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Pedigree Analysis for Population Management



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The long-term survival of a population depends on the maintenance of sufficient genetic variation for individual fitness and population adaptability. Inbreeding depression, the reduction of fecundity and viability in progeny of matings between close genetic relatives, has been extensively documented in domesticated livestock (Darwin 1868; Wright 1977; Falconer 1981), captive populations of wild animals (Ralls et al. 1988; Lacy et al. 1993), and in many, but not all, wild populations (Wildt et al. 1987; Thornhill 1993). The loss of individual heterozygosity that occurs with inbreeding results in the expression of deleterious recessive genes and the loss of heterotic effects at overdominant loci (both components of the "genetic load" of a normally outbreeding population). Even if an inbred population is viable in its present environment, a lack of allelic diversity due to fixation of alleles by genetic drift would preclude an adaptive response to natural selection when the environment changes (Robertson 1960; Selander 1983; Allendorf 1986).

One component of population viability analysis (PVA) is the assess-

ment of the genetic health of a population (Gilpin 1989). At the most general level, genetic analysis and management could consist of the application of the 50/500 rule for a minimum population size (Franklin 1980) or perhaps of an estimation of the fraction of the census population contributing to the genetically effective population size (N_e), and substitution of N_e into a standard equation for the loss of genetic variation (Lande and Barrowclough 1987). Unfortunately, this is as far as genetic analysis has been taken for many recovery programs for endangered species. The specific status of a particular population must be determined and its genetic vulnerability assessed before an effective management program for its preservation and recovery can be designed (e.g., Haig et al. 1993). This more intensive population management requires analyses tailored to the population's history, present status, and management needs. This approach requires an understanding of general processes, with focus on their impact on the specific case; this is the essence of population viability analysis.

Pedigree analysis, broadly defined as the genetic study of a particular multigenerational population with ancestral linkages that are known, knowable, or can be reasonably assumed or modeled, encompasses this class of case-specific analyses of genetic change. The emphasis is on examining the genetic structure imparted to the population by its pedigree relationships and evaluating the consequences of that structure on the long-term conservation of the population. The purpose of this study is to review the application of specific pedigree analysis techniques to the conservation of small populations and to discuss how genetic management is affected by the quality and quantity of the information available.

THE ASSUMPTION OF NEUTRALITY

Although the concern of genetic management for maintaining the viability of a population is to prevent its decimation caused by rapid selective removal of inbred animals and to allow for continued adaptive evolution via natural selection, pedigree analyses usually begin with an assumption of selective neutrality of the genetic variation under study. Because of the regularity of Mendelian inheritance, the transmission of a neutral genetic variant follows simple probabilistic rules. Results obtained for neutral variants at one genetic locus are applicable to all un-

linked, neutral loci. The effect of selection on the maintenance of genetic variation is much more complex and is unpredictable when the agents of selection are not well understood. Natural selection can take on any of a number of forms (directional selection against an allele, balancing heterozygote superiority, disruptive homozygote superiority, frequency-dependent selection, epistatic dependence between loci), can fall anywhere along the spectrum of no selection to lethal alleles, and is dependent on the environment.

Because of the simplicity of the transmission of neutral alleles, because neutral variation represents the limiting case of weak selection, and because much existing genetic variation in natural populations is likely neutral or near neutral under existing conditions (Kimura 1983), models of change in neutral variation serve as very useful baselines for studying genetic change in pedigreed populations. Even the genetic variation necessary for adaptation to future environments is probably not under selection most of the time, for example, when populations bred in benevolent captive environments are to be used for releases into natural habitats. Thus, analysis of the fate of presently neutral variation may, in fact, accurately model the changes in the genetic variation that will be critical for a population's long-term viability. The use of pedigree analysis in population viability analysis will presumably be restricted to relatively small populations of up to several thousand individuals. The viability of larger populations would be affected minimally by stochastic changes in gene frequencies, and the use of pedigree analysis on a larger scale is difficult even when accurate data are available. Neutral models of genetic change in pedigree analysis will thus be inappropriate only for those genes under selection sufficiently strong to control genetic dynamics in the face of random genetic drift in small populations. Clearly, some traits do come under such strong selection during intensive management, and other methods of analysis should be used to consider the likely effects of modified natural or inadvertent artificial selection (see Arnold, essay 13 of this volume).

