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Demographic and Genetic Management of Captive Populations

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The last fifteen years have been a time of revolutionary change in the focus and goals of zoos. This change has been motivated by a fundamental philosophical shift in the zoo community toward establishing conservation, through both captive propagation and public education, as a primary purpose. A large part of the material included in this volume has resulted as much from this shift as from the development and application of new technology.

The material discussed in this chapter has also resulted from this new conservation ethic. Two decades ago, the primary focus of zoo animal management was the exhibition, maintenance, and occasional breeding of individual specimens. Collection from the wild, rather than reproduction in captivity, was the usual means of acquiring animals for zoo exhibits. As animals became increasingly difficult to obtain from the wild, however, captive propagation became a more important means for replenishing zoo collections. At the same time, zoos began to recognize their potential contribution to wildlife conservation: the preservation of wild animal species in captivity over long periods of time and the potential to reintroduce captive-bred animals into the wild.

Significant biological problems confront this effort. Small and fragmented populations, such as those that exist in zoos and to an increasing extent in the wild, have a low probability of long-term survival. Random catastrophic demographic events, reduced vigor due to inbreeding depression, and loss of genetic diversity due to genetic drift and inbreeding all have an effect on the survival of small populations (Gilpin and Soulé 1986). Success in managing these populations ultimately rests on managing them as populations, not just as individuals.

There are also organizational problems involved in managing groups of individual zoo collections as cross-institutional biological populations. The international zoo community has responded to this additional responsibility by forming associations and programs to organize and coordinate cooperative population management efforts (Hutchins and Wiese 1991; Shoemaker and Flesness, appendix 4, this volume). The primary purpose of such programs is to contribute to the conservation of species by providing reservoirs of genetic and demographic material that can be used periodically to reinforce, revitalize, or reestablish populations in the wild. This goal requires the development of propagation programs oriented to the maintenance of genetic diversity and demographic security. It is envisioned that conservation programs for many endangered species will interactively manage both wild and captive populations for mutual support and survival.

This chapter delineates the principles, concepts, and techniques necessary to manage captive populations, concentrating on those aspects critical to the long-term maintenance of genetic diversity and demographic security. However, the scope of "population" management is broad and includes many subjects considered elsewhere in this volume: reproductive and behavioral research, data management, genetic research, program administration, and of course, basic husbandry.

The chapter begins with a discussion on establishing management goals to guide the formulation of a propagation and management plan. Genetic and demographic analyses are a critical part of this process, but can only be conducted after basic pedigree and demographic data on the current and historical population have been compiled and organized. Methods of data collection and organization are discussed in the second section, as well as by Shoemaker and Flesness (appendix 4, this volume). This is followed by a discussion of methods and techniques for both genetic and demographic analyses, using examples to illustrate various analytic procedures. The chapter concludes with a section on population management, which covers the basic strategies and concepts for combining propagation goals with the re-

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sults of the demographic and genetic analyses to form the basis for the program's specific institution-by-institution and animal-by-animal breeding recommendations.

CAPTIVE MANAGEMENT GOALS

The goals of most captive management programs approach one of two extremes: individuals are either intentionally selected to be well adapted to captive environments, or they are managed to preserve genetic diversity (Foose et al. 1986; Frankham et al. 1986). Which goal is chosen depends on the managers' objective for the population. Frankham et al. (1986) distinguish among four types of captive populations of primary interest to zoos:

1. Common display species
   Population goal: Establish a tractable, easily managed population well adapted to the captive environment
   Management strategy: Select for traits adapted to captivity
   Example: Fallow deer, *Cervus dama* (Hemmer 1986)
2. Endangered species in captivity for long-term conservation
   Population goal: Long-term maintenance of a viable population and preservation of genetic diversity
   Management strategy: Maximize retention of the founders' genetic diversity and maintain a demographically stable population compatible with the limits of the captive environment's carrying capacity
   Example: Golden lion tamarin, *Leontopithecus rosalia* (Kleiman et al. 1986); Siberian tiger, *Panthera tigris altaica* (Foose and Seal 1986)
3. Rare species being propagated for immediate release into natural habitats
   Population goal: Rapid population growth and large-scale reproduction for immediate release
   Management strategy: Maximize reproduction in a captive environment as similar as possible to the natural environment
   Example: Guam rail, *Rallus ownstoni* (Derrickson 1987)
4. Rare species not yet capable of self-sustaining reproduction in captivity
   Population goal: Develop husbandry techniques for achieving self-sustaining capabilities
   Management strategy: Preferentially propagate individuals capable of reproducing in the captive environment. Once the population has grown to self-sustaining status, manage the population as type 2 above
   Example: Micronesian kingfisher, *Halcyon cinnamomina* (Bahner 1991)

Adapting a species to captivity is appropriate for populations of type 1 and, initially, type 4. Frankham et al. (1986) and Foose et al. (1986) discuss basic population management strategies for these types of populations. Maintenance of genetic diversity is paramount for populations of type 2 and, eventually, type 4.

Although the intent of this chapter is to describe population management techniques specifically for populations designated for long-term conservation, many of the concepts and techniques can be appropriately applied to populations under other objectives. For example, data should be collected and demographic and genetic calculations routinely performed for *all* types of populations.

MANAGEMENT OF GENETIC DIVERSITY

Maintaining genetic diversity and demographic security are the primary population management goals for long-term conservation. Management for genetic diversity minimizes change in the genetic constitution of the population while in captivity so that if and when the opportunity arises for animals to be reintroduced into the wild, they will represent, as closely as possible, the genetic characteristics of the original founders used to establish the captive population (Hedrick et al. 1986; Lacy et al. 1995). Genetic variation is also the basis for adaptive evolution and must be retained to maintain the population's potential to adapt to changing environments. Furthermore, there are a growing number of studies that indicate a general, although not universal, positive relationship between genetic variation and both individual and population fitness (Hedrick et al. 1986; Allendorf and Leary 1986; Mitton and Grant 1984). These include a number of studies that have documented the deleterious effects of inbreeding in captive populations (Ralls, Ballou, and Templeton 1988; Lacy, Petric, and Warneke 1993) as well as the effects of low levels of variation on reproductive condition (Wildt et al. 1987; O'Brien et al. 1985). Last, maintaining genetic diversity preserves future management options, a strategy that will become increasingly important as knowledge of the genetic and demographic requirements of wild and captive populations expands.

There are several kinds of genetic variation. Animals carry many thousands of genes located on chromosomes. The exact location of a gene on the chromosome is referred to as its locus. The terms gene and locus are often used interchangeably. Each gene may occur in alternative forms, called alleles, that may produce slightly different genetic effects, such as different pelage colors, eye colors, and so forth. The number of alleles per gene or locus can vary from one (no diversity, or monomorphic locus) to many (polymorphic locus). Most vertebrate species carry two copies of each gene (they are diploid), one inherited from each parent. A few species carry only one copy of each gene (they are haploid). Both copies may represent the same allele, in which case the animal is described as homozygous for that locus, or different alleles, in which case the animal is heterozygous.

Genetic diversity comprises both allelic diversity and heterozygosity. Allelic diversity refers to the number of different alleles at any given locus in the population. Heterozygosity is the percentage of heterozygous loci in a population or individual. Thus, genetic diversity can be measured in both individuals and populations. Both allelic diversity and heterozygosity are desirable in captive populations; allelic diversity is important for a population's long-term ability to adapt, while heterozygosity is important for immediate adaptation (Allendorf 1986).

Both allelic diversity and heterozygosity are lost in small populations (numbering a few tens to a few hundreds)

through the process of genetic drift. The alleles passed from parents to offspring represent only a sample of the allelic variation of the parental generation. When only a few offspring are produced, the genetic diversity of the offspring may be unrepresentative of the genetic diversity present in the parents. By chance alone, some alleles may not be passed to the offspring; others may increase or decrease in frequency. These changes in the number and frequency of alleles, as well as changes in heterozygosity due to this biased sampling process, are termed genetic drift.

The population's average heterozygosity is often used as an overall indicator of genetic diversity since it lends itself well to theoretical considerations and usually provides a simple, accurate indicator of the loss of allelic diversity (Allendorf 1986). This is not always the case, however. During bottleneck events, allelic diversity is lost much more readily than heterozygosity, and using heterozygosity alone overestimates the amount of genetic diversity retained after a bottleneck. Moreover, rare alleles (those occurring at low frequencies in the population) may also be lost faster than average heterozygosity. The genetic goals of most captive propagation programs are currently based on maintaining heterozygosity but also consider bottleneck effects in the pedigrees.

In managing genetic variation, it is important to distinguish between single-locus and multilocus, or quantitative, variation. Single-locus variation is variation in traits regulated by single genes, while quantitative variation is variation in traits regulated by many genes. Although quantitative variation is probably more important than single-locus variation for long-term evolutionary adaptation, heterozygosity and additive quantitative variation are lost at approximately the same rate. Consequently, management strategies based on maintenance of heterozygosity generally apply to maintenance of additive genetic diversity as well (Lande and Barrowclough 1987).

Selection can potentially retard or accelerate loss of genetic diversity. However, little is known about the role selection plays in captive populations (Frankham et al. 1986; Arnold 1995). Variation can be selective (influenced by selection pressures) or selectively neutral (influenced not by selection pressures but by the random process of genetic drift). The conservative approach is to assume selective neutrality, particularly in small populations in which genetic drift is likely to be a stronger force than selection. Discussions of the management and maintenance of genetic variation in this chapter refer primarily to single-locus neutral variation. (See Lacy et al. 1995; Lande and Barrowclough 1987 for further discussions of this issue.)

Loss of genetic diversity is a function of population size and time. In general, the smaller the population, the faster the loss; the longer the period of time, the greater the total loss (fig. 26.1). Therefore, those developing management plans to conserve genetic diversity must consider the questions, "How much genetic diversity is required?" and "How long should it be maintained?"

The question of how much genetic diversity is required to retain long-term fitness and evolutionary potential in captive populations is difficult to answer, since little is known about minimum genetic requirements of populations. One approach might be to maintain as much genetic variation as possible. This does not provide useful guidelines for the development of management programs, however, because populations would have to be "as large as possible" to achieve this result. The finite availability of captive resources strictly limits the size and number of captive populations that can be managed.

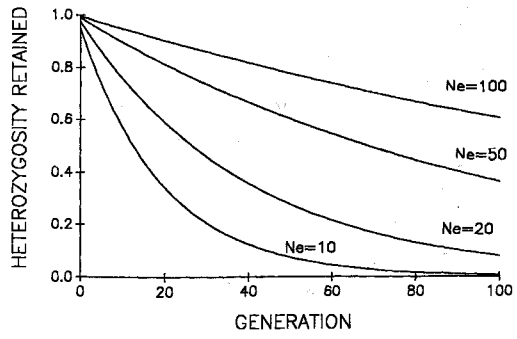


FIG. 26.1. Percentage of original heterozygosity retained over 100 generations for effective population sizes (N_e) varying from 10 to 100.

