection

Selection alters gene frequencies and the resultant genotypic proportions in a quantitative and qualitative fashion through differential reproductive success (Li, 1955; Falconer, 1964). The influence of selection is not on the genotype per se, but rather on the phenotypic expression of the genotype (Waddington, 1976), and there can be no selection if a locus is monomorphic (Wright, 1969). Selective pressures arise from either biotic or abiotic elements of the ecosystem. Although both species nest in conjunction, this does not necessarily imply selection will affect both species equally or in the same manner.

S. hirundo: The gene pool uniformity over the sampling range suggests that several possibilities for selective pressures may exist. Selective pressures may be equal over the sampling range. Conversely, selection may

not operate during the reproductive stage, but during the migratory period of the life cycle. A third selective process may operate only on the regulatory genes that are interrelated to the observed variability at the structural loci.

If selection operates during the reproductive period, then uniform selective pressures must be affecting the population across the sampled area. If selection pressures were not uniform, then gene pool divergence would result (Endler, 1973; Williams et al., 1974), requiring gene flow to negate this effect. If selection coefficients are uniform and large, then the data would deviate from Hardy-Weinberg equilibrium expectation, and would be detectable by the total organismal sample size (n = 88). Since this last statement is in contradiction to observed results, the alternative is low uniform selective pressures across the sampled range.

Alternatively, selection may act on individuals on migration and on the wintering range. Flyway convergence and identical wintering ranges (Haymes, unpublished data) suggests equal selective pressures on individuals from the Great Lakes, and the Atlantic coast colonies as indicated by the high juvenile mortality (Austin, 1940; 1942; 1949; Palmer 1941A). Such a selective regime would generate uniform genotype distributions over the sampling range, and this selection would not be countered by gene flow as all members of all colonies would have essentially similar genetic components. Increased winter range fitness would decrease winter range selection (Lowther, 1977), and concommitently increase the size of the organismal sample necessary to detect the effects of selection.

Although selective pressures may shape the population on the wintering range, the Oest-1 locus is expressed only during the egg-laying period.

Winter range selection cannot be invoked to explain the gene pool homogeneity at this locus. However, if this locus is linked to another locus, which is being affected by winter range selection, then both loci would appear to respond to winter range selection (Kimura and Ohta, 1972; Hedrick, unpublished manuscript). Alternatively, OEST-1 may be exposed to a different selection, that involves the enzymes' physiological function in either chick development or the hatching process.

L. argentatus: Ldh-A gene pool heterogeneity may arise from differential selective pressures that vary with colony location (Endler, 1973). Furthermore, the physiological function of LDH in anaerobic metabolism (Everse and Kaplan, 1973), and the avian ventilatory mechanism, in conjunction with an alteration of selective pressures following species (Avise, 1976), may account for the different patterns of genetic variability in the two species. The long distance migration undertaken by S. hirundo (Austin, 1938; 1940; 1942; 1953; Palmer, 1941A; 1941A; Haymes, unpublished data; Haymes and Blokpoel, 1978) may result in conditions of temporary anaerobiosis during flight. This may create an increased selective pressure maintaining the observed LDH monomorphism. However, the lack of genetic variability at this locus in S. hirundo is not evidence for selection (Wright, 1969). In L. argentatus, the slow dispersal, the soaring method of flight, and the relatively sedentary habits (Kadlec and Drury, 1968; Moore, 1976), may prevent conditions of anaerobiosis from developing in this species. This would reduce the physiological constraints on LDH, and reduce selection allowing greater genetic variability to be maintained at this locus. This variability may be maintained, as well, by differential selection or by

heterosis (Li, 1955; Falconer, 1964; Wright, 1968; 1969; 1977; Ehrlich and Raven, 1969; Endler, 1973).

Genetic variability at the Alb locus may be maintained by balancing selection, or the 98 allele may be selected against. The heterozygous state that this allele was found in, and the restricted geographical distribution precludes the possibility of any further definitions of the genetic variability at this locus.

Since selection affects population structure, alterations in selective pressures may alter the distributional characteristics of a population or species. The increasing exploitation by L. argentatus of wastes generated by man's activity (Kadlec and Drury, 1968; Hunt, 1972), has been related to the increase of L. argentatus juveniles and sub-adults wintering on the Great Lakes (Moore, 1976). Furthermore, these non-migrants have a lower rate of mortality than the migrants (Moore, 1976). This shift in selection to favour non-migrants may be indirectly generating the low gene flow, especially if the development of group adherence and site tenacity is an ontogenetic process. The summation of these events would then be gene pool heterogeneity, the proximate cause being low levels of gene flow, while the ultimate cause would be selection.

Uniform selection as described for S. hirundo, may also generate gene pool heterogeneity. Since selection operates on the phenotype (Waddington, 1976), different phenotypes may have the same fitness, depending upon the total phenotypic expression.

The gene pool heterogeneity may be due to selective pressure differing in the different colony environments. However, both polymorphic loci appear to have similar geographic distribution patterns in the sampled areas.

Consequently, equal selective coefficients would have to be assigned to each of the structural loci. This equality would appear unlikely, and suggests that a reduction in gene flow is generating the observed result. If both structural loci are controlled by the same regulatory gene(s), then selection at the regulatory loci may not be discounted. In such a system, both structural loci would show equal selection coefficients (Hedrick, pers. comm.). To clarify this situation, both larger organismal and loci sample sizes are required.

Small Sample Size

Small sample surveys generally do not detect rare alleles yielding underestimates of population genetic variability. Conversely, if a rare allele is detected, population allelic frequencies would be inflated. These sampling errors may lead to conclusions of gene pool heterogeneity, or homogeneity, when the converse is true. Such a process may be occurring with the sampled populations of both species. L. argentatus gene pool heterogeneity at the Ldh-A locus may arise from these errors. Further complicating the clarification of the results are the processes of population sampling (Li, 1955; Cain and Curry, 1963, in Wright, 1970; Wright 1970; Kimura and Ohta, 1972), and gametic sampling (Li, 1955; Wright, 1970), and the number of alleles at this locus. As four alleles assort to produce ten genotypes, small sampling may detect disproportionate amounts of one genotype or the other. Also occurring is lack of sensitivity to Hardy-Weinberg equilibrium expectations deviations (Hubby and Lewontin, 1966). All of these factors may combine to generate data that can fail to

detect the actual population structure.

Considerations of genetic data at a single locus may convincingly argue that small sample data represent an artifactual situation. However, by invoking ethological and eco-demographic considerations (Richardson, 1970), and genetic data from other polymorphic loci, a countering argument can be proposed. However, the data for the estimation of some of these parameters is lacking, and small sample errors cannot be definitely refuted.

Genetic Markers

Assessment of the utility of polymorphic loci as genetic markers should follow the criteria established by Maurer (1968). Ease of sampling to reduce colony disturbance should be the next major criteria in sampling. Oest-1 would be the prime choice for a genetic marker in S. hirundo. The remaining three loci may serve as population markers, however bleeding of adults would result in severe colony disturbances. If either Ldh-A, or Est-5 or Alb were used to monitor the populations, then my sampling procedure (see Materials and Methods) should be used.

Correlated with studies of genetic markers, is necessary eco-demographic data (Tracey, 1974). If both systems generate approximate results, then the duplicity may indicate that the genetic markers may function alone in population monitoring. The eco-demographic data are required because changes in allelic frequencies may arise from multiple sources (Dobzhansky, 1966). Parameters generated by or approximated by such data, when coupled with larger sample sizes, may allow the assessment of the major mechanism(s) influencing the gene pool structure of these two species.

One good tern deserves another.

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Appendix 1

A Listing of

Solutions, Buffers and Chemical Composition

Starch Gel Electrophoresis

Poulik Gel Buffer (pH 8.65)

9.08 g of Tris (2-Amino-2-hydroxymethyl-1,3-propanediol)

1.29 g of citric acid

Dissolved in 500 ml of distilled water, pH adjusted to 8.65 with 4.0 N sodium hydroxide or 1.0 N hydrochloric acid and diluted to 1 litre with distilled water.

Poulik Bridge Buffer (pH 8.1)

18.55 g of boric acid

2.4 g of sodium hydroxide

Dissolved in 500 ml of distilled water, pH adjusted to 8.1 with 4.0 N sodium hydroxide or 1.0 N hydrochloric acid and diluted to 1 litre with distilled water.

Polyacrylamide Disc Gel Electorphoresis

Stock Solutions

Solution A (pH 8.9)

48 ml of 1.0 N hydrochloric acid

36.6 g of Tris (2-amino-2-hydroxymethyl-1,3-propanediol)

0.23 ml of Temed (N,N,N',N'-tetramethylethylenediamine)

Adjusted to pH 8.9 and diluted to 100 ml with distilled water.

Solution B (pH 6.9)

48 ml of 1.0 N hydrochloric acid

5.98 g of Tris (2-amino-2-hydroxymethyl-1,3-propanediol)

0.46 ml of Temed (N,N,N',N'-Tetramethylethylenediamine)

Adjusted to pH 6.9 and diluted to 100 ml with distilled water.

Solution C

28.0 g of acrylamide

0.735 g of Bis (methylene-bis-acrylamide)

Dissolved and diluted to 100 ml with distilled water.

Soltuion D

10.0 g of acrylamide

2.5 g of Bis (methylene-bis-acrylamide)

Dissolved and diluted to 100 ml with distilled water.

Solution E

4 mg riboflavin

Dissolved and diluted to 100 ml with distilled water.

Solution F

40 g sucrose

Dissolved and diluted to 100 ml with distilled water.

Small Pore Solution II

0.14 g ammonium persulphate

Dissolved and diluted to 100 ml with distilled water.

Reservoir Stock Buffer (pH 8.3)

28.0 g glycine

6.0 g Tris (2-amino-2-hydroxymethyl-1,3-propanediol)

Dissolved in 500 ml of distilled water, adjusted to pH 8.3 and diluted to 1000 ml.

Working Solutions

Stacking Gel (Large Pore) Solution

1.25 ml Solution B

2.50 ml Solution D

1.25 ml Solution E

5.00 ml Solution F

Small Pore Gel Solution

3.5 ml Solution A

7.0 ml Solution C

3.5 ml distilled water

14.0 ml Small Pore Solution II

Layering Solution

0.1 ml of Photo-Flo 200

100 ml distilled water

Electrophoresis Reservoir Buffer

100 ml Reservoir Stock Buffer

Dilute to 1000 ml with distilled water.

