

GEOGRAPHICAL GENETICS: CONCEPTUAL FOUNDATIONS AND EMPIRICAL APPLICATIONS OF SPATIAL GENETIC DATA IN WILDLIFE MANAGEMENT

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Abstract: Molecular-genetic technology and statistical methods based on principles of population genetics provide valuable information to wildlife managers. Genetic data analyzed in a hierarchical, spatial context among individuals and among populations at micro- and macro-geographic scales has been widely used to provide information on the degree of population structure and to estimate rates of dispersal. Our goals were to (1) provide an overview of spatial statistics commonly used in empirical population genetics, and (2) introduce analytical designs that can be employed to extend hypothesis-testing capabilities by incorporating space-time interactions and by using information on habitat quality, distribution, and degree of connectivity. We show that genetics data can be used to quantify the degree of habitat permeability to dispersal and to qualify the negative consequences of habitat loss. We highlight empirical examples that use information on spatial genetic structure in areas of harvest derivation for admixed migratory species, wildlife disease, and habitat equivalency analysis.

JOURNAL OF WILDLIFE MANAGEMENT 69(4):1434–1453; 2005

Key words: autocorrelation, Canada geese, disease ecology, habitat equivalency analysis, metapopulations, population genetics, spatial genetic structure, white-tailed deer.

A variety of tools are available to help natural resource professionals quickly and efficiently collect and analyze data and apply findings to problems in wildlife conservation and management (DeSalle and Amato 2004). Recent developments in molecular technology such as high-throughput DNA sequencing, single nucleotide polymorphisms (SNPs), and microsatellites (Smith and Wayne 1996, Baker 2000) have led to novel analytical approaches that are widely used in many biological sciences. Noninvasive DNA sampling methodologies have helped expand the use of genetics in applied, field-oriented disciplines including wildlife management (Mills et al. 2000). With the advent of DNA technologies, particularly methods based on polymerase chain reaction (PCR), sampling can be accomplished easily using noninvasive procedures to collect biological ma-

terials such as hairs or feathers, and samples can be preserved for long periods (weeks or months) at ambient (field) conditions (Palsboll 1999). Spatial statistical analyses based on population genetic principles provide a commonly used framework for making inferences in molecular ecology and evolutionary biology, but they have not been fully exploited in wildlife management.

Stewardship of wildlife resources necessitates a fundamental understanding of where and how to invest limited resources to conserve organisms. Two important questions in wildlife management are: (1) over what spatial scales are population characteristics (e.g., demographic characteristics such as age structure and sex ratios, abundance, genetic characteristics) autocorrelated or nonindependent, and (2) at what scales and by what criteria should populations be managed separately? Genetic markers, which were first used as a wildlife management tool in the 1970s (e.g., Manlove et al. 1975), provide a means to define population boundaries and monitor levels of dispersal through a landscape.

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In conservation biology and wildlife management, the effects of habitat fragmentation on population genetic structure and viability are a major focus of concern (Lacy 1987, Lande and Barrowclough 1987). Fragmentation can increase the genetic differentiation among populations by increasing the degree of reproductive isolation, and fragmentation can reduce genetic variation within populations via genetic drift. Spatial subdivision also has potentially important consequences to population viability when selection pressures vary from place to place. The mixing of individuals from genetically differentiated populations through translocations or other human activities can disrupt locally co-adapted genotypes, potentially leading to loss of fitness (Lynch 1991).

Even within small areas and contiguous habitats, wildlife populations are rarely composed of a genetically homogeneous set of individuals, but rather, these populations represent a matrix of spatially segregated subgroups (Scribner and Chesser 1993). The degree of genetic cohesion within subgroups, and spatial scales over which this cohesion exists, will be determined by a species' life history, propensity for movements over short and long distances, behavioral ecology, and social structure (Sugg et al. 1996). For example, spatial genetic structure arises in a matrilineal social system due to the aggregation of genetically related individuals and their spatial segregation from nonrelatives (Chesser 1991*a,b*; Matthews and Porter 1993). Knowledge of geographic variation in gene frequencies can be used to explore how ecological characteristics of populations and the impacts of features (or changes in features) of the landscapes they inhabit lead to nonrandom spatial associations (Sokal et al. 1997, Epperson 2003).

The definition of regions of genetic discordance between individuals or populations is important for the management of wildlife, and it represents a necessary first step to more complex analyses and hypothesis testing. Genetic data sampled from natural populations can complement ecological studies of population demography and behavior, and this data can aid in the development of effective management plans in the face of threats to population survival and future adaptive potential. Genetic markers and population genetic theory can help managers identify constraints imposed by environmental, habitat, or anthropogenic factors that have led to increased reproductive isolation, demographic independence among populations, and declining probabilities of population persistence.

We wrote this paper for the practicing wildlife professional who has little knowledge of population genetics and who has interests in quantitative approaches to understand animal movements and processes affecting spatial structure in natural and anthropogenically altered landscapes. Our objectives were to review past analytical methods and recent advances in empirical population genetics that are relevant to the definition of spatial genetic structuring of wildlife populations. We provided an overview of population genetic principles that relate animal movements and degree of reproductive isolation to spatial variation in genetic characteristics that form the basis for analyses. The empirical examples we provide demonstrate how information on degree of spatial structure can be used for hypothesis testing, and they emphasize the management implications of each application.

TRADITIONAL USES OF SPATIALLY EXPLICIT GENETICS DATA IN WILDLIFE MANAGEMENT

Methods for Estimating Dispersal

Traditional Research Tools in Wildlife Management.—There is increasing interest in methodologies for estimation of dispersal and spatial aspects of recruitment dynamics. When species are numerically declining, it is important to know whether future recruitment will likely occur due solely to natality within the population or if immigration and subsequent breeding by individuals from other populations contribute to future generations. For many species of management concern, it is impossible to monitor large numbers of individuals over space and time in an exhaustive fashion. As such, traditional radiotelemetry and capture–mark–recapture (CMR) methods have been used to estimate degree of spatial cohesion, movements, and inferentially, levels of recruitment via immigration from outside groups (e.g., Nichols et al. 2000, Lebreton et al. 2003).

However, there are numerous reasons to expect that direct measures of movements, as estimated using telemetry or CMR methods, and indirect measures of gene flow, as afforded by genetic markers, may differ (Slatkin 1985, Neigel 1997). Gene flow, in the strict sense, refers to the transfer of genes from one population to another (i.e., individuals dispersing from one population to another breed in the population to which they dispersed). Migration, as quantified by direct observations, documents the physical presence of an individual in >1 population at 2 or more different time periods, and it does not

provide information regarding breeding and thus genetic contributions to recipient populations. Further, gene flow can occur over larger spatial scales than what is monitored through direct observation of marked individuals. Genetic-based estimates provide a cumulative measure of dispersal and subsequent breeding over large spatial scales. Direct observations chronicle the extent of movements only over the period of observation, without revealing anything about historical levels of dispersal. Genetic measures of gene flow record the cumulative effects of historical and contemporary gene flow. Finally, CMR programs are often not feasible, or when they are possible, they are conducted using small sample sizes or over spatial or temporal scales that are smaller than a species' dispersal capabilities, and thus provide limited information on migration.

In the absence of information on movements, genetic markers can be used to estimate parameters that provide surrogate measures of rates of dispersal or degree of population uniqueness (Slatkin 1985, Forey et al. 1994, Petit et al. 1998). Sampling may be comparatively easier for genetic samples using noninvasive methods that do not require handling of individuals (e.g., hairs, feathers, feces), than to capture, mark, and recapture comparable numbers of individuals. Further, individuals genetically identified as immigrants using individual assignment tests or similar methods (Paetkau et al. 1995, see below) would be a valuable addition to CMR programs to identify temporary emigration (i.e., transitional individuals whose observational stage changes with immigration and emigration from the population; Pollock 1982, Kendall and Nichols 2002).

Using the Right Marker for the Right Job.—Different research questions require different genetic markers. Choice of a marker depends on the desired application and on the level of variation required, and it should be consistent with limitations imposed by collection and preservation of biological material. Choice of genetic marker can also be made based on the mode of inheritance. Many genetic markers such as microsatellite loci are inherited in a Mendelian fashion. Other markers are transmitted from a single sex. For example, mitochondrial DNA is an extra-chromosomal genome in the cell mitochondria that resides outside of the nucleus, and it is inherited from mother to offspring with no paternal contribution (Avice 1991). There are other sex-linked markers (e.g., located on the Y chromosomes or W chromosomes of heterogametic males and females in mammals and birds, respectively). Markers that

have different inheritance patterns can be particularly useful based on the research question and knowledge of the ecology of the animal in question (e.g., Favre et al. 1997). For example, if females are more philopatric to natal areas than are males, mitochondrial DNA can be a useful means of documenting female-mediated gene flow. Importantly, using highly variable genetic markers and noninvasive sampling methods, researchers can genetically identify individuals without capture or handling, and thus large amounts of information about individual organisms can be gathered. Ecological data obtained based on genetic identity is qualitatively similar to data obtained using traditional wildlife management tools (e.g., Woods et al. 1999).