Because loss of genetic diversity is a function of time, it is also important to consider how long genetic diversity must be maintained. The time scale for management programs will vary. Some species may need the support of a captive population for a relatively short time before they can be returned to the wild. However, for many, if not most, species, captive populations will have to be maintained for the long term, often over hundreds of years. The safest approach is to initiate all programs as if they will be for the long term. They can always be concluded earlier if conditions permit.

A crude but general strategy that has been suggested in response to the questions "how much" and "for how long" is to preserve 90% of the founders' heterozygosity over a period of 200 years (Soulé et al. 1986). This "90%/200 year rule" originated from considerations of how long human population growth and development will continue to reduce wildlife habitat. Its authors estimated that this "demographic winter" will last between 500 and 1,000 years. However, they observed that some stabilization of human population growth is expected in the next 150 to 200 years. More importantly, they hypothesized that the current rapid development of biological technology, especially long-term storage of germ plasm (cryopreservation), will decrease dependence on populations of living animals for the preservation of gene pools by the end of the twenty-first century. The authors despaired of the feasibility of developing human-managed programs that would continue for hundreds of years and concluded that 200 years would be a reasonable time frame for management of captive populations. The recommendation to retain 90% of the original heterozygosity was based on the authors' consensus that the 10% loss "represents, intuitively, the zone between a potentially damaging and a tolerable loss of heterozygosity" (Soulé et al. 1986, 107).

Although this 90%/200 year rule of thumb is somewhat arbitrary, it does provide a starting point for establishing

population size goals. We have chosen to use this approach to determine genetic goals for captive propagation programs and will focus our discussions on populations being managed under this goal. However, the questions "how much" and "for how long" will normally require species-specific answers (see "Demographic Analyses" below). Individual programs can modify both the time period of concern and the level of genetic diversity to be retained in response to the circumstances of the species. For example, populations that are to be reintroduced soon after a captive colony is established will require less concern about long-term maintenance of genetic diversity than populations destined to remain in captivity for many generations. In fact, more recently, population size objectives have been formulated in terms of 100 rather than 200 years, since this results in smaller, more realistic population sizes (Foose et al. 1995). Nevertheless, the general techniques for developing a plan remain the same.

Small populations are subject to demographic as well as genetic problems, and similar questions about demographic security should be considered in establishing goals for captive propagation programs. Many demographic threats are stochastic (random) in nature. They include such easily appreciated chance events as environmental variation, natural disasters, and disease epidemics (Dobson and May 1986; Goodman 1987) as well as more subtle fluctuations in birth and death rates, including distortion of sex ratios, due to simple variation among individuals.

Risks of demographic problems, like genetic risks, are functions of population size and time. The smaller the population and the longer the time period of management, the greater the risks. The relevant question is, what is the probability of a population surviving (i.e., not going extinct) for a specified period of time? Or, in other words, what population size is necessary to achieve a high probability (e.g., 95%) of survival over a long time period (e.g., 200 years) (Shaffer 1987)? In most cases, captive populations large enough to achieve the usual genetic objectives will also be large enough to insure high survival probability over the time period of concern because management in captivity will usually, though not always, be able to moderate demographic stochasticity caused by environmental variation. This is not likely to be the case for small wild populations, in which environmental variation has a tremendous effect on population survival (Goodman 1987).

DATA COMPILATION

The most important task in the development of a captive propagation plan is compiling the basic data required for population analysis and management. Data may already have been compiled in a variety of different forms if a captive population exists or has existed in the past. The best source of compiled data is a studbook, which is a chronology of a captive population listing vital information on animal identities, sexes, parentage, and birth and death dates, as well as information on animal movements between institutions (Shoemaker and Flesness, appendix 4, this volume; Glatston 1986). Currently there are approximately 250 international and regional studbooks (T. J. Foose, pers. comm.), many of which are available as computerized data bases, and the number is growing annually.

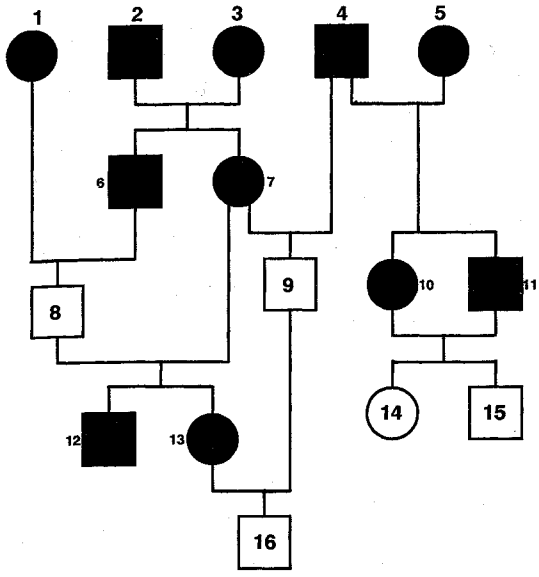
If a studbook does not exist or is out of date, one must be compiled from original sources. Historical and current data should be collected from all institutions that have had or currently have individuals of interest. Historical data are critical for determining the ancestry of living animals and estimating certain genetic and demographic parameters (e.g., population growth rates, generation lengths, effective population sizes).

Data compilation should begin with reference to a number of sources that summarize data on captive populations. Potential sources of data are:

- **International Species Information System (ISIS).** ISIS is a computerized data base containing information on animal identities, birth and death dates, genealogies, and movements (Seal, Makey, and Murtfeldt 1976; Shoemaker and Flesness, appendix 4, this volume). ISIS collects data from institutions worldwide and is the best starting point for compiling population data if no studbook is available.
- **International Zoo Yearbook (IZY).** IZY provides an annual list of birds, mammals, reptiles, amphibians, and fishes bred in captivity (Olney 1986). Although only numbers and locations are presented, these annual listings are useful for identifying institutions that once had or currently have specimens of interest.
- **Species Registries.** Registries are single-species listings of numbers and locations of animals. They do not contain the detailed vital information necessary for population analysis, but do provide a starting point for locating institutions that once held specimens (Shoemaker and Flesness, appendix 4, this volume).
- **In-House Institutional Records.** In-house inventory records are the primary source of data. Once institutions that have had or currently have specimens of interest are identified, they can be contacted for information on the history, status, and details of their collection. Again, it is important to stress the importance of collecting historical data.

The basic data required on each animal for population analysis and management are:

- Individual identification: a simple numeric lifetime identity (i.e., studbook number). To achieve this identification, it may be necessary to link a series of different ID numbers (e.g., the local ISIS specimen numbers) the animal has had as it has moved among institutions
- Sex
- Birth date
- Death date (it is vital to record stillbirths and aborted fetuses)
- Parentage
- Whether the individual is wild-caught
  Date and site of capture
  Possible relationship to other wild-caught animals (i.e., several animals captured in a nest or herd)
  Date animal entered captivity
- Date animal left captivity or was lost to follow-up (reintroduced into the wild, escaped, lost track of)
- Institutions/facilities where it has been, with dates of shipments



ID	Sex	Dam	Sire	Status
1	F	Wild	Wild	Dead Founder
2	M	Wild	Wild	Dead Founder
3	F	Wild	Wild	Dead Founder
4	M	Wild	Wild	Dead Founder
5	F	Wild	Wild	Dead Founder
6	M	3	2	Dead
7	F	3	2	Dead
8	M	1	6	Living
9	M	7	4	Living
10	F	5	4	Dead
11	M	5	4	Dead
12	M	7	8	Dead
13	F	7	8	Dead
14	F	1D	11	Living
15	M	10	11	Living
16	M	13	9	Living

FIG. 26.2. Pedigree of a population founded with 2.3 individuals. Squares, males; circles, females; open squares and circles, living animals. Numbers are unique identifiers for each individual. The pedigree listing is presented on the right.

- Information on circumstances and cause of death
- Reproductive condition (e.g., castrated male, postreproductive female)
- Group compositions (who is housed with whom)
- Reproductive opportunities (whether animal was given opportunities to breed, and when)
- Information on past breeding experience (e.g., proven breeder?)
- Tattoo or other permanent identification marks (e.g., transponder number)
- Carcass disposition and tracer (e.g., "Sent to Univ. Kansas Museum, #12345")
- Miscellaneous comments (unusual behavior or phenotype, etc.)

When dealing with unknown or missing data, record as much information as possible. Dates or events that are partially or completely unknown should be noted as such. Unknown dates are a particular problem. Usually events are dated to the nearest day, month, or year. Uncertain parentage is also a common problem, particularly in herd situations. Record all potential parents and, if possible, indicate the likelihood (e.g., based on behavioral data) of each being the actual parent (e.g., "*Comment:* Potential Sires/Likelihood: Stbk 123/50%; Stbk 1221/25%; Stbk 1212/25%).

Most analyses require that the data be computerized for easy access and manipulation. Standard formats for pedigree data have been developed (Shoemaker and Flesness, appendix 4, this volume), and a number of computerized studbook management and analysis software packages are available, including the Single Population Animal Record Keeping System (SPARKS: ISIS 1991), and the Zoo Research Studbook Management System (Princée 1989).

GENETIC ANALYSES

The purpose of genetic analyses is to describe the genetic characteristics of a population that are important for its management. These include information on the number of founders, the distribution of their genes among living animals, the relationships among individuals in the living population, and the capacity of the population to retain genetic variation. Results of genetic analyses are used in conjunction with results of demographic analyses to arrive at a carrying capacity for the captive population and formulate recommendations for managing the population at this carrying capacity. A step-by-step procedure for calculating these genetic characteristics follows.

1. Construct the pedigree for each animal in the population.

This "pedigree" can be in the form of a standard pedigree chart and/or simply a listing of each individual with its parents (fig. 26.2) that will be used with various pedigree analysis algorithms and computer programs. Pedigree charts are particularly useful for identifying pedigree bottlenecks as well as ancestors of special interest.

2. Identify the founders of the population.

A founder is an animal that

- is from outside the population (usually the wild)
- has no known ancestors in the population at its time of entry
- has descendants in the living population or is currently living and capable of reproduction (a potential founder)

Unless it is known otherwise, founders are assumed to be unrelated to each other. When the relationships of wild-caught animals are known or suspected (e.g., several chicks captured in the same nest), it is necessary to create "hypothetical" parents (or other ancestors) to define those relationships. These hypothetical ancestors are then defined as founders. It is useful to name all hypothetical founders in an easily identifiable fashion (e.g., studbook numbers beginning with the letter H).