Coomassie Blue Stock Solution

2.5 g Coomassie Brilliant Blue R250 C.I. 42660

0.1 g sodium EDTA (sodium ethylenediaminetetraacetate)

0.2 M Sodium Phosphate Buffer (pH 6.8)

31.202 g sodium dihydrogen orthophosphate

Dissolve and dilute to 1000 ml with distilled water.

71.63 g disodium hydrogen orthophosphate

Dissolve and dilute to 1000 ml with distilled water

For 2 litres of buffer:

980 ml of sodium dihydrogen orthophosphate solution

1020 ml of disodium hydrogen orthophosphate solution

Appendix 2

LDH-A 100 Thermostabilities

Appendix 2

LDH-A^{100} Thermostabilities

Electrophoretograms of the LDH phenotypes observed are summarized in Figure 2A. The Ldh-A^{100} allele is fixed in all samples from all nesting locations of Sterna hirundo, and is found in samples from six of the seven Larus argentatus nesting locations. Initial tests suggested that S. hirundo LDH-A^{100} was more thermolabile than that from L. argentatus. After a two minute exposure to 60¼C, spectrophotometric criteria indicate that S. hirundo LDH-A^{100} activity is reduced to 50% to 60% of the control activity (Figure 2B). Increasing the length of exposure time did not appear to cause a further reduction in enzyme activity.

LDH-A^{100} from L. argentatus (Figure 2C) appeared remarkedly thermostable in comparison, although the control activity was considerably less than that observed in LDH-A^{100} from S. hirundo. An apparent slight decrease of activity was evident with increasing exposure times.

When LDH-A from Larus delawarensis was analysed a three banded electrophoretogram was observed. Thermostability profiles (Figures 2D, 2E) of all three electromorphs appear to resemble the profiles for LDH-A^{100} from L. argentatus. Reduction of control activity of the three electromorphs with respect to exposure times were tested by Two-Way Analysis of Variance. All F values claculated were not significant ($P > 0.05$).

With reference to Figure 2B, 2C, 2D and 2E, it is interesting to note the general similarity between the LDH thermostability profiles of both L. argentatus and L. delawarensis. Since no significant decrease of enzyme

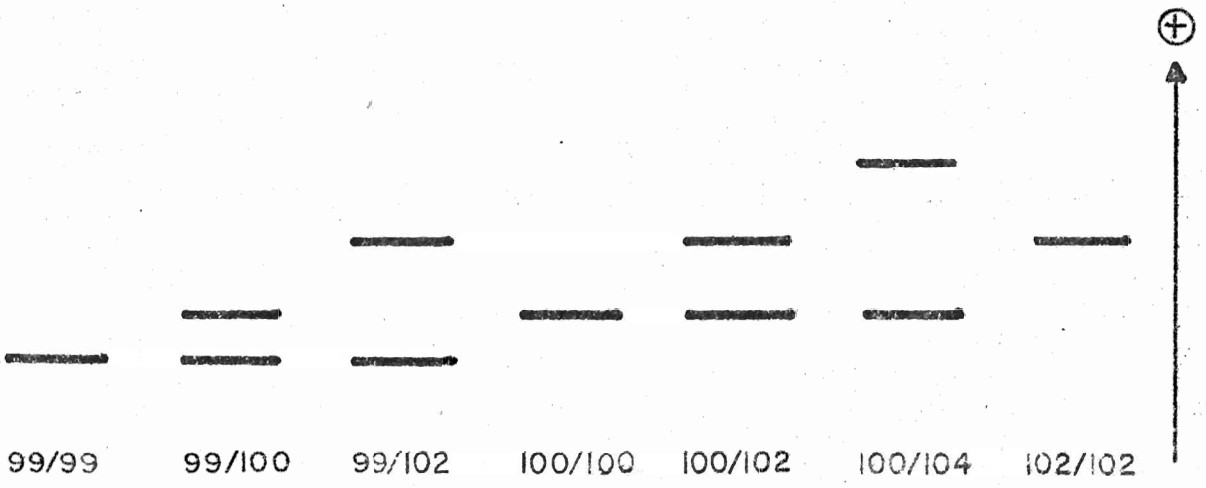


Figure 2A Diagrammatic Summarization of Ldh-A Variants as Resolved by Polyacrylamide Disc Gel Electrophoresis. Genotypic interpretations are recorded below the respective electrophoretic phenotypes.

Figure 2B Enzyme Activity in Relation to Length of Exposure Times for Ldh-A^{100A} from *Sterna hirundo*

Ldh-A^{100A} from an individual from Prince Edward Island

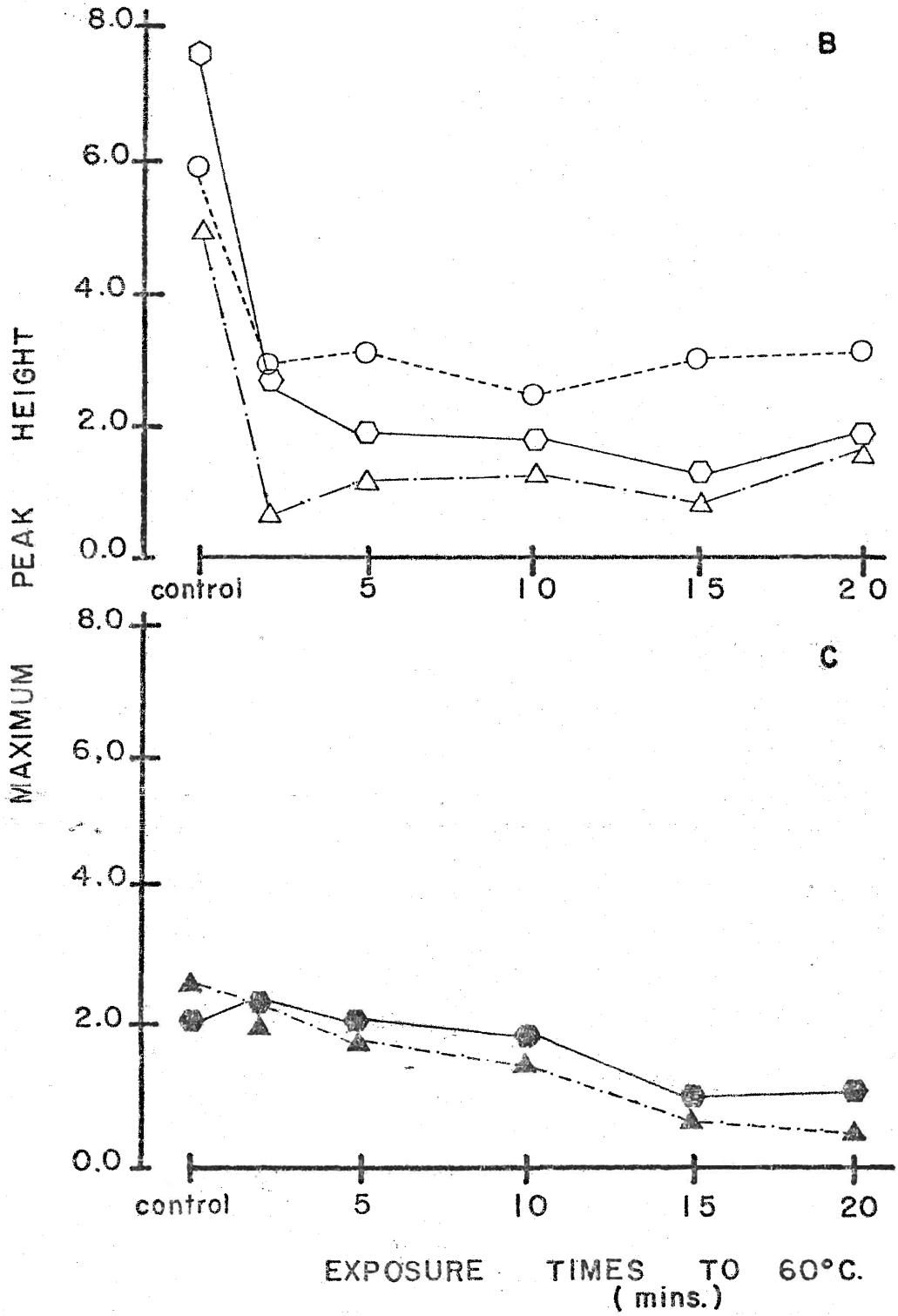
Ldh-A^{100A} from an individual from Presqu'île