TOOLS FOR PEDIGREE ANALYSIS

The methods described in the following essays build upon earlier work by these authors and others. Previously available methods fall into three general classes: (1) the analytical calculation of genotype probabilities

in completely known pedigrees, (2) the simulation of possible pedigrees resulting from known aspects of a population's structure, and (3) the determination of equations that broadly describe population genetic processes (table 4.1).

Analytical Calculation of Genotypes and Pedigree Relationships

The most complete and fundamental pedigree analysis (short of the empirical measurement of the state of each gene in every individual) is the specification of exact genetic relationships between every pair of individuals in a population. Measures of genetic relatedness (coefficient of kinship or consanguinity, coefficient of relationship) and the related concept of the inbreeding coefficient (which is a measure of the relatedness of the maternally inherited haploid genome of an individual to the paternally inherited haploid complement) were developed by Wright (1921, 1922), Malécot (1948), and others. Techniques for calculating genetic relatedness between every pair of individuals and the inbreeding coefficient of each individual are provided by Wright (1969) and Crow and Kimura (1970). The additive matrix method (Ballou 1983; Boyce 1983) provides an efficient means of calculating all pairwise kinships for even large populations. If the pedigree is known and if management calls for and allows precise control over each pairing, or accurate monitoring of the effects of inbreeding, the additive matrix should be calculated. This matrix also provides substantial information on the distribution of alleles descended from each founder (see below).

Every pedigree analysis must assume a starting population (the founders) among which there are no known genetic relationships. These founders are assumed to be unrelated and all subsequent calculations of genetic relatedness trace common ancestors only as far back as this founder stock. If two initial members of the population are thought to be related, ancestors of these animals, perhaps never directly observed, would be considered the genetic founders of the population, thereby preserving the condition that no two founders share a known common ancestor. Except for mutations, no closed population can ever have more genetic variation than did the founder stock, and several authors have suggested guidelines for the minimum numbers of founders needed for maintaining viable populations for conservation (e.g., Denniston

Table 4.1 Tools for Pedigree Analysis

METHOD	USE	REFERENCES*
I) Calculations of genotype or relationship probabilities from pedigrees:		
Path analysis	Kinships, inbreeding coefficients, causal basis for inherited traits	Wright 1921; Wright 1969; Ballou 1983; Lacy 1994*
Additive matrix	Kinships, inbreeding coefficients	Boyce 1983; Ballou 1983; Lacy 1994*
Mean kinship	Identification of genetically important individuals	Ballou and Lacy, essay 5, this vol.; Lacy 1994*
Founder analysis	Determination of gene diversity retained from founder stock and identification of under-represented lineages	Lacy 1989; Ballou and Foose in press; Lacy 1994*
Joint probabilities ("peeing")	Inference of ancestry of rare alleles; probability of survival of founder alleles	Thompson et al. 1978; Thompson 1983; 1986; Thomas 1986; Geyer and Thompson 1988; Thompson, essay 6, this vol.; Thomas 1991*
Trimming	Reduction of pedigree complexity to simplify calculations	Geyer et al. 1989; Thomas 1991*
II) Simulation of genotype or pedigree relationships:		
Gene drop	Simulation of gene transmission; determination of gene diversity and allelic loss; genetic relationships	MacCluer et al. 1986; Princece 1988; Lacy 1994*
Pedigree simulation	Elucidation of likely pedigree structure and genetic consequences from social biology	Harris et al. 1986; Seal and Lacy 1989; Princece, essay 7, this vol.; Starfield et al., essay 8, this vol.; Lacy 1993*
Gibbs sampler	Estimation of missing genotypes within a pedigree	Sheehan 1990; Thomas, essay 11, this vol.
III) Equations for describing genetic consequences of pedigree structure:		
Effective population size	Calculation of expected rate of loss of gene diversity	Wright 1931; Wright 1969; Crow and Kimura 1970; Chesser 1983; Lande and Barrowclough 1987; Harris and Allendorf 1989
Calculated loss of alleles	Probability of allele loss	Crow and Kimura 1970; Allendorf 1986; Denniston 1977

* Computer software

1977; Foose 1983; Foose et al. 1986; Soulé et al. 1986; Lacy 1989). Because each generation is a genetic sampling from the previous one, some of the variation present in the founders will be lost in each generation by random drift. The goal of maintaining genetic diversity is equivalent to selecting pairings that maximize the retention of the founders' diversity.