Figure 26.3 illustrates the identification of founders in the captive population of black-footed ferrets, *Mustela nigripes* (Ballou and Oakleaf 1989). "Willa," "Emma," "Annie,"

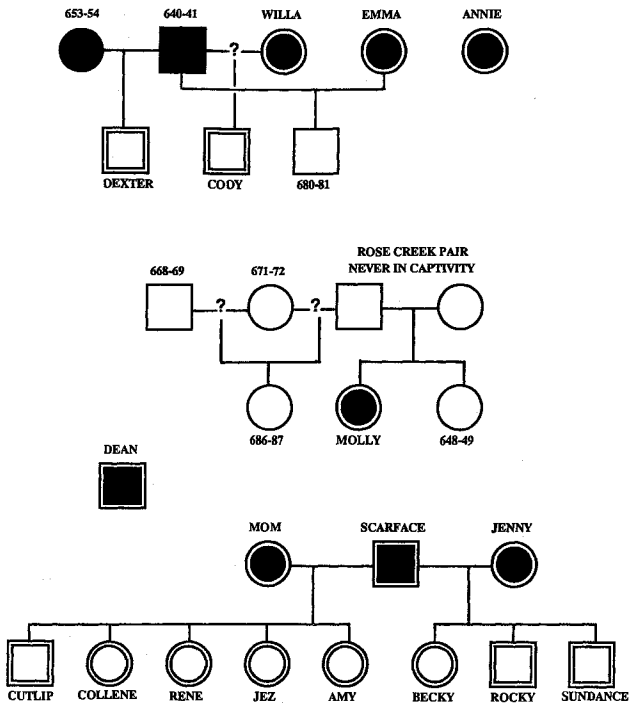


FIG. 26.3. Pedigree of the founding population of black-footed ferrets. Squares, males; circles, females; solid squares and circles, founders; double-bordered squares and circles, living animals. A question mark indicates uncertain parentage. (Reprinted with permission from U. S. Seal et al., eds., *Conservation Biology and the Black-footed Ferret* [New Haven: Yale University Press, ©1989].)

"Mom," "Jenny," "Dean," and "Scarface" are shown as founders since they are wild-caught, have no known ancestors in the captive population, and are thought not to be closely related to each other. Although "Molly" has known relatives, they were either never in captivity or died without producing offspring; she is therefore considered a founder. Female "653-54" and male "640-41" are also founders because "Dexter," who is living, is an offspring of both and "Cody" is an offspring of male "640-41."

Molecular genetic analyses (e.g., DNA fingerprinting) can be useful in examining relationships of wild-caught animals or even captive-born animals without pedigrees (Ryder and Fleischer, chap. 25, this volume; Morin and Ryder 1991; Avise et al. 1995; Ashworth and Parkin 1992; Geyer et al. 1993). However, these techniques may be useful for determining only first-order relatedness (e.g., full sibling or parent-offspring relationships).

3. Compute the genetic contribution of each founder to each living individual as well as to the living population as a whole.

Founder contribution is the percentage of an individual's or a population's genes that have descended from each founder. Calculations are based on the Mendelian premise that each parent passes (on average) 50% of its genes to its offspring, 25% to its grandoffspring, and so forth. Each founder's genetic contribution to living individuals can be calculated by constructing each individual's pedigree back to the founders and applying these Mendelian rules of segregation.

TABLE 26.1. Founder Contributions for the Pedigree Illustrated in Figure 26.2

	Living individuals					Pop.	
Founder	8	9	14	15	16	avg.	Retention
1	.50	0	0	0	.13	.126	.500
2	.25	.25	0	0	.31	.162	.484
3	.25	.25	0	0	.31	.162	.487
4	0	.50	.50	.50	.25	.350	.803
5	0	0	.50	.50	0	.200	.612
Mean kinship	.150	.228	.238	.238	.244		

Note: Average proportion of each individual's genes that has descended from each founder. See text for explanation of retention and mean kinship.

The founder's genetic contribution to the current population's gene pool is its contribution averaged across all living individuals (table 26.1). Algorithms and computer programs are available for calculating founder contributions from pedigree data (Ballou 1983; Lacy 1990a).

Founder contributions in most captive populations are highly skewed, usually due to disproportionate breeding of a small proportion of the founders early in the population's history (fig. 26.4). Genetic diversity potentially contributed by the underrepresented founders is thus lost or at high risk of being lost due to genetic drift.

4. Calculate the loss of founder alleles due to genetic drift and pedigree bottlenecks.

Further loss of genetic diversity occurs when genetic drift causes founder alleles to be lost from the population. Extreme cases of genetic drift are often referred to as pedigree bottlenecks, occurring when the genetic contribution of a founder passes through only one or a few individuals. For example, only 50% of a founder's genes survive to the next generation if it produces only one offspring, 75% survive if it produces two offspring, and so forth. Bottlenecks may occur during the first generation of captive breeding if only one or two offspring of a founder live to reproduce. However, the genetic drift caused by such bottlenecks can occur at any point in the pedigree, resulting in gradual erosion of the founders' alleles. The more "pathways" a founder's genes have to the living population, the less loss will occur. Therefore, even though a large proportion of a population's gene pool may have descended from a particular founder, the population may represent only a fraction of that founder's genetic diversity.

The proportion of a founder's genes that survive to the current population is referred to as gene retention or gene survival. Although exact methods for calculating retention have been developed (Cannings, Thompson, and Skolnick 1978), it is often estimated using Monte Carlo simulation procedures ("gene dropping": MacCluer et al. 1986). "Gene drop" procedures assign two uniquely identifiable alleles to each founder. Alleles are passed, randomly, from parents to offspring according to the rules of Mendelian segregation, and the distribution and pattern of alleles among living animals are examined after each simulation (fig. 26.5). The simulations are repeated several thousand times, and the re-

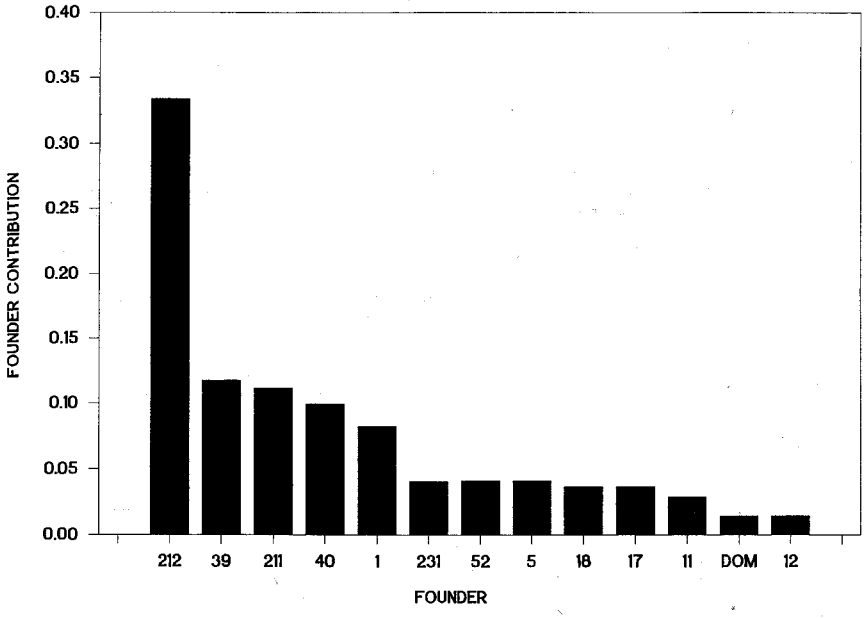


FIG. 26.4. Founder contributions in the 1988 captive population of Przewalski's horses, *Equus przewalskii*. The distribution is heavily skewed due to disproportionate breeding among the founders early in the population's history. "DOM" is a Mongolian domestic mare that was bred to a Przewalski's horse in 1960.

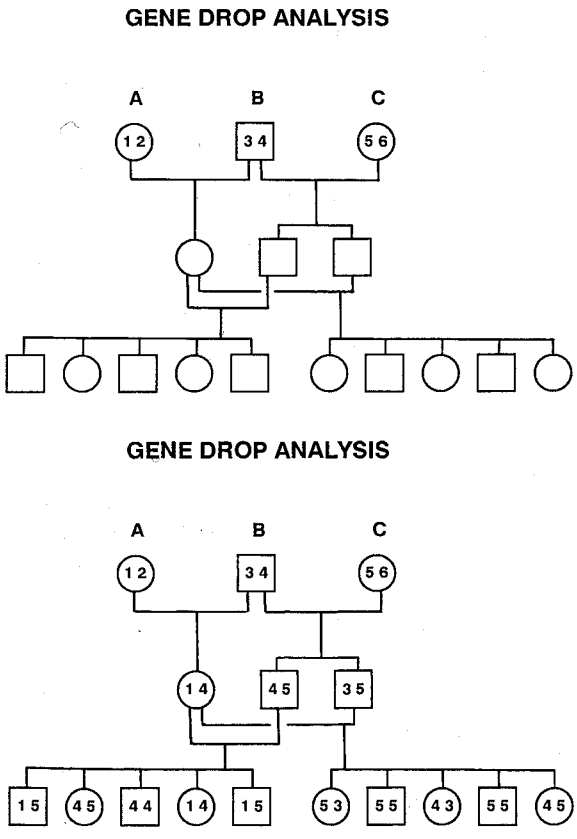


FIG. 26.5. Gene drop analysis. *(a)* Each founder is assigned two unique alleles. *(b)* The alleles are then "dropped" through the pedigree according to the rules of Mendelian segregation; each allele has a 50% chance of being passed on to an offspring. At the end of the simulation, the pattern and distribution of alleles in the living population (bottom row) are examined. The simulation is repeated several thousand times and results are averaged across simulations to give gene retention. Note that allele 2 from founder A and allele 6 from founder C have been lost.

tention for each founder is calculated as the average percentage, across all simulations, of the founder's alleles that have survived to the living population. The retention estimates for the sample pedigree shown in figure 26.2 are listed in table 26.1. The retention for founder 1 is only 50% because she produced only one offspring, while the retention for founder 4 is higher because his genes have multiple pathways to the living population.

Gene drop analyses provide information about the distribution of founder genes in the living population that data on founder contribution do not. This is particularly true for deep, complex pedigrees, in which using founder contribution alone to determine the founders' genetic contribution to the population can be very misleading. Figure 26.6 illustrates the effects of pedigree structure on gene flow in two pedigrees that have equal levels of inbreeding and founder contribution but different levels of gene retention.