Ldh-A^{100A} from an individual from Port Colborne

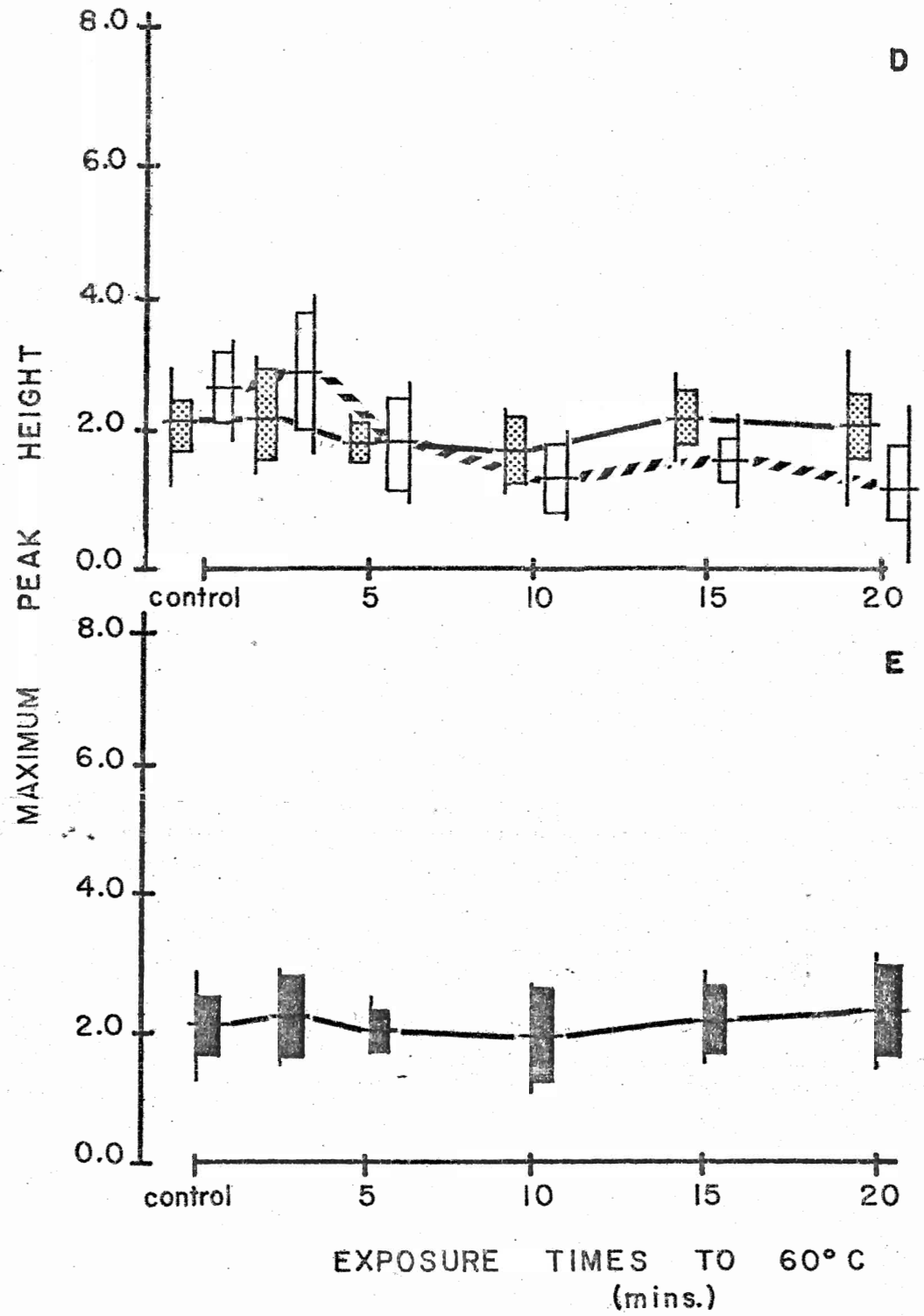
Figure 2C Enzyme Activity in Relation to Length of Exposure Times for Ldh-A^{100A} from *Larus argentatus*

Ldh-A^{100B} from an individual from Prince Edward Island

Ldh-A^{100B} from an individual from Port Colborne


B
C
8.0
6.0
4.0
2.0
0.0
control
5
10
15
20
MAXIMUM PEAK HEIGHT
EXPOSURE TIMES TO 60°C.
(mins.)

Figures 2D and 2E — Enzyme Activity in Relation to Length of Exposure Times for the Three LDH Electromorphs from Larus delawarensis. Mean (horizontal line), standard deviation (vertical bar), 95% confidence limits (vertical line) are recorded for a sample size of six repetitions. Unshaded vertical bars represent values for the fastest migrating LDH electromorph, stippled vertical bars represent the intermediate LDH electromorph, shaded vertical bars represent the slowest LDH electromorph.


D
8.0
6.0
4.0
2.0
0.0
control
5
10
15
20
E
8.0
6.0
4.0
2.0
0.0
control
5
10
15
20
MAXIMUM PEAK HEIGHT
EXPOSURE TIMES TO 60° C
(mins.)

activity occurred with L. delawarensis, it may be that no significant decrease of enzyme activity occurred with L. argentatus LDH-A^{100}. However, LDH-A^{100} from S. hirundo shows a considerable decrease in activity compared to the other two larid species. Possible explanations for these differences may lie at the DNA base sequence level of the LDH locus, especially between S. hirundo and L. argentatus. Although both charge and molecular shape have not been altered, a difference exists between these two allelic products.

Appendix 3

Sample Genotypes

Table A3A: Egg-White Protein Genotypes for Samples from Four Nesting Locations of Sterna hirundo.

Location	Sample Numbers	Locus					
		Opro-1	Opro-2	Opro-3	Opro-4	Oalb	Oest-1
Port Colborne	075-C12 [1]						
	075-C13	100	100	100	100	100	106
	075-C14						
	075-C15						
	075-C16	100	100	100	100	100	100
	075-C17						
	075-C18						
	075-C19	100	100	100	100	100	100
	075-C20						
	075-C21	--[2]	--	--	--	--	100/106
	075-C22	--	--	--	--	--	--
	075-C23	--	--	--	--	--	--
	075-C24	--	--	--	--	--	--
	075-C25	--	--	--	--	--	--
	075-C26	--	--	--	--	--	--
	075-C27	--	--	--	--	--	--
	075-C28	--	--	--	--	--	--
	075-C29	--	--	--	--	--	--
Presqu'île	175-C1						
	175-C2	100	100	100	100	100	100
	175-C3						
	175-C4						
	175-C5	--	--	--	--	--	100/106
	175-C6						
	175-C7	--	--	--	--	--	106
	175-C8	--	--	--	--	--	100/106
	175-C9	--	--	--	--	--	106
	175-C10	--	--	--	--	--	--
	175-C11	--	--	--	--	--	--
Limestone Island	275-C1	100	100	100	100	100	100
	275-C2	--	--	--	--	--	--
	275-C3	--	--	--	--	--	[3]
	275-C4	--	--	--	--	--	--

1. Brackets indicate a 3-egg clutch was analysed, and subsequently evaluated as 1 sample, as egg-white proteins represent the geotype of the female parent.

2. Bars indicate that the sample had the same genotype as the preceding sample

3. Indicates that the locus could not be scored accurate, or no activity occurred.

Table A3A, p. 2

Location	Sample Numbers	Locus					
		Opro-1	Opro-2	Opro-3	Opro-4	Oalb	Oest-1
Prince Edward Island	375-C1	100	100	100	100	100	100
	375-C2	--	--	--	--	--	--
	375-C3	--	--	--	--	--	--
	375-C4	--	--	--	--	--	101
	375-C5	--	--	--	--	--	100
	375-C6	--	--	--	--	--	100/101
	375-C7	--	--	--	--	--	--
	375-C8	--	--	--	--	--	--
	375-C9	--	--	--	--	--	--
	375-C10	--	--	--	--	--	--
	375-C11	--	--	--	--	--	100
	375-C12	--	--	--	--	--	--
	375-C13	--	--	--	--	--	--
	375-C14	--	--	--	--	--	100/101
	375-C15	--	--	--	--	--	100
	375-C16	--	--	--	--	--	100/101
	375-C17	--	--	--	--	--	101
375-C1	375-C18	--	--	--	--	--	100/101
	375-C19	--	--	--	--	--	100
	375-C20	--	--	--	--	--	100/101
	375-C21	--	--	--	--	--	100
	375-C22	--	--	--	--	--	--

Table A3B Egg-White Protein Genotypes for Samples from Four Nesting Locations of Larus argentatus.[1]

Location	Sample Numbers	Locus				
		Opro-1	Opro-2	Opro-3	Opro-4	Oalb
Port Colborne	075-H1	100	100	100	100	98
	075-H2	--[2]	--	--	--	--
	075-H3	--	--	--	--	--
	075-H4	--	--	--	--	--
	075-H5	--	--	--	--	--
	075-H6	--	--	--	--	--
	075-H9	--	--	--	--	--
	075-H10	--	--	--	--	--
	075-H11					
	075-H12	--	--	--	--	--
	075-H13					
Presqu'île	175-H1	100	100	100	100	99
	175-H2					
	175-H3	--	--	--	--	--
	175-H4					
	175-H5	--	--	--	--	--
	175-H6	--	--	--	--	--
Limestone Island	275-H1					
	275-H2	100	100	100	100	99
	275-H3					
	275-H4	--	--	--	--	--
	275-H5					
Prince Edward Island	375-H1	100	100	100	100	99
	375-H2	--	--	--	--	--

1. Egg-white proteins were sampled from only four locations.

2. Dashes indicate that the sample genotype is identical to the preceding sample genotype.

Table A3C: Blood Serum Protein Genotypes for Samples from Four Nesting Locations of *Sterna hirundo*.

Location	Sample Numbers	Locus														
		Pro-1	Pro-2	Pro-3	Pro-4	Pro-5	Alb	Est-1	Est-2	Est-3	Est-5	Est-6	Ng	Ldh-A	To-1	To-2
Port Colborne	075-C35[1]													100A	100	100
	075-C44	100	100	100	100	100	100	100	100	100	100	100	100	--	--	--
	075-C45	--[2]	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	075-C46	--	--	--	--	--	--	--	--	--	98	--	--	--	--	--
	075-C47	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	075-C48	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	075-C49	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	075-C52	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	075-C54	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	075-C55	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	075-C56	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	075-C57	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	075-C58	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	075-C59	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	075-C60	--	--	--	--	--	--						--	--	--	--
	075-C61	--	--	--	--	--	--	100	100	100	98/100	100	--	--	--	--
	075-C65	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	076-C1	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	076-C2	--	--	--	--	--	--	--	--	--	98	--	--	--	--	--
	076-C3	--	--	--	--	--	--	--	--	--	98	--	--	--	--	--
	076-C4	--	--	--	--	--	--	--	--	--	98	--	--	--	--	--
	076-C5	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	076-C6	--	--	--	--	--	--						--	--		
	076-C7	--	--	--	--	--	--	100	100	100	98/100	100	--	--	--	--
	076-C8	--	--	--	--	--	--	--	--	--	98	--	--	--	--	--
	076-C9	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	076-C10	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--

Table A3C, p. 2

Location	Sample Numbers	Locus													
		Pro-1	Pro-2	Pro-3	Pro-4	Pro-5	Alb	Est-1	Est-2	Est-3	Est-5	Est-6	Ng	Ldh-A	To-1	To-2
Presqu'île	175-C106	100	100	100	100	100	100	100	100	100	98	100	100	100	100	100
	175-C107	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	175-C108	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	175-C109	--	--	--	--	--	--	--	--	--	98	--	--	--	--	--
	175-C111	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	175-C112	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	175-C113	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	175-C114	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	175-C115	--	--	--	--	--	--	--	--	--	98	--	--	--	--	--
	175-C116	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	175-C118	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
Limestone Islands	275-C119													100A	100	100
Prince	375-C50	100	100	100	100	100	100	100	100	100	98	100	100	100	100	100
Edward	375-C51	--	--	--	--	--	--							--	--	--
Island	375-C52	--	--	--	--	--	--	100	100	100	100	100	100	--	--	--
	375-C53	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	375-C54	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	375-C55	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	375-C56	--	--	--	--	--	--	--	--	--	100	--	--	--	--	--
	375-C57	--	--	--	--	--	--	--	--	--	98/100	--	--	--	--	--
	375-C58	--	--	--	--	--	--	--	--	--		--	--	--	--	--

1. No entry under the locus column indicates that the sample was not scored for this locus.

2. Dashes indicate that the genotype of that sample was identical to the preceding sample.

Table A3D. Blood Serum Protein Genotypes for Samples from Seven Nesting Locations of Larus argentatus.