For this reason, much of the present genetic management of captive populations focuses on the genetic representation of each founder in the descendant population (Foose et al. 1986). The expected representation of each founder's genes in each descendant can be determined simply as the genetic relatedness between the founder and each descendant. (A founder, by definition, can have no relatives in the pedigree other than direct descendants.) The total contribution of each founder to the population is simply the summed relationships to the living descendants.

Each founder's contributions can also be obtained from computer simulation (MacCluer et al. 1986; Prince 1988) of the stochastic process of Mendelian transmission through the pedigree. Simulations provide not only the mean number of copies of a founder's genome present in the descendant population but also the probability distribution for the number of extant copies of each founder allele. Lacy (1988; 1989) presented metrics for summarizing the retention of the founders' variation. Ballou and Foose (in press) presented measures for assessing the genetic importance of each descendant for the maintenance of genetic diversity, based on the rareness of the founder alleles that constitute the descendants' genomes. Haig et al. (1990) compared the utility of these metrics in identifying a maximally diverse set of Guam rails (*Rallus owstoni*) from a captive population to be reintroduced to the wild. In essay 5 of this volume Ballou and Lacy present additional such metrics and evaluate their effectiveness in managing hypothetical populations modeled by computer simulation. Tonkyn (1993) described the use of mathematical optimization techniques to extend metrics that identify genetically valuable individuals to the identification of genetically optimal sets of animals for breeding or release.

Thomas and Thompson (1984) and Thompson (1986) provided an exact method for calculating the probability of each possible distribution of founder alleles in the descendant population. Although the requirements for computer memory and computational time currently prohibit the use of this technique on highly complex pedigrees, methods developed to reduce a pedigree to just the information essen-

tial to an analysis of the living population allow calculations to be performed on most managed pedigrees ("peeling" methodology; Cannings et al. 1978; Thompson et al. 1978; "likelihood factorization": Thomas 1986; Thompson 1986, and "trimming": Geyer et al. 1989). An example of the use of these exact methods on a complex pedigree that could be reduced to a manageable analysis has been given for the Przewalski's horse (*Equus przewalskii*) (Geyer and Thompson 1988; Geyer et al. 1989). A survey comparing this method with the simulation method is described by Thomas (1990).

In essay 6 of this volume, Thompson develops further the use of exact techniques to identify individuals and groups of individuals containing unique genetic information that is at risk of being lost from the population. Thomas (essay 11 of this volume) uses a simulation technique from the field of image processing to estimate missing genomic information in a pedigree with partial information about the genotype of some individuals. This allows the simulation of genotypes in a pedigree subject to constraints of known phenotypes.

General Guidelines from Population Genetics Theory

The exact computation of relationships within known pedigrees as described above is necessary for intensive management of populations, where optimal matings are to be chosen for each generation. At a less specific level, population genetic theorists have provided analytical formulas describing the expected fate of alleles within generalized populations under varying assumptions about breeding structure, selection, and mutation (Wright 1969; Crow and Kimura 1970; Falconer 1981). While this large body of population genetic theory provides insights into the genetic processes of populations and forms the basis for most of our understanding of microevolutionary dynamics, it is both too general and too simplified to provide a complete guide to the selection of breeders in an intensive management program. Although theoretical formulas could be derived for the specific population structure of each population managed, such a case-by-case development of theory is not always practical; population genetics theory is appropriately focused on the elucidation of general principles.