Since both skewed founder contributions and loss of alleles due to genetic drift result in the loss of founders' genetic diversity, the genetic contribution of the founders to the gene pool may be less than expected. Lacy (1989) introduced the concept of founder genome equivalent (f_g) to illustrate the combined effect skewed founder contribution and genetic drift have on the genetic diversity of a population. f_g is the number of founders that would be required to obtain the levels of genetic diversity that are observed in the current population if the founders were all equally represented and had retained all their alleles in the living population. It is calculated as

$$f_g = \frac{1}{\sum_{i=1}^{N_f} (p_i^2/r_i)} \qquad (26.1)$$

where N_f is the number of founders, p_i is the founder contribution of founder i to the population, and r_i is founder i's retention. Our sample population in figure 26.2 has 5 foun-

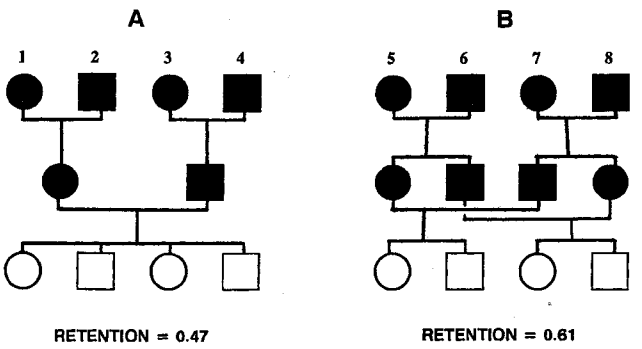


FIG. 26.6. Gene drop analysis applied to two similar pedigrees. Squares, males; circles, females; open squares and circles, living animals. Pedigrees A and B each have four founders and four living animals. Founder contribution to living animals is identical for both pedigrees (25% from each founder) and all animals are non-inbred. However, genes from each founder in pedigree A pass through only one individual, creating a severe bottleneck. Genes from each founder in pedigree B pass through two individuals, creating less severe bottlenecks. As a result, more of the founder alleles in pedigree B are retained in the living population than in pedigree A.

ders, but because of retention problems and skewed founder contribution, they have an f_g of only 2.8. In essence, they behave genetically like 2.8 idealized founders.

The f_g values are often calculated with living founders excluded from the analysis. Living founders have 100% retention, and including them assumes that their alleles have been "captured" in the population, even though they may have no living descendants. Excluding living founders provides a more realistic summary of the genetic status of the population, particularly if there are many founders who are not likely to contribute offspring to the gene pool. Comparing the f_g calculated with living founders excluded with the f_g when they are included shows the contribution that genetic management can make if 100% of the living founders' genes can be retained in the population.

5. Calculate measures of genetic importance for each individual.

When selecting animals for breeding, it is useful to rank individuals according to their genetic "importance." Individuals carrying genes from overrepresented founders are not as genetically valuable as those carrying genes from underrepresented founders. A number of methods have been used to rank animals according to their genetic importance. One is the Founder Importance Coefficient (*fic:* Ballou and Lacy 1995), which is the weighted average of the founder contributions within each individual, with the population founder contribution acting as the weights. However, the *fic* does not take into consideration the effect of retention on an individual's genetic value and could potentially produce misleading results. For this reason, it has not been extensively used to measure genetic importance.

A more appropriate measure of genetic importance is mean kinship (*mk*). Mean kinship is the average of the kinship coefficients between an individual and all living individuals (including itself) in the population (Ballou and Lacy 1995; Lacy 1990a):

$$mk_i = \frac{\sum_{j=1}^{N} k_{ij}}{N} \qquad (26.2)$$

where mk_i is the mean kinship of individual i; k_{ij} is the coefficient of kinship between individuals i and j; and N is the number of living animals in the population (Ballou and Lacy 1995). The kinship coefficient is the probability that two alleles, taken at random from two individuals, are identical by descent (Crow and Kimura 1970). It is a measure of the genetic similarity of the individuals and is the same as the inbreeding coefficient of any offspring they would produce. Individuals who are carriers of rare genes will have low values of *mk* because they have few relatives in the population, whereas individuals who carry genes shared with many individuals will have a high *mk*. Ranking individuals according to their *mk* values provides a quick method for identifying genetically important animals.

Both *mk* and f_g relate directly to maintenance of genetic diversity in populations. Gene diversity, the expected level of heterozygosity of the population, can be calculated as either $1 - mk$ or $1 - 1/2f_g$; the two expressions are equivalent. Thus, breeding strategies to minimize *mk* or to maximize f_g will both maximize gene diversity (Ballou and Lacy 1995). Computer programs are available for calculating *mk* values (Lacy 1990a). Values of *mk* for the sample pedigree in figure 26.2 are shown in table 26.1.

Another measure of genetic importance is genetic uniqueness, which is the probability that a gene carried by an individual is unique (i.e., not carried by any other living animal). Genetic uniqueness is calculated using the gene drop analysis described above and can also be used to rank individuals by genetic importance (Ballou and Lacy 1995).

6. Calculate inbreeding coefficients of all individuals in the population as well as kinship coefficients between all living individuals.

Inbreeding is the mating of related individuals. If two parents are related, their offspring will be inbred, and the more closely related the parents are, the more inbred their offspring will be. The degree to which an individual is inbred is measured by its inbreeding coefficient *(f)*, which is the probability of its receiving the same allele from each parent (i.e., that the alleles are identical by descent). Offspring of father/daughter, mother/son, or full-sib matings are 25% inbred; offspring of first-cousin matings are 6.25% inbred. Inbreeding coefficients are used to examine the effects of inbreeding in the population (see below) and to determine the degree of relatedness between individuals. Algorithms and computer programs for calculating inbreeding coefficients from computerized pedigrees are available (Ballou 1983; Boyce 1983; Lacy 1990a; ISIS 1991).

7. Estimate the population's effective population size.

The extent and rate of loss of genetic diversity depends on the size of the population. However, the size of relevance is not simply the number of individuals; rather, it is the genetically effective population size (N_e). The effective size of a population is a measure of how well the population maintains genetic diversity from one generation to the next.

Genetic diversity is lost at the rate of $1/2N_e$ per generation. Populations with small effective population sizes lose genetic diversity at a faster rate than those with large effective population sizes (see fig. 26.1).

The concept of N_e is based on the genetic characteristics of a theoretical or ideal population that experiences no selection, mutations, or migration and in which all individuals are asexual and have an equal probability of contributing offspring to the next generation. Extensive population genetic models have been developed to examine the loss of genetic diversity over time in an ideal population (Kimura and Crow 1963). However, real populations differ greatly from the ideal. Estimating how rapidly a real population loses genetic diversity requires comparison of the genetic characteristics of the real population with those of the ideal population. A real population that loses genetic diversity at the same rate as an ideal population of size 50 (1% per generation) has an effective population size of 50, regardless of its actual size. Strictly defined, the effective size of a population is the size of a theoretically ideal population that loses genetic diversity at the same rate as the population of interest (Hedrick 1983). Once an effective population size is calculated, the rate at which the population loses genetic diversity can be estimated.

In general, the effective size of a population is based primarily on three characteristics: the number of breeders, their sex ratio, and the relative numbers of offspring they produce during their lifetime (their "lifetime family size"). Each of these characteristics can strongly influence a population's effective size. In general, a large number of breeders will pass on a larger proportion of the parental generation's genetic diversity than will only a few breeders. A heavily biased sex ratio in the breeders will likely result in loss of genetic diversity since the underrepresented sex will contribute an unequally large proportion of the offspring's genetic diversity. An equal sex ratio is preferable since it assures that the gene pool will receive genes from a larger number of breeders than when the sex ratio is highly skewed. Differences in family size also result in loss of genetic diversity since some individuals contribute few or no offspring to the gene pool while others producing large numbers of offspring contribute more to the gene pool. The amount of genetic diversity passed from one generation to another is, in general, maximized when all breeders produce the same number of young (i.e., family sizes are equal and the variance in family size is zero).

One method commonly used to calculate N_e is to assume that the population is not growing, has nonoverlapping generations, and that family sizes have a Poisson (random) distribution—this is the theoretically expected distribution if each individual in the population has an equal opportunity to breed. Under these assumptions the effective population size can be calculated from

$$N_e = \frac{4 * N_m * N_f}{N_m + N_f} \qquad (26.3)$$

where N_m and N_f are the total numbers of different adult males and females in the population over one generation.

Unfortunately, in captive populations, family size distributions are rarely determined by random mating and are not Poisson in form. In unmanaged populations many more adults than expected may fail to produce offspring, while in intensively managed populations fewer adults than expected may fail to produce. A more accurate method of estimating N_e incorporates information on family size. The family size of an individual is the total number of offspring it produces during its lifetime and that survive to adulthood. Ideally, only individuals who have completed their reproductive lives (are postreproductive or have died) should be used for these calculations. However, Lande and Barrowclough (1987) describe a method for estimating future reproductive performance for individuals still breeding. Both the mean family size ($\bar{k}$) and the variance in family size (V_k) need to be calculated across all individuals; individuals who fail to breed must be included, contributing family sizes of zero. These parameters can be calculated directly from studbook data.

Since $\bar{k}$ and V_k are measured over individual lifetimes, they provide accurate estimates only if the population has been stable for a relatively long time (several generations). This is unlikely for most rapidly changing captive populations, and calculations of $\bar{k}$ and V_k may not represent current population trends. Accurate estimates of current effective sizes are therefore difficult to calculate.

With estimates of $\bar{k}$ and V_k for each sex (if available), it is possible to calculate N_e separately for each sex. The effective size of males is:

$$N_{e(m)} = \frac{N_m * \bar{k}_m - 1}{\bar{k}_m + \frac{V_{km}}{\bar{k}_m} - 1} \qquad (26.4)$$

where $\bar{k}_m$ is the average number of young surviving to adulthood across all males; N_m is the number of adult males in the population during a generation; and $V_{k(m)}$, the variance in number of young surviving to adulthood, is defined as:

$$V_{k(m)} = \frac{\Sigma\,(k_m - \bar{k}_m)^2}{N_m} \qquad (26.5)$$

where the sum is over the number of adult males in the population, and k_m is the number of offspring surviving to adulthood for each male.

The effective size for females ($N_{e(f)}$) is calculated from equation (26.4) using family size data for females. The effective size for the overall population is then determined using equation (26.3), replacing N_m with $N_{e(m)}$ and N_f with $N_{e(f)}$.

The effective population size can be compared with the true population size *(N)* by calculating the ratio of N_e/N. It is theoretically possible for the effective size to be almost twice the true size if the variance in family size is zero. In reality, N_e is almost always less than the true size. Ratios of N_e/N in captive populations not genetically managed have been measured at between 0.3 and 0.5 (Flesness 1986; table 26.2).

Effective size may change radically over time. Lack of genetic management in the past may have caused N_e/N ratios to be very low. Therefore, the data used to estimate the current effective size should be relatively recent (over the last 5 years). Likewise, estimates of future effective sizes should be based on future management goals (i.e., attempts to maxi-

TABLE 26.2. Effective Population Size for the Captive Population of Golden Lion Tamarins during a One-Generation (6-year) Period between 1981 and 1987

Variable	Males	Females
Number of adults in the population[a]	$N_m = 269$	$N_f = 275$
Mean number of offspring[b]	$\bar{k}_m = 1.7$	$\bar{k}_f = 1.6$
Variance in number of offspring[c]	$V_{km} = 12.1$	$V_{kf} = 13.5$
Effective size by sex (equation 26.4)	$N_{em} = 58.4$	$N_{ef} = 48.6$
Overall effective size (equation 26.3)	$N_e = 106$	
Actual population size[d]	$N = 357$	
Ratio of effective size to real size	$N_e/N = 0.30$	

[a] Calculated from total number of males and females that lived in the population between 1981 and 1987.
[b] Mean number of offspring surviving to age of sexual maturity (18 months) per adult.
[c] Variance in number of offspring surviving to age of sexual maturity.
[d] Harmonic mean of the population size between 1981 and 1987.

mize N_e while also aspiring to other objectives, such as zero population growth). Moreover, N_e/N ratios may be very different during the growth and carrying capacity phases of the population. Table 26.2 illustrates a calculation of the effective population size for one generation in the captive history of the golden lion tamarin.