Location	Sample Numbers	Locus												
		Pro-1	Pro-2	Pro-3	Pro-5	Alb	Est-1	Est-2	Est-3	Est-4	Ng	Ldh-A	To-1	To-2
Port Colborne	075-H38	100	100	100	100	100	100	100	100	100	100	99/102	100	100
	075-H50	--[1]	--	--	--	--	--	--	--	--	--	102	--	--
	075-H51	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H62	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H63	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H64	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H66	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H67	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H68	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H69	--	--	--	--	--	--	--	--	--	--	--	--	--
	075-H70	--	--	--	--	--	--	--	--	--	--	--	--	--
	076-H10	--	--	--	--	--	--	--	--	--	--	--	--	--
	076-H11	--	--	--	--	--	--	--	--	--	--	100B/104	--	--
Presqu'île	175-H100	100	100	100	100	100/98	100	100	100	100	100	102	100	100
	175-H110	--	--	--	--	100	--	--	--	--	--	100B/102	--	--
	175-H126	--	--	--	--	100	--	--	--	--	--	102	--	--
Limestone Island	275-H100	100	100	100	100	100	100	100	100	100	100	102	100	100
	275-H101	--	--	--	--	--	--	--	--	--	--	--	--	--
	275-H102	--	--	--	--	--	--	--	--	--	--	--	--	--
	275-H104	--	--	--	--	--	--	--	--	--	--	--	--	--
Prince Edward Island	375-H3	100	100	100	100	100	100	100	100	100	100	100B	100	100
	375-H4	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H5	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H6	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H7	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H8	--	--											

Table A3D, p. 2

Location	Sample Numbers	Locus												
		Pro-1	Pro-2	Pro-3	Pro-5	Alb	Est-1	Est-2	Est-3	Est-4	Ng	Ldh-A	To-1	To-2
Prince Edward Island	375-H9	100	100	100	100	100	100	100	100	100	100	100B	100	100
	375-H10	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H11	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H12	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H13	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H14	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H15	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H16	--	--	--	--	--	--	--	--	--	--	--	--	--
	375-H17	--	--	--	--	--	--	--	--	--	--	--	--	--
	376-H50	--	--	--	--	--	--	--	--	--	--	--	--	--
	376-H51	--	--	--	--	--	--	--	--	--	--	--	--	--
	376-H52	--	--	--	--	--	--	--	--	--	--	--	--	--
	376-H53	--	--	--	--	--	--	--	--	--	--	--	--	--
Chantry Island	476-H1	100	100	100	100	100	100	100	100	100	100	100B	100	100
	476-H2	--	--	--	--	--	--	--	--	--	--	100B/102	--	--
	476-H3	--	--	--	--	--	--	--	--	--	--	--	--	--
	476-H4	--	--	--	--	--	--	--	--	--	--	100B	--	--
	476-H5	--	--	--	--	--	--	--	--	--	--	102	--	--
	476-H6	--	--	--	--	--	--	--	--	--	--	99/102	--	--
	476-H7	--	--	--	--	--	--	--	--	--	--	99/100B	--	--
	476-H8	--	--	--	--	--	--	--	--	--	--	--	--	--
	476-H9	--	--	--	--	--	--	--	--	--	--	99	--	--
	476-H10	--	--	--	--	--	--	--	--	--	--	99/100B	--	--

Table A3D, p. 3

Location	Sample Numbers	Locus												
		Pro-1	Pro-2	Pro-3	Pro-5	Alb	Est-1	Est-2	Est-3	Est-4	Ng	Ldh-A	To-1	To-2
Scotch Bonnet Island	576-H1	100	100	100	100	98/100	100	100	100	100	100	98/100B	100	100
	576-H2	--	--	--	--	100	--	--	--	--	--	98	--	--
	576-H3	--	--	--	--	100	--	--	--	--	--	98	--	--
Mohawk Island	676-H1	100	100	100	100	100	100	100	100	100	100	100B/102	100	100
	676-H2	--	--	--	--	--	--	--	--	--	--	98	--	--
	676-H3	--	--	--	--	--	--	--	--	--	--	98/100B	--	--

