Demographic and Genetic Management of Captive Populations

by:

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In Press: Devra G. Kleiman, Kaci Thompson, and Charlotte Kirk-Baer. (ed). Wild Mammals in Captivity. Univ. of Chicago Press.

1 Table of Contents

1 Table of Contents 2
2 Introduction 4
3 The Value of Population Management 6
3.1 Increasing value to conservation 6
3.2 Ensuring the availability of captive animals 6
3.3 Improving animal welfare 7
3.4 Verifying taxonomic origin 7
3.5 Managing zoo space efficiently 7
3.6 Buffering against unexpected changes in regulations 7
3.7 Reducing collection from the wild and shipping costs 8
4 Data for Population Management 8
5 Maintaining Viable Populations: Demography 11
5.1 Small population dynamics 11
5.2 Unstable age/sex structures 11
5.3 Unreliable reproduction 12
6 Maintaining Viable Populations: Genetics 13
6.1 What is genetic diversity? 13
6.2 Measuring genetic diversity 15
7 Defining a Purpose, Goals and Targets for Population Management 16
7.1 Determining a population's purpose 16
7.2 Setting genetic goals 17
7.3 Setting demographic goals 18
7.4 Setting targets 19
7.5 1. Common display species, species for education and research 19
7.6 2. Endangered species in captivity for long-term conservation 20
7.7 3. Rare species being propagated for immediate release into natural habitats 20
7.8 4. Species not yet capable of self-sustaining reproduction in captivity 21
8 Evaluating a Population's Demographic Status 21
8.1 Population size and distribution 21
8.2 Age and sex structure 22
8.3 Historical demographic patterns 23
8.4 Summary parameters calculated from the life table 29
9 Evaluating a Population's Genetic Status 30
9.1 Founders 32
9.2 Founder contribution 33
9.3 Allele retention 35
9.4 Founder genome equivalents 36
9.5 Gene diversity retained 37
9.6 Average inbreeding 37
9.7 Potential genetic diversity 38
9.8 Effective population size 39
9.9 Use of molecular genetic analyses 40
9.10 Genetic summary table 40
10 General Management Strategies 41

10.1 Obtain a sufficient number of founders – the Founding Phase 41
10.2 Expand the population size as rapidly as possible – the Growth Phase 42
10.3 Stabilize the population at carrying capacity – the Management Phase 43
10.4 Consider subdividing the population 43
10.5 Utilize available reproductive technology 43
11 Developing Population Management Recommendations 44
11.1 Step 1: Calculate the target population size. 44
11.2 Step 2: Calculate desired growth rate. 44
11.3 Step 3: Calculate number of births and breeding pairs needed. 46
11.4 Step 4: Calculate mean kinship values 47
11.5 Step 5: Calculate genome uniqueness values 48
11.6 Step 6: Calculate kinship coefficients of all possible pairings. 48
11.7 Step 7: Use the mean kinship table to identify pairings 48
11.8 Step 9: Make recommendations for every animal in the population. 50
12 Particular Challenges 50
12.1 Managing new founders 50
12.2 Immigration and emigration 51
12.3 Unknown ancestry 52
12.4 Management of deleterious and adaptive traits 55
12.5 Group management 56
13 Genetics of reintroductions 57
14 Acknowledgement 58
15 Literature Cited 59
16 APPENDIX A: Software programs for managing and analyzing data for population management. 69
17 APPENDIX B: Demographic definitions. 71
18 APPENDIX C: Genetic definitions. 73

2 Introduction

The purpose of population management is to ensure that populations of species of our choosing are available, healthy and viable for the foreseeable future. Thus, the contribution of zoos to ex-situ conservation via captive breeding programs requires prudent population management planning. Population management does result in successful conservation. The rescue from extinction of species like the black-footed ferret (*Mustela nigripes*), California condor (*Gymnogyps californianus)*, Guam rail (*Rallus owstoni*), Lord Howe Island woodhen (*Gallirallus sylvestris*), greater stick-nest rat (*Leporillus conditor*), and mala (*Lagorchestes hirsutus*)) are living testaments to the potential of the international zoo community's response to the needs of species under the imminent threat of extinction. Successful reintroduction of captive born individuals back into the wild to re-establish natural free-ranging populations of golden lion tamarins (*Leontopithecus rosalia)*, black-footed ferrets, Przewalski horses (*Equus caballus przewalskii)*, chuditchs (*Dasyurus geoffroyii*), and greater bilbies (*Macrotis lagotis*) are also testaments to the direct role of zoos in conservation. All of these programs and more reflect the implementation of successful population management programs.

The World Zoo and Aquarium Conservation Strategy developed by the World Association of Zoos and Aquariums (WAZA 2005) recognizes this need and calls for increased attention and implementation of animal management at the population level and the need to establish truly viable populations. This is both a biological and organizational challenge.

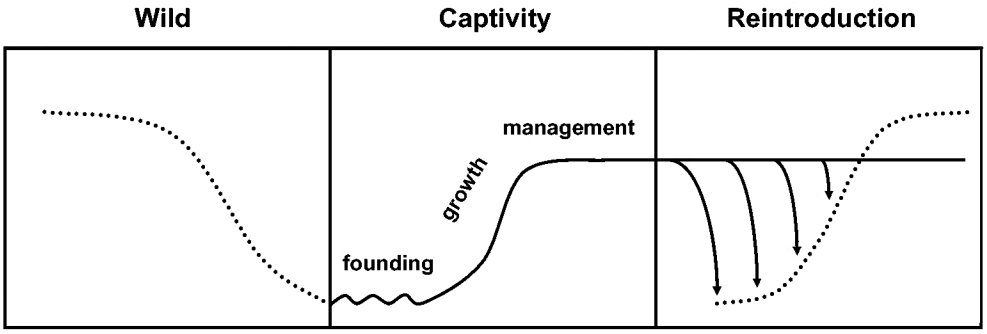

Figure 1. A hypothetical history of the events in a captive population.

Some of the biological challenges are illustrated in Figure 1, which shows a hypothetical, but not atypical, history of a population rescued by captive breeding. The original wild population may have declined for any number of reasons – habitat loss, competition with invasive species, disease, etc. Some or all of the few remaining wild-born individuals may be captured to establish the captive breeding program in the founding phase. If these founders are the last remaining individuals of the species, they represent the total genetic future of their species (e.g., black-footed ferrets). Unfortunately, captive breeding programs are often initiated with few founders, compromising the genetic health of the program from the start. Basic husbandry knowledge may be lacking, so the population initially remains small, further compromising the genetic health of the population. Lack of reproduction may even cause the population to go extinct (e.g., i'iwi,

apapane, and omau). As knowledge is gained, reproduction becomes more reliable, generating the population's growth phase. Population managers will set a target size for the population based on resources available, the genetic and demographic status of the population and the captive breeding needs of similar species competing for limited captive resources. The population will be maintained during the management phase at zero population growth to establish a stable population. And for certain populations, reintroduction of individuals back into the wild may be an option (Chapter XX by Earnhart).

The overall demographic goal for captive populations is, as rapidly as possible, to increase the population to a sufficient size to avoid extinction due to accidental or chance events, and then to maintain that population with an age and sex structure that promotes reliable reproduction when needed (and possible surplus reproduction for a reintroduction program). The demographic challenges here are to maintain stable populations that neither overshoot the capacity available, nor leave zoos with empty exhibits.

The genetic goal for these populations is to retain the founders' genetic diversity, as unchanged as possible over time, so that the population can serve as a genetic reservoir for the species (from which genetic diversity may be reintroduced back into the wild). Achieving this goal means confronting the challenges of loss of genetic diversity, inbreeding and inbreeding depression, and adaptation to captivity (Frankham et al. 2002; Bryant and Reed 1999). Management strategies attempt, as much as possible, to retain every aspect of the genetic diversity of the founders over time: essentially stopping evolution in the captive population.

There are organizational challenges 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 regional zoo associations and programs to organize and coordinate cooperative population management efforts, e.g., Species Survival Plan (SSP) of the Association of Zoos and Aquariums (AZA, based in the US and Canada); European Endangered species Programme (EEP) of the European Association of Zoos and Aquaria (EAZA); and the Australasian Species Management Program (ASMP) of the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA) (Hutchins and Wiese 1991; Shoemaker and Flesness 1991). However, plans based on the science of population management do not always coincide with desires of individual institutions. More zoos may want to breed than is needed for zero population growth during the management phase. Ideal genetic management recommendations to transfer a particular animal to another zoo may conflict with the holding zoo's desire to keep that individual. Managers of captive breeding populations are continually struggling to balance the science with institutional wishes.

This chapter does not address the sometimes competing needs of population management vs. institutional wishes. Rather it presents and outlines the basic principles, concepts, and techniques that are involved in managing captive populations, concentrating on those aspects critical to the long-term maintenance of genetic diversity and demographic security (Ballou and Foose 1994). The chapter begins with the basic data needed for the basis of a management plan and is followed by a description of defining the overall purpose and goals of the captive population. The demographic and genetic characteristics that are used to define the current status of a population are presented. This is followed a description of the basic management strategies that

are applied to population management and a description of the more detailed analyses that form the basis of the individual-by-individual animal recommendations – the heart of any population management plan. We end by addressing particularly difficult issues (how to proceed when data are poor and how to manage groups of individuals where individual identity is not known).

3 The Value of Population Management

Managing captive populations is time consuming (maintaining the data, making recommendations), costly (shipping animals), and sometimes risky (disease transfer between institutions, stress on animals). However, its benefits are clear. These include:

Increasing value to conservation
Intensive management can help populations to retain the genetic characteristics of wild counterparts. This increases their value as genetic reservoirs for use in reintroduction, should this be needed.

Ensuring the availability of captive animals
Many captive populations that were once large and well distributed have subsequently crashed, particularly populations of small mammals and birds (Amori and Gippoliti 2003; Figure 2). Although there are many reasons why populations crash, many do so because individual collections are not managed as an integrated population. The result is not having specimens available when desired. For example, when the giraffe (Giraffa camelopardalis) SSP was changed to a Population Management Plan (PMP) in 2004, recommendations became voluntary rather than mandatory (PMP recommendations are voluntary, as opposed to recommendations made in a SSP). Over the next two years 35 giraffes, representing over half of the giraffes shipped in North America, were transferred out of the AZA population. This resulted in a waiting list of 17 institutions wanting roughly 50 giraffes; an additional six institutions wishing to build and stock new giraffe exhibits found few available.

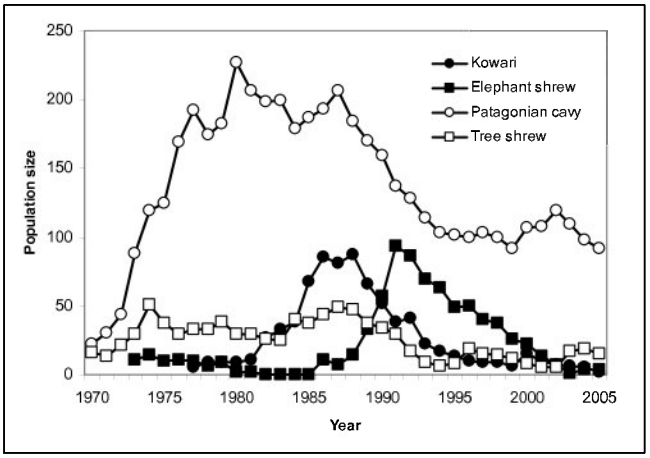

*Figure 2. Captive population crashes and declines in four small mammal species: kowari (*Dasyuroides byrnei*), elephant shrew (*Macroscelides proboscideus*), Patagonian cavy, (*Dolichotis patagonum*), and tree shrew (*Tupaia glis*).*

3.1 Improving animal welfare

Population management attempts to avoid production of inbred animals, as inbred animals often suffer from a vast assortment of ailments. These include: reduced longevity, inanition (failure to thrive), metabolic diseases, morphological deformities, abnormal birth weights and growth, organ (eye, brain, spleen, adrenal gland, thyroid) malformations, impaired reproductive traits, modified temperament, immune diseases, reduced temperature tolerances, and increased susceptibility to stress (Wright 1977; Frankham et al. 2002). In theory, any trait partially or wholly determined by genetics is a candidate for being degraded by inbreeding (see below). Though considerations of animal welfare alone should be sufficient to encourage inbreeding avoidance, there is also the increased cost of treating such a variety of ailments. For example, Willis (pers. comm..) found that inbred prairie chickens (Tympanuchus cupido attwateri), at the Minnesota Zoo received veterinary attention significantly more often than non-inbred chickens.

3.2 Verifying taxonomic origin

Because captive breeding plans require effort in ensuring accurate studbook data, working within a population management plan increases the chances that zoos actually receive what they ask for. When the giraffe SSP program was initiated in the early 1990s, a studbook was compiled and for the first time a complete pedigree was available. Many curators were unpleasantly surprised to discover that about 30% of living giraffes were subspecific hybrids or had minimally traceable pedigrees. Furthermore, between 1979 and 2000, 27 giraffes were purchased by Japanese zoos from US zoos. Having assumed these were reticulated giraffe (G.c. reticulata), they were surprised when on consulting the studbook after the animals had already been shipped, that 13 of them were subspecific hybrids and therefore useless to their breeding programs. Not examining the studbook cost these zoos up to $50,000 for each giraffe.

3.3 Managing zoo space efficiently

Population management is not only for species that we want to maintain over the long term, but also can be used to control populations of common species that compete for space with more endangered species. Examples among AZA populations include limiting population growth in plains zebra (Equus burchellii quagga) and warthog (Phacochoerus africanus) to increase available space for Grevy's zebra (E. grevyi) and Red River hog (Potamochoerus porcus), respectively.

3.4 Buffering against unexpected changes in regulations

Unexpected and unplanned-for regulations that limit imports can result in populations becoming closed, and, unless managed, vulnerable to extinction. For example, Australia suspended all artiodactyl imports in 2001 due to disease concerns, which so far has resulted in demographic extinction of the Australian populations of greater kudu (Tragelaphus strepsiceros), sable (Hippotragus niger) and collared peccaries (Pecari tajacu), with other species in decline. Likewise, unmanaged bird populations will probably not be sustainable if avian flu concerns prevent importation from affected regions. Only demographically robust, cooperatively managed populations are likely to survive these restrictions. Similar effects on native taxa can result from

changes in policy/attitude towards wild collection or retention in captivity of injured wildlife. Zoos need to be able to weather these shifts in policies and regulations.

3.5 Reducing collection from the wild and shipping costs

Programs are designed to reduce the frequency and distance of shipping and/or to reduce the rate of wild collection. This saves time and costs of collecting trips, permit applications and international transaction arrangements.

4 Data for Population Management

The most important task in the development of a captive breeding 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, sex, parentage, and birth and death dates, as well as information on animal movements between institutions (Shoemaker and Flesness 1996; Glatston 1986). Studbooks serve as excellent data sources because studbook keepers validate and edit data to enhance quality. Currently there are over 1150 regional and 145 international studbooks (ISIS 2007), most of which are available as computerized databases on the ISIS/WAZA Studbook Library CD-ROM distributed annually (ISIS/WAZA 2004).

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 relationships between living animals and estimating important population parameters.

Potential sources of data are:

International Species Information System (ISIS). ISIS is a computerized database containing information on animal identities, birth and death dates, genealogies, and movements (Flesness 2003; ISIS 2007). ISIS collects data from over 700 institutions from 70+ countries worldwide and is the best starting point for compiling population data if no studbook is available. ISIS is currently developing a single web-based global Zoological Information Management System (ZIMS 2007; ISIS 2007; Cohn 2006). This will provide, for the first time, a single unbroken record of an animal's significant events throughout its life. ZIMS will be replacing the current ISIS animal record keeping software currently being used by most zoos worldwide (ARKS, SPARKS, MedARKS).