There is an appreciable literature on effective population sizes (Lande and Barrowclough 1987; Ballou 1987a; Ryman et al. 1981; Hill 1972; Kimura and Crow 1963). Most computational methods (including those above) are derived for populations with nonoverlapping generations, rarely the case in vertebrate species. Lande and Barrowclough (1987) and Harris and Allendorf (1989) present methods for calculating effective population sizes in populations with overlapping generations. Those interested in a more detailed discussion should refer to their original articles.

8. Conduct various biochemical analyses that measure genetic variability and relationships.
Estimates of genetic variation are helpful primarily for identifying the extent of genetic differences between populations or taxa (Wayne et al. 1986; Ryder and Fleischer, chap. 25, this volume). If large differences (e.g., chromosomal differences) are found within a managed population, it may be necessary to reevaluate the goal of the program and possibly manage the population as two separate units (Templeton et al. 1986). In the words of an emerging terminology, large genetic differences may be evidence that there is more than one "evolutionarily significant unit" (ESU) within a species (see Barrowclough and Flesness, chap. 24, this volume). Interbreeding individuals from different ESUs may result in reduced survival and reproduction (outbreeding depression; see below). Unfortunately, criteria have not yet been developed to indicate what magnitude of genetic differences constitutes separate ESUs. Where different ESUs are suspected, additional analyses on morphological, behavioral, and biogeographical considerations should be conducted and considered.

Levels of genetic variation may provide information on the demographic and genetic history of the population. However, the goal of maintaining genetic diversity should not be abandoned if little or no variation is measured. It is not yet clear how representative currently measurable variation may be of the actual genetic diversity in an individual or population. There may be more diversity than can be detected by existing methods, and in the face of such uncertainty, the only prudent course of action is to manage as if diversity were present. In any case, it may be imperative to maintain what little genetic variation is present for the long-term fitness of the population.

As mentioned earlier, biochemical analyses may also be useful in resolving questions regarding parentage and in identifying relationships among founders. Long-term biochemical studies can be used to monitor the change of genetic variation in a population over time (Wayne et al. 1986). A comparison of the empirically estimated loss of variation with the theoretical loss of variation estimated from "gene drop" or similar analyses might provide insight into the types and degree of selection acting on captive populations.

It is not recommended that selection of breeding individuals be based on individual levels of heterozygosity estimated from biochemical methods. Heterozygosity at a few isozyme loci is often a poor indicator of overall individual heterozygosity (Hedrick et al. 1986; Lande and Barrowclough 1987). In addition, specific selection for known heterozygous loci (e.g., MHC loci: Hughes 1991) may select against heterozygous loci not sampled electrophoretically and decrease the overall level of genetic diversity in the population (Haig, Ballou, and Derrickson 1990; Miller and Hedrick 1991; Gilpin and Wills 1991; Vrijenhoek and Leberg 1991).

9. Adjust for uncertain parentage.
Lack of individual identification and uncertain parentage will complicate genetic analyses. This problem is common in species managed as herds, in which individual dams are often not identified, and in species in which more than one breeding male has access to females, resulting in uncertain paternity. Depending on the extent of unknown parentage, a number of different approaches can be taken.

a. Exclude individuals with unknown parentage or ancestors from the managed population. This approach is practical only if few individuals are involved and they are not otherwise important to the population. In such cases, a determining factor in the decision will be the percentage of an individual's genes that have descended from unknown ancestors. Small percentages of unknown ancestry may be acceptable. Animals who have some degree of unknown ancestry but also have ancestors whose genes are relatively rare could be kept in the population to perpetuate the contribution of underrepresented founders (see "Population Management" below). Willis (1993) points out that excluding animals of unknown parentage may result in maintaining lower levels of diversity than retaining them.

b. If questionable parentage is limited to only a few individuals, run the genetic and demographic analyses under all possible combinations to give the complete range of outcomes. If the results are insensitive to parentage possibilities, the questionable parentage should have little effect on management decisions. If the results are

highly dependent on parentage, other options for analyzing the pedigree should be explored. An alternative strategy is to select the worst-case scenario as the basis for management decisions.

c. Use the potential parent most likely to be the true parent for the pedigree analysis.

d. Create hypothetical parents that represent an agglomeration of all potential parents. If the potential parents are all equally likely to be the true parent, then a new, average, "hypothetical" parent can be created. It is given a "dummy" ID number for the genetic analysis and considered as the sire (or dam) of the offspring in question. The founder contribution of the "hypothetical" parent is then calculated as the average of the founder contributions of the possible parents. Creating an "average" parent is most appropriate if the founder contributions of the potential parents are not too different. If the differences between the potential parents are very large (especially if the potential parents are founders), other options should be considered. Inbreeding coefficients are calculated by assuming that the "hypothetical" parent is unrelated to its mate and the rest of the population. In most cases, this will underestimate inbreeding coefficients for the descendants of the unknown parent(s). It is better to assume worst-case scenarios: that is, the closest relationships among putative parents.

e. When groups have been managed for several generations without individual animal identification, create hypothetical pedigrees. "Black box" populations are common in herding species kept in large groups. An example of how a worst-case strategy can be used to utilize at least some of the founder potential in such groups is the AZA Species Survival Plan for Grevy's zebra, *Equus grevyi*. With this species, there were a number of very large herds in which individual parentage was not recorded. However, considerable useful information was known: each herd had been established by a number of founder animals (usually one stallion and several mares); there had been a limited number of further immigrants of known origin to the herds; only one stallion was in each herd in any breeding season; and the dates of birth of all individual foals born into the herds were documented.

It was first assumed that a single founder female established the herd; that is, all actual founder females were amalgamated into a "hypothetical" founder female that was assigned a "dummy" ID number. All offspring born during the first few years (or a period of time equal to the age of sexual maturity for the species) were then considered to be offspring of the herd stallion and this hypothetical dam. After this first cohort, it was assumed that daughters of this pair would have matured and bred with their father. Therefore, an F_1 hypothetical female was created. The parents of this female were the herd stallion and the hypothetical founder female. Thereafter, all offspring born in the herd traced 75% of their genes to the founder stallion and only 25% to the hypothetical founder female.

Such a strategy is most useful if the herd was established by known founders. Obviously, this strategy will underestimate the actual number of founders for the herd as well as the genetic diversity involved. Inbreeding coefficients will be overestimated when a number of different breeding animals are combined under one "hypothetical" parent. However, within the herd, inbreeding coefficients will be relative, and closely related individuals will have higher coefficients than less closely related individuals.

When "hypothetical" parents or founders are created to satisfy genetic analysis requirements, individuals with unknown ancestors in their pedigree should be clearly labeled to indicate that both their founder contributions and inbreeding coefficients are based on hypothetical data.

DEMOGRAPHIC ANALYSES

The purposes of demographic analyses are to calculate basic life tables and population dynamics for the captive population; determine a carrying capacity for the captive population compatible with genetic, demographic, and resource limitations; and determine lifetime and annual reproductive objectives for each individual.

1. Demographic Characteristics of the Population

Basic demographic data of interest to the captive manager are:

a. Size of the current population and number of institutions and geographic regions over which it is distributed. This tabulation will usually be an immediate result of the data collection process (see above). It may also be useful to estimate the numbers and distribution of other taxa with similar "captive ecologies" (i.e., space and resource requirements) in order to estimate the total captive carrying capacity for the species.

b. Age and sex structure of the population. These distributions show the proportion and sex ratio of the population in each age class (fig. 26.7).

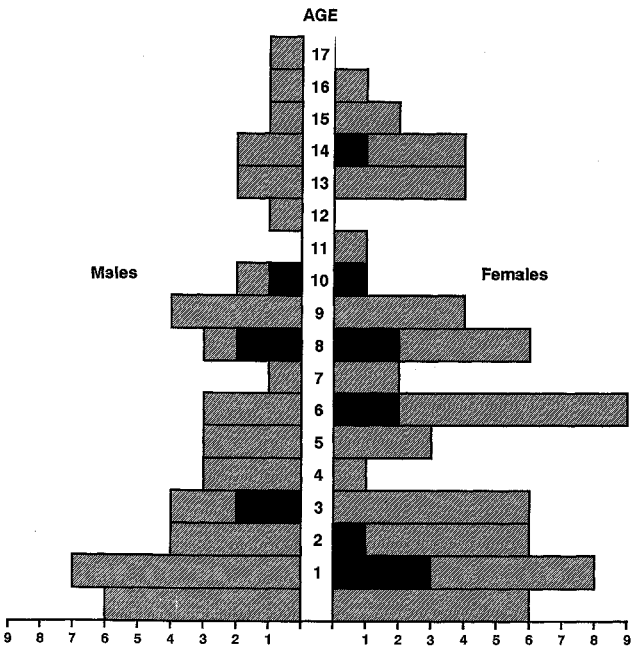


FIG. 26.7. Male and female age structures for the 1983 captive Sumatran tiger, *Panthera tigris sumatrae*, population. The solid area shows the number, sex ratio, and ages of proven breeders in the population. (From Ballou and Seidensticker 1987.)

c. Age-specific survivorship and fertility rates. Survivorship and fertility rates are calculated separately for each sex from age-specific tallies of birth and death events in the population and are usually presented in the form of a life table (Caughley 1977). A variety of different procedures have been developed to calculate life tables (Caughley 1977; Foose and Foose 1983; Foose and Ballou 1988). Table 26.3 is a life table for the captive population of golden lion tamarins.

TABLE 26.3. Life Table Calculations for Captive Female Golden Lion Tamarins for the Period 1981–1987

Age class (years)	p_x[a]	l_x[b]	m_x[c]
0	0.61	1.00	0.00
1	0.87	0.61	0.00
2	0.90	0.53	0.32
3	0.92	0.48	0.60
4	0.92	0.44	0.74
5	0.91	0.40	0.78
6	0.90	0.37	0.72
7	0.90	0.33	0.59
8	0.89	0.30	0.53
9	0.88	0.27	0.53
10	0.86	0.23	0.53
11	0.82	0.20	0.65
12	0.76	0.17	0.89
13	0.78	0.13	0.88
14	0.88	0.10	0.52
15	0.97	0.09	0.13
16	1.00	0.08	0.00
17	1.00	0.08	0.00
18	1.00	0.08	0.00
19	0.75	0.08	0.00
20	0.25	0.06	0.00
21	0.00	0.02	0.00

[a] Proportion of females surviving from age class x to age x + 1.
[b] Proportion of offspring surviving to age class x.
[c] Average number of female offspring born to a female of age x.
Source: Ballou 1987b.
Note: Demographic calculations (see Caughley 1977):
Net reproductive rate (R_o)

$$R_o = \sum_{x=0}^{21} l_x m_x = 2.43$$

Exponential growth rate (r)

$$\sum_{x=0}^{21} e^{-rx} l_x m_x = 1.00$$

Solution for $r = 0.149$
$\lambda = e^r = 1.16$

Generation length (T)

$$T = \sum_{x=0}^{21} x e^{-rx} l_x m_x = 5.28$$

Growth rate per generation $= \lambda^T = 2.19$

No. female births required for zero population growth at carrying capacity of 250 females (see Keyfitz 1968)

$$= 250^* \frac{1}{\sum_{x=0}^{21} l_x} = 41$$

Because life tables derived from historical data may reflect past rather than current population trends, life tables should be based on relatively recent data (e.g., the last 5 years). However, in many populations there may not be enough recent data to construct a reliable life table, and in those cases historical data can be used to increase sample sizes.