1. Dashes indicate the genotype of that sample is identical to the preceding sample genotype.

Appendix 4

Computer Programs Used in Data Analysis

```
10REM THIS 'PRIMES'
20SELECT PRINT 005:PRINT "INPUT SPECIES CODE;LARUS ARGENTATUS(0)
,STERNA HIRUNDO (1)":INPUT Z:SELECT PRINT 211
30IF Z=0THEN 40:IF Z=1THEN 50
40PRINT "LARUS ARGENTATUS":GOTO 60
50PRINT "STERNA HIRUNDO"
60SELECT PRINT 005:PRINT "INPUT LOCUS CODE":PRINT MEM(0900):PRIN
T "OMST-1(0);  MST-5(1);  LDH-A(2);  ALB(3);":INPUT M:SELECT PRI
NT 211
70IF M=0THEN 80:IF M=1THEN 90:IF M=2THEN 100:IF M=3THEN 110
80PRINT "OMST-1":GOTO 120
90PRINT "MST-5":GOTO 120
100PRINT "LDH-A":GOTO 120
110PRINT "ALB"
120SELECT PRINT 005:PRINT "INPUT LOCATION CODE"
130PRINT MEM(0909):PRINT "PORT COLBORNE(0);  PEISQU'ILE(1);  LIM
ESTONE ISLAND(2);  PRINCE EDWARD ISLAND(3);  CHANTRY ISLAND(4);
 SCOTCH BONNET ISLAND(5); MONAMY ISLAND(6);  TOTAL(7)"
140INPUT M:SELECT PRINT 211
150IF M=0THEN 160:IF M=1THEN 170:IF M=2THEN 180:IF M=3THEN 190:I
F M=4THEN 200:IF M=5THEN 210:IF M=6THEN 220:IF M=7THEN 230
160PRINT "PORT COLBORNE":GOTO 240
170PRINT "PEISQU'ILE":GOTO 240
180PRINT "LIMESTONE":GOTO 240
190PRINT "PRINCE EDWARD ISLAND":GOTO 240
200PRINT "CHANTRY ISLAND":GOTO 240
```

```
210PRINT "SCOTCH BONNET ISLAND":GOTO 240
220PRINT "HOHAWK ISLAND":GOTO 240
230PRINT "TOTAL"
240RESTORE :SELECT PRINT 005:REMEND :LOAD "MARVAR"
```

```
10REM THIS HARWAR:DIM A(36),T(8),B(36)
20SELECT PRINT 005:PRINT "INPUT SAMPLE SIZE(N)":INPUT N
30PRINT "INPUT NUMBER OF ALLELES(M)":INPUT M:IF M=1THEN 50
40K=K+1:L=L+K:IF K=MTHEN 60:GOTO 40
50SELECT PRINT 211:PRINT "P!2=1.0,2PQ=0.0,Q!2=0.0":GOTO 350
60FOR I=1TO L:PRINT "A(";I;")=";:INPUT A(I):NEXT I
70PRINT HEX(03);:FOR I=1TO L:PRINT "A(";I;")=";A(I),:NEXT I
80PRINT "CORRECT MISTAKES NOW":STOP :SELECT PRINT 211:PRINT :PR
INT "HARDY-WEINBERG EXPECTATION VALUES"
90 W=(2*A(29)+A(30)+A(31)+A(32)+A(33)+A(34)+A(35)+A(36))/(2*N)
100 V=(2*A(22)+A(23)+A(24)+A(25)+A(26)+A(27)+A(28)+A(36))/(2*N)
110 U=(2*A(16)+A(17)+A(18)+A(19)+A(20)+A(21)+A(28)+A(35))/(2*N)
120 T=(2*A(11)+A(12)+A(13)+A(14)+A(15)+A(21)+A(27)+A(34))/(2*N)
130 S=(2*A(7)+A(8)+A(9)+A(10)+A(15)+A(20)+A(26)+A(33))/(2*N)
140 R=(2*A(4)+A(5)+A(6)+A(10)+A(14)+A(19)+A(25)+A(32))/(2*N)
150 Q=(2*A(3)+A(2)+A(6)+A(9)+A(13)+A(18)+A(24)+A(31))/(2*N)
160 P=(2*A(1)+A(2)+A(5)+A(8)+A(12)+A(17)+A(23)+A(30))/(2*N)
170 Z=P+Q+R+S+T+U+V+W
180T(8)=W/Z:T(7)=V/Z:T(6)=U/Z:T(5)=T/Z:T(4)=S/Z:T(3)=R/Z:T(2)=Q/
Z:T(1)=P/Z
190FOR J=1TO 8:IF J=8THEN 230:READ G$:PRINTUSING 210,G$,T(J);
200FOR I=J+1 TO 8:READ G$:PRINTUSING 210,G$,2*(T(J)*T(I));
210Z###=.#####
220NEXT I:READ G$:PRINTUSING 210,G$,T(J)!2;:GOTO 240
230PRINT "W=";T(8),"W!2=";T(8)!2:J=9
240NEXT J:PRINT :PRINT "CONTINUE FOR OBSERVED GENOTYPE FREQUENCI
ES":STOP
```

```
10 DIM D(2),E(2):REM THIS PROGRAM CALCULATES SMALL-SAMPLE CHI-SQ
UARE
20 REM A=FREQ. OF HETEROZYGOTES OBSERVED, B=FREQ. OF HETEROZYGOT
ES EXPECTED
30 PRINT "INPUT A,B,N":INPUT A,B,N
40 D(1)=A*N:E(1)=B*N:D(2)=(1-A)*N:E(2)=(1-B)*N:F=(A-B)/B
50 SELECT PRINT 215(40)
60 PRINT "OBSERVED HETS=";D(1)
70 PRINT "OBSERVED HOMO=";D(2)
80 PRINT "EXPECTED HETS=";E(1)
90 PRINT "OBSERVED HETS=";E(2)
100 M=D(1)-E(1):IF M]0THEN 120
110 M=-M
120 M=(M-0.5)!2:N=D(2)-E(2):IF N]0THEN 140
130 N=-N
140 N=(N-0.5)!2:Q=M/E(1):R=N/E(2):C=Q+R
150 PRINT "HET CHI-SQUARE=";Q
160 PRINT "HOMO CHI-SQUARE=";R
170 PRINT "CHI-SQUARE=";C
180 PRINT "F=";F
190 SELECT PRINT 005:RESTORE :END
```

```
10 PRINT "SINGLE LOCUS GENETIC IDENTIITY, AND DISTANCE"
20PRINT "FOR A MAXIMUM OF 40 ALLELES."
30PRINT "X(I) IS THE FREQUENCY OF THE ITH ALLELE"
40PRINT "IN POPULATION X."
50PRINT "Y(I) IS THE FREQUENCY OF THE ITH ALLELE"
60PRINT "IN POPULATION Y."
70PRINT "N IS THE NUMBER OF ALLELES "
80PRINT "BOTH X(I) AND Y(I) MUST BE THE SAME"
90PRINT "ALLELE IN BOTH POPULATIONS"
100 REM NEIS GEN ID
110 COM X(40),Y(40):INPUT "NO. OF ALLELES OVER ALL LOCI ([40) ",
 N
120 FOR I=1 TO N
130 INPUT "X AND Y", X(I), Y(I)
140 NEXT I
150 FOR I=1 TO N
160 PRINT "X(";I;")"; X(I);" Y(";I;")"; Y(I);
170 NEXT I: STOP
180 FOR I=1 TO N
190 S1=S1+ X(I)*Y(I)
200 S2=S2 + X(I)!2 : S3=S3 + Y(I)!2
210 NEXT I : S4=SQR(S2 * S3): I1=S1/S4
220 PRINT "I=";I1, "D="; -1*LOG(I1):END
```

```
10 REM THIS BASCHI
20 PRINT "BRANDT-SNEDECOR CHI SQUARE TEST"
30 PRINT "DATA FORMAT"
40 PRINT "A(1),A(2),A(3),.....A(J), A(TOTAL)"
50 PRINT "B(1),B(2),B(3),.....B(J), B(TOTAL)"
60 PRINT "N(1),N(2),N(3),.....N(J), N(TOTAL)"
70 DIM A(20), N(20), C(20),Q(20)
80 PRINT "INPUT J":INPUT J
90 FOR I=1 TO J:PRINT "INPUT A(I),N(I)":INPUT A(I),N(I)
100 PRINT "A(I)=";A(I), "N(I)=";N(I):NEXT I
110 PRINT "INPUT A,B,N":INPUT A,B,N
120 M=(A!2)/N
130 P=(N!2)/(A*B)
140 FOR I= 1 TO J:C(I)=((A(I)!2)/N(I))
150 PRINT "C(I)=";C(I):NEXT I
160 S=0
170 FOR I= 1 TO J:S=S+C(I):NEXT I
180 H=P*(S-M): D=(J-1)+(J-1)
190 PRINT "CHI SQUARE VALUE=";H
200 PRINT "P=";P
210 PRINT "S=";S
220 PRINT "M=";M
230 PRINT "DEGREES OF FREEDOM=";D
```

```
10REM "DATASAVE":COM A(28),B(11),A$(4)64,B$6,K$3,L$3:PRINT HEX(0
3);"THIS PROGRAM ASSUMES A FILE LABELLED 'DATA' EXISTS FOR 13 PO
PU- LATIONS."
20PRINT "THIS PROGRAM STORES ON A TAPE CASSETTE DATA FOR THE COM
PUTE PRO-GRAM"
30PRINT "TO OPEN A DATA FILE %% FOLLOW THESE INSTRUCTIONS %%"
40PRINT "1ST. PRESS CLEAR/EXEC..(!!DO NOT REWIND THE TAPE!!)"
50PRINT "THEN TYPE AND ENTER THE COMMAND;DATASAVE OPEN 'DATA'"
60PRINT "(THIS ESTABLISHES THE HEADER FOR THE DATA FILE"
70PRINT "THIS HEADER MUST BE ON TAPE FOR DATA STORAGE)"
80PRINT "THE END OF FILE MARKER IS PART OF THIS PROGRAM"
90INPUT "NO. OF FIRST POPULATION FOR TODAY",N:DATA LOAD "DATA":S
KIP END
100FOR I=1TO 28:A(I)=0:NEXT I:N=1
110READ B$,P:K=0:FOR I=1TO 11:B(I)=0:NEXT I:PRINT :PRINT "FOR PO
PULATION";N;" LOCUS  ";B$;"INPUT THE NO. OF ALLELES TO BE ENTERE
D";
120INPUT K:IF K[]0THEN 130:B(1)=9.999:GOTO 140
130FOR I=1TO K:INPUT "VALUE OF ALLELE",B(I):NEXT I
140K=0:FOR I=NTO N+P-1:K=K+1:A(I)=B(K):NEXT I:N=N+P:IF N]=28THEN
150:GOTO 110
150RESTORE :N=0
160READ B$,P:PRINT HEX(03);"POPULATION ";N;" LOCUS  ";B$:FOR J=1
TO P:PRINT "A(";N+J;")",A(N+J):NEXT J:INPUT "IS DATA CORRECT (Y=
YES)",K$:IF K$="Y"THEN 170:STOP "MAKE CORRECTIONS"
```

```
170M=M+P:IF M[28THEN 160:PACK(#.###)A$()FROMA():DATA SAVE A$():
RESTORE :INPUT "ARE YOU FINISHED FOR TODAY (Y=YES)",L$:IF L$="Y"
THEN 190
180M=M+1:IF M[14THEN 100
190DATA SAVE END :END
200DATA "OPRO-1",1,"OPRO-2",1,"OPRO-3",1,"OPRO-4",1,"OALB",2,"OE
ST",2,"LDH",4,"TO-1",1,"TO-2",1,"EST-1",1,"EST-2",1,"EST-3",1
210DATA "EST-4",1,"EST-5",2,"EST-6",1,"NG",1,"PRO-1",1,"PRO-2",1
,"PRO-3",1,"PRO-4",1,"PRO-5",1,"ALB",2
```

```
10REM "COMPUTE"THIS PROGRAM COMPUTES NEI'S IDENTITY AND DISTANCE
 FOR ALL LOCI, FOR 21 LOCI AND 15 POPULATIONS:DIM A$(4)64,X(31),
Y(31),B$6:N=1
20 FOR I=1TO 14:DATA LOAD "DATA":FOR J=1TO I:DATA LOAD A$():NEXT
J:UNPACK(#.####)A$()TO X():READ B$,P
30 FOR J=I+1TO 15:SELECT PRINT 211(40):PRINT "POPULATION";I;"COM
PARED TO POPULATION";J;,"LOCI COMPARED=";:DATA LOAD A$():UNPACK(
#.####)A$()TO Y()
40 IF X(N)=9.999THEN 60:IF Y(N)=9.999THEN 60
50 FOR K=N TO N+P-1:S1=S1+X(K)*Y(K):S2=S2+X(K)!2:S3=S3+Y(K)!2:NE
XT K:PRINT B$;",";
60 N=N+P:IF N]=31THEN 70:READ B$,P:GOTO 40
70 S4=SQR(S2*S3):I1=S1/S4:PRINT :PRINT "I=";I1:PRINT "D=";-1*LOG
(I1):PRINT :RESTORE :S1,S2,S3,S4=0:N=1:READ B$,P:NEXT J
80 REWIND :RESTORE :NEXT I:SELECT PRINT 005:END
90 DATA "OPRO-1",1,"OPRO-2",1,"OPRO-3",1,"OPRO-4",1,"OALB",2,"OE
ST-1",2,"LDH",5,"TO-1",1,"TO-2",1,"EST-1",1,"EST-2",1,"EST-3",1
100DATA "EST-4",1,"EST-5",2,"EST-6",1,"NG",1,"PRO-1",1,"PRO-2",1
,"PRO-3",1,"PRO-4",1,"PRO-5",1,"PRO-6",1,"ALB",2
```

Appendix 5

Hardy-Wienberg Expectation

and Sample Genotype Frequency Calculations

STERNA HIRUNDO
OEST-1
PORT COLBORNE

HARDY-WEINBERG EXPECTATION VALUES

P =.54166	2PQ=.49652	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.29340	Q =.45833	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.21006	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.16666 B(2)=.75000 B(3)=.08333
ESTIMATED HETEROZYGOSITY= .496527777778
ACTUAL HETEROZYGOSITY= .75

STERNA HIRUNDO
OEST-1
PRESQU'ILE

HARDY-WEINBERG EXPECTATION VALUES

P =.28571	2PQ=.40816	2PR=.#####	2PS=.#####	
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####	
P!2=.08163	Q =.71428	2QR=.#####	2QS=.#####	
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####	
Q!2=.51020	R =.#####	2RS=.#####	2RT=.#####	
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####	
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####	
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####	
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####	
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####	
2VW=.#####	V!2=.#####	W= 0	W!2= 0	

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.14285 B(2)=.28571 B(3)=.57142
ESTIMATED HETEROZYGOSITY= .408163265309
ACTUAL HETEROZYGOSITY= .285714285714

STERNA HIRUNDO
OUST-1
LEWISTON

HARDY-WEINBERG EXPECTATION VALUES

P =.33333	2PQ=.44444	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.11111	Q =.66666	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.44444	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.33333 B(2)=.##### B(3)=.66666
ESTIMATED HETEROZYGOSITY= .44444444445
ACTUAL HETEROZYGOSITY= 0

STERNA HIRUNDO
OUST-1
PRINCE EDWARD ISLAND

HARDY-WEINBERG EXPECTATION VALUES

P =.68181	2PQ=.43398	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.46487	Q =.31818	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.10123	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.50000 B(2)=.36363 B(3)=.13636
ESTIMATED HETEROZYGOSITY= .43388429752
ACTUAL HETEROZYGOSITY= .36363636364