Methods of Analysis and the Basis for Spatial Variation among Populations

One common approach to the identification of unique populations is to compare 2 or more populations using statistical tests to determine whether statistically significant differences exist between population estimates of allele frequencies. Inferences about allele frequencies when combined with knowledge of the ecology of the organism and management goals help inform decisions. If the statistical tests suggest no difference in allele frequency, then populations might be managed as a single population, whereas if the populations show significant allele frequency differences, they might be managed separately. More complex models have been developed to quantify levels of genetic variation within and among subpopulations or other breeding groups. Models differ in assumptions and in the relative importance placed on parameters estimated from data (see below).

It is important to know the mechanisms by which spatial variance arises if spatial variation in allele frequencies and measures of genetic distance or variance forms the empirical basis for analytical approaches to define geographic genetic structuring of wildlife populations. Changes in allele frequencies within a population and variance among populations will accrue in a time-dependent manner and as a function of each population's effective size (N_e). Over short time periods where gene flow is limited or absent, we would expect to see changes in allele frequency accrue between populations (Fig. 1, Time I). Genetic relatedness (or coancestry) within a population will be greater than among populations. The genetic affinities among populations can be estimated across alleles and loci using fixation indices (pro-

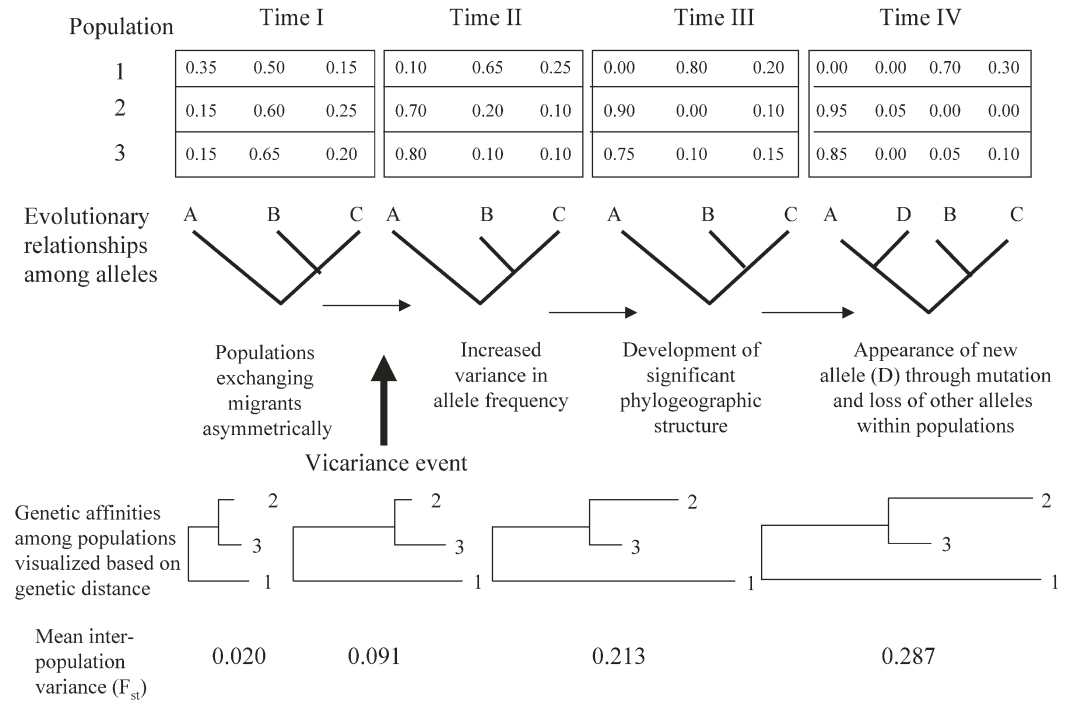


Fig. 1. Hypothetical scenario showing trajectories of increasing inter-population variance in allele frequencies as a function of isolation time (after Moritz 1994). Allele frequency data is commonly used to estimate genetic distance among populations and F_{st} -statistics.

portion of total variance; F_{st} or D_{st}) or by genetic distances as qualitatively shown based on the branch lengths and branching topology of dendrograms (or trees; Fig. 1) constructed based on metrics of genetic distance.

Greater genetic differences between populations can result from isolation due to physical barriers, geographic distance (Fig. 1, Time II), or behavioral or other ecological isolating mechanisms such as timing of reproduction. Over intermediate lengths of isolation (i.e., tens or hundreds of generations), we expect to see alternate fixation of alleles in different lineages. Over longer periods of reproductive isolation, due to the time-dependent coalescence process by which lineage's diverge or are lost (Hudson 1990), we expect to see accumulations of mutations that are novel to each population resulting in further divergence in allele frequencies and increased genetic differentiation among populations (Fig. 1, Time IV). The magnitude of differentiation in allele frequencies at neutral genes can be used to identify units (populations, metapopulations, taxonomic groups, species assemblages) for purposes of conservation (Forey et al. 1994, Petit et al. 1998) or to estimate time since population separation (Hudson 1990) based on the time-depen-

dent process by which variance in allele frequency accumulates via genetic drift.

One approach to quantify degree of reproductive isolation based on genetic data involves apportioning variation in allele frequency (or counts of alleles). Using a hierarchical sampling design, genetic diversity within a species can be systematically apportioned among individuals, social groups, populations, and metapopulations. At the lowest level of the hierarchy within a population, interbreeding individuals are genetically more similar to one another than they are to individuals in other populations. In lieu of information on pedigree relationship, calculation of coefficients of relatedness (e.g., S_{xy} , Bowcock et al. 1994; r_{xy} , Queller and Goodnight 1989) that are formulated based on the proportion of alleles shared between individuals, can be used as a surrogate measure of genealogical relationship. Estimates of relatedness, when made for pairs of individuals separated by increasing spatial distances, can be used to describe characteristics of population social and breeding structure, impediments to gene flow, and degree of population cohesion (Sugg et al. 1996).

Historically, most analyses have focused on populations as the sampling unit of management con-

cern. Significant genetic differentiation among populations is indicative of reproductive isolation and demographic independence. Populations representing long-standing evolutionary lineages (Fig. 1, populations 1 and 2 during Time IV) can be identified to add weight to the priority placed on management. Genetic methods also allow population boundaries to be identified where no obvious barriers exist. Pritchard et al. (2000) and Dawson and Belkhir (2001) demonstrated that the number of genetically differentiated clusters that are consistent with the genotypic data can be inferred, and posterior probabilities of population assignment can be estimated conditional on the most strongly supported number of inferred genetic groups. The Pritchard et al. (2000) approach can be extended to obtain probabilities of admixture (i.e., an individual possessing genotypes arising from a mating of parents from different populations).

An important development in conservation biology is the realization that populations are often not independent, but instead, they are inter-connected to some degree by dispersal and gene flow. Each population may thus be considered as belonging to a larger metapopulation whose dynamics are inter-connected (Hanski and Gilpin 1997). In a metapopulation, where individual populations are expected to go extinct with some probability each generation, recolonization can occur via gene flow from other populations. Time periods over which metapopulations are predicted to persist can greatly exceed those for individual populations.

Metapopulation structure can have important effects on parameters of interest for management, particularly in landscapes where populations are fragmented. A metapopulation in which all local populations suffer extinction and recolonization will tend to lose genetic variation (alleles and heterozygosity), and effective population size will also typically be lower compared to a single population of comparable size or to a subdivided population with gene flow but without extinction (Hedrick and Gilpin 1997). Recently, methods were developed to determine the origin of founding groups and to assess the relative importance of biotic and abiotic factors that play a role in colonization events within a metapopulation (Gaggiotti et al. 2004).

Methods for Determining Degree of Geographical Structuring of Wildlife Populations

Fixation Indices.—Early methods developed to quantify variation in allele frequencies among populations were based on an island model, the

principal components of which centered on the effects of genetic drift (random fluctuations in allele frequency over generations due to the finite number of individuals breeding) and gene flow (Wright 1943). Models assumed random mating within subpopulations, equal reproductive contributions among breeding adults, a large number of populations of equal size each contributing dispersers to the pool of migrants, and equal and constant probabilities of dispersal from (and immigration into) a population for all populations.