In situations in which no data are available (e.g., because no captive population has previously existed), life table data can be estimated from basic life history data on the species (age of first reproduction, age of last reproduction, litter size) as well as from data on similar species in captivity. ISIS is a valuable source for rough survival and fecundity rates of captive populations (Shoemaker and Flesness, appendix 4, this volume).

d. Any factors that adversely affect survival and reproduction rates and patterns. Evidence of reproductive failure and high mortality rates should be investigated immediately. In addition to medical, nutritional, physiological, and behavioral causes, potential genetic causes should be examined. The deleterious effects of inbreeding on survival and reproduction (inbreeding depression) have been observed in many captive populations (Ralls and Ballou 1983; Templeton and Read 1984). Although genetic in cause, its effects are demographic and can include lower population growth rates, smaller populations, and, consequently, even higher rates of inbreeding (Gilpin and Soulé 1986). If such inbreeding depression is severe, inbreeding should be minimized.

Outbreeding depression, a reduction in fitness caused by hybridization between individuals from differently adapted or coadapted populations, can also reduce breeding success (Templeton et al. 1986). Although rarely documented in mammals or other vertebrates, outbreeding depression is most likely when ESU boundaries are transgressed (see Barrowclough and Flesness, chap. 24, this volume), either knowingly or not (e.g., owl monkeys, *Aotus trivirgatus:* Cicmanec and Campbell 1977). Templeton and Read (1984), Templeton et al. (1986), and Lynch (1991) discuss methods for examining the effects of outbreeding in captive populations. Careful consideration of the ESU status of populations should mitigate potential outbreeding problems.

2. Demographic Parameters Estimated from Life Table Data

A number of different demographic parameters are calculated directly from life tables:

a. Generation length *(T).* Generation length is the average age at which a parent produces young (Hedrick 1983). It can be calculated directly from estimates of survival and fecundity rates (see table 26.3; Caughley 1977) and is used to estimate a minimum viable population (MVP) size for the captive population (see below). It should be calculated for each sex separately.

b. Population growth rate (λ). Life tables provide estimates of the expected growth rate of the population, assuming the estimated survival and fecundity rates remain stable over time (Caughley 1977). The growth rate is used to estimate the MVP size and the capacity of the population for

self-sustainment. If it is less than 1, the population is declining; if greater than 1, the population is growing; and if equal to 1, the population size is stationary (constant).

If the growth rate is inadequate for the population to be self-sustaining, the focus of the management program should shift to research on reproductive, behavioral, and other biological and husbandry aspects of management to resolve the problems.

c. Stable age structure. The stable age structure is the eventual sex and age structure of the population if survival and fecundity rates remain stable over time (Caughley 1977).

d. Net reproductive rate (R_0). The net reproductive rate is the number of same-sex offspring produced by an average individual during its lifetime (see table 26.3). Conceptually, it is the number of same-sex animals an individual "replaces" itself with in the population. For stationary populations (zero population growth), R_0 is 1: each animal exactly replaces itself in the population every generation. R_0 is used to calculate animal lifetime reproductive objectives for population management.

e. Annual reproductive rates. The number of animals born each year in a stable population with growth rate λ is a function of the survival rate and the population growth rate. The annual number of female (or male) births required to achieve a population growth rate of λ for a stable population of size N is:

$$\text{Number of births} = \frac{N * \lambda}{\Sigma \lambda^{-x} l_x} \qquad (26.6)$$

where the summation in the denominator is over all age classes. The number of births are for the same sex from which the l_x values are calculated. For zero population growth ($\lambda = 1$), the number of births is $N/\Sigma l_x$. For example, 41 female golden lion tamarins need to be born each year to achieve zero population growth at a stable population size of 500 animals (250 females: see table 26.3). If the survival rates for males and females are the same, and if the sex ratio at birth is 1:1, the total number of births required is double the number calculated above.

f. Fertility, survival, and harvest rates necessary to maintain a stationary population. These parameters are used to develop management recommendations for designation of surplus and breeding rates, as well as to predict what effects managerial modifications of survival and fertility rates will have on the population (Beddington and Taylor 1973; see below).

* * *

Several computer programs are available to calculate these demographic parameters from life table data as well as to estimate life table data directly from computerized pedigrees (Bingaman and Ballou 1993; ISIS 1991). Table 26.3 presents calculations of values for generation length, population growth rate, and fertility rates for the captive population of golden lion tamarins.

3. Carrying Capacity Determination

For a managed population, the carrying capacity is an analytically established target size to which the program aspires. The process of establishing a carrying capacity involves reconciling the genetic and demographic goals of the population with the limited resources of zoological institutions.

Losses of both genetic diversity and demographic stochasticity are functions of population size. The smaller the population, the faster the loss of diversity, and the more unstable and susceptible to extinction it is. Thus, purely for genetic and demographic reasons, the captive population should be as large as possible. However, limited resources place severe restrictions on the sizes of captive populations. Similar species "compete" for captive habitat. Maintaining too large a population of any one taxon may deprive other needy taxa of captive resources; therefore, the carrying capacity for each taxon needs to be a compromise between maintaining some minimum viable population (MVP) size large enough for genetic and demographic goals to be realized and still allowing enough resources for other similar species' programs. While the MVP size determines the lower limit of the carrying capacity, the upper limit is determined by resource limitations.

a. Determine the lower limit of carrying capacity: minimum viable population size. The lower limit of the carrying capacity, the MVP, will be determined primarily by the long-term genetic and demographic objectives of the program and the biological characteristics of the population. As discussed above, the primary goal of most conservation-related captive propagation programs is to maintain genetic diversity and demographic security. More specifically, MVP size depends on:

- The kind and amount of genetic diversity to be preserved
- The length of time the population is to be managed
- The probability that the population will survive this time period
- The biological characteristics of the population (i.e., number of founders, generation length, effective size, and population growth rate)

The 90%/200 year rule of thumb (see "Captive Management Goals" above) is a common approach to determining how much diversity is required and for how long it should be maintained (Soulé et al. 1986). Calculating the MVP size necessary to maintain 90% of the original heterozygosity for 200 years requires modeling the population's growth from its founding number to its carrying capacity through the 200-year period. Loss of genetic diversity can be conveniently visualized as occurring during three phases: the founding event, the growth to carrying capacity, and the management of a stable population at carrying capacity (fig. 26.8; Ballou 1987c). During each phase genetic diversity is lost at a different rate, and the overall loss of heterozygosity is the cumulative loss over all three phases. Loss of heterozygosity during the founding phase is a function of the effective size of the founding population. Equation (26.1) can be used to roughly estimate the effective size of the founding population from its sex ratio. Loss of heterozygosity during the growth phase is a function of the population's growth rate and how long (measured in animal generation lengths) it remains in the growth phase. Loss of heterozygosity during the carrying capacity phase is deter-

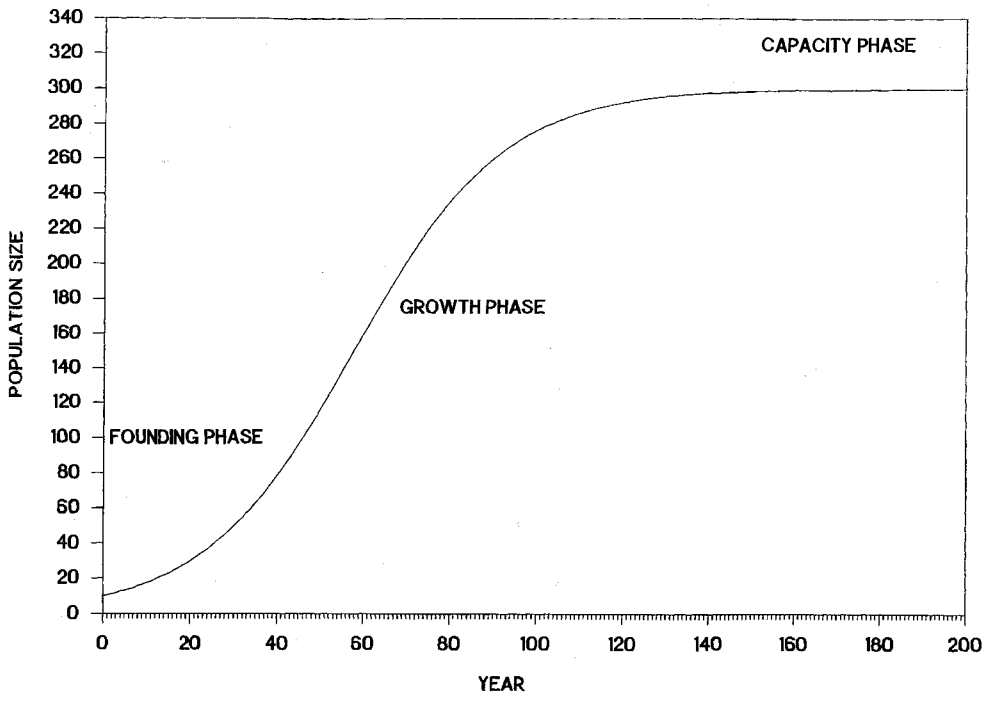


FIG. 26.8. Theoretical growth curve of a captive population showing the founding, growth, and capacity phases used to model loss of genetic diversity.

mined by the effective size of the population at carrying capacity and how long it stays at capacity, again measured in generations.

If the founder effective size, generation length, N_e/N ratio, and population growth rate are known, the carrying capacity required to maintain X% (e.g., 90%) of the variation for Y (e.g., 200) years can be calculated (Ballou 1987c). Graphs, algorithms, and computer programs have been developed for this purpose (Gilpin 1987; Ballou 1986; Soulé et al. 1986). Table 26.4 illustrates the MVP sizes required for a range of N_e/N ratios and effective founder sizes for a population growing at 8% per year.

A secondary consideration for determining the MVP size is demographic stochasticity and the susceptibility of the population to extinction due to chance or catastrophic events. Populations smaller than 50 or even 100 may be particularly vulnerable to "crashes" or extinctions due to random demographic events such as disease epidemics, natural disasters, or sex ratio distortions (Gilpin and Soulé 1986). Therefore, for demographic reasons, MVPs should be no smaller than 50 individuals (Foose et al. 1986). The MVP based on genetic considerations will probably be large enough to insure a high probability of survival for 200 years for most captive populations, since distribution of animals among many zoos decreases the likelihood of total population extinction due to environmental stochasticity or catastrophe (Shaffer 1987). Demographic simulations can be conducted to estimate how susceptible populations with given demographic characteristics are to such chance events (Ewens et al. 1987; Goodman 1987; Lacy 1990b; Shaffer 1987). Demographic MVP models are discussed in detail in Soulé (1987).