International Zoo Yearbook (IZY). IZY, published yearly by the Zoological Society of London, provides an annual list of birds, mammals, reptiles, amphibians, and fishes bred in captivity from 1961 until 1998. Although only numbers and locations are presented, these annual listings are useful for identifying institutions that once held specimens of a particular taxon.

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.

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

- Individual identification: a simple numeric lifetime identity (e.g., studbook number). To achieve this identification, it may be necessary to link a series of different local institutional ID numbers assigned to an animal as it has moved among institutions
- Sex
- Birth date and location
- Death date and location (it is vital to record stillbirths and aborted fetuses)
- Parentage
- Rearing type
- If an individual is wild-caught:
- Date and site of capture
- Estimate age at time of capture
- Possible relationship to other wild-caught animals (e.g., several animals captured from a nest or herd)
- Date and institution when animal entered captivity
- Date animal left captivity or was lost to follow-up (e.g., reintroduced into the wild, escaped, sent to an animal dealer and no longer tracked)
- Institutions where it has been, with dates of transfers and the local ID at each institution
- Information on circumstances and cause of death
- Reproductive condition (e.g., castrated male, post-reproductive female with relevant dates)
- Group compositions (which animals are housed together and during what time period)

- 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 University of Kansas Museum. #12345")
- Miscellaneous comments (e.g., unusual behavior or phenotype) that might affect its reproduction, social behavior and husbandry

Missing and incomplete information is a characteristic of any kind of data, and animal records data are no different:

1) When dealing with unknown or missing data, as much information should be recorded as possible. However, data should never be invented to fill in missing or incomplete information.

2) Uncertain parentage is a common problem, particularly in herd situations. All potential parents should be recorded with, if possible, their likelihood of being the parent (e.g., based on behavioral data).

3) Records must correctly reflect the extent of uncertainty in an animal's history. While assumptions often need to be made when analyzing a population in preparation for making management recommendations, the practice is to create an "analytical" version of the studbook where documented assumptions replace missing or unknown data. These assumptions, however, should never be transferred to the official "true" studbook.

4) The fundamental data needed for demographic analysis are birth dates, death dates and dates of reproduction. Uncertainty of any of these events, especially birth dates and death dates, can have significant effects on the demographic analyses. Any individual with unknown dates (especially unknown birth dates) are generally excluded from analyses (while some software allows them to be included but in proportion to rates from known-aged animals). Informed estimates should be recorded wherever possible.

5) The fundamental information needed for genetic analyses is parentage. The complete set of parentage information for a population constitutes the population's pedigree. Captive pedigrees are plagued with unknown or missing parentage. Pedigrees with many unknowns (more than 15% is a rough threshold) can make pedigree analyses useless. Significant efforts go into trying to resolve unknown parentages or making assumptions so that genetic analyses can be completed; these strategies are discussed in their own section below.

Most analyses require that the data be computerized for easy access and manipulation. Standard formats for pedigree data have been developed (Shoemaker and Flesness 1996), and a number of

computerized studbook management and analysis software packages are currently available, or soon will be, including the Single Population Analysis and Record Keeping System (SPARKS: ISIS 2004a), PopLink (Faust et al. 2006a) and ZIMS (ZIMS 2007) (see Appendix A for more details).

5 Maintaining Viable Populations: Demography

The purpose of demographic management depends on the goals of the population. While for most populations of conservation concern, the goal is to establish a stable population of sufficient size to mitigate risks of extinction, for other populations the goal might be to reduce the population to extinction at a managed and predictable rate. The major demographic risks that populations face are small population dynamics, unstable age structures, and unreliable reproduction.

5.1 Small population dynamics

Small populations are more vulnerable to extinction than large populations not just because they are smaller, but because synergistic interactions in their dynamics can lead to an "extinction vortex" (Gilpin and Soule 1986; Shaffer 1987; Lande 1988; Vucetich et al. 2000; Lande et al. 2003; Drake and Lodge 2004; Fagan and Holms 2006). One of the main sources of demographic vulnerability for small populations is demographic stochasticity -- the random variation in reproduction, mortality, and offspring sex ratio at the individual level. This variability is magnified when population size is small, resulting in fluctuations in a population's vital rates (mortality and fecundity) and sex ratios (Lande 1998; Lacy 2000a; Lande et al. 2003).

In addition to the effects of demographic stochasticity, small captive populations may become demographically vulnerable because of inbreeding depression, which can decrease survival and reproduction (see below). Although there is no rigid cutoff for when a population becomes susceptible to these types of dynamics, general estimates range from 20 to 100 individuals in the population or in a particular life stage (Goodman 1987; Lande 1988; Lacy 2000a; Morris and Doak 2002; Lande et al. 2003) or an effective population size (see below) of fewer than 100 (Keller and Waller, 2002). For further discussion about the implications of small population dynamics for captive populations, see Faust et al. (in review).

5.2 Unstable age/sex structures

Although there is no strict definition for what makes a population's age structure unstable, there are some situations that can be harbingers of demographic problems, including:

- Large discrepancies in sex ratio of age classes or life history stages (e.g., pairing all reproductive-aged females and males) for monogamous species: these uneven sex ratios may result in difficulty in forming monogamous pairs for breeding or social housing.

- Inappropriate sex ratio for polygynous or group-housed species: if sex ratio at birth is equal but management is in polygynous social groups, the excess individuals of one sex must be managed as single-sex groups or solitary individuals [e.g., gorillas (Gorilla gorilla), elephants (Loxodonta africana and Elephas maximus), and hoofstock species such as wildebeest (Connochaetes), waterbucks (Kobus), and gazelles (Gazella)] and planned for in long-term space requirements. It is often important, however, to manage these excess individuals as potential future breeders in the population rather than export, neuter or otherwise remove them from the breeding pool; in the future, they may become important genetically or demographically and be essential to maintaining population stability. .

- Few individuals in the youngest age classes: as those individuals become reproductively mature, there may not be enough individuals to form breeding pairs to sustain the population.

- Too few individuals in the reproductive age classes: this leads to relatively few births, which decreases population size; this factor should be taken into consideration in harvesting animals from captive populations for release.

- Large numbers of individuals in the oldest age classes; if these individuals are close to the maximum longevity of the species, managers may want to anticipate their deaths in the near future and the resulting need to fill empty exhibit spaces.

Managers can detect many of these problems using demographic models that project future population growth (see below).

5.3 Unreliable reproduction

Understanding the reproductive biology of captive species and the husbandry necessary to reliably produce offspring when desired is essential to good population management. When populations are in their initial growth phase, it is important that reproduction be spread across participating institutions rather than focused at a few institutions to mitigate the risk of wiping out a population's breeding potential if an essential institution experiences a random catastrophe (e.g., disease, natural disaster). When a population reaches the phase when it needs to be maintained at a certain size, the number of allowable breedings will be severely limited. For example, in a tiger population at capacity, a zoo might get only one breeding recommendation in 12-15 years; this interval may mean that no staff at that zoo have relevant breeding management experience. Managers need to think creatively about sharing the collective experiences of those working in the wider managed program to ensure valuable husbandry information is disseminated. Many captive breeding programs have husbandry manuals (and/or other management protocols). Example: The Tiger SSP published a husbandry manual in 1994, which includes not only husbandry, veterinary care, etc. but also details on how to introduce (breed) and raise tigers. This manual has been translated into 5 languages (Russian, Chinese, Thai, Vietnamese and Indonesian) and distributed among zoos in all tiger range countries.

In addition, managers may need to be careful about ensuring that individual females remain viable, especially if breeding is being delayed because the population is being maintained at zero population growth. There are suggestions that in several species females may require a breeding early in their reproductive lifespan to remain viable breeders in the future [(e.g., elephants and rhinos (Rhinoceros, Ceratotherium, Dicerorhinus, Diceros), Hermes et al. 2004, Hildebrandt et al. 2006; Australian dasyurids such as Tasmanian devils (Sarcophilus harrisii), (C. Lees, pers comm.); lions (Panthera leo) (B. Wiese, pers. comm.)]. Although it is not clear whether such examples are exceptions or the rule, individual program managers and scientific advisors should carefully consider whether species may be susceptible to such an effect. Managers should also be careful that if contraceptives are used to limit reproduction, that females can be reliably returned to reproduction once contraceptives are removed; the North American population of Goeldi's monkey (Callimico goeldii) experienced a serious demographic crash that threatened long-term viability when contraception, believed to be reversible, permanently sterilized females.

6 Maintaining Viable Populations: Genetics

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 (Figure 1) 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 (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 environmental change. Furthermore, a large number of studies 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; Frankham 1995a; Saccheri et al. 1998; Vrijenhoek 1994). In addition, most studies on the effects of inbreeding, in both captive and wild populations, have documented deleterious effects (Ralls et al. 1979; Ralls et al. 1988; Lacy 1997; Keller and Waller 2002; Crnokrak and Roff 1999). 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.

6.1 What is genetic diversity?

Genetic diversity comes in many forms. It can be haploid (DNA of the mitochondria), diploid, or even polyploid. Genetic traits can be based on the alleles at a single locus or many dozens of loci. Not surprisingly then, there are several different terms and different types of genetic variation (refer to Frankham et al. 2002 for more details). Two common terms are 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 loci that are heterozygous in a population or individual (Frankham et al. 2002). A heterozygous locus is one in which the two alleles (one inherited from the dam, the other from the sire) are different (e.g., Aa as opposed to AA or aa). When the alleles are the same, the locus is said to be homozygous. Genetic diversity can be measured in both individuals and populations. Both allelic diversity and heterozygosity

are desirable. Allelic diversity is important for a population's long-term ability to adapt, while heterozygosity is important for more immediate individual health (Allendorf 1986).

Both allelic diversity and heterozygosity are lost in small populations (populations with individuals numbering fewer than a few hundreds) through the process of genetic drift. Alleles are passed randomly from parents to offspring (each parent has a 50% chance of contributing either of its alleles at each locus to an offspring) and thus the alleles the offspring receive across all loci 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 sampling process, are termed genetic drift.

Another term, quantitative variation, refers to those traits of high concern that are related to the overall fitness of individuals (e.g., reproductive success and survival rates, litter size). Rather than being determined by a single locus, these traits involve many loci. Quantitative traits vary among individuals due to genetic differences and environmental differences. The most important genetic component of the variation in quantitative traits is called additive genetic variation (Frankham et al. 2002). However it is difficult to determine how much of the differences observed in a quantitative trait are due to additive genetic variation vs. environmental without extensive research and experimentation (Frankham et al. 2002). Conveniently, overall heterozygosity and additive quantitative variation are lost at approximately the same rate. Consequently, management strategies based on maintenance of heterozygosity will generally promote the maintenance of additive genetic diversity as well (Lande and Barrowclough 1987).

Genetic traits can also be selectively beneficial, deleterious, or neutral. Thus selection can potentially retard or accelerate loss of genetic diversity. Little is known about the role selection plays in captive populations, although it is undoubtedly important and has been shown to be a significant factor (Frankham and Loebel 1992). Variation can be selective (influenced by selection pressures) or selectively neutral (influenced not by selection pressures but by the random process of genetic drift) (see Lande and Barrowclough 1987; Lacy et al. 1995; for further discussions of this issue).

Genetic management needs to focus on maintaining all these levels of genetic variation – diversity at the single locus as well as diversity for quantitative traits, loci that are under selection and those that are not (but may be in the future). Average heterozygosity appears to be the best single measure of diversity that encompasses most of this variation. It 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). The genetic goals of most captive breeding programs are currently based on maintaining overall levels of average heterozygosity.

The primary threat to the genetic health of a population is the loss of genetic diversity. This is a function of population size (actually effective population size, see below) and time. In general,

the smaller the population, the faster the loss; the longer the period of time, the greater the total loss (Figure 3). Therefore, those developing breeding programs to conserve genetic diversity must consider the questions, "How much genetic diversity is required?" and "How long should it be maintained?" This is discussed in the section on Population Goals below.

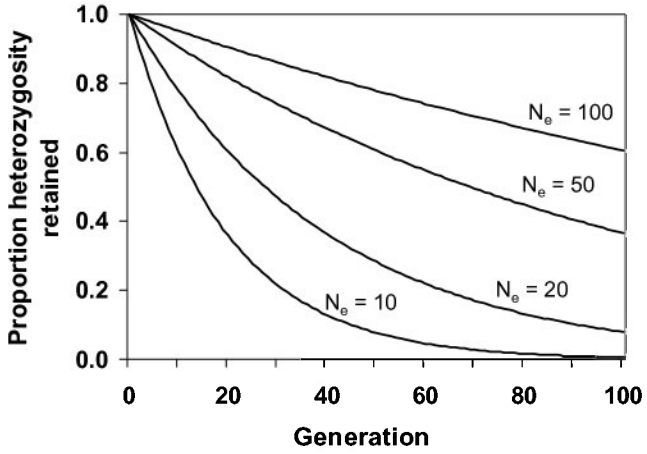

Figure 3. Proportion of original heterozygosity from the source population retained over 100 generations for effective population sizes (N_e) ranging from 10 to 100.

6.2 Measuring genetic diversity

Genetic variation is typically measured by collecting a sample of DNA from an organism (from blood, tissues, hair, feathers, bones, feces, etc.) and, using one of a variety of molecular techniques that are available, measure the frequency of alleles or the frequency of heterozygotes for a set of loci (see Schlötterer 2004 for a comprehensive review of techniques). Common techniques used at the time of publishing include analyzing microsatellites, mitochondrial DNA haplotypes, and even exact sequences of genes.

Most of these techniques have in common the ability to identify genetic differences among individuals and provide information about allele diversity and heterozygosity. Changes in diversity over time can be measured. In an ideal world, molecular techniques could be used to identify the genetic diversity of the founders, and through continuing monitoring of individuals over generations, guide a management program that maximizes retention of all of the founders' genetic diversity.

Unfortunately, molecular analyses that measure the diversity at the individual level across the entire genome do not (yet) exist. Even the most extensive studies are able to sample only several score of loci among the many tens of thousands genes that make up an animal's genome. Managing based on the diversity of only a few loci will not achieve the goal of genome-wide diversity, as it will tend to result in populations with high diversity at the monitored loci, but loss of diversity at all others (Slate et al. 2004; Fernandez et al. 2005).

However, managing genetic diversity at the whole-genome level can be achieved using pedigrees. When pedigrees are known, calculating kinships among individuals and inbreeding coefficients give us genome-wide estimated or average levels of diversity in individuals relative to the source population. Studies show that genetic management based on pedigree estimates of genetic diversity performs better at maintaining genetic diversity than molecular-based methods (e.g., Fernandez et al. 2005). The primary difference between molecular- and pedigree-based methods is that molecular methods provide empirical estimates of absolute or real levels of diversity of only a few loci, while pedigree-based methods provide a statistical measure of average genome-wide diversity but relative to the source population as opposed to absolute levels of diversity. Since an overall goal of management programs is to preserve the genetic diversity of the source population, the pedigree-based method works very well.