Nevertheless, this theory can be, and has been, applied to the devel-

opment of guidelines for population management. Chesser (1983) used inbreeding theory and several formulations of effective population size to examine the genetic consequences of a range of dispersal rates and mating structures and provided some general suggestions for the development of breeding programs for conservation. Another such derivation of a general guideline is provided by Thompson (essay 6 of this volume). Thompson shows that with the typical number of linkage groups in vertebrate genomes derived from the arrangement of genes along chromosomes, twelve progeny would be sufficient to obtain the entire genome of a progenitor with 99% certainty. The presence of linkage among genes is ignored in most analyses of gene transmission through pedigrees, but Thompson provides methods for utilizing the linkage information in deriving rules for effective genome conservation. Using general analytical formulas of the dynamics of additive genetic variance in quantitative traits, Lande (essay 14 of this volume) provides guidelines for the size of populations necessary to maintain particular levels of quantitative genetic variation. These results build on the earlier work of Franklin (1980) and Soulé et al. (1986), discussing the impact of population size on the conservation of genetic diversity.

Simulating Pedigrees

Simulation methods can be valuable for examining populations whose structure and dynamics are at least partially known (e.g., numbers of animals, sex ratio, social structure, fecundity and mortality rates, migration rates), even though individuals may not be identifiable, and therefore the existing pedigree cannot be reconstructed. These methods usually generate multiple simulated pedigrees from what is known about the dynamics of the population. These multiple pedigrees are then analyzed by one or more of the pedigree analysis techniques described above for general trends. Computer models of idealized populations thought to be representative of typical managed populations have been used to provide general guidelines for management, without addressing a particular pedigree structure or even the biological parameters of any specific population (e.g., Allendorf 1986; Lacy 1987; Ballou and Lacy, essay 5 of this volume).

Population viability analyses have made extensive use of pedigree simulation to examine the genetic consequences of the range of pedigree relationships possible given the constraints of known biological parameters. These analyses of genetic effects can be incorporated into overall assessments of the interacting genetic, demographic, and environmental risks faced by small populations and can then be used in developing conservation strategies (e.g., Mace 1990, Haig et al. 1993). The Captive Breeding Specialist Group (CBSG) of the International Union for the Conservation of Nature (e.g., Seal and Lacy 1989) and others have been using simulations to examine the likely retention of genetic variability and the consequent impact on a population's survival based on knowledge of basic population parameters (age-specific birth and death schedules, population numbers and age distribution, current and projected habitat availability). For example, Foose et al. (1991) used a computer simulation of a subdivided population structure to examine the loss of genetic diversity likely to occur subsequent to the fragmentation and isolation of black rhinoceros (*Diceros bicornis*) populations into small parks and preserves in Kenya. This assessment provided indications of the minimal size of a reserve capable of sustaining a population of rhinos and of the amount of managed migration necessary to prevent severe loss of diversity within the isolates. Harris et al. (1986) and Lacy (1993) have provided flexible and comprehensive simulation packages for these types of population projections.

The above studies used simulated pedigrees to examine likely genetic changes across a population and then to make recommendations as to the numbers of animals having to be maintained in the population or its subdivisions. Each assumed random mating (at least within local isolates), thus explicitly ignoring the pedigree structure that arises from nonrandom breeding systems. Yet, the social structure as well as the geographical structure of a population delineates the range of pedigrees possible as well as their genetic consequences. In Prince's study in this volume (essay 7) pedigree simulations that incorporate the breeding structure of a population are used to help guide the selection of specific breeding designs for captive populations. Starfield et al. (essay 8 of this volume) uses a similar approach to develop management techniques for African lions (*Panthera leo leo*) that utilize manipulation of the social structure in free-ranging populations. Information on social behavior

allows a considerable refinement of analyses of genetic change; the manipulation of a population's social structure allows further opportunity for genetic management.

Selection of Appropriate Methods for Pedigree Management

The methods described above were developed to provide insight into the maintenance of genetic variability in small populations subject to stochastic genetic drift, and all are used to guide management programs designed to minimize losses of genetic variation. Although focused on the same overall management objective, the methods require different sorts and amounts of data as input, provide different kinds of information at varying levels of precision, and attend to different management subgoals (e.g., preservation of a particular genetic variant, assurance of no allelic losses, or management without identification of individuals within the population). Accordingly, the methods most appropriate for a management program will depend on available or attainable information, intended intensity of management, and specific needs of the population or population manager.