TABLE 26.4. Carrying Capacities Necessary for Maintaining 90% of the Founders' Heterozygosity for 200 Years in a Population with Generation Length of 5 Years and $a\lambda$ of 1.08 (8% Growth Rate per Year)

N_e/N ratio	Effective founder number				
	10	15	20	25	30
0.1	3620	2452	2084	1917	1822
0.3	1207	817	695	639	607
0.5	724	490	417	383	364
0.7	517	350	298	274	260
0.9	402	272	232	213	202
1.1	329	223	189	174	166

Source: After Soulé et al. 1986.

Finally, it should be emphasized that there is no single MVP size that applies to all species or populations, nor is there a single magic-number MVP size that categorically applies to any one species all the time. Determination of MVPs depends on a number of factors. The simplistic determination of MVP described here is an example of the more general process known as population viability analysis (PVA: Soulé 1987; Gilpin and Soulé 1986).

b. Determine the upper limit of carrying capacity: captive resources. The upper limit on carrying capacity should be derived from an analysis of the amount of "captive habitat" (space and resources) currently being used by the target population and other taxa with similar "captive ecologies" (enclosure and resource requirements, exhibit value, etc.). Current population sizes and information on expansion plans can be used to estimate the captive habitat available. For example, Foose and Seal (1986) calculated the total number of enclosure spaces utilized by all large felids to determine the captive carrying capacity for Siberian tigers.

In addition, the number of different taxa in need of assistance from captive propagation programs and potentially competing for this captive space should be determined. This may require additional information on the status and trends of wild populations as well as consideration of taxonomic

uniqueness. Division of the available "captive" habitat by the number of "competing" taxa will suggest the upper limit on carrying capacity for each taxon. These estimates can be refined if additional information is known about the MVP size requirements of the other "competing" taxa (Conway 1987; Foose, Seal, and Flesness 1987).

c. Establish the carrying capacity. With the lower limit of carrying capacity determined by MVP size requirements and the upper limit determined by captive resource allocation, a carrying capacity for the captive population can be established. The carrying capacity should be as large as possible within these limits. If the MVP size is larger than the population size allowed by resource allocation, then either the MVP requirements will have to be relaxed (reduce the time frame of concern and/or decrease the levels of diversity to be retained) or the biological characteristics of the population will have to be improved (acquire new founders, extend generation length, increase N_e/N ratio, and/or increase growth rate). Otherwise, it will be necessary to prioritize and select among competing taxa. The development of criteria for prioritizing taxa in need of conservation measures is complex and continues to be discussed by a number of conservation organizations (Foose, Seal, and Flesness 1987; Oates 1986; Foose 1983).

POPULATION MANAGEMENT

Genetic and demographic analyses provide the basis for formulating a captive propagation and management program, such as an AZA Species Survival Plan Masterplan (Foose and Seal 1986). Ideally, the program should provide specific recommendations for each individual in the population. More specific guidelines for population management include:

1. Attempt to obtain a sufficient number of founders to sample adequately both the heterozygosity and the allelic diversity in the source population.

Allelic diversity is lost much more rapidly than heterozygosity during bottleneck and founding events (Allendorf 1986; Fuerst and Maruyama 1986). Therefore, the primary concern is adequate sampling for allelic diversity, since this may require more founders than sampling for heterozygosity alone. Sampling for heterozygosity does, however, establish a lower limit for the effective founder size required. A sample of N effective founders retains on average $(1/2N)$ * 100% of the source population's heterozygosity. A general rule of thumb is to try to sample at least 95% of the source population's heterozygosity; this requires an effective founder size of at least ten (Denniston 1978).

The number of founders required to sample allelic diversity adequately depends on the allele frequencies in the source population. Marshall and Brown (1975), Denniston (1978), and Gregorius (1980) discuss the effective founder sizes required given various allele frequency distributions (table 26.5). Unfortunately, information on the distribution of allele frequencies in the source population is often not available. Marshall and Brown (1975) suggest that founder numbers adequate for effectively sampling allelic diversity be based on the most likely allele distributions, and conclude that effective founder sizes between twenty-five and fifty are sufficient in most cases. They emphasize that potential differences in genetic variation over the range of a population should be considered. Sampling strategies should attempt to compensate for and/or exploit known geographic patterns of genetic variation to optimize the levels of genetic diversity sampled, while at the same time striving to remain within the geographic boundary of the ESU.

TABLE 26.5. Founder Sizes Necessary to Sample All Alleles with Frequencies Equal to or Greater Than p with 95% and 99% Certainty

Allele frequency (p)	Certainty	
	95%	99%
.500	6	8
.300	11	15
.200	22	28
.100	51	66
.040	152	192
.010	754	916
.008	972	1,174

Source: After Gregorius 1980.

Additional perspectives on the number of founders required will also derive from the MVP analysis described above. Specifying genetic and demographic objectives and other population characteristics will prescribe a minimum number of founders. The MVP analysis approach will also consider demographic as well as genetic factors in establishing minimum founder numbers.

It should be appreciated that founders will not necessarily or optimally enter the population only at the inception of a captive propagation project. Immigrants from the wild should periodically be incorporated into the captive population if possible. It should also be noted that failure to obtain an optimal genetic number of founders is *not* justification for cancelling plans to establish a captive propagation program. Wild-caught specimens, however, should be obtained only after extremely careful consideration of the potential effects of such removals on the wild population.

2. Expand the population size as rapidly as possible to the carrying capacity.

Genetic diversity is lost when growth rates are slow because small populations lose genetic diversity at a faster rate than large populations.

3. Stabilize the population at carrying capacity.

The current population size and growth rate determine whether the population is at, or when it will be at, carrying capacity. If the population is at or is approaching carrying capacity, demographic analysis can be used to determine how fertility and survivorship rates can be managed by "removals" of animals (harvests, culls) and/or regulation of reproduction (birth control) to stabilize the population at the desired carrying capacity (Beddington and Taylor 1973). This process may entail much "what if" analysis to determine how such managerial modifications of survivorship and fertility patterns will affect population size, growth rate, age distribution, and so forth. Table 26.6 shows how such an analysis can be applied to Siberian tigers. The ef-

TABLE 26.6. Management Options for Stabilizing the Siberian Tiger Population at 250 Animals

Option	If reproduction is	Percentage of 0–1-year-olds to be removed	Percentage of each age class to be removed
1	Equivalent to 1956–1980 and litter size of 2.43 cubs	46	7
2	Adjusted to compensate for mortality and equally distributed over all ages	0	0
3	One litter of 2.43 cubs at any age	This level of reproduction appears insufficient to sustain the population with present mortality rates	
4	One litter of 3 cubs at age 4	0 (probably)	0 (probably)
5	Two litters of 2.43 cubs at age 5	This level of reproduction appears insufficient to sustain the population with present mortality rates	
6	Two litters of 2.43 cubs at ages 5 and 10	30	5
7	Two litters of 2.43 cubs at ages 4 and 7	35	8
8	Three litters of 2.43 cubs at ages 4, 9, and 12	53	10
9	Litters of 2.43 cubs in alternate years	72	15

Source: Foose and Seal 1986.

fects of these modifications on the effective population size should also be examined, since a reduction in the number of breeders can reduce N_e. Modifications that maintain a large effective size while still accomplishing the goal of stabilizing the population at carrying capacity should be explored (Dyke et al. 1986; Ryman et al. 1981).

4. Extend generation length as much as possible without jeopardizing demographic security.
Because genetic diversity is lost each generation, extending generation length *(T)* will reduce the amount of diversity lost during a given number of years. Alternatively, the same level of diversity can be retained with a smaller N_e if T is extended. Generation time can be lengthened by shifting the mean age of reproduction to later in life. This strategy, however, incurs greater risk of stochastic losses of animals before they can breed and may also result in reduction of fertility due to age-dependent factors.

5. Adjust representation of founder lineages to be proportional to the probable distribution of founder alleles surviving in the living population.
The most substantial part of any captive propagation program is the process of identifying which animals are to breed, how often, and with whom. The basic objective of this process is to compensate for highly skewed founder contribution distributions and loss of founder alleles by preferentially breeding descendants of underrepresented founders and restricting reproduction in those of overrepresented founders. However, this must be done within the framework of the demographic requirements of the population. The process involves four steps: (1) determining the *target founder contributions* that define the objectives for adjusting the population founder contributions; (2) determining *individual lifetime reproductive objectives* according to the genetic characteristics of each individual (i.e., how often animals are to breed); (3) determining *individual annual reproductive objectives* so that yearly population demographic needs are met (i.e., which animals are to breed each year); and (4) recommending *pairing* to accomplish all of the above (i.e., who is to breed with whom).

a. Determine the target founder contribution objectives for the population. Equalization of founder representation is usually not the optimal objective. Founder representation should not be equalized if some proportion of a founder's alleles have been lost as a result of bottlenecks in the pedigree (see "Genetic Analyses" above). With fewer genes to contribute, adjusting this founder's contribution to the same level as that of other founders not having experienced a bottleneck will overrepresent this founder's remaining genes in the population. For such founders, the founder contribution goals must be reduced according to their level of retention. For example, if a founder's retention is 50%, it could be considered only "one-half" of a founder and its contribution to the living population managed to a level of one-half that of the other founders.

Results of the gene drop and founder contribution analyses (see "Genetic Analyses" above) are used to compute a target distribution of founder representation that more accurately reflects how much of the founders' genetic diversity has survived to the living population (retention):

$$TF_i = \frac{r_i}{\sum_{x=1}^{N_F} r_x} \qquad (26.7)$$

where TF_i is the target founder contribution for founder i; r_i is the proportion of founder i's alleles surviving to the living population (retention); and N_F is the number of founders in the living population. Genetic representation of founders with low retention should be managed at a lower level than that of well-represented founders. This strategy will increase the number of unique founder alleles maintained in the population. Table 26.7 shows the target founder representations for the pedigree in figure 26.2. Note that founders 2 and 3 are adequately represented according to the target founder contribution goal, whereas before they appeared to be underrepresented. The objective of genetic management then becomes attempting to shift the observed founder contributions toward the target founder contributions.

b. Combine genetic and demographic objectives to ar-

TABLE 26.7. Target Founder Contributions for Genetic Management of the Pedigree Shown in Figure 26.2

Founder	Current founder contribution	Parity[a] founder contribution	% genes surviving[b] (retention)	Target[c] founder contribution	Status of contribution[d]
1	.13	.20	.50	.17	Under
2	.16	.20	.48	.17	Adequate
3	.16	.20	.49	.17	Adequate
4	.35	.20	.80	.28	Over
5	.20	.20	.61	.21	Adequate

Note: Target founder contributions are based on the proportion of a founder's genes surviving to the living population (retention).