7 Defining a Purpose, Goals and Targets for Population Management

One of the most important steps in population management is to define the reasons why a particular species needs a captive breeding program. The goals of captive programs can be described at three levels. At the highest level, the program will have broad, qualitative goals that define the purpose of applying management, such as sustaining a population to meet zoo exhibition needs or generating a sufficient number of animals for release to the wild. These are referred to here as the program's "purpose". At the second level are the population "goals", which translate program purpose into quantifiable genetic and demographic measures that answer the questions "how much" (genetic diversity), "how many" (animals) and "for how long". These are the characteristics of the population that will determine whether or not the program achieves its purpose. At the third level are a series of targets for those program parameters directly influenced by day-to-day or year-by-year program management of individual animals and which, over time, will determine whether population goals are met. These might include targets for maximum level of inbreeding, annual birth rate, effective population size, rate of input of new founders and generation length (all of these are described in detail elsewhere in this chapter). These targets interact closely with each other such that changes in performance of one can often be compensated for by careful management of another. As a result, they are the most dynamic of the three levels.

7.1 Determining a population's purpose

Populations in captivity can serve a number of purposes. Different purposes lead to different management needs, different levels of management intensity and different goals and targets. 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. Similarly, populations primarily managed for zoo display will need less ambitious genetic management, possibly reflecting a need to only manage average inbreeding levels rather than maintain evolutionary potential. On the other hand, a species that is extinct in the wild and exists only in captivity will require long-term intensive genetic and demographic management.

Before a program's purpose can be determined, analyses must be done to examine the potential of the population to serve that purpose. This involves a detailed analysis of the population's current demographic and genetic status. The status will determine whether the population in its current state can meet the proposed purpose and if not, what potential there is for bringing it closer to what is required. For example, a population that currently retains very little gene diversity may not be a useful starting point for a long-term conservation insurance program unless additional founders can be acquired. Similarly, a highly inbred population founded on only four individuals may not be a suitable source of animals for re-stocking a wild area.

ZooRisk (Earnhardt et al. 2005) is a software program that uses the current demographic and genetic structure of a population along with historic fecundity and mortality rates to stochastically model and categorize a population's viability in captivity. This categorization is based on: 1) the population's probability of extinction; 2) the distribution of breeding-age groups (e.g.. determining whether the population's reproductive stock is limited to only a few institutions); 3) current number of breeding-aged animals (ensuring that there are enough potential pairs); 4) reproduction in the last generation (determining whether there is historic breeding success;, and 5) the starting and/or projected level of gene diversity. This multi-faceted approach to evaluating viability helps identify the genetic, demographic, and management factors that may be increasing the risk to the population. This tool is very useful in helping managers evaluate the suitability of a population to meet its intended purpose.

In addition to population characteristics, there are some practical constraints that impact a population's potential to meet its goals. For example, is there sufficient husbandry expertise and adequate cooperation from studbook keepers, program coordinators, and holding institutions to meet a program's proposed purpose? Is there sufficient zoo space available? Consideration must be given to the needs of other taxa competing for similar zoo resources. Frameworks for prioritizing the allocation of zoo space at regional and sometimes global levels have been developed around the world as regional collection plans (this topic is covered in some detail in Chapter XX by Allard).

Based on an analysis of the current status, practical considerations and availability of resources, it may be necessary to modify a program's purpose. Determining a population's purpose may be an iterative process. For example, there simply may not be enough space or husbandry expertise to develop a reintroduction program, and the purpose might change to holding the population in zoos for a longer time period with the hope of acquiring additional founders and gaining husbandry experience.

7.2 Setting genetic goals

Setting genetic goals essentially asks how much for how long and how many. The time scale for management programs will vary. Some species may need only the temporary 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.

For these populations, 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 source population's 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). Although this 90%/200 year rule of thumb is somewhat arbitrary, it does provide a starting point for establishing targets for population size. More recently, targets for population size have been formulated in terms of 100 rather than 200 years, since this results in smaller, more realistic population sizes (Foose et al. 1995). Maintaining 90% of the original heterozygosity for 100 years is the starting point advocated here for populations that are without more specific guiding influences.

Once a genetic goal has been selected, then the number of animals needed to achieve that goal can be calculated (Soulé et al. 1986) using PM2000 (Pollak et al. 2007), given the population's potential growth rate, effective size, current level of gene diversity and generation time. Thus, a genetic goal can be directly translated into a demographic goal to answer the demographic question of how many.

7.3 Setting demographic goals

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 populations – that is, how many and for how long. 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 then 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., 100 years) (Shaffer 1987)? Or, alternatively, for common display species, what rates of supplementation will confer a 95% probability of persistence for a population at or above the size needed to meet regional exhibit needs? In most cases, captive populations large enough to achieve standard genetic goals will also be large enough to insure high survival probability over the time period of concern. ZooRisk can help evaluate if this is true.

7.4 Setting targets

Analysis programs such as PM2000 (Pollak et al. 2007) and ZooRisk (Earnhardt et al. 2005) are used to convert the genetic and demographic goals into specific targets. They are often used to explore what combination of management actions and targets would be needed to ensure that the population meets its goals or, conversely, what goals could be met using the population under consideration, within the range of possible management actions. Typically, the first target set is the target for population size. The Goals module in PM2000 allow managers to determine what population size is needed to reach the genetic goals set earlier. This will depend on the population's generation length, effective population size, current population size, population growth rate, founder supplementation rate and captive carrying capacity – all of which can be influenced directly through management.

Once a specific target population size is set, then a decision can be made about whether the population needs to grow, shrink, (and how fast to grow or shrink) or remain the same size, in order to meet that target. This decision will determine the number of births needed (or the number of animals that need to be removed from the population) to meet the desired growth rate (or to meet zero population growth).

With a realistic set of initial targets for key program parameters established, and population goals and program purpose refined as appropriate, a more detailed management strategy can be drawn up. Program performance should be evaluated regularly against both population goals and parameter targets, and adjustments made as necessary. Through these iterative steps, program management can continue to adapt to population and program needs.

Listed below are a number of scenarios describing programs with different purposes with examples of the kinds of goals and targets that might be established for each (Lees and Wilcken 2002; AZA 2007). Goals and targets need to reflect realistic benchmarks for the specific populations being managed and hence will vary between different programs and regions.

7.5 1. Common display species, species for education and research

Characteristics: Species is not threatened in the wild and is periodically available to zoos through importation, wild collection or rehabilitation centers. Reliable, consistent breeding is established. Populations that exist in zoos for research or education purposes would also fit into this program category, many having relatively short-term goals with little or no need for genetic and demographic management.

Program purpose: To sustain a healthy population able to meet zoo display needs.

Management strategy: Maintain a demographically stable population at the size required without generating unwanted surplus. Minimize inbreeding where possible. Monitor status of supply and intensify management as needed.

Example population goals: Maintain population size at 50 for 25 years.

Example targets: Maintain inbreeding below f = 0.25; maintain breeding rate at approximately 8 births per year for the next 5 years.

7.6 2. Endangered species in captivity for long-term conservation

Characteristics: Captive population that is closed or has few new founders available. Breeding is reliable and consistent.

Program purpose: To maintain a long-term viable population and preserve genetic diversity.

Management strategy: Maximize retention of genetic diversity (using mean kinship values to select optimal pairings) and maintain a demographically stable population compatible with the limits of the captive environment's carrying capacity.

Example of population goals: Focus on maintaining genetic diversity and program duration. Usual goals would be to maintain 90% of wild source heterozygosity for 100 years.

Example targets: Maintain population at 250; produce 30 births next year; raise first age of breeding to 7 years in females to extend generation length; raise N_e/N ratio to 0.4 by increasing ratio of males:females.

7.7 3. Rare species being propagated for immediate release into natural habitats

Characteristics: Management applied from the founder phase. Wild recruitment, if possible, is likely to be limited. Breeding is reliable and consistent.

Program purpose: To sustain a genetically diverse, demographically robust population able to sustain a harvest of animals for release.

Management strategy: Manage reproduction to maximize initial growth and retain founder genetic diversity. At captive capacity, manage reproduction to generate required harvest for release. Retain genetic diversity in both captive and release populations until reintroduction is complete. Minimize inbreeding in release animals. Manage appropriate age structures in both captive and wild populations. Ideally, manage population in a captive environment as similar as possible to the natural environment.

Example population goals: Maintain 95% of wild source heterozygosity for 25 years. Maintain population size at 100 (to allow a harvest of 20 animals per year for release).

Example targets: Maintain breeding rate at 40 births per year; maintain inbreeding at or below f = 0.125.

7.8 4. Species not yet capable of self-sustaining reproduction in captivity

Characteristics: Breeding is not reliable and consistent. Species may be new to captivity or one for which husbandry remains poorly known. . Further recruitment may or may not be possible.

Program purpose: To establish the conditions required to manage a demographically viable and genetically healthy captive population.

Management strategy: Encourage proliferation of individuals breeding well in captivity in order to sustain demographic stability. Focus husbandry research and resources on specimens not breeding well. Once techniques are firmly established, document and wind-down program or manage as one of the other categories.

Example population goals: Focus on sustaining the population at a particular size for a specified period (e.g., sustain population size at 50 animals for 5 years; retain at least 85% genetic diversity).

Example targets: Reduce juvenile mortality to below 20%; maintain breeding rate at approximately 20 births per year; maintain inbreeding at or below 0.125; breed every available female.

Some programs will not fit neatly into any of these categories. Some will span several of the purposes described and for any program, both the purpose and the supporting goals may change over time with shifting circumstance. Despite this, clearly identifying a program's purpose and setting goals and targets to underpin that purpose remain key to successful management.

Evaluating a Population's Demographic Status
As mentioned above, an important part of determining the goals of a captive breeding program is evaluating the genetic and demographic status of the population.

Although zoo and aquarium populations are typically dispersed across institutions, because animals are transferred between these institutions, they meet the basic definition of biological populations. The first step in evaluation a population's status is to assess its current size, structure, and distribution, as well as determining any historical demographic patterns that may be relevant to future population management; all of these analyses are dependent on the data collected in a studbook.

7.9 Population size and distribution

The size of the current population, while seemingly easy to determine using studbook data, is dependent on how the managed population is defined. A captive population may include: 1) all individuals of that species (and/or subspecies) held globally; 2) all individuals held in a region; 3) all individuals at a subset of institutions participating in a regional management program (such as an SSP or EEP); and/or 4) specific specimens from the set of institutions participating in a regional management program (e.g., an individual institution may have some individuals that are

excluded or surplus to the managed population). Also note that in subsequent analyses (see below) specimens are often excluded from the genetic managed population for various reasons, but that these genetically excluded individuals are still regarded as part of the overall population size—they will still be included in the final recommendations as they will take up exhibit space and will need to be appropriately placed for social reasons.

When analyzed, the total population size is also often placed in the context of the amount of space available to the population (the carrying capacity) and/or the target population size set by the management program, for example: "The Okapi SSP population size at the time of analyses was 86 individuals (37.43.0; or 37 males, 43 females and 0 unknown sex) distributed among 24 institutions. The SSP Management Group has set the target population size at 200" (Petric and Long 2006).

7.10 Age and sex structure

Populations have structure – they are composed of individuals that differ in sex, age, birth origin, medical status, and/or other assorted phenotypic or genotypic traits. This underlying structure is important because these traits influence an individual's chance of reproducing or dying in a given year, and therefore the population's overall potential for growth. The most conventional visual representation of a population is an age pyramid, which delineates the number of individuals in each age and sex class (Figure 4). Specific regions of interest in an age pyramid are:

- the base of the pyramid, or the number of individuals in the youngest age classes: these are the surviving offspring from the most recent years of breeding;

- the individuals in the reproductive age classes (e.g., the middle of the pyramid—bounded by the ages at first and last reproduction): these are the individuals being paired for reproduction, and the sex ratio of these individuals (e.g., relative number of males and females) can influence management and the ability to form pairs or breeding groups;

- the individuals at the top of the pyramid: these are the oldest living individuals in the population (but note that they may be younger than the species' maximum longevity); often they are non-breeding individuals that occupy available zoo space until death.

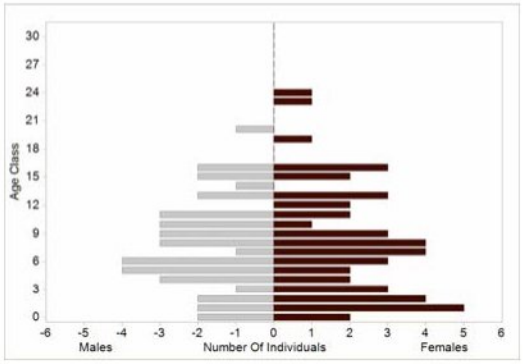

Figure 4. Age pyramid of the Okapi SSP population as of March 2006 (Okapia johnstoni).

Understanding the structure of age pyramids can reveal a good deal about a population's past growth pattern and potential for future growth. Populations that have a strong base of young individuals are usually growing populations (e.g., Figure 5a); these populations will have a strong potential for future reproduction as the youngest individuals advance to the reproductive age classes. Populations that have few individuals in the youngest age classes (e.g., they are top heavy, Figure 5b) are usually declining populations; these populations may experience further difficulty as current breeders age and are replaced by a smaller number of breeders, as there may not be enough individuals to form breeding pairs or sustain the population.

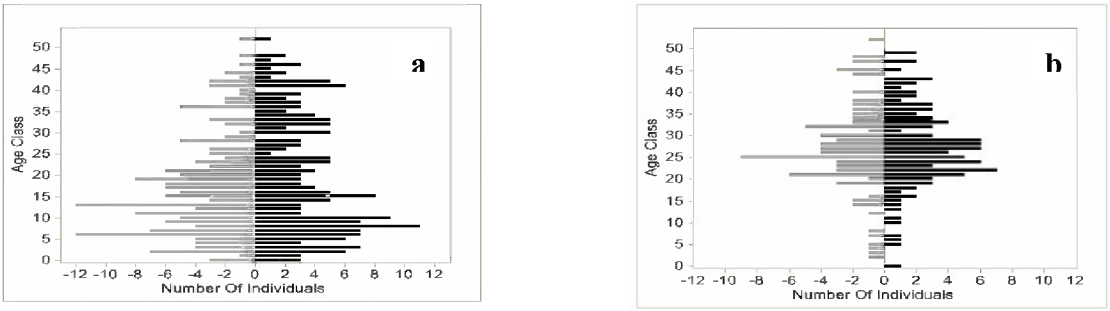

Figure 5. Comparisons of age structures in a growing (left) or declining (right) population.

7.11 Historical demographic patterns

7.11.1 Population Size

Assessment of a population's historical pattern of growth is important in determining its potential for future growth. Most commonly this is done using census graphs of population size over time, often divided by sex (Figure 6a) or origin (Figure 6b).

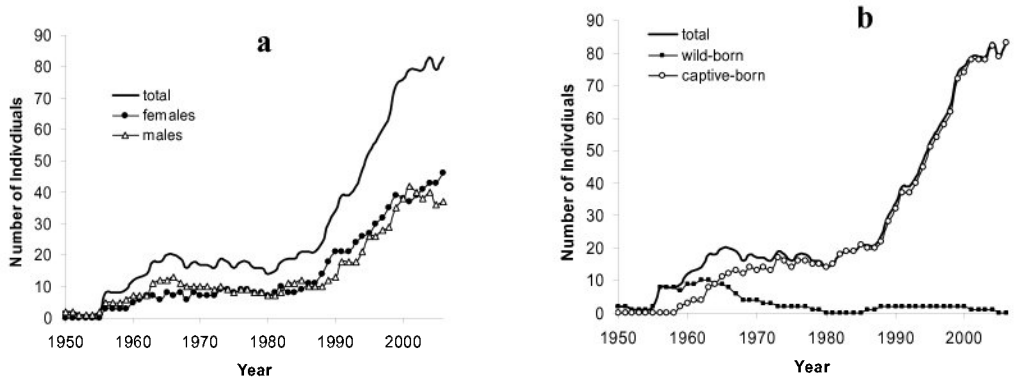

Figure 6. Census of okapi in the SSP by sex (a) and origin (b).