Cockerham (1969, 1973) and Weir and Cockerham (1984) demonstrated that statistics generated from Wright's models (e.g., fixation indices; Wright 1965) could be determined using gene correlations ($F = F_{it}$, $\phi = F_{is}$, $\theta = F_{st}$) where F is the correlation between genes within individuals (i) across all populations sampled (t); θ , or coancestry, is the correlation between genes of different individuals within populations; and f is the correlation of genes within individuals (i) within the population (s). Cockerham (1969, 1973) used a hierarchical analysis of variance to derive genetic variance components apportioned within and among spatially subdivided populations.

An alternative to Wright's model (Nei 1973) can be utilized when 2 levels of spatial organization are present (i.e., population and metapopulation) as:

$$H_T = H_S + D_{ST} \quad (1)$$

where H_T equals the total genetic diversity in the metapopulation and represents the probability that any 2 alleles chosen at random, 1 from each of 2 individuals, are independent (Nei 1973). The average, expected genetic diversity within a population can be estimated as the average frequency of heterozygotes in a population (H_S) under Hardy-Weinberg equilibrium. The remaining genetic variance in a metapopulation is the divergence among the populations, which can be estimated by the average genetic distance among populations (D_{ST}). Estimates of F_{st} (or D_{ST}) change with increasing inter-population variance in allele frequencies (Fig. 1).

Genetic Distance.—Metrics of genetic similarity or genetic distance are frequently used to summarize relationships between pairs of individuals or populations based on allele or haplotype frequencies at nuclear or mitochondrial genes. Distance-based methods are frequently used to construct trees as a quantitative means of summarizing genetic relationships among groups based on a single metric. When they are analyzed using clustering algorithms such as neighbor-joining (Satiou and Nei 1987), dis-

ance-based methods provide a means of visualizing genetic relationships. Measures of statistical support, quantified based on the frequency in which populations co-occur in the same cluster on the tree, can be generated by resampling (e.g., bootstrapping) across different loci. Tree branching topology and branch lengths that jointly summarize population relationships change as a function of increasing variance in allele frequency among populations (Fig. 1). Populations that share alleles and whose allele frequencies are more similar (e.g., Fig. 1, pop2 and pop3), will cluster together and will be separated by short branch lengths relative to other populations.

Group-structured Models.—Interpretation of spatial variance in gene frequency across natural populations centers upon knowledge or inferences of movements of genes among individuals within and among populations. Dispersal, aspects of the mating system, and variance in male and female reproductive success are all critically important parameters if we are to understand how genetic variation is partitioned spatially and maintained (Scribner and Chesser 2001).

Researchers have shown that assumptions of Wright's models are not often met in most wildlife species. Group-structured models (Chesser 1991a, 1991b, Sugg and Chesser 1994, Chesser and Baker 1996) have been developed that expand upon Wright's original models to incorporate aspects of organismal demography, life history, and behavioral ecology into the estimation of gene correlations. These models account for the manner in which genes are transmitted among individuals within and among groups, and for differential probabilities of dispersal among groups, (e.g., sex-bias or bias based on different population size, etc).

Parameterization of group-structured models using genetic, demographic, and behavioral ecological data can lead to greater accuracy in estimation of population ecological and behavioral traits, and to greater predictability in forecasting future population or metapopulation change. Understanding the processes that affect gene correlations of individuals within and among populations can be critical in predicting changes in levels of relatedness, inbreeding, and effective population size. Awareness of the plausible trajectories of population change is increasingly important in situations of accelerated anthropogenic changes leading to loss of population connectivity, decreases in abundance, and changes in age structure and sex ratios that increase the likelihood of generation to generation accumulation of gene correlations, inbreeding, and loss of genetic variation.

Group-structured models have been used in wildlife management. Scribner et al. (2001) used demographic and genetic data (maternally inherited mtDNA and bi-parentally inherited microsatellite loci) to estimate effective population size and rates of male and female gene flow in the 3 remnant populations of endangered populations of spectacled eiders (*Somateria fischeri*) in Russia and Alaska. Genetic differences among populations were much lower for nuclear DNA loci than was observed for mtDNA. Estimates of generational female and male rates of gene flow among populations differed greatly (3.7×10^{-4} and 3.0×10^{-2} , respectively), revealing higher natal philopatry of females than for males. High levels of genetic differentiation among females nesting in the 3 remnant breeding populations suggested that the populations should be managed separately.

Individual Assignment Test.—Individual assignment tests (IA; Paetkau et al. 1995) can be employed to assign unknown individuals to population of origin or to identify individuals as migrants (Wilson and Rannala 2003, Paetkau et al. 2004). Individual assignment tests have been used extensively in ecological and evolutionary studies and are increasingly used for management-related activities (e.g., detection of wildlife poaching [Primmer et al. 2000]), determination of population of origin for wildlife disease cases (Blanchong et al. 2002), degree of mixing of released hatchery and wild individuals (Hansen et al. 2000), and assessing the extent of gene flow among populations (Cegelski et al. 2003).

The assignment test is essentially a maximum-likelihood decision rule where probabilities of population origin are based on the product of expected genotype probabilities over all loci scored for an individual, conditioned on the genetic characteristics of each potential contributing population. Estimates of the expected frequency of an individual's multilocus genotype are made for each of the putative source populations. Individuals are classified as belonging to the population with the highest probability of origin. For example, given estimates of allele frequencies $\hat{\theta}_A$ and $\hat{\theta}_B$ determined from samples in 2 populations (A and B), the goal is to use the genotype of an individual of unknown origin to assign it to 1 of the 2 potential source populations. An individual is assigned to population A if the ratio:

$$\frac{L_A}{L_B} = \frac{(\text{Prob}(\text{genotype})|\hat{\theta}_A)}{(\text{Prob}(\text{genotype})|\hat{\theta}_B)} \quad (2)$$

was >1, and they are assigned to population B if the ratio was <1. In Equation 2, L_A is the probability of

the individual's multilocus genotype (assuming both Hardy-Weinberg and linkage equilibrium within the source population), conditional on its origin being in a population with allele frequencies θA . Estimates of statistical confidence in individual assignment decisions can be obtained from posterior population-probabilities using Bayesian models (e.g., Rannala and Mountain 1997).

Several measures are available that provide estimates of true or predictive accuracy: cross-validation accuracy, bootstrap accuracy, and leave-one-out accuracy as a specific case of cross-validation (see review in Shao 1993). Leave-one-out is most commonly used, since it has been shown to be unbiased (i.e., on average, the true accuracy is correctly estimated). Details concerning calculations of the statistic and its application can be found in Paetkau et al. (1995), Cornuet et al. (1999), and Waser and Strobeck (1998), respectively.

APPLICATIONS OF SPATIAL GENETIC DATA: TECHNICAL ASPECTS

Research and management applications of spatial genetic data are limited not by availability of markers or methods of analysis but by lack of knowledge regarding how these techniques can be applied. In the remaining sections, we highlight several emerging areas of importance in wildlife management where spatial genetic data can be used.

Spatial Autocorrelation

Definition and Concepts.—Spatial autocorrelation is the dependence of values of a variable on values of the same variable at other locations (Sokal and Oden 1978, Oden and Sokal 1978). Autocorrelation techniques when applied to alleles or genotypes describe nonrandom patterns in allele frequencies and distances over which such spatial structure occurs. Measures of levels of autocorrelation provide information on whether spatially distributed data violate standard statistical assumptions of independence, and accordingly, whether standard (nonspatial) methods are acceptable (Epperson 2003). Spatially autocorrelated patterns in data can also be used to estimate parameters including migration rates, degree of reproductive isolation as a function of geographic distance, and space-time patterns. Autocorrelation analysis has advantages in describing population structure over standard techniques, such as variance in allele frequencies (F_{st}), because the degree of nonrandom patterns of alleles are described explicitly as a function of distance (Barbujani 1987, Sork et al. 1999).

Autocorrelation in wildlife studies can be important in several areas. First, spatial structure in many situations is inextricably tied to the ecology and habitats used by species of management interest. As such, definition of degree of autocorrelation and the distances over which traits are autocorrelated provide valuable information on basic elements of a species' life history and interactions with the environment. Secondly, because spatial patterns can be changed in substantial and often characteristic ways by anthropogenic forces, including management actions (e.g., Scribner et al. 1984, Blanchong et al. 2005), analyses of spatial patterns can help to detect the impact of these forces.