STENIA MINUTO
OUST-1
TOTAL

HARDY-WEINBERG EXPECTATION VALUES

P =.55681	2PQ=.49354	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.31004	Q =.44318	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.19641	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.34090 B(2)=.43181 B(3)=.22727
ESTIMATED HETEROZYGOSITY= .49354338843
ACTUAL HETEROZYGOSITY= .43181818181818

STENIA MINUTO
EST-5
POINT COLBORNE

HARDY-WEINBERG EXPECTATION VALUES

P =.43750	2PQ=.49218	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.19140	Q =.56250	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.31640	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.20833 B(2)=.45833 B(3)=.33333
ESTIMATED HETEROZYGOSITY= .4921875
ACTUAL HETEROZYGOSITY= .45833333333333

STERNA HIRUNDO
EST-5
PIESQU'ILE

HARDY-WEINBERG EXPECTATION VALUES

P =.45454	2PQ=.49586	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.20661	Q =.54545	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.29752	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.27272 B(2)=.36363 B(3)=.36363
ESTIMATED HETEROZYGOSITY= .49586776859
ACTUAL HETEROZYGOSITY= .3636363636364

STERNA HIRUNDO
EST-5
PRINCE EDUARD ISLAND

HARDY-WEINBERG EXPECTATION VALUES

P =.21428	2PQ=.33673	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.04591	Q =.78571	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.61734	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.14285 B(2)=.14285 B(3)=.71428
ESTIMATED HETEROZYGOSITY= .336734693873
ACTUAL HETEROZYGOSITY= .142857142857

SIERRA MENUDO
MST-5
TOTAL

MARDY-WEINBERG ESTIMATION VALUES

P =.40476	2PQ=.48185	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.16383	Q =.59523	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.35430	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES

B(1)=.21428 B(2)=.38095 B(3)=.40476

ESTIMATED HETEROZYGOSITY= .481859841043

ACTUAL HETEROZYGOSITY= .380952380952

LARUS ARGENTATUS
LDH-A
PORT COLBORNE

HARDY-WEINBERG EXPECTATION VALUES

P =.03846	2PQ=.00295	2PR=.06804	2PS=.00295
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.00147	Q =.03846	2QR=.06804	2QS=.00295
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.00147	R =.88461	2RS=.06804	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.78254
S =.03846	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.00147	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES

B(1)=.#####	B(2)=.#####	B(3)=.#####	B(4)=.84615
B(5)=.07692	B(6)=.#####	B(7)=.#####	B(8)=.#####
B(9)=.07692	B(10)=.#####		

ESTIMATED HETEROZYGOSITY= .213017751478
ACTUAL HETEROZYGOSITY= .1538461538462

LARUS ARGENTATUS
LDH-A
PRESQU'ILE

HARDY-WEINBERG EXPECTATION VALUES

P =.16666	2PQ=.27777	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.02777	Q =.83333	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.69444	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES

B(1)=.#####	B(2)=.33333	B(3)=.66666

ESTIMATED HETEROZYGOSITY= .277777777782
ACTUAL HETEROZYGOSITY= .3333333333333

LARUS ARGENTATUS
LDH-A
LIMESTONE
P!2=1.0,2PQ=0.0,Q!2=0.0

LARUS ARGENTATUS
LDH-A
PRINCE EDWARD ISLAND

HARDY-WEINBERG EXPECTATION VALUES

P =.97500	2PQ=.04875	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.95062	Q =.02500	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.00062	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.95000 B(2)=.05000 B(3)=.#####
ESTIMATED HETEROZYGOSITY= 4.87500000E-02
ACTUAL HETEROZYGOSITY= 5.00000000E-02

LARUS ARGENTATUS
LDH-A
CHANTRY ISLAND

HARDY-WEINBERG EXPECTATION VALUES

P =.30000	2PQ=.27000	2PR=.15000	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.09000	Q =.45000	2QR=.22500	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.20250	R =.25000	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.06250
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.10000 B(2)=.30000 B(3)=.20000 B(4)=.10000
B(5)=.10000 B(6)=.20000
ESTIMATED HETEROZYGOSITY= .645
ACTUAL HETEROZYGOSITY= .6

LARUS ARGENTATUS
LDH-A
SCOTCH BONNET ISLAND

HARDY-WEINBERG EXPECTATION VALUES

P =.83333	2PQ=.27777	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.69444	Q =.16666	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.02777	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TW=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.66666 B(2)=.33333 B(3)=.#####
ESTIMATED HETEROZYGOSITY= .277777777782
ACTUAL HETEROZYGOSITY= .3333333333333

LARUS ARGENTATUS
LDH-A
MOHAWK ISLAND

HARDY-WEINBERG EXPECTATION VALUES

P =.50000	2PQ=.33333	2PR=.16666	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.25000	Q =.33333	2QR=.11111	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.11111	R =.16666	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.02777
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TW=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.33333 B(2)=.33333 B(3)=.##### B(4)=.#####
B(5)=.##### B(6)=.33333
ESTIMATED HETEROZYGOSITY= .611111111112
ACTUAL HETEROZYGOSITY= .6666666666666

LARUS ARGENTATUS
LDH-A
TOTAL

HARDY-WEINBERG EXPECTATION VALUES

P =.13392	2PQ=.12675	2PR=.10044	2PS=.00473
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.01793	Q =.47321	2QR=.35491	2QS=.01690
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.22393	R =.37500	2RS=.01339	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.14062
S =.01785	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.00021	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES

B(1)=.07142	B(2)=.08928	B(3)=.37500	B(4)=.32142
B(5)=.03571	B(6)=.07142	B(7)=.#####	B(8)=.#####
B(9)=.03571	B(10)=.#####		

ESTIMATED HETEROZYGOSITY= .617187500004
ACTUAL HETEROZYGOSITY= .232142857142

LARUS ARGENTATUS
ALB
PRESQU'ILE

HARDY-WEINBERG EXPECTATION VALUES

P =.16666	2PQ=.27777	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.02777	Q =.83333	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.69444	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES

B(1)=.#####	B(2)=.33333	B(3)=.66666

ESTIMATED HETEROZYGOSITY= .277777777782
ACTUAL HETEROZYGOSITY= .333333333333

LARUS ARGENTATUS
ALB
SCOTCH BONNET ISLAND

HARDY-WEINBERG EXPECTATION VALUES

P =.16666	2PQ=.27777	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.02777	Q =.83333	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.69444	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.##### B(2)=.33333 B(3)=.66666
ESTIMATED HETEROZYGOSITY= .277777777782
ACTUAL HETEROZYGOSITY= .3333333333333

LARUS ARGENTATUS
ALB
TOTAL

HARDY-WEINBERG EXPECTATION VALUES

P =.01785	2PQ=.03507	2PR=.#####	2PS=.#####
2PT=.#####	2PU=.#####	2PV=.#####	2PW=.#####
P!2=.00031	Q =.98214	2QR=.#####	2QS=.#####
2QT=.#####	2QU=.#####	2QV=.#####	2QW=.#####
Q!2=.96460	R =.#####	2RS=.#####	2RT=.#####
2RU=.#####	2RV=.#####	2RW=.#####	R!2=.#####
S =.#####	2ST=.#####	2SU=.#####	2SV=.#####
2SW=.#####	S!2=.#####	T =.#####	2TU=.#####
2TV=.#####	2TW=.#####	T!2=.#####	U =.#####
2UV=.#####	2UW=.#####	U!2=.#####	V =.#####
2VW=.#####	V!2=.#####	W= 0	W!2= 0

CONTINUE FOR OBSERVED GENOTYPE FREQUENCIES
B(1)=.##### B(2)=.03571 B(3)=.96428
ESTIMATED HETEROZYGOSITY= 3.507653206E-02
ACTUAL HETEROZYGOSITY= 3.571428571E-02

Appendix 6

All Calculated Chi-square Probability Values

Table A6A. Chi-Square Probabilities for H_O, H_E, H_L and G_O, G_E, G_L at the Oest-1 Locus in Sterna hirundo. Observed H_O, G_O, expected (at Hardy-Weinberg equilibrium) H_E, G_E, Levene's (1949) correction for small samples sizes, H_L, G_L, heterozygosities (H), homozygosities (G), Chi-square Probabilities, P, and gene sample sizes are recorded for three nesting locations and the pooled sample.

	Sterna hirundo									
Location	Heterozygosity				Homozygosity				Total	Gene Sample Size
	H_O	H_E	H_L	P	G_O	G_E	G_L	P	P	
Port Colborne	0.75	0.50		0.30	0.25	0.50		0.30	0.14	24
	0.75		0.52	0.36	0.25		0.48	0.34	0.19	24
		0.50	0.52	0.92		0.50	0.48	0.92	0.90	24
Presqu'île	0.29	0.41		0.83	0.71	0.59		0.86	0.78	14
	0.29		0.44	0.74	0.71		0.56	0.77	0.66	14
		0.41	0.44	0.87		0.59	0.56	0.89	0.83	14
Prince Edward Island	0.36	0.43		0.74	0.64	0.57		0.77	0.65	44
	0.36		0.44	0.69	0.64		0.56	0.72	0.59	44
		0.43	0.44	0.93		0.57	0.56	0.94	0.90	44
Total	0.49	0.43		0.61	0.51	0.57		0.66	0.50	88
	0.49		0.50	0.98	0.51		0.50	0.98	0.98	88
		0.43	0.50	0.56		0.57	0.50	0.61	0.44	88

Table A6B. Chi-Square Probabilities for H_O, H_E, H_L and G_O, G_E, G_L at the Est-5 Locus in Sterna hirundo. Observed, H_O, G_O, expected (at Hardy-Weinberg equilibrium), H_E, G_E, Leven's (1949) correction for small sample sizes, H_L, G_L, heterozygosities (H), homozygosities (G), Chi-square probabilities, P, and gene sample sizes are recorded for three nesting locations, and the pooled sample

Location	Sterna hirundo									
Location	Heterozygosity				Homozygosity				Total	Gene Sample
	H_O	H_E	H_L	P	G_O	G_E	G_L	P	P	Size
Port Colborne	0.46	0.49		0.93	0.54	0.51		0.93	0.90	48
	0.46		0.50	0.86	0.54		0.50	0.88	0.82	48
		0.49	0.50	0.94		0.51	0.50	0.94	0.92	48
Presqu'île	0.36	0.49	0.49	0.68	0.64	0.51		0.69	0.56	22
	0.36			0.62	0.69		0.51	0.60	0.47	22
		0.49	0.49	0.92		0.51	0.51	0.92	0.88	22
Prince Edward Island	0.14	0.34		0.58	0.86	0.66		0.69	0.49	14
	0.14		0.36	0.51	0.86		0.64	0.62	0.41	14
		0.34	0.36	0.84		0.66	0.64	0.88	0.80	14
Total	0.38	0.48	0	0.41	0.62	0.52		0.43	0.25	84
	0.38		0.49	0.31	0.62		0.51	0.43	0.20	84
		0.48	0.49	0.97		0.52	0.51	0.97	0.96	84

Table A6C. Chi-Square Probabilities for H_O, H_E, H_L and G_O, G_E, G_L at the Ldh-A locus in Larus argentatus. Observed H_O, G_O, expected (at Hardy-Weinberg equilibrium) H_E, G_E, Levene's (1949) correction for small sample sizes, H_L, G_L, heterozygosities (H), homozygosities (G), Chi-square probabilities, P, and gene sample sizes are recorded for six nesting locations, and the pooled sample.