These graphs can show important trends, such as the different phases in a population's growth (Figure 1), the point when captive births began overtaking importation of wild-caught

individuals as a consistent source of population growth (in the mid-1960s for okapis, Figure 6b), or patterns of rapid growth or decline. Explanations should be sought for periods of rapid decline, especially if they took place during a period of population management, as they can pose serious threats to population viability. The demographic data that exist in the studbook can provide some indication of reasons for such declines (see life table section below), but ultimately population managers will have to provide the context of whether the changes were planned or unplanned. If the change was not planned, then managers should attempt to determine whether the changes had a biological cause (limitations in breeding biology or population structure, issues related to health, veterinary care, behavior, husbandry) or were a result of simple lack or failure of management (lack of cooperation, failure to monitor births/deaths/aging structure).

7.11.2 Population Growth Rate

Rates of change in population size, which are called growth rates regardless of whether the population is increasing or decreasing, are typically expressed as a function of time (e.g., percent per year). There are two avenues of change in population size: intrinsic, which arise from births and deaths, and extrinsic, which arise from immigration (or importation) and emigration (or exportation). From one year to the next, change in population size is determined by the formula

$$N_{t+1} = N_t + (B - D) + (I - E) \qquad \text{Equation (1)}$$

where N = population size at time t or t+1, B = births, D = deaths, I = immigration, and E = emigration. For most captive populations immigration and emigration are typically low because of the logistical, financial, and ethical considerations of bringing wild individuals into captivity and/or transporting exotic species across international borders. However, importations are important when a captive population is being initiated, and after a population is established they can still be an important strategy for improving genetic health (by bringing new founders into a population) or demographic stability (by adjusting sex ratios, bringing in individuals of breeding age, etc.) For the most part, however, managers of captive populations are primarily focused on the intrinsic properties of population growth.

Using a population's size over time, managers can calculate a historic average growth rate, or rate of change, symbolized by λ (lambda). When $\lambda > 1.00$, the population is increasing; when $\lambda < 1.00$, population is decreasing, and when $\lambda = 1.00$, the population is stationary. The difference between the value of lambda and 1.00 indicates the magnitude or annual rate of change: $\lambda = 1.04$ denotes a population increasing at 4% annually while $\lambda = .94$ indicates an annual decline of 6%. λ for an individual year is calculated as

$$\lambda_t = \frac{N_t}{N_{t-1}} \qquad \text{Equation (2)}$$

An average λ for a series of years is calculated as the geometric mean of each year's λ (Case 2000). Annual and average λs can be found in the census reports of SPARKS (ISIS 2004) and

PopLink (Faust et al. 2006a). For example, the Okapi SSP female population experienced an observed average growth rate of 1.072 (7.2% increase) over the period 1981-2006 (Figure 6a).

7.11.3 Life Tables

Although the most general way to categorize a population's demography is to look at population-level rates of birth and death, in reality population growth is determined by how age-specific patterns in those rates interact with the population's structure. For many species, males and females have different age-related patterns of reproduction and mortality. These differences are conveniently summarized in a life table (Caughley 1977; Ebert 1999). Table 1 is a life table for the AZA SSP population of female okapi (Petric and Long 2006).

Table 1. Life table for female okapi in the AZA SSP based on a demographic filter of data between 1/1/1981 – 29/2/2006 and restricted to individuals at institutions in the SSP. See Appendix B for definitions of life table parameters.

Age (x)	Q_x	P_x	l_x	M_x	V_x	E_x	*Risk* (Q_x)	*Risk* (M_x)
0	0.110	0.890	1.000	0.000	1.058	16.336	66.200	59.300
1	0.020	0.980	0.890	0.000	1.200	16.448	55.600	55.600
2	0.020	0.980	0.872	0.035	1.295	15.763	50.400	49.500
3	0.020	0.980	0.855	0.093	1.360	15.065	45.700	45.700
4	0.020	0.980	0.838	0.128	1.367	14.352	44.300	43.700
5	0.020	0.980	0.821	0.143	1.338	13.624	41.700	41.700
6	0.020	0.980	0.804	0.150	1.290	12.882	41.600	41.300
7	0.022	0.978	0.788	0.150	1.231	12.140	38.300	37.300
8	0.027	0.973	0.771	0.153	1.173	11.425	34.600	34.600
9	0.032	0.968	0.749	0.158	1.112	10.747	29.900	29.400
10	0.038	0.963	0.725	0.160	1.046	10.100	27.300	26.300
11	0.040	0.960	0.698	0.160	0.975	9.467	25.400	24.500
12	0.040	0.960	0.670	0.160	0.898	8.819	23.400	22.900
13	0.058	0.943	0.643	0.165	0.820	8.219	18.600	18.600
14	0.093	0.908	0.606	0.175	0.748	7.800	18.000	17.900
15	0.110	0.890	0.550	0.180	0.674	7.562	14.900	14.000
16	0.110	0.890	0.490	0.180	0.587	7.373	10.100	10.100
17	0.110	0.890	0.436	0.180	0.484	7.161	9.000	8.500
18	0.113	0.888	0.388	0.180	0.362	6.931	8.000	8.000
19	0.138	0.863	0.344	0.150	0.219	6.773	8.200	8.200
20	0.180	0.820	0.297	0.075	0.087	6.849	7.000	6.000
21	0.150	0.850	0.243	0.015	0.015	7.018	5.000	4.400
22	0.050	0.950	0.207	0.000	0.000	6.717	4.600	4.600
23	0.000	1.000	0.197	0.000	0.000	5.867	4.500	4.500
24	0.000	1.000	0.197	0.000	0.000	4.867	3.400	2.900
25	0.000	1.000	0.197	0.000	0.000	3.867	2.000	2.000
26	0.000	1.000	0.197	0.000	0.000	2.867	2.000	2.000
27	0.125	0.875	0.197	0.000	0.000	1.992	2.000	1.400

28	0.500	0.500	0.172	0.000	0.000	1.417	1.000	1.000
29	0.875	0.125	0.086	0.000	0.000	1.111	1.000	0.600
30	1.000	0.000	0.011	0.000	0.000	1.000	0.000	0.000
31	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

r = 0.0559
λ = 1.0575
T = 9.34
N = 43.50
N (at 20 yrs) = 132.99

A life table displays the vital rates (mortality, Qx; fecundity, Mx; and related rates) for each age class; male and female rates are usually tabulated separately. Vital rates are calculated based on age-specific tallies of birth and death events and the number of individuals at risk for those events using data from a studbook. Studbook data are generally limited to a defined subset of data using a date span and a geographic/institutional filter. Although the specific parameters and calculations used to create life tables for captive populations vary somewhat between software programs (SPARKS, PM2000, ZooRisk, PopLink), the basic concepts are applicable across all software.

Although life tables may display a sometimes overwhelming amount of data, population managers can focus on specific spots for key information about their population's demography (Table 1):

- Age-specific patterns of fecundity (M_x) can indicate the reproductive lifespan (e.g., those years with non-zero M_x rates, or ages 2-21 for okapi)

- Patterns in M_x can also indicate the period of peak reproduction (those years with the highest fecundity rates, roughly ages 8-19 for okapi).

- Age-specific patterns of mortality (Q_x) should be examined for the rate of infant (first-year) mortality (0.11, or 11%, for okapi females) and any other unusual age-specific spikes in mortality

- When the age-specific mortality rates reach 1.0 or $l_x = 0$, that is generally the maximum observed longevity for the population (30 for female okapis).

- Age-specific patterns of survivorship (l_x) can indicate the median survivorship (the age where $l_x = 0.5$), also called the median life expectancy; half of the individuals in the dataset died before this age and half of the individuals survived longer (between 15 and 16 for okapi females).

- The Risk columns indicate the sample size upon which the vital rate calculations are based. In general, if a particular age class has fewer than 30 individuals at risk of events

(death or reproduction), the vital rates calculated for that age class should be viewed with caution. This occurs after age class nine for okapi female vital rates.

Evidence of reproductive failure and high mortality rates should be investigated immediately. In addition to medical, nutritional, physiological, and behavioral causes, potential genetic causes (inbreeding and outbreeding depression) should be examined.

These patterns can also frequently be determined by viewing graphs of age-specific vital rates (e.g., Figure 7). Note, however, that when curves include jagged peaks and valleys between vital rates (as in the variable mortality rates for female okapis after age class 12), it can indicate potential sampling error due to small sample size. More details on reproductive patterns can be found in the reproductive reports of SPARKS and PopLink; more details on analyzing and interpreting survival data can be found in the SPARKS Ages report and PopLink Survival Tool.

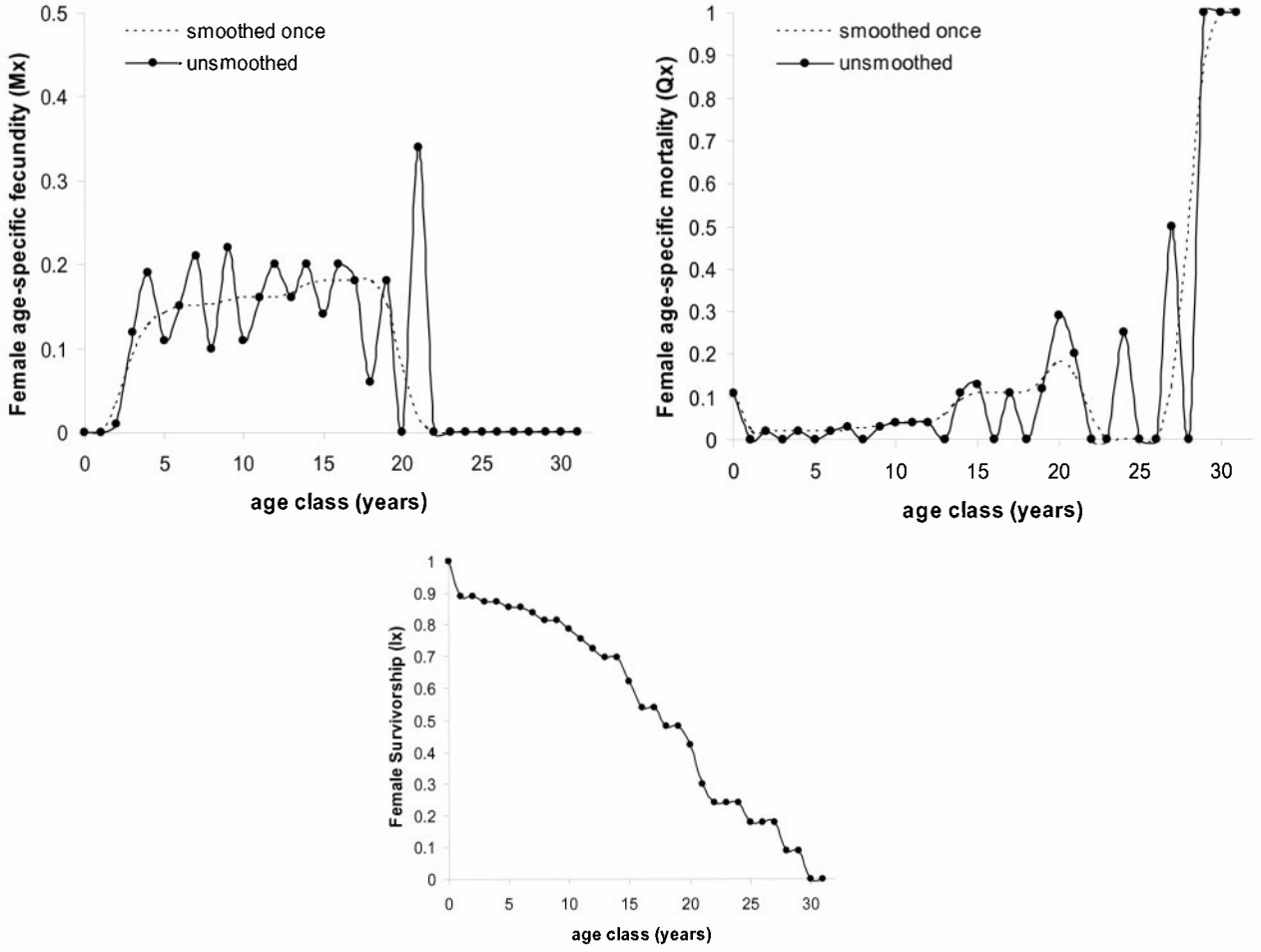

Figure 7. Age-specific fecundity (a), mortality (b), and survivorship (c) rates for female okapis in the AZA SSP population based on a demographic filter of data between 1/1/1981 – 29/2/2006 and restricted to individuals at institutions in the SSP. Note the different scale on (a) and (b).

Life tables are derived from historical data but are used to project future population trends (see below); because of this, it is important that the life table is representative of the population's true capacity for reproduction and mortality. The general strategy for defining the filter used to extract these data is to limit the life table to the period of modern management – those years in which a managed program has been in place (e.g., for many AZA populations, from the 1980s to the present) or when modern husbandry was established for the species. A common starting point is when intrinsic growth of the historic population (e.g., growth fueled by births rather than importations) becomes strong. However, several additional items should be considered when setting a filter, as life table vital rates are influenced by:

- **The amount of studbook data used to create the life table**: In some populations there may not be enough recent data to construct a reliable life table, or there may be specific age classes in which sample sizes are not sufficient to calculate reliable vital rates. The cutoff of 30 individuals in a given age class is a somewhat arbitrary definition but is based partially on statistical conventions of small sample sizes (Lee 1980). More recently, attempts have been made to quantify data quality for data used in mortality analyses; these data quality routines can be found in the Survival Analysis Tool in PopLink.

- **The husbandry practices within the demographic filte**r: As captive managers' understanding of each species' nutritional, behavioral, reproductive, and medical needs evolves, the species' vital rates are likely to change. For example, when a population is being established in captivity and breeding is sporadic, fecundity rates will be very low; if nutrition or husbandry have not been fully perfected, mortality rates may be higher. Certain aspects of the life table are likely to be more susceptible to these changes, including infant survival (e.g., for species with changing philosophies on hand-rearing), maximum longevity (as veterinary knowledge and nutrition practices improve), and fecundity rates (as husbandry knowledge of breeding biology increases). Also, if sample sizes are already small, care should be taken that husbandry practices at an individual institution do not overly affect life table values (e.g., only a single institution has successfully bred but fecundity rates look high because of small sample sizes, or a catastrophe at a single institution inflates mortality rates).

- **Which individuals are considered at risk for events**: Life table fecundity calculations in current software consider all females "at risk" for reproduction, regardless of whether they are physically separated from males or contracepted to prevent breeding. Fecundity data are therefore highly impacted by whether the demographic filter reflects a time frame where breeding was actively pursued vs. being limited to a few individuals or institutions. Because of this, fecundity data are generally underestimates of a population's true biological potential to breed (e.g., what reproductive rates could be if all individuals were in breeding situations). When fecundity rates are low or 0, especially for the oldest age classes (for example, 22-30 in female okapis), one cannot determine from the life table whether these rates are due to reproductive senescence (e.g., they are biologically unable to breed) or lack of access to mates. In the future, better recording of reproductive data (e.g., tracking an individual's opportunities to breed) should enable calculation of more accurate at risk values and more appropriate fecundity rates.

- **The particular life history of the species**: In general, it is more difficult to create accurate life tables for long-lived species because data accrue more slowly in such populations. Long-lived species will often have small sample sizes, especially in the oldest age classes, which can make it challenging to accurately assess maximum longevity and other parameters of the survival curve.