Estimates of Lack of Spatial Independence.—Statistical measures of spatial patterns in natural wildlife-populations are based on the distribution of genetic characteristics (usually allele frequencies) in pairs of populations (see review in Epperson 2003). The null hypothesis tested is that the allele frequencies have the same expected (mean) value over all sampled populations. Pair-wise, spatial autocorrelation statistics (e.g., Moran's I) are essentially a type of product-moment correlation coefficient that measures levels of inter-population covariation in allele frequency within a distance class for individual alleles. Where populations sampled may be irregularly spaced, investigators can use different weighting schemes with Moran's I statistics to increase power, or population genetic characteristics could vary as a nonlinear function of distance. For example, aquatic organisms inhabiting linear, stream environments may experience higher rates of downstream dispersal relative to dispersal upstream. Standard Moran's I statistics represent a 1-dimensional representation of data. Oden and Sokal (1986) developed a procedure for detection of spatial trends as a function of distance and ordination.

Investigators are frequently interested in documenting nonrandom spatial associations among traits sampled at the level of individuals (genotypes) rather than populations (allele frequencies). A number of techniques including Moran's I statistics (Dewey and Heyward 1988) and joint-count statistics (Cliff and Ord 1981) can be used to estimate degree of autocorrelation and spatial genetic patch structure of individual genotypes. Smouse and Peakall (1999) developed a multi-allele and multilocus approach by defining a genetic distance between pairs of individuals based on sharing of alleles. The approach of Smouse and Peakall (1999) differs from other methods where estimates of spatial autocorrelation are made for each allele separately.

Autoregression Analyses of Space-time Processes

Although spatial patterns of genetic variation when estimated from one time period can be used to quantify the distance of effective gene flow, use of spatial-temporal data allows additional inferences to be made. For example, if gene frequencies are influenced only by genetic drift and rates of migration among populations, then when spatial genetic data is collected in one time period it allows limited inferences. Dispersal is a continuous process that is best monitored when populations are sampled over a series of time periods so that rates of migration between populations that are separated by various distances generally can be accurately determined.

If migration rates are the same in all directions, then the spatial pattern is primarily determined by the variance of the migration distances and the amount of drift (inverse of effective population size; Malécot 1948). In a system of populations existing essentially in 2 spatial dimensions, if migration is greater along 1 axis or dimension than it is in the other, then such dimensional directionality can be detected in spatial patterns (Oden and Sokal 1986, Epperson 2003). More generally, spatial patterns should be viewed as a spatial cross-section of an underlying space-time process (Fig. 2). One can model a specific space-time process and compare the spatial patterns produced to empirical observations. Unfortunately, it is often the case that more than 1 spatial-temporal process can produce the same spatial patterns. For example, the genetic change in a population (e.g., changes in allele frequency) may be influenced by immigrants. Then the change depends on the sum of products of migration rates from the source populations and degree of genetic differences among the source populations. The sum of products may be the same for many different source and recipient populations. In contrast, the use of space-time data has the potential to filter the effects of migration into spatial scales (or lags) and also into temporal scales.

Recently, it was shown that a spatial-time series-model known as space-time autoregressive, STAR (Epperson 1993), subsumes and greatly extends standard population genetics models of gene flow (e.g., stepping stone model of migration and drift; Kimura and Weiss 1964). STAR is a special case of STARMA, which is the space-time extension of an autoregressive moving average (ARMA), time-series model (Box and Jenkins 1976). The STAR treats a variable, $z_{\underline{x},t}$, as a set of time-series that do not evolve independently, rather they interact in ways that reflect degree of spatial proximity. If $z_{\underline{x},t}$

is taken to be the value of some variable, for example gene frequency, at a location defined by coordinates in a vector \underline{x} , at time period t , then:

$$z_{\underline{x},t} = \sum_{s=1}^m \sum_{\underline{b}} \phi_{\underline{b},s} z_{\underline{x}+\underline{b},t-s} + a_{\underline{x},t} \quad (3)$$

Each $\phi_{\underline{b},s}$ is a coefficient of autoregression, measuring the strength of influence of the value of the variable at location $\underline{x} + \underline{b}$ at time period $t-s$. For the migration model, $\phi_{\underline{b},1}$ is the rate of migration from a population existing at a distance specified by the spatial lags in the vector \underline{b} . Theoretical models are usually based on a lattice, where the features of spatially lagged autoregressive effects are exemplified (e.g., Fig. 2). Genetic drift acts through the spatially random (white noise) stochastic inputs $a_{\underline{x},t}$.

An analogous equation can be written for observed values for space-time data (e.g., Pfeiffer and Deutsch 1980). For example, STAR and the broader STARMA model provide a statistical model (as opposed to model of a stochastic process) for data collected from multiple locations and across multiple time periods. In general, STARMA uses space-time data to estimate the strengths of influences of locations at different spatial distances or lags at various, previous time periods. The STARMA analyses include steps of process identification, parameter estimation, and model fit. Once a model is fitted, it can be used for forecasting by applying the autoregression equation to the existing state of the system. For example, once migration patterns are determined and the migration rates are estimated, that information can be used together with the current spatial pattern of genetic variation to project the spatial pattern of future time periods. Moreover, autoregressive coefficients could be modified by suggested managerial strategies, and the various outcomes could be compared and contrasted (e.g., with and without changes in landscape connectivity due to development).

Habitat Connectivity Influences Spatial Structuring of Populations on a Landscape Level

Autocorrelation is a general property of ecological and genetic variables examined along spatial or temporal axes (Legendre 1993), and it can have significant consequences for design and analysis of ecological or genetic field surveys (Legendre and Fortin 1989, Legendre et al. 2002), particularly when data are collected with the intent to relate biological response variables (e.g., inter-population

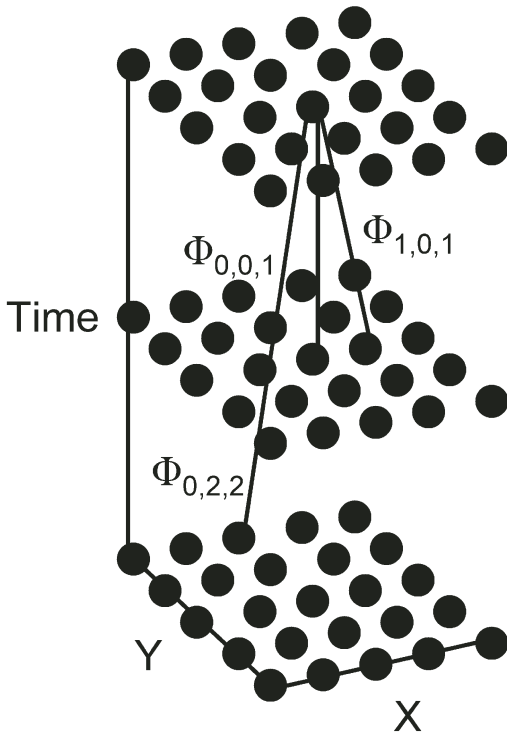


Fig. 2. Example of autoregression coefficients for a Space Time Autoregression (STAR) or Space Time Autoregression with Moving Averages (STARMA) stochastic process. Here, the location vector has 2 coordinates (x, y) . Thus, for example, $N_{0,2,2}$ is the autoregressive coefficient for a location zero spatial lags in the x dimension, 2 spatial lags in the y dimension, and 2 time-period lags; $N_{0,0,1}$ is the effect of the value at the same location on itself 1 period later. In migration models this would be the rate of nonimmigration.

differences in allele frequency) to explanatory environmental variables (Dale et al. 2002).

Understanding patterns of gene flow and processes that lead to local adaptation requires detailed knowledge of how landscape characteristics structure populations (Manel et al. 2003). Landscape connectivity, the degree to which landscape features facilitate or impede movements and gene flow between populations (Taylor et al. 1993, D'Eon et al. 2002), is an essential feature of landscape structure because of effects on movements among populations, population persistence, and probabilities of recolonization. Landscape connectivity can be quantified, in a relative sense, based on indices that characterize the spatial dispersion of landscape habitat types and based on proportional contributions of each landscape type to landscape matrices between populations (Fig. 3C).

Landscape connectivity or permeability can play a critical role in the structuring of populations, particularly in situations where habitats are fragmented

by human activities. In most wildlife management applications, direct measurements of connectivity that are typically quantified by observations of animal movements are not logistically feasible (Tishendorf and Fahrig 2000). The degree of genetic differentiation among populations can be used as a surrogate measure of movements and reproduction following immigration into new populations.