	Larus argentatus									
Location	Heterozygosities				Homozygosities				Total	Gene
	H_O	H_E	H_L	P	G_O	G_E	G_L	P	P	Sample Sizes
Port Colborne	0.15	0.21		0.87	0.85	0.79		0.93	0.86	26
	0.15		0.31	0.45	0.85		0.69	0.62	0.37	26
		0.21	0.31	0.66		0.79	0.69	0.82	0.62	26
Presqu'île	0.33	0.28		0.71	0.67	0.72		0.82	0.67	6
	0.33		0.33	0.62	0.67		0.67	0.72	0.54	6
		0.28	0.33	0.71		0.72	0.67	0.82	0.67	6
Prince Edward Idland	0.05	0.05		0.63	0.95	0.95		0.91	0.62	40
	0.05		0.05	0.62	0.95		0.95	0.91	0.61	40
		0.05	0.05	0.63		0.95	0.95	0.91	0.62	40
Scotch Bonnet Island	0.33	0.28		0.71	0.67	0.72		0.82	0.67	6
	0.33		0.33	0.62	0.67		0.67	0.72	0.54	6
		0.28	0.33	0.71		0.72	0.67	0.82	0.67	6
Chantry Island	0.60	0.65		0.98	0.40	0.35		0.98	0.98	20
	0.60		0.86	0.50	0.40		0.14	0.07	0.051	20
		0.65	0.86	0.51		0.35	0.14	0.37	0.27	20
Mohawk Island	0.67	0.61		0,81	0.33	0.39	0.76	0.76	0.69	6
	0.67		0.67	0.72	0.33		0.33	0.62	0.54	6
		0.61	0.67	0.81		0.39	0.33	0.76	0.69	6
Total	0.23	0.62		$3.4x^{1}$ 10^{-4}	0.77	0.38		$5.9x^{1}$ 10^{-6}	$1.43x^{1}$ 10^{-8}	112
	0.23		0.75	$7.9x^{1}$ 10^{-4}	0.77		0.25	$1.3x^{1}$ 10^{-5}	$7.4x^{1}$ 10^{-9}	112
		0.62	0.75	0.25		0.38	0.25	0.13	$5.9x$ 10^{-2}	112

1. Significance values of Chi-Square Probabilities (P), indicating departure from Hardy-Weinberg equilibrium expectations, and Levene's small sample size corrected heterozygosities (1949).

Table A6D. Chi-Square Probabilities for H_O, H_E, H_L and G_O, G_E, G_L, at the Alb Locus in Larus argentatus. Observed, H_O, G_O, expected (at Hardy-Weinberg equilibrium), H_E, G_E, Levene's (1949) correction for small sample size, H_L, G_L, heterozygosities (H), homozygosities (G), Chi-square probabilities, P, and gene sample sizes are recorded for two nesting locations and pooled samples.

	Larus argentatus									
Location	Heterozygosity				Homozygosity				Total	Gene Sample Size
	H_O	H_E	H_L	P	G_O	G_E	G_L	P	P	
Presqu'île	0.33	0.28		0.71	0.67	0.72		0.82	0.67	6
	0.33		0.33	0.62	0.67		0.67	0.72	0.59	6
		0.28	0.33	0.71		0.72	0.67	0.82	0.68	6
Scotch Bonnet Island	0.33	0.28		0.71	0.67	0.72		0.82	0.67	6
	0.33		0.33	0.62	0.67		0.67	0.72	0.54	6
		0.28	0.33	0.71		0.72	0.67	0.82	0.67	6
Total	0.04	0.04		0.74	0.96	0.96		0.95	0.73	112
	0.04		0.04	0.74	0.96		0.96	0.95	0.73	112
		0.04	0.04	0.74		0.96	0.96	0.95	0.73	112

Appendix 7

Print Out of

Total Genetic Identities and Genetic Distances

The following printout gives total genetic identities and genetic distances for all pairwise combinations of the sampled nesting locations of both species, and the loci used in these calculations. The following list correlates species, and sampled locations to population numbers as used in the printout.

Sterna hirundo	Port Colborne	Population 1
	Presqu'île	Population 2
	Limestone Island	Population 3
	Prince Edward Island	Population 4
	All Great Lakes Colonies	Population 5
	Pooled sample	Population 6
Larus argentatus	Port Colborne	Population 7
	Presqu'île	Population 8
	Limestone Island	Population 9
	Prince Edward Island	Population 10
	Chantry Island	Population 11
	Scotch Bonnet Island	Population 12
	Mohawk Island	Population 13
	All Great Lakes Colonies	Population 14
	Pooled sample	Population 15

POPULATION 1 COMPARED TO POPULATION 2
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9967428119139
D= 3.26250427E-03

POPULATION 1 COMPARED TO POPULATION 3
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,
I= .994912850537
D= 5.10013305E-03

POPULATION 1 COMPARED TO POPULATION 4
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9965630842187
D= 3.44283554E-03

POPULATION 1 COMPARED TO POPULATION 5
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9993950579497
D= 6.05125101E-04

POPULATION 1 COMPARED TO POPULATION 6
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9999871501945
D= 1.28498881E-05

POPULATION 1 COMPARED TO POPULATION 7
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8879153498755
D= .1188788672507

POPULATION 1 COMPARED TO POPULATION 8
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8871660018898
D= .1197231643635

POPULATION 1 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8823529411765
D= .125163142954

POPULATION 1 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8836208070904
D= .1237272596256

POPULATION 1 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .5999448253485
D= .5109175857468

POPULATION 1 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9244309469268
D= 7.85769232E-02

POPULATION 1 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9409392739466
D= 6.08766750E-02

POPULATION 1 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8975162122315
D= .1081240950152

POPULATION 1 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8987118012786
D= .1067928729045

POPULATION 2 COMPARED TO POPULATION 3
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,
I= .9997479168391
D= 2.52114939E-04

POPULATION 2 COMPARED TO POPULATION 4
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9893978819986
D= 1.06587208E-02

POPULATION 2 COMPARED TO POPULATION 5
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9989441106643
D= 1.05644717E-03

POPULATION 2 COMPARED TO POPULATION 6
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9963550460516
D= 3.65161297E-03

POPULATION 2 COMPARED TO POPULATION 7
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8879153498755
D= .1188788672507

POPULATION 2 COMPARED TO POPULATION 8
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8871660018898
D= .1197231643635

POPULATION 2 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8823529411765
D= .125163142954

POPULATION 2 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8836208070904
D= .1237272596256

POPULATION 2 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .5999448253485
D= .5109175857468

POPULATION 2 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9244309469268
D= 7.85769232E-02

POPULATION 2 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9409392739466
D= 6.08766750E-02

POPULATION 2 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8975162122315
D= .1081240950152

POPULATION 2 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8987118012786
D= .1067928729045

POPULATION 3 COMPARED TO POPULATION 4
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,
I= .9858132316804
D= 1.42883625E-02

POPULATION 3 COMPARED TO POPULATION 5
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,
I= .998866571132
D= 1.13407168E-03

POPULATION 3 COMPARED TO POPULATION 6
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,
I= .9941487507121
D= 5.86843491E-03

POPULATION 3 COMPARED TO POPULATION 7
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,
I= .7601554928087
D= .2742322708277

POPULATION 3 COMPARED TO POPULATION 8
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,
I= .7633722333626
D= .2700095116633

POPULATION 3 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,
I= .75
D= .2876820724517

POPULATION 3 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,
I= .7522956534512
D= .2846258761128

POPULATION 3 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,
I= .7513045401677
D= .285944196543

POPULATION 3 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,
I= .6998599251146
D= .3568750709418

POPULATION 3 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,
I= .7470891047026
D= .2915708175592

POPULATION 3 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,
I= .7785733263687
D= .2502921028453

POPULATION 3 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,
I= .780721096813
D= .247537303276

POPULATION 4 COMPARED TO POPULATION 5
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9943110525938
D= 5.70519110E-03

POPULATION 4 COMPARED TO POPULATION 6
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9966406973008
D= 3.36495782E-03

POPULATION 4 COMPARED TO POPULATION 7
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8879153498755
D= .1188788672507

POPULATION 4 COMPARED TO POPULATION 8
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8871660018898
D= .1197231643635

POPULATION 4 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8823529411765
D= .125163142954

POPULATION 4 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8836208070904
D= .1237272596256

POPULATION 4 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .5999448253485
D= .5109175857468

POPULATION 4 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9244309469268
D= 7.85769232E-02

POPULATION 4 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9409392739466
D= 6.08766750E-02

POPULATION 4 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8975162122315
D= .1081240950152

POPULATION 4 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8987118012786
D= .1067928729045

POPULATION 5 COMPARED TO POPULATION 6
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,OEST-1,LDH,TO-1,TO-2,EST-1,
EST-2,EST-3,EST-5,EST-6,NG,PRO-1,PRO-2,
PRO-3,PRO-4,PRO-5,ALB,
I= .9992193145252
D= 7.80990368E-04

POPULATION 5 COMPARED TO POPULATION 7
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8879153498755
D= .1188788672507

POPULATION 5 COMPARED TO POPULATION 8
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8871660018898
D= .1197231643635