Fecundity and mortality data need to be interpreted in the context of these issues.

In situations where data quality is very poor or the life table is not considered representative of the species' life history, population biologists may simply use the data as is or may: 1) expand the demographic and/or geographic filter (include additional years or additional institutions/regions), or use another region's studbook to include more data in the analyses; 2) use different filters for mortality calculations and fecundity calculations (this may be appropriate if reproduction in a population is concentrated in a short window but mortality-related management practices have been stable for a wider time frame); 3) smooth mortality and fecundity data to remove some of the variability; 4) adjust data based on basic life history data on the species (e.g., ages of first and last reproduction, litter size, maximum longevity); and/or 5) utilize data from a closely related species or taxon (and/or a species that may be distantly related but might be expected to have similar demographic rates), which may be accessed on the WAZA/ISIS Studbook Library (ISIS/WAZA 2004)

7.12 Summary parameters calculated from the life table

The age-specific vital rates in a life table can also be summarized into parameters that can be used to describe the population's demographic characteristics over the historic period covered in the life table:

7.12.1 Population Growth Rate (λ, r)

Earlier we described λ as a parameter calculated from observed population sizes; life tables can also provide estimates of the expected growth rate of the population. The λ calculated from life table vital rates is the value of λ that solves the Euler equation:

$$1 = \Sigma \lambda^{-x} l_x M_x \qquad \text{Equation (3)}$$

where the summation is over all age classes in the life table (Caughley 1977; Ebert 1999). λ is calculated separately for each sex; if a population level λ is reported it is generally the average of the male and female rates.

The intrinsic rate of natural increase (r) is an analogous growth rate calculated from the life table, except that r is centered around 0.00 rather than 1.00 (e.g., $r < 0.0$ describes a declining population, $r > 0.0$ describes an increasing one). λ and r can be derived from each other as:

$$\lambda = e^{r} \quad \text{or} \quad r = \ln(\lambda) \qquad \text{Equation (4)}$$

Growth rates calculated from the life table are based on the assumption that estimated survival and fecundity rates remain stable over time and that the population is at stable age distribution (Caughley 1977).

Since λ can be calculated in two different ways (from observed changes in N and from the life table), a population may therefore have two values of λ for the same time period. For example, the observed historic λ for okapi females from 1981-2006 was 1.072, while the calculated λ from the life table for the same period was 1.0575 (Table 1). Differences between the two rates can arise if demographic characteristics of the population have been changing, if imports and exports have contributed to changes in population size, or if the population structure is very different from stable age distribution.

7.12.2 Generation Length (T)

Generation length is the average age at which all parents produce young. Generation length is not the age at which animals begin to reproduce. It can be calculated directly from estimates of survival and fecundity rates in the life table (Caughley 1977; Ebert 1999; Case 2000). T is calculated for each sex separately; if T is reported for an entire population it is generally the average of the male and female generation lengths. Generation length is important in captive management because it determines the rate at which genetic diversity is lost; a longer T results in a slower loss over time.

7.12.3 Stable Age Distribution (SAD)

The stable age distribution is the eventual sex and age structure the population would reach if the survival and fecundity rates in the life table remained constant over time (Caughley 1977). If a population were at its SAD, the population and each age class within the population would grow at the same rate each year. Although the SAD is a useful theoretical concept, in reality most captive (and likely many wild) populations are not necessarily at or near their SAD. A population's deviation from SAD can arise by stochastic fluctuations in the number of offspring produced from year to year, in survival rates, in importation and exportation events where groups of individuals are brought in or transferred out, or by other chance events. If a population is not near its SAD, its growth may deviate greatly from the λ calculated from the life table.

Definitions for demographic terms are provided in Appendix B.

8 Evaluating a Population's Genetic Status

The genetic history of a population can be represented as diagrammed in Figure 8. Any population can be traced back to some number of founding individuals. These may be wild-

caught individuals derived from a specific wild population or several different wild populations. Some of them may be individuals whose parentage cannot be traced back any further, but that are very likely to be unrelated to each other. Either way, these original founding individuals are assumed to be a sample of a Source or Base population, and the goal is to preserve, to the best extent possible, the genetic composition of the Source population over time by preserving the genetic diversity of the founders.

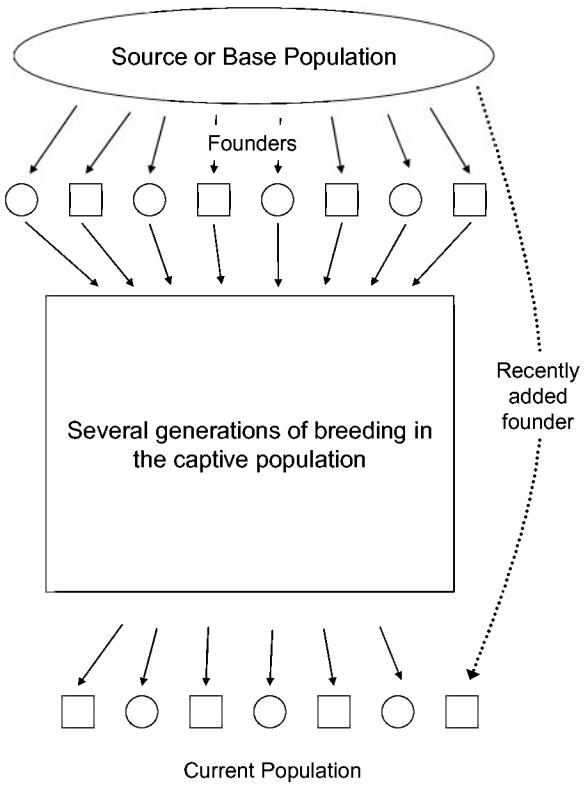

Figure 8. Diagram of the genetic events over time in a hypothetical captive population.

There may be several generations of breeding between the founding event and the current living population. The genetic characteristics of the current population can then be described in terms of:

- How many founding individuals have contributed genes to the current population (some lineages may have died out)?
- How much of each founder's genome has survived to the current population?
- What proportion of the gene pool of the Source or Base population has been retained in the current population?

The following sections present the concepts needed to answer these questions.

8.1 Founders

A founder is an animal who has no known ancestors either in the wild or in captivity at the time it entered the population and and who has descendents in the living population. As such, wild-caught animals are usually founders if they reproduce (and their parents are unknown wild individuals). Wild-caught animals that have not reproduced are not (yet) founders since they have not contributed genetically to the captive population (Figure 9). 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.

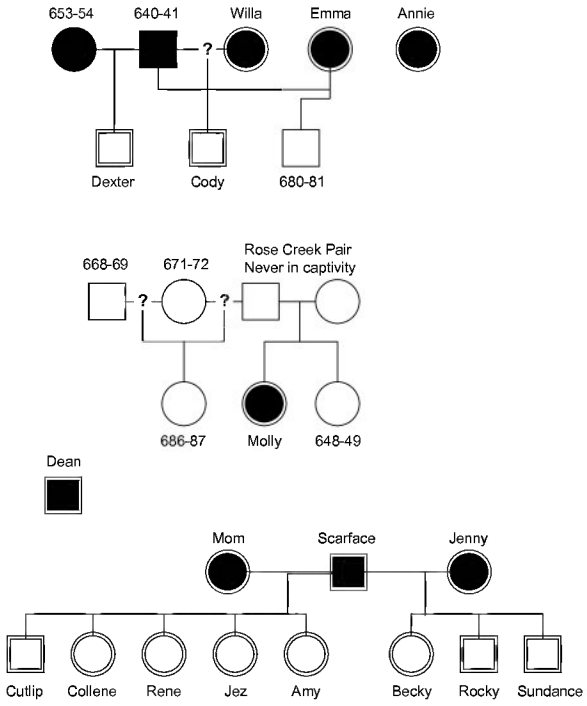

Figure 9. The identification of founders in the last remaining 18 black-footed ferrets brought into captivity (Ballou and Oakleaf 1989).Squares are males, circles females. Solid objects are founders. "?" indicates uncertain parentage. Double-outlined indicate living individuals at that time. Willa, Emma, Annie, Mom, Jenny, Dean, and Scarface are shown as founders since they are wild-caught, have no known ancestors in the group, 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. Even though they were never brought into captivity, 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 can be useful in examining relationships of wild-caught animals or even captive-born animals without pedigrees (Haig et al. 1990, 1994, 1995; Ashworth and Parkin 1992; Geyer et al. 1993; Jones et al. 2002; Russello and Amato 2004). However, these techniques typically have the resolution for determining only first-order relatedness (e.g., full sibling or parent-offspring relationships) and must be based on extensive molecular data to be useful. When information about founder relatedness is available, the PM2000 software does allow import of those data as a matrix of kinships or relatedness to apply to the founding generation.

The number of founders is a rough indication of how well the source population has been sampled to provide genetic diversity to the captive population. A large number of founders is indicative that the source population was well sampled and probably could be managed to retain much of its genetic diversity.

8.2 Founder contribution

Founders will typically have unequal genetic contributions to the current population. 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. 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.

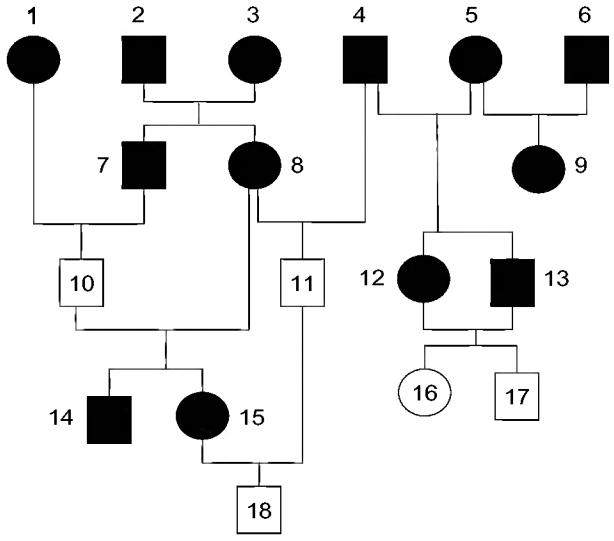

Figure 10. Pedigree of a population founded with 3.3 individuals. Squares = males; circles = females; open squares and circles = living animals. Numbers are unique identifiers for each individual. The pedigree listing is presented below.

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	Wild	Wild	Dead Founder
7	M	3	2	Dead
8	F	3	2	Dead
9	F	5	6	Dead
10	M	1	7	Living
11	M	8	4	Living
12	F	5	4	Dead
13	M	5	4	Dead
14	M	8	10	Dead
15	F	8	10	Dead
16	F	12	13	Living
17	M	12	13	Living
18	M	15	11	Living

A founder's genetic contribution to the current population's gene pool (pi) is its contribution averaged across all living individuals (Table 2). Algorithms and computer programs are available for calculating founder contributions from pedigree data (Ballou 1983). 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 (Figure 11). Genetic diversity potentially contributed by the underrepresented founders is at high risk of being lost due to genetic drift.

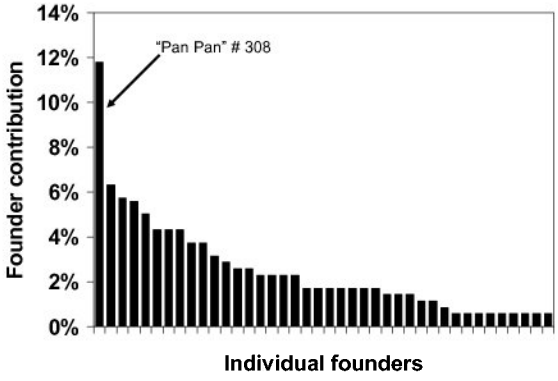

Figure 11. Founder contributions in the 2006 captive population of giant pandas (Ailuropoda melanoleuca). The distribution is heavily skewed due to disproportionate breeding among the founders. About 12% of the gene pool has come from one prolific male, panda #308 (Pan Pan), far left.

8.3 Allele retention

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% 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 founder alleles. The more pathways a founder's genes have to the living population, the less likely will be the loss of its alleles. . Therefore, even though a large proportion of a population's gene pool may have descended from a particular founder (i.e., its founder contribution is high), those genes may represent only a fraction of that founder's genetic diversity.

The proportion of a founder's genes surviving to the current population is referred to as gene retention (ri) or gene survival. Although exact methods for calculating retention have been developed (Cannings et al. 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 (Figure 12). The simulations are repeated several thousand times, and the retention 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 10 are listed in Table 2. 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. Founder genome survival is the sum of the founder retention across all founders.

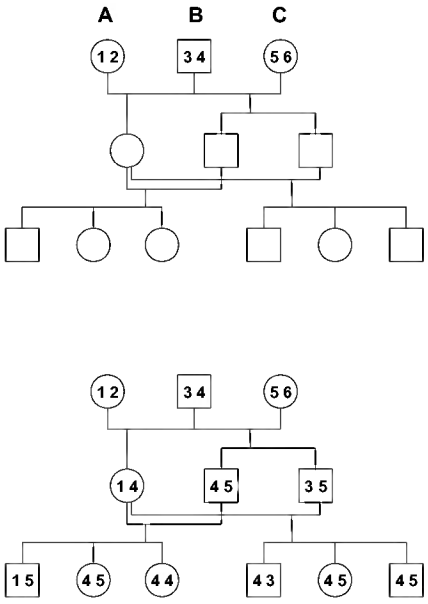

Figure 12. Gene drop analysis. (a) Each founder is assigned two unique alleles. (b) The alleles are then "dropped" through the pedigree according to the rules of Mendelian segregation; each allele has a 50% chance of being passed on to an offspring. At the end of the simulation, the pattern and distribution 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 allele retention. Note that allele 2 from founder A and allele 6 from founder C have been lost in the simulation shown.

Gene drop analyses provide information about the distribution of founder alleles in the living population not available from data on founder contributions. This is particularly true for deep, complex pedigrees, in which using founder contribution alone can be very misleading.

Table 2. Founder contributions for each living individual and allele retention for each founder from the pedigree in Figure 10.

Founder	Living individuals					Average Contribution p_i	Retention r_i
	10	11	16	17	18		
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
6	0	0	0	0	0	0	0

8.4 Founder genome equivalents

Since both skewed founder contributions and loss of alleles due to genetic drift result in the loss of founder genetic diversity, the genetic contribution of the founders to the gene pool may be less than expected. Lacy (1989, 1995) introduced the concept of founder genome equivalent (f_g) to illustrate the combined effect that 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 of their alleles in the living population. It is calculated as:

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

Equation (5)

where Nf is the number of founders, pi is the contribution of founder i to the population, and ri is founder i's retention. Our sample population in Figure 10 has six founders, 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 not have successfully reproduced or have any 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 s calculated with living founders excluded vs. included shows the contribution that genetic management can make if 100% of the living founder genes can be retained in the population.

8.5 Gene diversity retained

Gene diversity (GD) is the level of expected heterozygosity in a population. GD ranges from 0 to 1 and is the principle measure of genetic diversity in populations. In genetics of captive breeding, the gene diversity of interest is the proportion of heterozygosity of the Source population that currently survives in the living population:

$$GD_t = H_t / H_0 \qquad \text{Equation (6)}$$

where H_t is the expected heterozygosity in the current population (at time t) and H_0 is the expected heterozygosity in the Source population (i.e., time 0). Since there is no estimate of H_0, GD_t can be calculated from the allele frequencies generated by the gene drop simulation as follows:

$$GD_t = 1 - \sum_{i=1}^{2N_f} q_i^2 \qquad \text{Equation (7)}$$

where N_f is the number of founders and q_i is the frequency of allele i in the current population (Lacy 1989).