Populations of most species are limited in their movements to some extent by characteristics of habitat and by their degree of vagility. Populations are thus isolated as a function of the distance between other suitable habitats as well as by the type of intervening habitat. Not all habitat types are equally conducive to dispersal. Geographic proximity as measured by straight-line distance may not be predictive of probabilities of movements between populations. Landscape connectivity can be described using an approach whereby degree of permeability of any habitat type is weighted by landscape attributes that are tied to a species' ecological requirements (e.g., Ray 2005).

Models that can account for the influence of landscape connectivity on gene flow and changes in gene correlations within and among populations would be extremely valuable for hypothesis testing. Mantel (1967) developed a test of the association of between 2 sets of pair-wise matrices, for example, pair-wise inter-population measures of genetic distance and distance. Smouse et al. (1986) reformulated the Mantel statistic in terms of a product-moment correlation. The statistics can be extended to multiple regression analysis for any response-variable matrix (e.g., inter-population genetic distance) with several predictive, independent variable matrices to evaluate the influence of geographic distance and habitat permeability. For example, Scribner et al. (2000) found that inter-population variance in population levels of genetic variability and population size in populations of the common toad (*Bufo bufo*) were correlated with components of the terrestrial environment between breeding ponds as assessed using remote sensing and ground surveys.

APPLICATIONS OF SPATIAL GENETIC DATA: EMPIRICAL EXAMPLES

Autocorrelation at Individual and Population Levels

Spatial Analysis.—Blanchong (2003) used genetic markers and spatial statistics to characterize microgeographic genetic structure in a white-tailed deer herd in the Northeastern Lower Peninsula of Michigan (Fig. 3B). Genetic distances

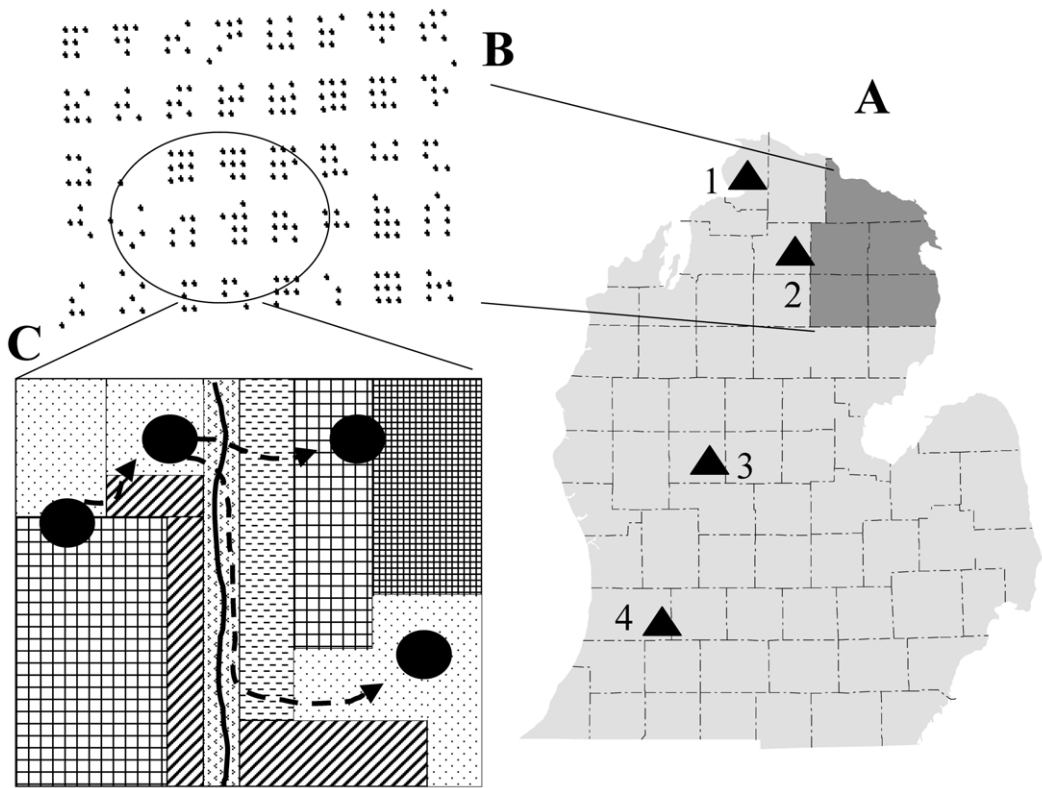


Fig. 3. Location of the bovine tuberculosis endemic in the white-tailed deer population in northeastern Michigan (A), juxtaposition of 6.8-km² sampling grids within the study area (B), and schematic representation of a habitat mosaic separating the different sampling grids (C). The permeability of different habitats to dispersal and gene flow among locations, independent of geographic distance, may not be homogeneous across all habitat types.

based on data from a battery of microsatellite loci were calculated between individual deer and for groups of deer apportioned spatially into 2.6-km² grids over a 2,323-km² region (Fig. 3A). Matrix regression (Mantel tests, Smouse et al. 1986) was used to correlate degree of genetic differentiation among individuals and among grids of deer (Fig. 3B) with increasing geographic distance. Analyses of grids were conducted using individuals grouped at 6.8-km² and 60.8-km² grids.

Blanchong (2003) detected significant genetic structure over short, inter-individual distances or inter-location distances (i.e., at the levels of individuals and among samples collected at the 6.8-km² intervals; Fig. 4). When deer were grouped at larger geographic scales, the sampling interval (inter-locality distance) exceeded patch diameter or the distance over which biologically meaningful autocorrelation existed; thus, no spatial genetic structure was evident.

Space-time Analysis.—We also applied STARMA statistical analysis to the Blanchong (2003) white-

tailed deer data set on allele frequencies at 3 microsatellite loci samples over the most coarsely defined spatial scale (in 60.8-km² grids; Fig. 4). In this case, the autoregressive coefficients were assumed to follow the spatial lag structure, such that autoregression coefficients defined as being at the same spatial lag or order had the same average value. The partial, space-time correlations (Hooper and Hewings 1981) averaged over all alleles (Table 1) were all small, indicating that there was little auto-regression in the data at this spatial scale. This fits with the finding of no significant spatial autocorrelation in the data at the same coarse (60.8-km²) spatial scale (see above; Fig. 4). However, when the genetic data were further refined by assignment to 6.8-km² (political map section) grids, there was significant spatial autocorrelation (Blanchong 2003; Fig. 4) suggesting that gene flow occurs at micro-geographic scales. This comparative analysis provides compelling evidence of the importance of geographic scale in design of a sampling program. Sampling across intervals that ex-

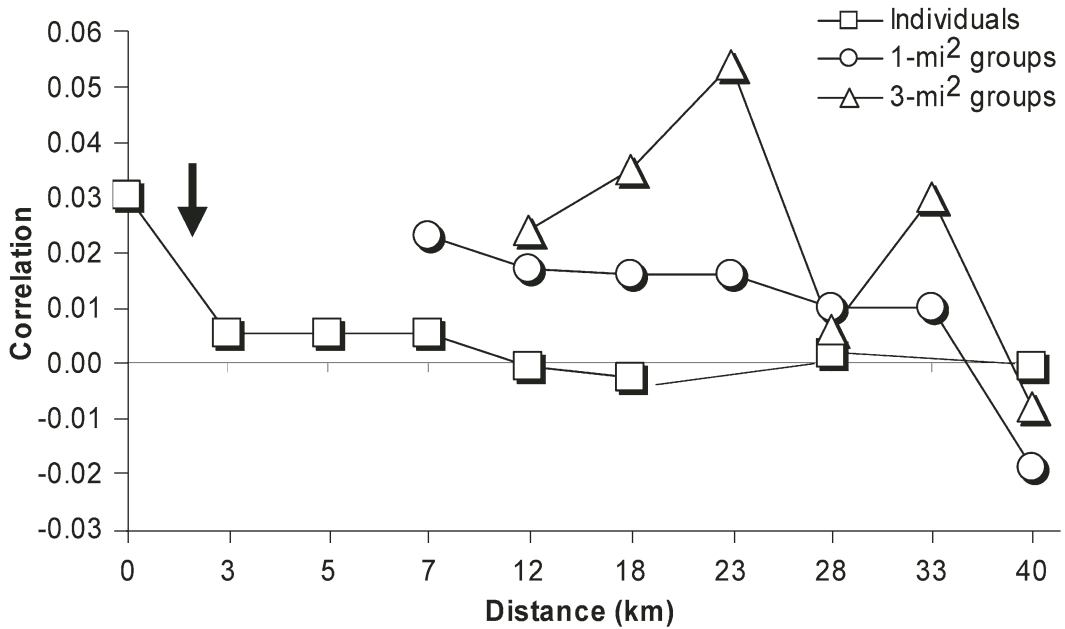


Fig. 4. The degree of genetic autocorrelation as a function of increasing geographic distance among deer that were aggregated at the level of individuals into 6.8-km² and 60.8-km² groups. Aggregating individuals into 60.8-km² groups resulted in high variance within sampling locations, which partially obscured variation among groups as a function of distance. Aggregation of individuals into 6.8-km² groups reduced intra-group variance, allowing detection of inter-group autocorrelation at biologically relevant distances. Spatially nonrandom associations can also be detected at the individual level, revealing that coefficients or relatedness decrease as a function of inter-individual distance. The arrow refers to the average home-range size for white-tailed deer across the study area (Garner 2001).

ceed effective distances of gene flow will result in measures of spatial inter-relationships that have little biological relevance.