Data used in pedigree analysis can be broadly categorized as information on the population biology of the species (e.g., mating system, litter size, period of dependency on parental care, timing and distance of dispersal, group size, and sex ratio) and information on each individual (e.g., parentage, membership in kinship groups, and genotype as determined by molecular genetic analysis). At one extreme are those populations managed as social groups, such as herd-living ungulates, colonial birds or bats, or schooling fish, in which the identification of individuals may be difficult and the assignment of parentage may not be possible without extensive and expensive genetic testing. While information on individuals may be lacking, the degree of polygamy, monopolization of mating opportunities, fecundity and mortality schedules, and other biological parameters of the population may be well enough known to allow genetic modeling. Models that simulate pedigrees may be accurate enough to provide guidelines for the management of the genetics of these populations.

At the other extreme of information about individual and population biology are populations such as captive *Okapia johnstoni*,

Sumatran rhinos (*Dicerorhinus sumatrensis*), and Puerto Rican crested toads (*Petropophryne lemur*). For each of these species, all animals in captivity are well known, pairings are arranged deliberately with little possibility of confusion of parentage, records are kept on each captive individual in a studbook, and, consequently, the ancestry of each animal can be traced back to the original wild-caught founders. Unfortunately, relatively little is known of the population biology of these species in their natural habitats. The management of captive populations can (and does) include intensive discussion of appropriate pairings, but we would not know what to expect demographically, socially, or genetically if the animals were kept more or less free-ranging, in loosely managed environments.

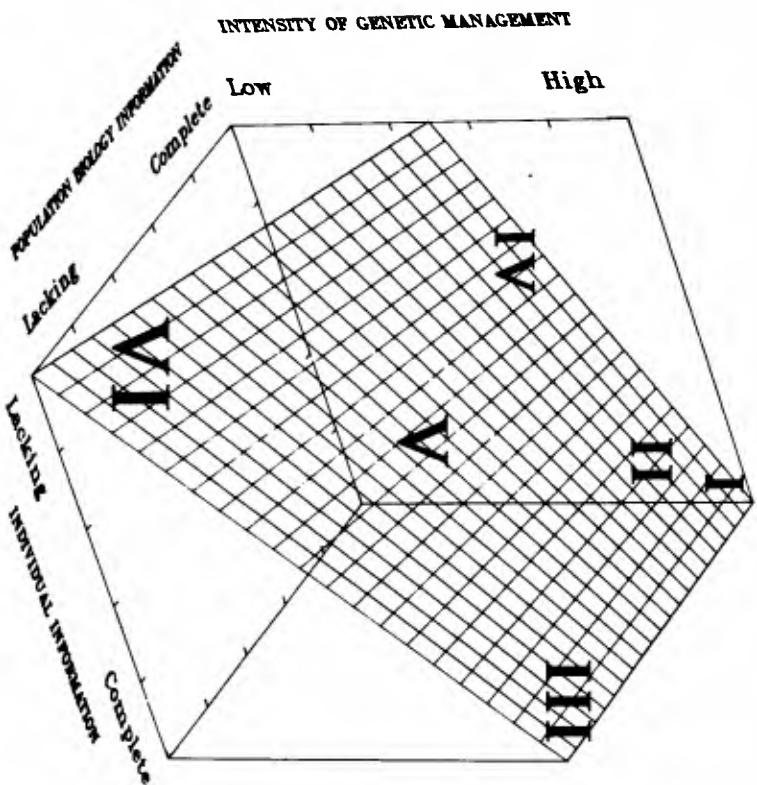
The amount and type of information available limit, therefore, the methods of analysis that can be applied and define the intensity of genetic management that is possible. Figure 4.1 crudely represents the constraint of information available about individual and population biology (the horizontal axes) on the scope of genetic management possible (the vertical axis). If we had complete information on both the population biology of the species and the individuals within the population under study (the back upper corner of the surface in figure 4.1; labeled as area I) we could apply any of the available analytical methods discussed earlier (although some might have little value in the case of complete information, because they are tools for estimating missing information based on partial knowledge). Inbreeding coefficients, genetic relatedness, and genotype probabilities could be calculated precisely, pairings could be made that would optimize the retention of genetic variation (either mean heterozygosity or number of allelic variants, but perhaps not both simultaneously), and a mating scheme could be designed that approximates the natural social behavior of the species.