POPULATION 5 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8823529411765
D= .125163142954

POPULATION 5 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8836208070904
D= .1237272596256

POPULATION 5 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .5999448253485
D= .5109175857468

POPULATION 5 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9244309469268
D= 7.85769232E-02

POPULATION 5 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9409392739466
D= 6.08766750E-02

POPULATION 5 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8975162122315
D= .1081240950152

POPULATION 5 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8987118012786
D= .1067928729045

POPULATION 6 COMPARED TO POPULATION 7
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8879153498755
D= .1188788672507

POPULATION 6 COMPARED TO POPULATION 8
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8871660018398
D= .1197231643635

POPULATION 6 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8823529411765
D= .125163142954

POPULATION 6 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8836208070904
D= .1237272596256

POPULATION 6 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .5999448253485
D= .5109175857468

POPULATION 6 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9244309469268
D= 7.85769232E-02

POPULATION 6 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .9409392739466
D= 6.08766750E-02

POPULATION 6 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8975162122315
D= .1081240950152

POPULATION 6 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,NG,PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .8987118012786
D= .1067928729045

POPULATION 7 COMPARED TO POPULATION 8
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9978434034812
D= 2.15892532E-03

POPULATION 7 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9995237976902
D= 4.76315730E-04

POPULATION 7 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9535082560131
D= 4.76071953E-02

POPULATION 7 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,EST-4,NG,
PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .60165261742
D= .5080750477042

POPULATION 7 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9410975137581
D= 6.07085169E-02

POPULATION 7 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9676576029386
D= 3.28769702E-02

POPULATION 7 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .995863221557
D= 4.14535858E-03

POPULATION 7 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9870068620192
D= 1.30782871E-02

POPULATION 8 COMPARED TO POPULATION 9
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9969864558694
D= 3.01809399E-03

POPULATION 8 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9604342292752
D= 4.03697746E-02

POPULATION 8 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,EST-4,NG,
PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .6063811151691
D= .5002465876699

POPULATION 8 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9442004942199
D= 5.74167474E-02

POPULATION 8 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .968685959662
D= 3.18148066E-02

POPULATION 8 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9958192696201
D= 4.18949406E-03

POPULATION 8 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9894710644781
D= 1.05847569E-02

POPULATION 9 COMPARED TO POPULATION 10
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9457259833284
D= 5.58024101E-02

POPULATION 9 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,OPRO-3,OPRO-4,LDH,
TO-1,TO-2,EST-1,EST-2,EST-3,EST-4,NG,
PRO-1,PRO-2,PRO-3,PRO-5,ALB,
I= .5976453960076
D= .5147576841805

POPULATION 9 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9303534943904
D= 7.21906635E-02

POPULATION 9 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9587053240617
D= 4.21715254E-02

POPULATION 9 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9928479150516
D= 7.17778371E-03

POPULATION 9 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,OPRO-2,OPRO-3,
OPRO-4,OALB,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .9822469820765
D= 1.79124930E-02

POPULATION 10 COMPARED TO POPULATION 11
LOCI COMPARED=OPRO-1,
OPRO-3,OPRO-4,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .6012320073906
D= .5087743833478

POPULATION 10 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9449054284522
D= 5.66704322E-02

POPULATION 10 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9730024977563
D= 2.73686297E-02

POPULATION 10 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,
OPRO-2,OPRO-3,OPRO-4,OALB,LDH,TO-1,TO-2,
EST-1,EST-2,EST-3,EST-4,NG,PRO-1,PRO-2,
PRO-3,PRO-5,ALB,
I= .972191403211
D= 2.82025770E-02

POPULATION 10 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,
OPRO-2,OPRO-3,OPRO-4,OALB,LDH,TO-1,TO-2,
EST-1,EST-2,EST-3,EST-4,NG,PRO-1,PRO-2,
PRO-3,PRO-5,ALB,
I= .9884995568928
D= 1.15670846E-02

POPULATION 11 COMPARED TO POPULATION 12
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9805403123701
D= 1.96515200E-02

POPULATION 11 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9975535506085
D= 2.44944683E-03

POPULATION 11 COMPARED TO POPULATION 14
LOCI COMPARED=OPRO-1,
OPRO-3,OPRO-4,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .610077000212
D= .4941700999252

POPULATION 11 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,
OPRO-3,OPRO-4,LDH,TO-1,TO-2,EST-1,EST-2,
EST-3,EST-4,NG,PRO-1,PRO-2,PRO-3,PRO-5,
ALB,
I= .6113577893884
D= .4920729111817

POPULATION 12 COMPARED TO POPULATION 13
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9910543383006
D= 8.98591436E-03

POPULATION 12 COMPARED TO POPULATION 14
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9689487099178
D= 3.15435994E-02

POPULATION 12 COMPARED TO POPULATION 15
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9690184677319
D= 3.14716087E-02

POPULATION 13 COMPARED TO POPULATION 14
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9887581067385
D= 1.13055609E-02

POPULATION 13 COMPARED TO POPULATION 15
LOCI COMPARED=LDH,TO-1,
TO-2,EST-1,EST-2,EST-3,EST-4,NG,PRO-1,
PRO-2,PRO-3,PRO-5,ALB,
I= .9919986439949
D= 8.03353863E-03

POPULATION 14 COMPARED TO POPULATION 15
LOCI COMPARED=OPRO-1,
OPRO-2,OPRO-3,OPRO-4,OALB,LDH,TO-1,TO-2,
EST-1,EST-2,EST-3,EST-4,NG,PRO-1,PRO-2,
PRO-3,PRO-5,ALB,
I= .9964253423071
D= 3.58106204E-03

APPENDIX 8

Further Statistical Analysis

Initial Chi-Square probabilities may be biased, as a result of the inclusion of complete broods in the sample size. This procedure, in conjunction with the small organismal sample size, may cause over-estimation of population allele frequencies. To circumvent this problem, complete broods were represented by only one randomly chosen individual, and where sample sizes were sufficient, observed heterozygosities were Chi-Square tested against Hardy-Weinberg equilibrium expectation heterozygosities (Table A8A). Chi-Square probabilities (P) were non-significant for all species at all locations, except for the Larus argentatus Ldh-A pooled sample ($P = 7.4 \times 10^{-9}$). This deviation from expectation suggests gene pool heterogeneity at this locus in the L. argentatus populations sampled.

Chi-Square analysis of sample genotype frequencies and Hardy-Weinberg equilibrium expectation genotype frequencies (Table A8B, A8C), suggest the identical data pattern of S. hirundo gene pool panmixis, and L. argentatus gene pool heterogeneity.

Table A8A: Statistical Analysis of Genetic Variation in Sterna hirundo and Larus argentatus. Gene sample sizes (2n) are twice the organismal sample size, and brood samples are represented by only one randomly chosen individual. Allele frequencies, observed (H_O) and Hardy-Weinberg expected (H_E) heterozygosities, and Chi-Square probabilities (P) are recorded for colonies represented br brood samples. Means and standard deviations of allele frequencies are recorded in the total column for alleles; H_O, H_E and P are pooled values.

Species	Locus	Alleles	Nesting Locations			
			Port Colborne	Presqu'ile	Prince Edward Island	Total
Sample Sizes			42	14	14	70
Sterna hirundo	Est-5	100	0.45	0.43	0.21	0.36 ± 0.13
		104	0.55	0.57	0.79	0.64 ± 0.13
		H_O	0.43	0.57	0.14	0.40
		H_E	0.49	0.49	0.34	0.48
		P	0.48			0.22
Larus argentatus	Ldh-A		20			104
		99	0.05			0.24 ± 0.32
		100B	0.00			0.30 ± 0.34
		102	0.90			0.45 ± 0.44
		104	0.05			0.01 ± 0.01
		H_O	0.20			0.25
		H_E	0.19			0.61
		P	0.90			7.4×10^{-9}

Table A8B: Statistical Analysis of Genetic Variation in Sterna hirundo
Gene Sample Sizes (2n) are twice the organismal sample sizes, allele frequencies and Chi-Square probabilities (P, P_L)[1] are recorded for nesting locations where sample sizes are sufficiently large. Means and standard deviations of allele frequencies are recorded in the total column for alleles; P and P_L are pooled values.

Locus	Alleles	Nesting Locations		
		Port Colborne	Prince Edward Island	Total
Sample Sizes		24	44	88
Oest-1	100	0.51	0.68	0.46 ± 0.18
	106	0.46	0.32	0.54 ± 0.18
	P	0.50	0.32	0.40
	P_L	0.15	0.32	0.07
Est-5	98	0.44		0.37 ± 0.13
	100	0.56		0.63 ± 0.13
	P	0.63		0.20
	P_L	0.56		0.12

[1] P: Chi-Square probability derived from the comparison of observed genotype frequencies to Hardy-Weinberg equilibrium expectation frequencies.

P_L: Chi-Square probability derived from the comparison of observed genotype frequencies to Levene's (1949) small sample corrected Hardy-Weinberg equilibrium expectation frequencies.

Table A8C: Statistical Analysis of Genetic Variation in Larus argentatus
Gene sample sizes (2n) are twice the organismal sample sizes, allele frequencies, and Chi-Square probabilities (P, P_L)[1] are recorded for nesting locations where sample sizes are sufficiently large. Means and standard deviations of allele frequencies are recorded in the total column for alleles; P and P_L are pooled values.

Locus	Alleles	Nesting Locations		
		Port Colborne	Prince Edward Island	Total
Sample Sizes		26	40	112
Ldh-A	99	0.04	0.00	0.13 ± 0.32
	100B	0.04	0.98	0.47 ± 0.34
	102	0.88	0.00	0.38 ± 0.44
	104	0.04	0.03	0.02 ± 0.02
	P	0.08	1.00	1.4×10^{-4}
	P_L	0.14	1.00	7.4×10^{-9}
Alb	98	0.00	1.00	0.98 ± 0.08
	100	1.00	0.00	0.02 ± 0.08
	P	1.00	1.00	1.00
	P_L	1.00	1.00	1.00

[1] P: Chi-Square probability derived from the comparison of observed genotype frequencies to Hardy-Weinberg equilibrium expectation frequencies.

P_L: Chi-Square probability derived from the comparison of observed genotype frequencies to Levene's (1949) small sample corrected Hardy-Weinberg equilibrium expectation frequencies.