Mantel Tests of Habitat Permeability.—Weighting matrices that include habitat variables can be used as independent variables to explain relationships between pairs of points (e.g., based on genetic affinities and inferentially rates of gene flow among populations). Measures of habitat permeability can thus be used to explain the degree of covariation in variable values (e.g., allele frequencies) in different locations. In situations where spatial heterogeneity in landscape connectivity is expected, the use of different weighting schemes will likely be more informative than analyses based on distance alone.

Expanding on analyses for white-tailed deer described above (Blanchong 2003), we incorporated features of the landscape as an additional explanatory variable of inter-population differences in allele frequencies. We used an index of thermal cover potential (TCP; Felix et al. 2004) to quantify white-tailed deer habitat suitability. We defined thermal cover potential between pairs of points as a composite measure of indices of forest species composition (a function of forest type and species

of coniferous species), forest structure (a function of average basal area, canopy cover, and tree size), and site quality (a function of geological attributes affecting forest growth and productivity; Merkel 1988). Areas with high TCP were those with closed canopy. Each habitat was indexed on a scale of zero to 1, where 1 had the highest TCP (Felix et al. 2004). We selected 50 random 6.8-km² grids across the study area (Fig. 3). Grids were used to group deer harvested and sampled during 2000. We estimated a weighted average TCP between all pairs of grid locations. We conducted a partial correlation coefficient summarizing the relationship between matrices of inter-grid genetic distance (a relative measure of gene flow among grids) and inter-grid TCP (a relative measure of habitat permeability) using a partial Mantel Test (Smouse et

Table 1. Partial space-time correlations (averaged across all alleles and loci) at several spatial lags, and temporal lags in years for white-tailed deer allele frequencies.

	0	1	2	3	4
1	0.056	-0.001	0.092	-0.009	-0.054
2	0.014	0.026	-0.013	-0.046	0.002

al. 1986) performed using program PASSAGE (Rosenberg 2000).

Analyses using 50 random grids resulted in a negative correlation ($r = -0.0954$, $P = 0.06$). As expected, greater genetic differences were negatively correlated with greater amounts of thermal cover potential among grids, so deer from grids separated by habitats with higher TCP were more similar genetically (i.e., alleles frequencies were more similar and exhibited lower genetic distance) than grids separated by lower average TCP. There was no significant correlation between geographic distance and genetic distance for these grids, suggesting that the degree of landscape connectivity estimated by incorporating habitat features related to white-tailed deer ecological requirements was generally more predictive than was inter-grid distance alone.

Geographical Genetics at the Individual Level: Applications to Wildlife Disease.—Emerging infectious diseases pose significant challenges to wildlife managers and directly affect the health and well-being of humans. Disease transmission in a wildlife population can be affected by the spatial distribution of infected individuals within a landscape (Fromont et al. 1998, Fulford et al. 2002). Knowledge of genealogical structure of host populations at a microgeographic scale can be used in wildlife epidemiological studies.

The white-tailed deer population in northeastern Michigan is infected with bovine tuberculosis (*Mycobacterium bovis*; TB). This is the only case of self-sustaining TB in a free ranging ungulate herd. Research has indicated that white-tailed deer are the reservoir host for TB in Michigan (Schmitt et al. 1997). Blanchong (2003) used 11 microsatellite markers to estimate inter-individual coefficients of relationship (r_{xy}) as a surrogate measure of pedigree relationship for white-tailed deer in the TB infected herd. Based on deer's social ecology in which females live in related groups, it was hypothesized that rates of contact among relatives were higher than contacts among nonrelatives. Accordingly, the risk of 2 individuals from the same locale being co-infected with TB would likely be higher for related individuals than for genetically independent individuals. Comparisons of genealogical relationships calculated between pairs of TB-positive and pairs of TB-negative individuals separated by increasing geographic distance indicated that mean relatedness among TB-infected deer was consistently higher than relatedness among noninfected deer harvested within distances consistent with data on deer movement in the study area (Garner 2001). Findings of higher average

genetic-relatedness among TB-infected deer relative to noninfected animals within distances consistent with telemetry data and direct estimates of home-range size (Garner 2001) supported the hypothesis that the social ecology of deer significantly influenced risk of TB infection. Knowledge gained from genetic data on the relationship between wildlife social ecology and disease transmission, and the spatial scale over which nonrandom genetic associations exist, can be used in predictions of the rate and spread of disease and the development of effective control programs.

Novel Applications of Assignment Tests in Wildlife Disease Ecology.—Assignment tests have been repeatedly used in Michigan to examine tissues from white-tailed deer found to be infected with TB. TB is endemic in the deer herd inhabiting the north-eastern portion of the Michigan Lower Peninsula (Fig. 3A). Recently TB has been found in individual deer in other regions of the state (Fig. 3A, locations 1, 2, 3, 4). Blanchong et al. (2002; J. A. Blanchong, University of Wisconsin, unpublished data) genotyped deer from each of the 4 locations. Based on individual assignment tests, each diseased individual was found to possess genotypes significantly more like those in the counties in which they were harvested relative to genotypes in the TB endemic area. Tests were important to alleviate public concerns of long-range dispersal or illegal transportation of diseased carcasses out of the TB management area. Findings suggested that there were multiple areas of endemism for the disease throughout Michigan.

Genetic Diversity, Metapopulations, and Habitat Equivalence

Many wildlife species exist as assemblages of spatially delimited local populations inhabiting a landscape of patchily distributed or fragmented habitats (i.e., a metapopulation) that are interconnected to varying degrees by gene flow (Hanski and Gaggiotti 2004). Management actions that are of increasing importance include actions developed on the basis of emerging metapopulation concepts and information pertaining to geographic genetic structuring of populations that successfully mitigate the negative effects of habitat loss and fragmentation, the leading threat to biodiversity in the United States (Wilcox and Murphy 1985, National Research Council 1995, Noss et al. 1997, Wilcove et al. 1998).

Genetic variation apportioned among and within populations represents measures of biodiversity that are widely recognized as being impor-