Gene diversity can also be calculated directly from f_g :

$$GD_t = 1 - \frac{1}{2f_g}. \qquad \text{Equation (8)}$$

8.6 Average inbreeding

Inbreeding is the mating of related individuals. If two parents are related, their offspring will be inbred; the more closely related the parents are, the more inbred will be their offspring. The degree to which an individual is inbred is measured by its inbreeding coefficient (f), which is the probability of receiving the same allele from each parent (i.e., the alleles are identical by descent). Figure 13 shows a father/daughter mating. The allele "A" has a 50% chance of being passed from the father to his daughter. When he breeds with his daughter, this male again has a 50% chance of passing "A" on to his offspring. Likewise, the daughter also has a 50% chance of passing on "A" if she carries this allele. The inbred offspring then have the potential to inherit allele "A" (with 12.5% probability) from both its father and mother. Allele "a" has the same chance. Therefore, the inbred offspring has a 25% chance of receiving two duplicate alleles in the form of "AA" or "aa". Inbreeding coefficients range from 0 (parents are unrelated) to 1.0. Offspring of father/daughter, mother/son, or full-sib matings are 25% inbred; offspring of first-cousin matings are 6.25% inbred. Many generations of full-sib matings result in offspring with inbreeding coefficients of 1.0. Inbreeding coefficients are used to examine the effects of inbreeding in the population and to determine the degree of relatedness between individuals. Methods for calculating inbreeding coefficients are available from Ballou (1983), Boyce (1983) and Frankham et al. (2002).

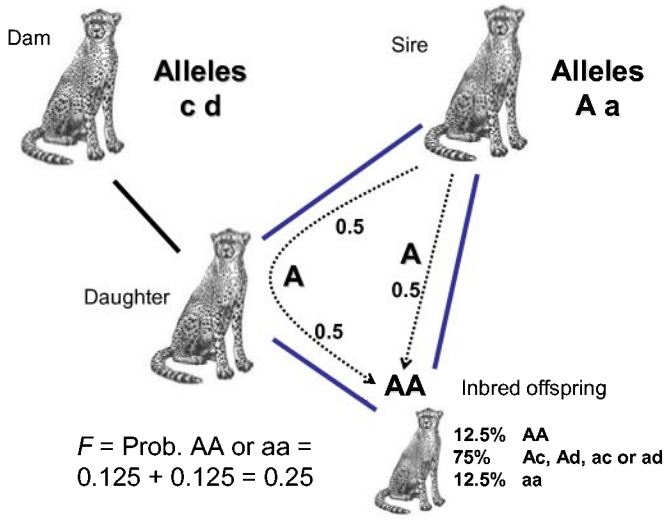

Figure 13. An example of inbreeding: a father/daughter breeding produces an offspring with an inbreeding coefficient of f = *0.25*

All naturally outbreeding plants and animals (including humans) have deleterious recessive alleles resulting from mutations. In Figure 13, if "a" is such an allele, it would not cause deleterious problems in the sire because it is masked by the dominant "A" allele. However, in the inbred offspring, there is a 12.5% chance of the locus being homozygous (aa) and therefore the alleles being expressed. Inbreeding depression results primarily when inbreeding unmasks these deleterious recessive mutations that reside in animals' genes and is the reason that deleterious consequences are expected and commonly observed in most species when inbred (Lacy 1997).

Average inbreeding is the average of the inbreeding coefficient of all animals in the current population and is a good indicator of the overall level of inbreeding in the population.

8.7 Potential genetic diversity

Living founders that have produced only a few offspring, or living animals that have no descendents in the population but are still capable of reproducing, represent individuals that can potentially still contribute genetic diversity to the population. Living founders who have only produced a few offspring have a chance, by producing additional offspring, to increase their allele retention (r_i) so that more of their genome is captured in the population. Equations (5) and (8) show that if r_i is increased for any founder, f_g and GD increase as well. Living animals that have no relatives in the population but can still breed are potential founders (e.g., recently acquired wild-caught animals).

A genetic summary of the population should indicate how many potential founders exist, and the values of GD and f_g if potential and living founders were ideally managed and bred.

8.8 Effective population size

The extent and rate of loss of gene diversity depends on the size of the population (Figure 2). 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 gene diversity from one generation to the next. Gene diversity is lost at the rate of $1/(2N_e)$ per generation. Populations with small effective population sizes lose gene diversity at a faster rate than those with large effective population sizes (Figure 2).

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. This "ideal" population is well understood, and loss of genetic diversity over time in an ideal population can be easily calculated (Kimura and Crow 1963). A real population differs greatly from the ideal, but is compared to an ideal population to determine its effective size. If a real population of say, 100 tigers, loses genetic diversity at the same rate as an ideal population of 15, then that tiger population has an effective population size of 15. 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 (Wright 1931). 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). In general, a large number of breeders will pass on a larger proportion of the parental generation's genetic diversity than only a few breeders. A heavily biased sex ratio in the breeders will result in greater 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).

Management procedures to maximize a population's effective size focus on maximizing the number of different breeding individuals, equalizing the sex ratio of breeders, and rotating breeding among many animals so that each breeding group or pair produces similar numbers of offspring. Managing a population using mean kinships (described below) also is an effective way to maximize a population's effective size.

By knowing the effective size of a population, it is possible to predict how rapidly heterozygosity will be lost in the future. Therefore, N_e is a useful indicator of the population's future genetic status. There are many methods for estimating a population's effective size. Some methods are based on demographic parameters that can be estimated from studbooks (sex ratios, variance in

family size, changes in population size, etc; Nunny and Elam 1994; Lande and Barrowclough 1997; Frankham et al. 2002). Other methods use changes in genetic diversity over time (Waples 1989). However, all of these methods require the assumption that trends in the past represent future trends. Nevertheless, understanding this caveat, N_e is useful as a general measure of how well the population has been managed. It is also needed to predict how well the population will retain future diversity – a measure needed to develop population level goals. Software (e.g., PM2000) is typically used to estimate N_e for captive populations based on the pedigree and life history (studbook) data as well as changes in genetic diversity over time.

Effective population sizes are also normally presented as the ratio of the effective size to the census size (N_e/N). The value of N_e can theoretically range from 0 to about twice the population's census size. However, rarely is it above N. The N_e/N ratios for most species in captivity typically range from 0.15 to 0.40 (average about 0.3), the low end being species managed as groups with unequal sex ratios (e.g., hoofstock herds) and the high end being long-lived and monogamously paired species (e.g., okapi). In the wild, N_e/N ratios are closer to 0.11 (Frankham 1995b).

8.9 Use of molecular genetic analyses

Estimates of genetic variation are helpful primarily for identifying the extent of genetic differences between populations or taxa. Large genetic differences may be evidence that there is more than one taxon or evolutionarily significant unit (ESU) within a species. 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 (Frankham et al. in prep; Deinard and Kidd 2000). Interbreeding individuals from different ESUs may result in reduced survival and reproduction (outbreeding depression, Frankham et al. in prep). Where different ESUs are suspected, additional analyses on morphological, behavioral, and biogeographical considerations should be conducted, and the purpose and goals of the population re-examined.

Levels of genetic variation may also 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. Molecular analyses only sample a very small proportion of the genome and there may be important diversity at highly functional genes that have not been screened. Management should strive to maintain what little genetic variation is present for the long-term fitness of the population.

8.10 Genetic summary table

Table 3 shows the summary of the genetic status of the global golden lion tamarin (GLT) captive breeding program. Based on 40 founders, much of the Source population gene diversity (96%) has been retained. If the GD_t was lower than 90% (the typical goal for many captive populations), this should raise some concern. GD_t lower than 80% indicates that a population has lost much of its evolutionary potential and its conservation value is questionable. In the GLT population, the GD_t represents the level of gene diversity retained if a new population were

established by 13 unrelated founders (i.e., $f_g = 13$). There are a few additional potential founders (illegally wild-caught tamarins recently confiscated by Brazilian authorities that have not yet bred). Including them in the program and breeding them to the fullest extent possible as well as successfully breeding the underrepresented founders would bring the gene diversity retained up to 98% and the founder genome equivalents up to 32. A high number of potential founders indicates that there may be opportunities to significantly increase genetic diversity by successfully reproducing them. In the GLT population, the average inbreeding is low at 3%. Population managers' tolerance for the level of inbreeding in a population vary. There is no level of inbreeding that indicates a threshold for inbreeding depression; inbreeding depression is expected to be a linear function of the amount of inbreeding (Frankham et al. 2002). However, many geneticists and population managers would probably feel uncomfortable with levels of inbreeding above 0.125.

Table 3. Summary of the genetic status of the international golden lion tamarin population as of January 1, 2007.

Founders	**40**
Potential Founders	**8 additional**
Living Descendants	**448**
GD_t retained	**0.9624**
Potential GD_t retained	**0.9842**
Founder genome equivalents (f_g)	**13.31**
Potential f_g	**31.59**
Average Inbreeding (f)	**0.0257**

9 General Management Strategies

9.1 Obtain a sufficient number of founders – the Founding Phase

How many founders are needed to start a captive population? Allelic diversity is lost much more rapidly than heterozygosity during founding events (Allendorf 1986; Fuerst and Maruyama 1986). Therefore, the primary concern is capturing 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. N effective founders retains on average 100 - [1/(2N)] x 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 10 (Denniston 1978).

The number of founders required to adequately capture 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. 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 25 and 50 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.

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. Failure to obtain an optimal genetic number of founders is not justification for canceling 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.

9.2 Expand the population size as rapidly as possible – the Growth Phase.

Genetic diversity is lost when growth rates are slow because small populations lose genetic diversity at a faster rate than large populations; therefore, until the population reaches its target size it should be managed to grow as rapidly as possible. This sometimes means compromising genetic management. The two primary objectives (population growth and genetic management) are not always complementary. Extreme focus on population growth (ignoring genetic management) might entail using only one or a very few highly successful males to accomplish all of the breedings during a given year. This might result in a higher number of offspring produced, and hence a larger population size, but would also result in all or most of the offspring being related to each other. As a consequence, as is often the case, future inbreeding would result in an unhealthy population with high mortality rates and low reproductive rates. This strategy would achieve a large, but genetically unhealthy, population.

On the other hand, an extreme focus on genetic management (ignoring demographics) might entail trying to breed only the most underrepresented males and females, who may be underrepresented due to advanced age or reproductive or behavioral problems and have little true reproductive potential Certainly the number of animals reproducing and number of offspring produced would decline. Reproductive rates might be too low to sustain the population. This strategy would result in a genetically healthy, but small or declining population.

Population management then becomes a balance between demographic management and genetic management: achieving sufficient (but not maximum) reproduction among a genetically good (but maybe not ideal) set of individuals. This often means compromising both population growth and genetic management. There will be some loss of reproduction when inexperienced males and female are paired and some genetic compromises when breedings are set up among some genetically over-represented pairs to ensure the production of a sufficient number of offspring. This is a challenge that all managed populations face.

The early history of a population is often where many genetic problems originate. For example, institutions that experience successful breeding right away tend to start dispersing offspring to those that are less successful. Underperforming founder males are paired with extremely

successful females to kick-start breeding and visa versa, resulting in one of the most difficult genetic challenges to correct: the linking of rare and common genetic lines. These problems will persist through the rest of the population's history and should be avoided if possible. Nevertheless, if populations are extremely small, or declining, it is always appropriate to focus more on growth than genetic management.

9.3 Stabilize the population at carrying capacity – the Management Phase

The current population size and growth rate determine whether the population is at, or when it will reach, carrying capacity. If the population is at or 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 (contraception) to stabilize the population at the desired carrying capacity (Beddington and Taylor 1973). This process may entail substantial "what if" analysis to determine how such managerial modifications of survivorship and fertility patterns will affect population size, growth rate, age distribution, and other population characteristics.

9.4 Consider subdividing the population

Subdivision of a population into several subpopulations or demes among which gene flow (usually exchange of animals but also potential exchange of gametes or embryos) is regulated is advantageous for protection against diseases, catastrophes, political changes, etc., (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, therefore, subdivision will maintain a higher overall level of allelic diversity; the theoretical conditions that support this argument do not always exist in real populations. Furthermore, while the smaller subdivided populations lose genetic diversity more rapidly than one single population because they are small and genetic drift dominates the evolutionary process, they experience fewer undesirable adaptations to captivity (i.e., adaptation is less effective in small than large populations; Margan et al. 1998). Margan et al. (1998) proposed that regional populations remain isolated until moderate levels of inbreeding accumulate, then exchange animals among regions to reduce inbreeding. This has the advantage of reducing adaptation to captivity as well as maintaining genetic diversity. 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 inbreeding depression and demographic stochasticity (Drake and Lodge 2004).

9.5 Utilize available reproductive technology

Reproductive technology (e.g., semen/ovum collection and storage, embryo transfer and freezing) should be considered a useful tool for assisting captive breeding 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 lifetime of founders and their immediate descendants. By increasing generation length, adequate levels of genetic diversity can be maintained in smaller populations, leaving more resources for populations of other species in need (Ballou and Cooper 1992). Living founders who have not yet contributed to the population should be considered immediate candidates for germ plasm storage. Artificial insemination can also help problem breeders contribute to the gene pool (black-footed ferrets; Wolf et al. 2000). Although reproductive technology is not yet available for most exotic species, it is a major focus of research by the reproductive community (Spindler and Wildt this volume).

10 Developing Population Management Recommendations

Most captive breeding programs periodically review the status of the population and generate or update recommendations for every individual in the population to produce an annual or bi-annual Master Plan for the population. The steps involved are fairly standard across species.

10.1 Step 1: Calculate the target population size.

This step has been described earlier when setting the goals and purposes for the population, but the target size needed to achieve a goal will vary over time as levels of gene diversity and population characteristics change.

10.2 Step 2: Calculate desired growth rate.

The difference between the target population size and the current population size help to determine the desired growth rate for the population. Population managers will need to decide how rapidly they wish to grow (or decline) to the target size, which may be dependent on genetic considerations, biological constraints, space availability, and other factors. They can then calculate the average growth rate needed over the defined period to reach their goals.

If the desired growth rate is negative (e.g., a population's target size is smaller than its current size), management of the decline needs to be carefully considered. If the final goal of the decline is to phase out the population from captivity, reproduction can be stopped and decline can be achieved through attrition as animals gradually reach the end of their lifespan. If the final goal of the decline is to simply decrease the population size but still maintain a stable population, care must be taken to ensure that the age structure of the population is not negatively affected. If a complete breeding moratorium is put in place, future viability may be jeopardized when no young individuals are available to fill the reproductive age classes. Instead, managers often utilize a gradual decline approach, in which a few births occur each year to ensure future reproduction but not to maintain the current size.

If the desired growth rate is positive, the population will need more births and/or imports than deaths and/or exports. If the population has grown strongly in the past (at the desired rate or higher), the population will likely be able to meet the demographic goals. However, the desired growth rate may be much higher than the growth rate observed historically or calculated from the life table as described earlier. This can be potentially confusing; in such cases, it becomes

difficult to determine whether the population actually has the biological potential to reach the desired growth rate. Remember that the historically observed rates reflect the management practices of a given period of time, and are often affected by small sample sizes; if so, how can demographic data be used to determine what the biological potential of the population might be?