[a]Parity (equal representation) = 1/(number of founders).

[b]Proportion of each founder's genome surviving to the living population is based on a gene drop analysis with 5,000 simulations.

[c]See equation 26.7.

[d]Under, founder's genetic contribution is below that of its target—it is genetically underrepresented in the population; over, founder's genetic contribution is above that of its target—it is genetically overrepresented in the population; adequate, founder's genetic contribution is approximately that of its target.

rive at animal-by-animal breeding recommendations. As discussed above, demographic analyses can be used to determine the average lifetime reproductive requirements for individuals in the population (R_o). However, in order to modify current founder contributions to match target objectives, it is desirable for individuals descended from underrepresented founders to produce more than the average number of progeny, while individuals descended from overrepresented founders should produce fewer.

These individuals can be identified by examining the founder contribution within each individual. Animals with a high founder contribution from underrepresented founders (as defined by the target founder contribution) should be considered high-priority breeders (e.g., individual 8 in the sample pedigree, table 26.1). However, identifying preferred breeders by scanning founder contribution charts is often difficult. An individual may be descended from both over- and underrepresented founders, and contribution from overrepresented founders may be highly correlated with contribution from underrepresented founders. Additionally, if there are a large number of founders, the quantity of information that must be considered is formidable.

Diagnostic methods like mean kinship and genetic uniqueness simplify the process of identifying priority individuals (see "Genetic Analyses" above). Ranking of animals according to mean kinship provides a fast and simple diagnostic tool for identifying animals that are genetically valuable to the population. Furthermore, these ranking methods can be combined with the demographic requirements of the population to develop specific animal-by-animal breeding recommendations for each individual in the population. One strategy is to use the distribution of mean kinship to determine lifetime reproductive objectives for each individual. Different lifetime reproductive objectives are assigned to different levels of mean kinship: the lower the individual's *mk* value, the higher its lifetime reproductive objective. However, the scale must be established such that average lifetime reproductive objectives across all individuals achieve the overall demographic objectives. Scaling reproductive contribution according to *mk* should not change the mean reproductive rate, only the variance across individuals.

The scaling of lifetime reproductive objectives with *mk* is dependent on how rapidly the current founder contributions are to be adjusted to match the target founder contributions. Large differences in lifetime reproductive objectives between descendants of over- and underrepresented founders will result in rapid convergence between current and target founder contributions. The range of lifetime reproductive objectives will most likely be determined by the reproductive biology of the species and how intensely the population can be managed. An example of scaling lifetime reproductive objectives according to mean kinship is shown in table 26.8.

If and when the population obtains its target distribution of founder representation, lifetime founder objectives (family sizes) should be equalized to maximize the effective size.

c. Schedule lifetime reproductive objectives to meet annual population growth objectives. Animal-by-animal breeding recommendations combine the population's yearly demographic requirements with the lifetime reproductive

TABLE 26.8. Lifetime Reproductive Recommendations for Individual Captive Golden Lion Tamarins Based on Distribution of Mean Kinship (*mk*) Values in the Population

Mean kinship range	% of population	Offspring objectives
< 0.019	12%	4
0.020 to 0.034	17%	3
0.035 to 0.050	45%	2
0.051 to 0.058	14%	1
> 0.058	12%	0
		Mean = 2.0

Note: The total number of offspring that should be produced and eventually bred per individual is a function of the individual's *mk* value. Individuals with low *mk* values carry genes that are uncommon in the population and should be bred more than individuals with common genes. Note that the mean number of births across all individuals is 2.0: each breeding pair only replaces itself and zero population growth is achieved.

goals for each individual. Demographic analyses determine the yearly number of births required to meet population growth objectives (e.g., rapid population growth or zero population growth). Given the species' litter size and breeding rates, this number can be translated into the number of pairs that need to be bred per year to accomplish the desired birth rate. For example, in golden lion tamarins, 82 births (41 female births) are needed each year for zero population growth (see table 26.3). The average litter size is 2.0, 25% of the breeding pairs fail to breed, 65% produce 1 litter per year, and 35% produce 2 litters per year. Sex ratios at birth are equal. Therefore, we need to maintain 40 breeding pairs per year to produce the 82 required births.

The animal-by-animal breeding recommendations must specify which individuals should be bred each year to meet these annual breeding requirements. The individuals selected for breeding are chosen from those who have not yet fulfilled their lifetime reproductive goals. Scheduling of which animals are to reproduce each year should take into consideration age and genetic importance so that aging, important animals are given reproductive priority. Scheduling should also take advantage of existing pairings or groups and institutions' capacities and interests. A schedule of which individuals should reproduce over the next 1–5 years is recommended.

d. Select pairings of animals among those scheduled for breeding. At this point, the specific individuals to be bred over the next several years will have been identified. The next, and final, step is to recommend pairings among those individuals. There are two principal criteria for determining who is to breed with whom. The first is to try to avoid pairing an animal from underrepresented founders with an animal from overrepresented founders. The offspring of such a pair would have founder contributions that are the average of the parents', and the underrepresented founder contribution would be linked to the overrepresented founder contribution; they could then no longer be managed independently. Therefore, when making pairing decisions, pair animals that are descended from underrepresented founders (i.e., low mean kinship) with similar animals. This strategy allows the underrepresented founder contributions to be increased in the population independently of the overrepresented founder contributions. At a later generation, when founder contributions are more evenly distributed, this is less of a concern.

It is often the case that pairings of animals with similar, underrepresented founder contributions will result in mates that are closely related to each other (a valuable brother/sister pair will have similar, if not the same, mean kinship). Therefore, it is also important to examine relationships among potential mates and exclude pairings of closely related animals. This objective accomplishes two goals: (1) it reduces the degree of relationship within the population as a whole, therefore retaining higher levels of heterozygosity than would otherwise be retained; and (2) it reduces the potentially detrimental effects of inbreeding depression on survival and reproductive rates. Inbreeding effects are highly variable among species, and it is not possible to predict at what level inbreeding will have significant deleterious effects on the population (Brewer et al. 1990). Inbreeding should be avoided or minimized if inbreeding depression is observed.

Unfortunately, inbreeding levels will increase in populations in which immigration is restricted. The minimum amount of inbreeding possible in a population depends on the levels of relatedness among the living animals. A rule of thumb often used in determining acceptable levels of inbreeding in a population uses the mean kinship value averaged across all living individuals. The average *mk* is equal to the expected inbreeding coefficient of the offspring that would be produced if all individuals in the population were bred randomly. To keep inbreeding levels low, pairings should be selected so that offspring have inbreeding coefficients no higher than the average *mk*.

It should be noted that minimizing inbreeding is not the primary criterion for genetic management. However, there should be an attempt to minimize inbreeding within the constraints of adjusting founder contributions toward target objectives and mating individuals to avoid linking over- with underrepresented founder contributions. There may be cases in which inbreeding is deliberately employed to purge a population of its deleterious alleles, as in the Speke's gazelle, *Gazella spekei,* program (Templeton and Read 1984). Intentional inbreeding of small populations is generally contrary to the goal of maintaining genetic diversity since it can drastically change the genetic characteristics of the population, possibly making it unsuitable for later release into the wild (Templeton and Read 1983).

6. Select against individuals with extreme outlying morphological and reproductive characteristics. Such characteristics would include traits such as albinism and dwarfism. This stabilizing selection should help control levels of genetic load in the population (Frankham et al. 1986). Selection can and should be imposed within families by replacing individuals to be selected against with their siblings. This strategy will allow selection to be implemented while working within the constraints of equalizing family size.

7. Consider dividing the population into several subdivisions or demes among which gene flow (usually exchange of animals but also exchange of gametes or embryos) is regulated. Subdivision of a population is advantageous for epidemiological protection (Dobson and May 1986) as well as for other practical reasons, such as reduction of shipping costs and hazards and simplification of management logistics. In addition, genetic advantages may accrue based on the theoretical argument that, without selection, random genetic drift will drive different alleles to fixation in different demes and, overall, maintain a higher level of allelic diversity (Chesser, Smith, and Brisbin 1980). However, the role of selection in captive populations is uncertain, and it is possible that similar types of selection, conscious or unconscious, will actually fix similar alleles in each deme, thereby decreasing the overall levels of genetic diversity. Furthermore, the smaller size of semi-isolated subdivisions may render them more vulnerable to demographic stochasticity. Subdivided populations with large numbers of animals in

each division will benefit from the practical advantages without the consequences of some of the genetic and demographic uncertainties. It is not possible in this chapter to describe methods to determine the optimal numbers or sizes of subdivisions or the extent and rate of genetic exchange among them. More analyses are needed on the role of population subdivision in maintaining genetic diversity. The reader is referred to Lacy (1987) for discussion.

8. If possible, continually introduce new wild-caught founders into the population.

Additional genetic material will help to minimize loss of variation due to genetic drift. In some cases, it may be appropriate to devise a program of continual exchange of individuals (or genetic material) between wild and captive populations, taking care to minimize the associated epidemiological problems.

9. Utilize available reproductive technology to the fullest extent possible.

Reproductive technology (semen/ovum collection and storage, embryo transfer and freezing, etc.) should be considered a primary tool for assisting captive propagation programs in the long-term maintenance of genetic diversity. Such technology can facilitate exchange of germ plasm between wild and captive populations as well as effectively increasing the reproductive lifetimes of founders and their immediate descendants. By increasing generation length, adequate levels of genetic diversity can be maintained in smaller populations, leaving more room for populations of other needy species (Ballou and Cooper 1992).

Living founders who have not yet contributed to the population should be considered immediate candidates for germ plasm storage. Although reproductive technology is not yet available for most exotic species, it is a major focus of research by the reproductive community (Wildt 1989).

CONCLUSIONS

Zoological institutions are making a major contribution to the conservation of threatened and endangered species through captive propagation programs. Their commitment to the long-term preservation and management of captive populations is dependent upon developing cooperative captive propagation programs based on sound genetic and demographic principles. The essence of any captive propagation program is the recommendations indicating which animals are to breed, how often, and with whom. These individual-by-individual and institution-by-institution recommendations are based on the results of genetic and demographic analyses. The final result is a conservation strategy that pools the genetic and demographic potential of all the individuals in the population to satisfy the genetic and demographic needs of the population. Whenever possible, conservation strategies for wild and captive populations should be integrated to provide a comprehensive conservation plan for the species.

The technology of genetic and demographic management is growing rapidly, and experts in many areas are directing attention to the problems unique to this field. Analytic and biochemical techniques are becoming increasingly available for population managers to use in the numerous analyses required. In addition, our understanding of the genetic and demographic needs of captive populations continues to expand as more is learned about natural populations. Advances will continue to be incorporated into the procedures for developing captive propagation programs as they become available.

ACKNOWLEDGMENTS

We thank Katherine Ralls, Laurie Bingaman, Susan Haig, and Kathy Cooper as well as an anonymous reviewer for making many helpful comments on this chapter.

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