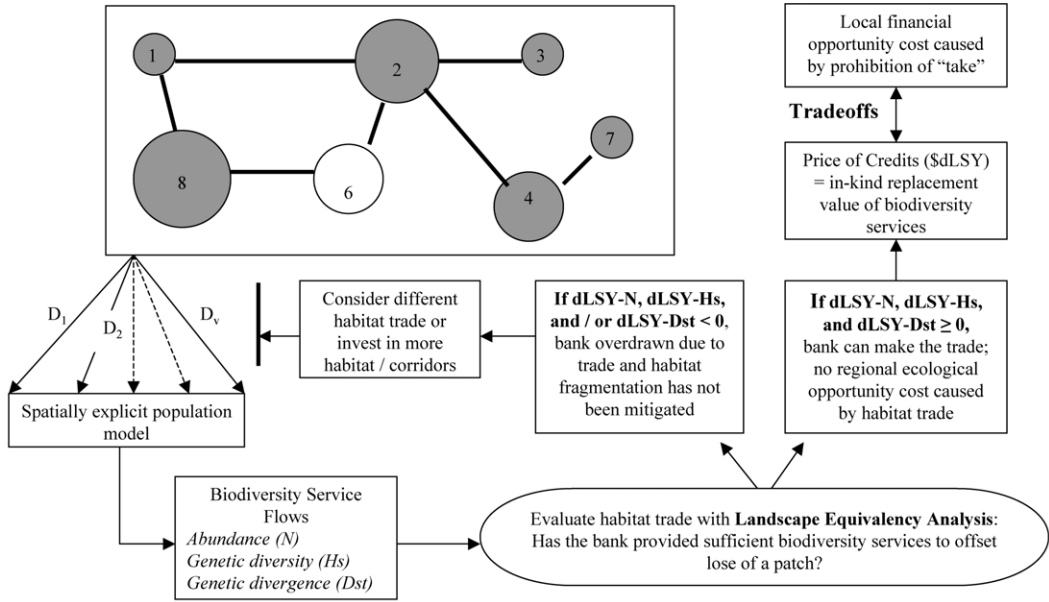


Fig. 5. Trading habitat patches using multiple biodiversity services with Landscape Equivalency Analysis. A hypothetical metapopulation is presented above. Gray circles represent existing habitat patches, lines represent existing corridors, and open circles represent conservation bank patch. D_1, D_2, \dots, D_v are possible decisions to trade habitat patches (i.e., v possible patch and corridor configurations). Patch 6 represents a conservation bank that may sell credits to owners of all other patches if they wish to develop their habitat. However, the credits acquired by restoring patch 6 may only be sufficient to offset patch 4 or to offset 1 or more of the small, peripheral patches. Loss of the peripheral patches will cause greater withdrawals of $dLSY-Dst$ (biodiversity credit representing genetic divergence) than credits representing abundance ($dLSY-N$) and genetic diversity ($dLSY-Hs$). Conversely, the loss of patch 2 would require large withdrawals of $dLSY-N$ and $dLSY-Hs$ and fewer $dLSY-Dst$ credits. In this landscape, selling credits from the bank to offset the loss of patch 2 is likely not a viable trade, unless the size and connectivity of patch 6 (the bank) were increased.

tant to fitness and continued adaptation (Amos and Balmford 2001). Development of habitats occupied by wildlife often will result in the loss of variation through reductions in population size and extinction of populations within larger metapopulations. The magnitude of loss in terms of increasing probabilities of metapopulation extinction resulting from habitat destruction and loss of a single population will not be the same for all populations. Habitats occupied by certain populations may be critical as corridors to dispersal and recolonization of other isolated habitats (e.g., Fig. 5, population 2). Certain populations may harbor disproportionately higher proportions of genetic diversity than do other populations; thus, their loss would disproportionately decrease total levels of genetic variability in the metapopulation (Petit et al. 1998). Methods are needed that could quantify the relative contributions to total metapopulation genetic diversity and provide a means to establish quantitative criteria of relative benefits of adding (or banking) new habitats to mitigate anticipated habitat (and population) losses elsewhere.

Ecological and evolutionary principles can be most effectively incorporated into management decisions when integrated with insights from the social sciences (Possingham et al. 2001), particularly in situations where economic and social values come into direct conflict with mandated stewardship responsibilities. Resource-based compensation is one method to integrate ecology and economics into management decisions regarding habitat loss and restoration (Jones and Pease 1997; National Oceanic and Atmospheric Association 1999a,b). Habitat is a form of natural capital, providing biodiversity services (attributes that contribute to metapopulation persistence such as abundance, genetic diversity, and genetic divergence among populations; Fig. 5) that indirectly contribute to human well-being (Loomis and White 1996, DeGroot et al. 2002). Resource-based compensation is used to determine if habitat loss in 1 location has been (or will be) offset by habitat restoration or acquisition at another location, such that biodiversity services do not decline over time or space despite habitat trading. Recently, Bruggeman et al. (2005) proposed a method to integrate

resource-based compensation with population genetic theory to estimate biodiversity credits. This novel method, called Landscape Equivalency Analysis (LEA; Bruggeman et al. 2005), captures the importance each population contributes to metapopulation processes—specifically population growth, migration among populations, and contributions to total metapopulation levels of genetic variation. When integrated with recent conservation banking policy under the Endangered Species Act (ESA), LEA may help direct management prescriptions to decrease fragmentation of wildlife habitat using market-based incentives.

Genetic variance within and among populations is important for adaptive evolution (McCauley 1991, Lande 1998). Within a metapopulation, there must be a balance between growth within each population (effective population size, N_e) and migration between populations (e.g., Fig. 5, among populations 1–8). This balance is necessary to prevent inbreeding and outbreeding depression and to maintain levels of genetic variance to maintain adaptive potential (Mills and Allendorf 1996). The spatial apportionment of genetic variance, as measured by neutral genetic markers, will be sensitive to genetic drift and migration that will result from changes in spatial associations of habitat when disruptions occur because of human disturbance within a landscape (Young and Clark 2000, Hanski and Gaggiotti 2004). Small population size and isolation increases the loss of genetic variance due to genetic drift and inbreeding; thus, it may accelerate probabilities of population and metapopulation extinction over expectations based on population numbers alone.

The LEA can be used to compare the ecological-economic equivalence of different landscape configurations (or habitat networks). Equivalent landscape configurations will mitigate potential declines in biodiversity services compared to baseline (pre-exploitation) levels (Bruggeman et al. 2005). Private landowners often base land-use decisions on the financial opportunity costs of not developing land. When financial opportunity costs are great enough and local economic decisions are implemented, spatial associations of habitat in the landscape are typically altered, which causes regional and local changes in genetic variance and biodiversity service flows (Young and Clark 2000). Local economic decisions often incur regional, ecological opportunity costs for a metapopulation (i.e., lost opportunities for metapopulation growth and adaptive evolution), measured as changes in these biodiversity service flows. Certain habitat network configurations (e.g., TCP indices utilized above) will be better than

others for maintaining gene flow and metapopulation growth and adaptive evolution.

The LEA estimates ecological costs at the regional scale due to different mitigation choices at the local (population) scale by capturing biological costs that may not be recognized when using Population Viability Analysis (PVA); specifically changes in genetic variance within and among populations (Hedrick 2002). Nei's (1973) method of apportioning neutral genetic variance at different spatial scales (i.e., within and among populations) is adapted to capture spatially explicit effects of local economic (land-use) decisions on regional levels of genetic variance. The LEA calculates the equivalency of different landscape configurations using estimates of average, expected genetic diversity (H_S); the average genetic divergence (D_{ST}); and abundance (N). Measures of H_S , D_{ST} , and N provide estimates of biodiversity services from a habitat network. Calculating biodiversity credits using LEA and service flows sensitive to habitat spatial structure (N , H_S , D_{ST}), which are estimated empirically for each situation, may replace general rules of thumb (e.g., 1 migrant per generation; Mills and Allendorf 1996) to prescribe adequate levels of migration for endangered metapopulations.

Spatially explicit simulation modeling can be used to generate expected biodiversity service flows for each landscape configuration (Dunning et al. 1995, Lacy 2000). The LEA calculates the marginal conservation value of patches within a metapopulation or ecological opportunity costs that would result from losing each patch or loss of connectivity among patches (Bruggeman et al. 2005). Expected discounted Landscape Service Years ($E[dLSY]$) are calculated for each biodiversity service flow individually. They represent the number of credits that must be purchased from the bank to offset the loss of a patch elsewhere in the landscape, thus preventing an ecological opportunity cost from being incurred (Fig. 5). The LEA captures information on societal preferences using a social discount rate; thus, it modifies the importance of biodiversity services at different times. Regardless of how large the societal discount rate is, the ESA stipulates that the habitat trades cannot cause a take or increase probability of extinction. Therefore, sustainability goals are not compromised by the market-based approach to habitat trades.

Estimation of Population Contributions to Harvest Mixtures

Management of harvested species requires maintenance of viable breeding populations that allow for sustained harvests. Management of harvested

populations often involves collecting information on levels of recruitment and mortality to meet user goals for species and populations. Wildlife managers rely on quantitative assessments that assume harvest estimates are representative of a specific breeding population. If harvest is composed of a mixture of breeding populations, then the relative contribution of each breeding population must be determined so that estimates of exploitation, mortality, and harvest rates can be apportioned correctly (for a recent review of stock identification methods see Cadrin et al. 2005).

Management of exploited migratory species is often necessary (e.g., when monitoring harvest composition in areas where individuals from multiple breeding populations or subspecies mix during harvest periods). For species where little information is available on the basis of marked individuals, analyses utilizing information on geographic genetic structure can be applied for purposes of harvest derivation. Genetic-based analyses have extensions to other ecological questions concerning characterization of migratory routes, timing of arrival, and locations of wintering grounds.