One frequently used method is to look at annual growth rates of the captive-born segment of the population; these annual rates can help managers determine whether the population has ever reached the desired growth rate in the past, and/or how long higher growth rates were sustained. Another important strategy is to evaluate vital rates in the life table and use simple "what if" modeling to assess the impact of potential management changes (Faust et al. in review). If fecundity rates in the life table are low (because they reflect a period in which a large portion of breeding-aged animals were not in reproductive situations), managers can adjust fecundity rates in the reproduction age classes to reasonable levels and determine how much impact those changes have on the projected growth rate. Setting these levels is often challenging, but simple scenarios of likely management actions such as "what if each female bred once every 5 years" or "what if all females were in a breeding situation but only half of the females bred successfully" would help assess the efficacy of such management actions. Similarly, if mortality rates in the life table are high and specific management practices can be identified that might lower these, the impact can be tested on the growth rate. Analyses such as these can help determine if a desired growth rate is achievable given the population's current structure and potential management actions. This analysis can also help managers decide where to invest research and management effort. For an example of how these types of analyses were applied to the management of the AZA Asian elephant SSP, see Faust et al. (2006b) and Figure 14.

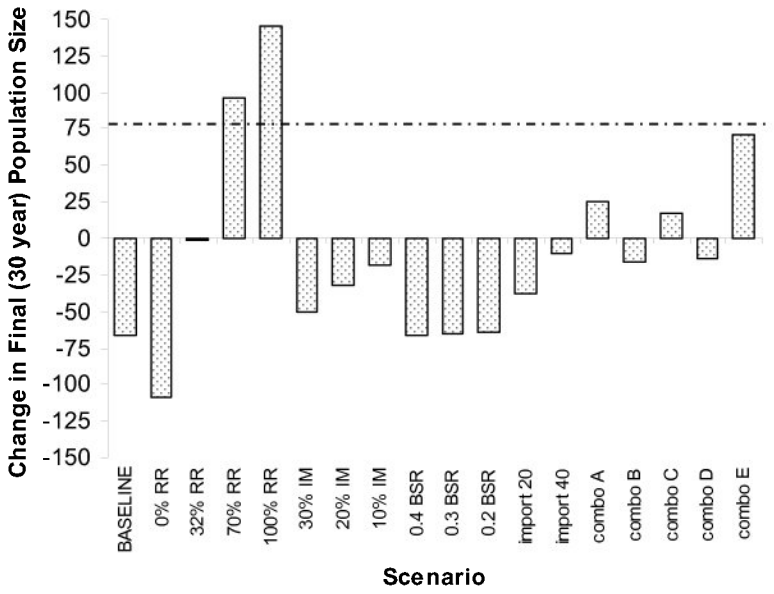

Figure 14. Change in final total size of the Asian elephant SSP population after 30 years under different model scenarios. The initial population size was 145 individuals; final population sizes are the mean size across 200 model iterations for each scenario. The dashed line represents the population change needed to meet the estimated number of spaces that will be available in SSP institutions by 2009 (218 spaces total, or an increase of 76 spaces from the initial population size). RR = % increase in reproductive rate, IM = % decline in infant mortality, BSR = birth sex ratio; Combos A-E changed multiple parameters simultaneously (e.g., improved RR and decreased IM). Reproduced with permission from Faust et al. 2006b.

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.

10.3 Step 3: Calculate number of births and breeding pairs needed.

Determining the number of births needed for a given planning session involves weighing multiple demographic, genetic, and management factors. The analysis combines the desired target size and time frame for growth to that size with the expected number of deaths in the upcoming year(s) based on the population's age structure and the mortality rates categorized in the life table (this includes infant mortality for the births needed). This produces a deterministic estimate of how many births will be needed to meet the population size goals; projections are likely most accurate for the short-term (0-10 years), as longer-term projections may be very different depending on how the population changes.

The number of breeding pairs needed to produce the desired number of offspring will then be determined by factors such as litter size, the proportion of pairs that successfully reproduce, and the likelihood that some breeding recommendations simply will not be successfully implemented. For example, 25% of the recommended breeding pairs of golden lion tamarins fail to breed each year. Of those that do reproduce, 65% produce one litter and 35% produce two litters per year, with an average litter size of 1.9. Therefore the production of 80 births requires 40 breeding pairs.

An alternative strategy is to assign a probability of success to each breeding pair as they are selected and to select enough breeding pairs so that the sum of the success probabilities sums to the number of desired litters. For example, a pair that had been successfully producing young over several years might receive a success probability of 0.9, while a newly established young pair that involved an animal transfer might receive a probability of 0.2. These probabilities can be based on analyses of past successes and failures to breed. For example, an analysis of 101 breeding recommendations from 1992 to 2001 by the Amur Tiger SSP found the greatest predictors of breeding success within one year to be the current location of the recommended breeders (same or different institutions) and previous reproductive success (Traylor-Holzer 2003). Recommended pairs located at the same institution and having both previously produced offspring (not necessarily with each other) had a 87% probability of success; pairs at the same institution but involving at least one unproven animal had a 50% of success; and pairs located at different institutions at the time of recommended breeding had a 14% success rate within one year. The Tiger SSP takes these probabilities into account when making annual breeding recommendations (Traylor-Holzer pers. comm.).

The ideal goal is to produce the desired number of offspring from the best possible genetic matches. Genetic considerations are critical, but not the only consideration. Pairings among the genetically best choices may not be sufficient to produce enough offspring; genetically less desirable pairings may need to be made simply for demographic reasons. Therefore, breeding pairs are selected on the basis of a number of factors including genetics, age, past breeding experience and location.

10.4 Step 4: Calculate mean kinship values.

When selecting animals for breeding, it is useful to rank individuals according to their genetic importance in preserving gene diversity in the population. Individuals carrying alleles from overrepresented founders are not as genetically valuable as those carrying alleles from underrepresented founders. Two measures of genetic value need to be calculated for each individual: mean kinship and genome uniqueness.

Before these calculations are made, animals that not likely to breed should be removed from the dataset, as they are genetically senescent and no longer relevant to the genetics of the population. This includes individuals that are sterilized, have debilitating medical problems, whose behavior will not allow breeding or who are post-reproductive. However, any animals that are capable of breeding at some point in the future should be left in the genetic analyses.

The mean kinship of an individual (mk_i) is the average of the kinship coefficients between an individual and all living individuals (including itself) in the population (Ballou and Lacy 1995):

$$mk_i = \frac{\sum_{j=1}^{N} k_{ij}}{N} \qquad \text{Equation (9)}$$

where 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; Toro 2000). 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 alleles will have low values of mk because they have few relatives in the population, whereas individuals who carry alleles 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.

Minimizing mean kinship is directly related to maximizing gene diversity retained:

$$GD_t = 1 - \overline{mk}. \qquad \text{Equation (10)}$$

where $\bar{m}\bar{k}$ is the average of the mk_i in the population. Thus, minimizing $\bar{m}\bar{k}$ maximizes gene diversity retained.

Management programs designed to minimize kinship using the mean kinship strategy have been demonstrated to work through computer simulations (Ballou and Lacy 1995) and experimental breeding (Montgomery et al. 1997; Rodriguez-Clark et al. in press; Toro 2000). Values of mk for the sample pedigree in Figure 10 are shown in Table 4.

Table 4. Kinship coefficients between all living animals from the pedigree in Figure 10. Mean kinship values are the average of the kinships for each individual and are shown on the bottom row. The genetically most valuable individual is #10 with the lowest mean kinship.

ID	10	11	16	17	18
10	0.500	0.063	0.000	0.000	0.188
11	0.063	0.500	0.125	0.125	0.328
16	0.000	0.125	0.625	0.375	0.063
17	0.000	0.125	0.375	0.625	0.063
18	0.188	0.328	0.063	0.063	0.578
***mk* =**	**0.150**	**0.228**	**0.238**	**0.238**	**0.244**

10.5 Step 5: Calculate genome uniqueness values.

Another measure of genetic importance is genetic uniqueness (gu_i), 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; Ebenhard 1995; Thompson 1995).

Genome uniqueness and mean kinship are often correlated, but there are certain pedigree configurations where mean kinship does not clearly identify valuable individuals whereas genome uniqueness does (offspring for which one parent is descended from over-represented founders and the other is from under-represented founders; Ballou and Lacy 1995). Typically, when screening individuals for genetic importance, mean kinships are considered first, and genome uniqueness is checked to insure carriers of vulnerable alleles are also included in the breeding recommendations.

10.6 Step 6: Calculate kinship coefficients of all possible pairings.

The kinship coefficient between two individuals is the same as the inbreeding coefficient of any offspring they produce. Since kinships are used to calculate mean kinship values, they can also serve to indicate potential offspring's inbreeding levels.

10.7 Step 7: Use the mean kinship table to identify pairings.

A mean kinship table (Table 5) is often used in conjunction with the kinship table (Table 4) when making pairings. Selecting breeding pairs involves three genetic considerations: the mean kinships of the individuals involved; the difference in their mean kinships; and their kinship to each other. Ideally, the lower the average mean kinship of the pair, the better, since minimizing mean kinship equates to maximizing genetic diversity. The mk of the male and female should also be similar. When the mk values are different, offspring produced have both rare and common alleles. If this occurs often, it is difficult to increase the frequency of the rare alleles

independently of the common ones. Finally, the kinship of the pair should be evaluated to keep inbreeding low. In some highly inbred populations (e.g., Przewalski's horse, where the average inbreeding coefficient in the population is above 0.30) it is impossible to avoid inbreeding. A common rule-of-thumb is to try to keep the inbreeding of offspring less than the average mean kinship of the population (some managers use less than one-half of the average mean kinship) – this provides a sliding scale that increases as closed populations become unavoidably more inbred. Taking these factors into consideration, the mean kinship table is used until the desired number of pairings has been made.

*Table 5. Mean kinships from a subset of the European sun bear (*Helarctos malayanus*) population for males and females sorted by ascending mean kinship values (courtesy of Dr. Lydia Kolter, Zoologischer Garten Köln). 'Known' is the percentage of an animal's pedigree that is known. Mean kinship values cannot be calculated for individuals with 0% known. Animals with mean kinship values of 0.0 are founders that have not yet produced offspring (i.e., potential founders).*

	Males					Females				
Rank	**Stbk#**	**MK**	**Known**	**Age**	**Location**	**Stbk#**	**MK**	**Known**	**Age**	**Location**
1	136	0.0000	100.0	25	ROSTOV	125	0.0000	100.0	27	ROSTOV
2	175	0.0000	100.0	20	JIHLAVA	167	0.0000	100.0	20	FRANKFURT
3	182	0.0000	100.0	18	USTI	173	0.0000	100.0	21	HILVARENB
4	207	0.0000	100.0	13	BELFAST	176	0.0000	100.0	20	JIHLAVA
5	210	0.0000	100.0	16	TOUROPARC	179	0.0000	100.0	18	USTI
6	122	0.0245	100.0	27	BASEL	180	0.0000	100.0	18	USTI
7	206	0.0245	100.0	18	KOLN	181	0.0000	100.0	18	USTI
8	169	0.0368	100.0	20	OLOMOUC	134	0.0245	100.0	25	BASEL
9	204	0.0368	100.0	12	FRANKFURT	172	0.0368	100.0	20	OLOMOUC
10	145	0.0951	100.0	23	LODZ	191	0.0368	100.0	14	BELFAST
11	203	0.1311	50.0	12	MADRID Z	197	0.0397	87.5	13	LA PLAINE
12	205	0.1392	100.0	11	BERLIN TP	159	0.0429	100.0	21	ZAGREB
13	218	0.1444	100.0	3	HILVARENB	201	0.0491	100.0	12	MADRID Z
14	124	---	---	27	KYIV ZOO	214	0.0491	100.0	7	USTI
15	149	---	---	23	BERLINZOO	217	0.0491	100.0	3	OLOMOUC
16	164	---	---	21	MUNSTER	211	0.0511	75.0	7	KOLN
17						213	0.0511	75.0	7	KOLN
18						165	0.0736	50.0	20	HILVARENB
19						185	0.0736	50.0	17	PARIS ZOO
20						192	0.0798	50.0	14	KOLN
21						193	0.0798	50.0	14	KOLN
22						139	0.0951	100.0	24	LODZ
23						142	0.1189	100.0	24	BERLINZOO
24						174	0.1281	100.0	18	BERLIN TP
25						212	0.1311	50.0	7	MUNSTER
26						198	0.1331	100.0	13	BERLIN TP
27						160	---	---	21	TOUROPARC
28						178	---	---	25	SOFIAZOO
29						195	---	---	14	TOUROPARC

An alternative to using the detailed mean kinship tables and PM2000 is to use the software MateRx. MateRx (Ballou 1999) calculates a single numeric index indicating the relative genetic benefit or detriment to the population of breeding for all possible male/female pair in the

population. This index, the mate suitability index (MSI), is calculated for each pair by considering the mean kinship values of both animals, the difference in the male's and female's mean kinships, the kinship of the male and female, and the amount of unknown ancestry in the pair. MSI ratings range from 1 (very beneficial) through 6 (very detrimental – pairing should only be used if demographic considerations override preservation of genetic diversity). MateRx is designed to simplify pairing decisions by condensing all that is known about the genetics of a pair into a single number. MateRx is useful for species such as colonial penguins in which managers cannot easily establish good breeding pairs but can discourage detrimental breeding pairs (by pulling eggs). MateRx is also useful for finding alternative pairings in species that require mate choice and for facilitating good genetic management in less intensively managed or less cooperative programs.

10.8 Step 9: Make recommendations for every animal in the population.

A captive breeding plan usually provides recommendations for every animal in the population. In addition to breeding recommendations, other recommendations are often made:

- Separating/contracepting individuals to prevent breeding
- Importing individuals to increase population size or improve population structure (age and/or sex)
- Exporting individuals to decrease population size or improve population structure
- removing individuals from a captive population for release into a reintroduced population
- Maintaining individuals to breed at another time
- Designating an individual as surplus to the program (no longer needed in the population)
- Conducting a reproductive evaluation (e.g., determine whether females are cycling, examine sperm quality)
- Collecting and banking gametes for future use
- Culling a specimen to make space available – note that this management option is somewhat controversial in application and is rarely utilized in some regions but well accepted in others.

These management actions can be used to manage a population's size and structure, and ultimately to ensure reaching the long-term demographic and genetic goals of population management.

11 Particular Challenges

11.1 Managing new founders

For species with short generation times, regular importation of founders, when possible, may be seen as an alternative strategy for maintaining high gene diversity when population sizes and growth rates in zoos cannot be high enough to compensate for the rapid loss of GD due to drift. For some species, particularly those regularly available through rehabilitation efforts, there are opportunities to incorporate new founders into the population. If this is possible, periodically

introducing new wild-caught founders into the population may completely counteract the loss of genetic diversity due to drift and inbreeding.

The genetic contribution of adding new founders can be measured as the change (increase) of genetic diversity in the population if that founder were to successfully breed. This is done by calculating the current f_g, adding to it one or some fraction of a f_g for each founder added, and converting it back into GD using the formulas presented above. It is probably unrealistic to assume that each founder will produce enough offspring to contribute a full f_g to the population. Mansour and Ballou (1994) found that over time, the average f_g contributed by a set of new founders of golden-headed lion tamarins was $0.4f_g$ per founder. For example, if four new founders were added to a population that had retained 92.0% of its gene diversity, how much might they boost gene diversity? 92% gene diversity equates to $6.25f_g$. Assuming each founder contributed 0.4fg, then the total f_g would be $6.25f_g + (0.4f_g \times 4) = 7.85fg$. This equates to 93.6% gene diversity retained: adding four founders increased gene diversity by 1.6%. The lower the gene diversity, the more it will be boosted by adding new founders. Odum (1994) provides a method for calculating the number of offspring each new founder should produce to ensure optimal representation of each founder in the population.