If some individual information is absent but data on the population biology are excellent, analytical methods can be used to solve some of the problems associated with missing individual data, and intensive genetic management can still be practiced (figure 4.1, area II). For example, when the mating system is well known, various scenarios for missing parentage can be modeled using some of the techniques discussed earlier. A "most likely" complete pedigree can then be used to calculate the needed genetic relationships. Generally, as less individual information is known about the pedigree structure, more information on the

population biology will be needed to design management programs that adequately address the genetic requirements for population viability.

If individual information is complete (and animals are amenable to all desired manipulations), then population biological information is not essential to the design of intensive genetic management plans that optimize various genetic criteria (figure 4.1, area III). At least among sexually reproducing diploid organisms, Mendelian inheritance is near-

Figure 4.1 Possible intensity of population management (vertical axis) constrained by the amount of information available on individuals within the population (x-axis) and on the population biology parameters of the species (y-axis). Roman numerals indicate regions of information availability and intended management intensity as described in the text.



ly universal and the stochastic effects of genetic drift are definable in terms of probability distributions if the complete pedigree structure is known. (Obviously, the management of diets, behaviors, epidemiology, and virtually all nongenetic aspects of biology does require more knowledge of the population.)

If less complete individual and population biology information is available, the methods of pedigree analysis possible are restricted and, consequently, the possible intensity of genetic management is reduced (figure 4.1, areas IV and V). Exact genetic relationships cannot be determined for any animals lacking a complete record of ancestry. It would, therefore, not be possible to determine the matings that would absolutely minimize inbreeding and maximize gene diversity. Willis (1993) assessed the possible costs in terms of lost gene diversity of incorporating or omitting individuals with unknown parentage in breeding programs. Pedigree and population simulation models that generate a range of possible pedigrees based on whatever individual and population biology data are available will be necessary to formulate more generalized recommendations for genetic management.

Molecular genetic analyses of DNA similarity can be used to fill in the gaps of incomplete pedigrees or to estimate relationships among animals when pedigree records are missing (Avisé et al., essay 9 of this volume). Morin and Ryder (1991) used mitochondrial DNA and DNA fingerprint analyses to generate sufficient information on relationships in a colony of lion-tailed macaques (*Macaca silenus*) to allow the animals to be incorporated into a population being managed via pedigree analyses. Haig et al. (1994) used the similarity of DNA profiles to examine hypotheses regarding the relationships among the founders of the captive population of Guam rails. They also tested the usefulness of DNA similarity profiles as a substitute for mean kinships (Ballou and Lacy, essay 5 of this volume) in identifying genetically important individuals when information about the pedigree is missing.

When little or no information is available on either the population biology or individual identities of the population (figure 4.1, area VI), guidelines for genetic management must be based on generalized population genetics theory without reference to specific details of the managed population. Management then can only be of very low intensity and is likely to be insufficient for the long-term conservation of genetic diversity in small populations.

The option of precise and intensive management may not necessarily always be desirable or even appropriate. Tragically, the number of endangered species grows daily, and monetary, facility, and human resources for the management of endangered species are limited. Thus, just as managers of endangered captive populations often strive to maintain no more than the minimum number of animals required for population viability in order not to exclude other needy taxa (Conway 1986; Soule et al. 1986), efficient use of limited resources would employ the least intensive management required to achieve success for each population. For example, if group management with minimal control of breeding can be shown to achieve adequate long-term demographic and genetic stability (see Princée, essay 7 of this volume), intensive efforts can be directed elsewhere.