Mixed Stock Analysis.—It is possible to estimate the relative contribution of each breeding population to mixtures, such as hunter harvests of migratory species (e.g., waterfowl or for neotropical migrants captured during migration), using genetic markers and information on population differences in allele frequency. Comparisons are typically made of distributions of genotypic frequencies of each breeding population with genotype frequencies observed from individuals of unknown origin that are captured during non-breeding time periods (e.g., during migration and on wintering grounds). Mixed stock analysis (MSA; Pella and Milner 1987) uses the relative differences in allele frequency among breeding populations to estimate the composition of an admixed sample. Precision and accuracy of MSA generally increases as differences in allele frequency increase among breeding populations. Analyses can be performed using a variety of computational approaches including maximum likelihood (Millar 1987, Wood et al. 1987), least squares (Xu et al. 1994), and Bayesian (Pella and Masuda 2001) methods. These methods use readily available computer programs such as the Statistical Package for Analyzing Mixtures (SPAM; Debevec et al. 2000). Genetic techniques allow for unambiguous estimates of harvest composition at spatial and temporal scales that provide feedback on the success of management programs.

Mixed Stock Analysis Derivations of Canada Goose Harvests in Michigan.—For seasonally migratory species such as Canada geese (*Branta Canadensis*) or Cackling geese (*B. hutchinsii*), hunting represents the primary source of mortality (Rextad 1992). Harvests routinely occur in areas far removed from breeding locales and in situations where individuals from multiple breeding populations co-occur in admixed flocks. In the absence of definitive information on harvest composition, numerically depressed populations or subspecies of conservation concern may be unintentionally overexploited.

To accurately estimate proportional contributions of populations or subspecies within a mixed flock, the harvest must be unambiguously identified to population/subspecies of origin. In addition, harvest samples must be representative of the entire harvest at desired spatial and temporal scales. Recently, molecular techniques and MSA have been applied to apportion Canada and Cackling goose harvests in several flyways using knowledge of degree of spatial genetic structure at the subspecies and population levels. Pearce et al. (2000) used mitochondrial DNA sequences and microsatellite loci to apportion harvests of Canada and Cackling geese to harvests in the Pacific Northwest. These authors found that subspecific assignments of harvested birds made on the basis of plumage and body size were inaccurate. Scribner et al. (2003) conducted MSA for Canada and Cackling geese harvested in Michigan over several years and in several locations across the state. Inman et al. (2003) expanded analyses using samples obtained from the standardized U.S. Fish and Wildlife Service parts collections to sex individuals on the basis of genotype at sex-linked loci (Griffiths et al. 1998) and to apportion harvests on a state-wide basis.

To highlight the utility of the MSA technique at different spatial and temporal scales, we present estimates (+SD) of harvests from state Goose Management Units (GMUs) that are managed to attract and retain migratory, interior Canada geese, and we also present nonGMU public and private areas state-wide and in the Southern Lower Peninsula of Michigan. Harvest derivations were based on multilocus, microsatellite genotypes from breeding populations of migratory and resident geese from the midcontinent regions of the United States and Canada (Inman et al. 2003, Scribner et al. 2003). Estimates of harvest revealed that there were substantial differences in the frequency of migratory (*B. c. interior*; *B. hutchinsii*) and resident (*B. c. maxima*) birds in GMU and nonGMU areas, in different areas of the state, and

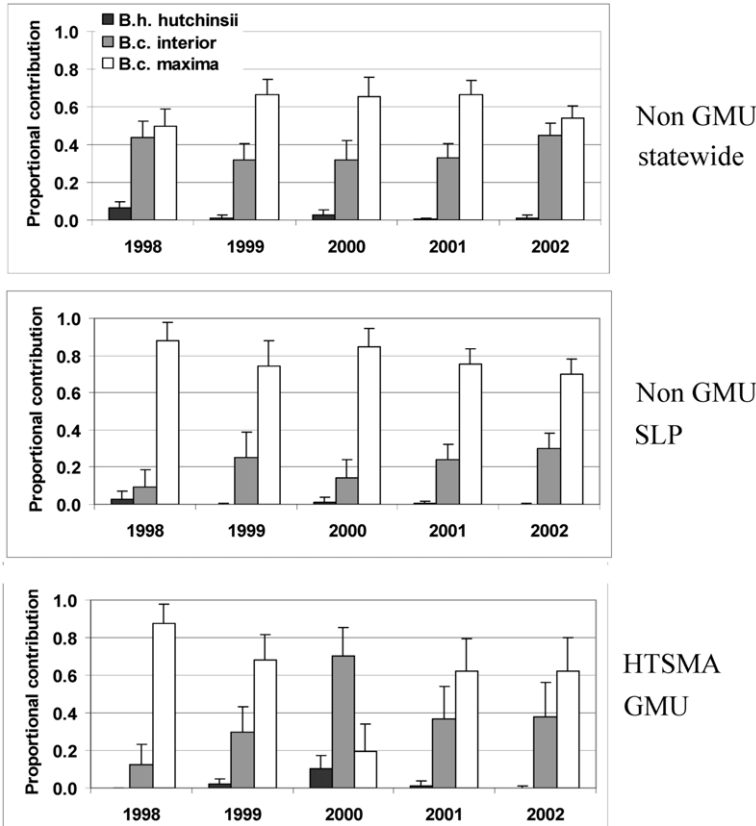


Fig. 6. Mean proportional contributions (+SD) of *Branta hutchinsii hutchinsii*, *B. canadensis interior*, and *B. c. maxima* to regular season harvests (16 Sep–31 Dec) in Michigan's 4 local Goose Management Units (GMU) including Huron/Tuscola, Saginaw, Muskegon, and Allegan (HTSMA), and Michigan's nonGMU counties statewide and in the Southern Lower Peninsula (SLP), 1998–2002.

among years. A higher proportion of the goose harvest was composed of *B. c. interior* in Michigan's Upper Peninsula and in the northern portion of the Lower Peninsula compared to harvest composition in the Southern Lower Peninsula (comparison of nonGMU state-wide estimates to nonGMU SLP estimates (Fig. 6). Differences in proportional contributions of migratory and resident Canada geese among years were attributed to annual variation in timing of migration (H. Prince, Michigan State University, unpublished data).

MANAGEMENT IMPLICATIONS

The application of genetic techniques to questions of interest to wildlife ecologists and managers is presently restricted more by lack of knowledge of applicable methods and by cost than by the availability of appropriate techniques. We reviewed traditional and novel approaches for using spatial genetic methods. Empirical examples demonstrate

a broad range of applications for genetic markers and spatial statistical methods of analysis to wildlife research and management questions.

Collection of spatially referenced genetic data from wildlife populations can provide a foundation for long-term monitoring of population responses to landscape changes, fragmentation, and management actions. In contrast to traditional assessments of habitat equivalency analysis, genetic concepts (specifically LEA) provide a means to quantitatively compare populations and assign relative values to lands considered for development (or for protection or purchase), and they provide a means to insure that limited resources are invested in management actions most likely to maintain biodiversity. The use of genetic markers and

mixed stock analysis to allocate harvests allows managers to distinguish among management units that are not easily discriminated morphologically or where banding data is lacking. Identification of contributions of populations to harvests as a function of spatial location and time period will enable managers to more carefully regulate harvest seasons to best achieve optimal harvests of numerically abundant populations while minimizing harvests for populations that cannot sustain excessive harvest-based mortality.

Analyses of the spatial genetic structure of wildlife will enable managers to more clearly identify significant population units. In addition, in conjunction with landscape data, spatial genetic data can help identify habitat variables that are most important for maintaining connectivity among populations and which variables serve as barriers to animal movement. Spatially explicit analyses will also be useful in situations such as

wildlife disease epizootics where managers need to quickly identify the most likely distance and direction of disease spread.

Use of spatial genetic methods will expand as new methods of collecting and analyzing genetic samples are applied to traditional and new wildlife management problems. Applications of spatial genetic methods to identify spatial genetic structuring in wildlife populations can improve planning and monitoring of population and habitat conservation strategies. We recommend that agencies broaden their background requirements to include familiarization with population genetic principles. We encourage managers to think strategically about creating state-wide data bases with spatially explicit genetic data for species of management concern.

ACKNOWLEDGMENTS

Funding for the case studies we presented were provided by the Michigan Department of Natural Resources through Federal Aid in Wildlife Restoration Act under Pittman-Robertson projects W-129-R and W-127-R. Additional support was provided by the Department of Fisheries and Wildlife at Michigan State University through the Partnership for Ecosystem Research and Management Program, and the Environmental Protection Agency's STAR Fellowship program.

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