Figure 4.1 can also be used to identify the approximate information and management intensity space addressed by the methods described in the following studies. The tools presented by Ballou and Lacy (essay 5 of this volume) and Thompson (essay 6 of this volume) for identifying genetically important individuals can be very powerful and precise, leading to optimal solutions to management goals. To be fully utilized, these approaches require that the ancestry of all animals can be fully traced back to the founder stock, but no knowledge of the population's biology is used in these analyses (figure 4.1, regions I to III). Ballou and Lacy also present the modifications to their techniques necessary to omit from consideration portions of pedigrees that are unknown. Thompson's (essay 6 of this volume) calculation of the probability that entire founder genomes have survived among progeny requires an accurate count of the founder's progeny but does not (yet) use information about descendants in later generations. This method can be applied to situations described by areas I, II, III, and perhaps V. The technique of genotype estimation presented by Thomas (essay 11 of this volume) applies to area II: it requires considerable information about each individual (the pedigree structure and some data on genotypes), makes use of additional information on genotype frequencies in the population, and provides access to additional individual information (the likely genotypes of unobserved individuals). Princée (essay 7 of this volume) utilizes information on the managed social structure of a population to simulate genetic dynamics and thereby assess the impact of the group structure on the goals of genetic management. Thus, modest informa-

tion on the population biology (the likely breeding outcomes resulting from a managed group structure) is used to determine whether the resulting pedigree would be adequate (area V). Starfield et al. (essay 8 of this volume) demonstrate computer modeling of the natural social system in a wild population of lions (thereby using considerable population biological information) to examine the genetic consequences of the resulting simulated pedigrees (area IV). Modifications of the social system are possible in order to achieve some genetic management but only within the constraints of the natural behaviors of free-ranging lions.

DIRECTIONS FOR THE FUTURE

The methods of pedigree analysis available in the literature and presented in the following studies leave many gaps on figure 4.1. For many populations we will have considerable information about individuals and the population as a whole, but the available information may not be sufficient to utilize fully the desired techniques. A single gap in a pedigree can confound an analysis of genetically important individuals; an uncertain migration rate can shift a simulation of population structure from a useful exploration to meaningless guesswork. Analysis can be restricted to those parts of pedigrees that are completely known (Ballou and Lacy, essay 5 of this volume) or to those populations with well-understood structure and dynamics, but gaps in data will then cause individuals or populations to be omitted from management plans. Often, assumptions can be made (about probable fathers or likely migration rates, for example) that allow an analysis of uncertain data to still be useful. If several equally likely possibilities exist, each can be assumed and the consequences can be assessed in turn, and then the impact of the missing data on management decisions can be examined (e.g., Willis 1993). Alternatively, a less demanding and less precise analytical method can be used that does not require information beyond what is available. Managers will need guidance as to when to stretch the reliability of the data to use powerful tools and when to fall back on simple tools that require fewer data.

Often multiple methods could be applied, independently or interactively, to increase the precision of results. A general simulation might indicate how much could be achieved with minimal management;

complete calculations of kinships and losses of diversity may indicate whether the additional gains from intensive management would be worth the effort. A simulation program may be developed to provide a sampling of possible relationships needed to fill in a gap in an otherwise complete pedigree, somewhat analogous to Thomas' use of partial information to estimate missing genotypic data (essay 11 of this volume). Molecular genetic analyses can be used to infer the most probable ancestries in an incomplete pedigree (e.g., Morin and Ryder 1991; Avise et al., essay 9 of this volume). It should be possible to use all the individual information available in an incomplete data set together with simulations that utilize population biology information to generate many possible resolutions—or even an enumeration of all possible resolutions—of uncertainties in order to maximize genetic criteria based on the available information.

Finally, we need to continue to develop, expand, refine, and evaluate techniques for genetic management. The genetic management of populations for conservation (as opposed to management of domesticated stocks for rapid improvement in production characteristics) is a very new field, but it can advance rapidly by adapting the analytical methods of fields such as human genetics and animal sciences. Methods used in other fields may have valuable applications to genetic management not yet recognized by wildlife managers having little familiarity with these approaches. The continued development and application of techniques for pedigree analysis will depend on continued feedback between those developing methods and those requiring them for population management.

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