Importation of new founders may take two forms: one large, one-time importation vs a series of imports of fewer animals over a longer time period. Factors include limitations on quarantine space, the ability to absorb a number of new animals, and founder availability now and in the future. PM2000 allows modeling of these various scenarios to determine optimum strategies for importing new founders into a particular population.

When founders are added, their lineages will be rare and their mean kinships will be 0.0 until they produce offspring. If possible, managers should avoid pairing new founders with over-represented lineages (high mean kinship animals) as this will link rare and common alleles in the offspring, which is difficult to correct later. However, pairing with a known successful breeder might be necessary to ensure capturing the new founder genetic diversity. If several new founders are available, consideration should be given to pairing them with each other. If several pairs of new founders exist, pairing them in several permutations may be possible. Further pairing of offspring from these founders may allow the mk values for the imports to begin to approach that of the rest of the population. Only after several generations would this new lineage be folded into the main population.

11.2 Immigration and emigration

Transfers between regions or with dealers can result in situations that compromise good population management. Often animals transferred from one region to another are individuals from the bottom of the mean kinship list in the shipping region. In the receiving region, these may be appropriately treated as founders and their genes incorporated into the population as such. However, if the source region later is interesting in importing animals from the receiving region, a global population analyses should be done to determine the relationships of potential imports to the current source population. This also applies to animals sent to dealers.

Sending animals to dealers who do not keep adequate records can result in the animals going to another zoo and then re-appearing in the managed population with the knowledge that it is related to the population in some way but not knowing the specific nature of the relationships (pedigree). This is not uncommon in hoofstock. All animals leaving the population should be marked with a transponder, brand or tattoo for permanent identification.

Zoos planning to receive animals from different regions should always check available studbooks (both regional and international), and the ISIS database. In the near future, ZIMS will also be available to provide one life-time record for each specimen in ISIS zoos and studbook.

11.3 Unknown ancestry

Lack of individual identification and uncertain parentage complicate both demographic and 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. Assumptions may be developed for demographic data in order to calculate fecundity or mortality rates for animals whose birth dates are not known. For example, the median age for first reproduction in the population could be used to determine a female's birth date when she gives birth for the first (known) time.

While molecular genetic analyses may be used to resolve pedigree unknowns, this is often too expensive or impossible if the unknown ancestors are no longer available for sampling. For animals with unknown ancestry, the options are: to exclude them from the population; to use only the known portion of the pedigree in the calculations; or to make various pedigree assumptions and compare the differences. In either case, replacing unknown parents with assumed parents should only be done in the analytical studbook, not the official studbook.

11.3.1 **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 alleles that have descended from unknown ancestors. Small percentages of unknown ancestry may be acceptable. Animals that have some degree of unknown ancestry but also have ancestors whose alleles are relatively rare could be kept in the population to perpetuate the contribution of underrepresented founders. Deciding what to do typically involves weighing the risks of losing genetic diversity against the risk of inbreeding: removing animals will remove their genetic diversity as well, but keeping them in and assuming they are unrelated may result in unwanted inbreeding. However, generally the genetic costs of excluding animals with unknown ancestry are greater than the costs of including them and making incorrect assumptions about their paternity (Willis 1993).

11.3.2 Leave unknown individuals in the population.

PM2000 software will calculate mean kinship values on only that proportion of the pedigree or genome that is known (Ballou and Lacy 1995). Again, this is suitable if only a small proportion of the pedigree is unknown (e.g., less than 20%). As the proportion of the pedigree that is unknown increases, the genetic calculations are based on a smaller and smaller proportion of the pedigree, and estimates of relationships among animals become unreliable.

11.3.3 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 sensitive, the pedigree should be explored. An alternative strategy is to select the worst-case scenario in terms of gene diversity or inbreeding as the basis for management decisions.

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

When using this strategy, be aware that parental assumptions based on behavior or dominance can be prone to error.

11.3.5 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, weighing the average by the probability associated to the likelihood of different parents being the true parent. Creating an "average" parent is most appropriate if the founder contributions of the potential parents are not too different. If the differences between 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). To avoid inbreeding, one could assume worst-case scenarios: that is, the closest relationships among putative parents. However, the worst-case scenario for inbreeding is usually not a good strategy for maintaining gene diversity (Willis 1993). Instead, a second set of assumptions and hypothetical pedigree could be constructed to represent the best-case scenario for retaining gene diversity by assuming no relationships among putative parents (Willis 1993).

11.3.6 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. 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 at the time of conception 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 F1 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 in the analytical studbook.

11.3.7 Estimate average kinship and create a hypothetical pedigree for a group of individuals with unknown pedigrees.

A more quantitative approach to constructing pedigrees in black-box populations is to estimate the average kinship of individuals coming out of the black-box. This is done by first estimating the number of individuals that likely founded or provided genetic input into the black-box and converting this into the number of unique founder alleles (Willis 2001). For example, if there were known to be one male and two female founders to the black-box, then three founders were involved, contributing a total of six alleles. If there were two males and two females, but they were known to be related (brothers and sisters), then only four alleles contributed. From the

number of founder alleles (A), the average kinship ($\bar{k}$) among the group of animals emerging from the black-box (N) can be calculated from:

$$\bar{k} = \frac{2N - A}{2A(N-1)} \qquad \text{Equation (10)}$$

(corrected from equation 10 in Willis 2001).

A hypothetical pedigree for the ancestors of the emerging animals can then be created so that the emerging animals have a level of kinship that best approaches $\bar{k}$ (often it is not possible to create a pedigree that exactly produces the desired $\bar{k}$). Table 6 shows several common pedigree structures that can be used to create animals with specific levels of kinship (Willis 2001).

Table 6. Pedigree structures that create specific average levels of kinship among a set of relatives.

Average kinship ($\bar{k}$)	Pedigree structure that creates that average kinship
0.375	full siblings of full siblings
0.25	full sibs (share 2 parents)
0.1875	share 1 parent and 1 grandparent
0.125	half-sibs (share 1 parent)
0.0625	first cousins (share 2 grandparents)
0.03125	share 1 grandparent
0	None

For example, if a black-box were founded by three individuals (so A = 6) and there were 10 animals emerging from the black-box (N = 10), then their average kinship from the above equation would be 0.129. This level of kinship among the 10 is most closely re-created by making them all half-sibs (Table 6). More details on using the approach are available in Willis (2001).

Other methods for dealing with incomplete pedigrees can be found in Marshall et al. (2002), Cassell et al. (2003) and Lutaaya et al. (1999).

11.4 Management of deleterious and adaptive traits

Relatively high frequencies of deleterious recessives have also been described in a number of captive animal populations that were founded by a small number of individuals (Laikre 1999). Examples include, blindness in wolves (Canis lupus) (Laikre et al. 1993), albinism in bears (Ursus sp.)(Laikre et al. 1996), gingival hyperplasia in silver foxes (Vulpes vulpes) (Dyrendahl

and Henricson 1959) and hairlessness in red-ruffed lemurs (Varecia variegata rubra) (Ryder 1988; Nobel et al. 1989).

Typically, most deleterious alleles will be rare in a large normally outbreeding population (Frankham et al. 2002). However, when populations pass through a bottleneck, such as founding a captive population, previously rare alleles that do make it through the bottleneck may significantly increase in frequency. If an allele with a low pre-bottleneck frequency survives passing through the bottleneck, its frequency will increase to at least 1/(2N) after the bottleneck, where N is the number of animals in the bottleneck. After the bottleneck, additional inbreeding will increase the chance of expressing any deleterious recessive alleles that do persist in the population.

Deleterious alleles will be detected in increasing frequency in many captive breeding programs as they become more inbred. Deleterious alleles are a natural component of the genetic diversity of all species, and the inbreeding in small populations typical of many captive breeding programs will bring these to light. The temptation will be to exclude from reproduction those animals exhibiting the trait (i.e., select against it). It will be important to first ascertain, through pedigree analysis, veterinary examination and others kinds of research, that the traits observed are truly genetically determined. This will be difficult in some cases where sample sizes are small and genetic mode of inheritance complicated. Secondly, it is important to understand the ramifications of strategies to select against the trait. Ralls et al. (2000) and Laikre et al. (1993) carefully evaluated the effects of selecting against traits on the overall genetic diversity of the population. Until both the genetic basis is determined and the implications of selection are evaluated, captive breeding programs should be very hesitant to automatically impose selection strategies.

Some suggest that captive breeding programs should select for specific or adaptive traits or allow natural mate choice in captive breeding programs to enhance reproduction (e.g., variation at the MHC loci, Hughes 1991; Wedekind 2002). It has also been recommended that selection of breeding individuals be based on individual levels of heterozygosity estimated from biochemical methods. As mentioned earlier, heterozygosity at a few loci is often a poor indicator of overall individual heterozygosity. In addition, specific selection for known heterozygous loci (e.g., MHC loci: Hughes 1991) may select against heterozygous loci not sampled and decrease the overall level of genetic diversity in the population (Haig et al. 1990; Miller and Hedrick 1991; Gilpin and Wills 1991; Vrijenhoek and Leberg 1991). Any selection, be it for specific genetic markers or phenotypic traits, will further reduce genetic diversity and increase inbreeding since selection will reduce the number of animals breeding and hence the effective population size (Lacy 2000b). Additionally, such selective measures will enhance the adaptation to the captive environment and reduced fitness in the wild (Margan et al. 1998; Kraaijeveld Smit 2006; Ford 2002).

11.5 Group management

The management strategy of minimizing mean kinship may not be practical for populations in which animals are not individually identified (e.g., herd species, tanks of fish, colonies of birds).

Populations such as these, for which detailed pedigree information is unknown and/or specific breeding pairs cannot be reliably controlled, are generally referred to as "groups." Groups can range from species in which individuals are identifiable, but pairings cannot be controlled (e.g., some penguins) to species in which individuals cannot be distinguished or counted at any life stage (corals, eusocial insects).

Genetic management of groups is a developing science and not frequently done (except for Partula snails, Pearce-Kelly et al. 1995). Proposed methods for group management include:

11.5.1 Maximizing Effective Population Size

Through introduction and/or removal of individuals, the factors that contribute to increases in effective population size can be manipulated. Such management actions include managing for equal sex ratio among breeders, producing an equal number of offspring per female, frequently rotating males in and out of breeding situations, maintaining a constant population size, and regularly moving animals (4-5 effective migrants per generation) among groups. For example, Princeé (1995) proposed a scheme that minimizes inbreeding and maximizes Ne by a regular system of rotating males in a systematic manner among groups. How much can be accomplished will depend on the social and husbandry requirements of specific species.

11.5.2 Group Mean Kinship

In a metapopulation of groups, average inbreeding and mean kinship values of groups (average relatedness of one group to all groups in the metapopulation) can be calculated using information on changes in group sizes (number of individuals), migration among groups, and sexual mode of reproduction (e.g., selfing vs cloning; Wang 2004). Much like mean kinship of individuals, these calculations allow managers to identify which groups should send or receive migrants with other groups. Research is this area is continuing.

11.5.3 Molecular Analysis of Population Structure

Molecular genetic analyses of samples from groups can be used to calculate measures of genetic divergence between groups (Fst, genetic distance; Frankham et al. 2002). Animals can then be moved to reduce genetic differences. This strategy is controversial because, as mentioned above, it bases genetic management on a small set of loci, ensuring maintaining diversity at those loci, but likely reducing it over the remainder of the genome .

12 Genetics of reintroductions

The selection of individuals for reintroduction should consider genetics (Ralls and Ballou 1992; Ballou 1992, 1997). A common genetic goal of reintroduction programs is to eventually plan to release all of the potential genetic diversity contained in the captive population back into the wild

(Earnhardt 1999). Reintroduced animals should not be inbred as they may be substantially less able to cope with the wild environment than non-inbred individuals (Jiménez et al. 1994). During experimental reintroductions, when risks to animals may be high, animals should be chosen for reintroduction with care so as not to release animals whose removal from the captive population will reduce its genetic diversity (e.g., under-represented animals or founders should not be released; Russell et al. 1994). However, as reintroductions become more successful, release of animals of higher genetic value is acceptable in order to transfer the full component of genetic diversity from the captive population into the wild (Ballou 1992). The software MetaMK (Ballou 1999) and PM2000 (Pollak et al. 2007) both assist with choosing individuals to move between populations and have been used in selecting animals for reintroduction (Ralls and Ballou 1992).

13 Acknowledgement

This chapter is dedicated to the memory of Dr. Tom Foose, one of the founders of the science of population management of zoo collections. Thanks to Kevin Willis and Peter Riger for material. Many thanks to Kathy Traylor-Holzer and Kristen Leus for extensive comments that significantly improved earlier versions.

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14 APPENDIX A: Software programs for managing and analyzing data for population management.

Software	Developer	Primary purpose	Features	Source
ARKS	ISIS	Animal record management for individual zoos	Animal records management with some analyses; multiple species	Available to staff of ISIS member zoos. (ISIS 2004b)
SPARKS	ISIS	Studbook records management	Manages studbook data with some basic analyses of demography, genetics, census and reproduction	Available to staff of ISIS member zoos. (ISIS 2004)
GENES	R. C. Lacy	Genetic management	Using a pedigree exported from SPARKS, calculates inbreeding coefficient, mean kinships, founder statistics. Evaluates effect of making pairings on genetics of population. OUTDATED	Free. Distributed with SPARKS software. (Lacy 1993)
Demog	J. D. Ballou and L. Bingaman Lackey	Demographic analyses	A spreadsheet that calculates a life table from data exported from SPARKS. Limited demographic modeling. OUTDATED	Free. (Ballou and Bingaman 1992)
PM2000	J. P. Pollak, R. C. Lacy and J. D. Ballou	Population management	Pedigree and demographic analyses, setting population goals, genetic management recommendations. Uses data exported from SPARKS and PopLink.	Free. Available from website of R. C. Lacy. (Pollak et al. 2007)
PMx	J. P. Pollak, R. C. Lacy and J. D. Ballou	Population management	Update of PM2000 currently under development. Includes genetic management of groups, multiple parents. Bootstrap demographic analyses.	Free. Will be available from website of R. C. Lacy
MateRx	J. D. Ballou, J. Earnhardt, and S. Thompson	Genetic management	Assigns a rating from 1 to 6 for all possible breeding pairs in the population to simplify genetic management. Uses a data file produced by PM2000.	Free. Distributed with PM2000. (Ballou et al. 2001)
Meta MK	J. D. Ballou	Genetic management	Evaluates effects on genetic diversity of moving animals between two populations.	Available from J. D. Ballou website at

				National Zoo. (Ballou 1999)
ZooRisk	J. M. Earnhardt, A. Lin, L.J. Faust, and S.D. Thompson	Population viability analysis	Uses simulations to evaluate the degree of risk for a captive population. Uses data from a SPARKS or PopLink dataset.	(Earnhardt et al. 2005)
PopLink	L. J. Faust, Y. M. Bergstrom, and S. D. Thompson	Studbook records management and analysis	Helps maintain, analyze and export population data for demographic and genetic management. Uses SPARKS dataset, user-entered data, or (in the future) ZIMS data.	(Faust et al. 2006a)
Vortex	R. C. Lacy	Population viability analysis	PVA modeling with options to import studbook information from SPARKS and determine pairings based on genetic criteria.	Free. Available from website of R. C. Lacy (Lacy et al. 2007)
ZIMS	ISIS	Global animal records information system	Animal husbandry, health, studbook, pathology, etc., global web-based information system currently under development. Being built by ISIS to replace ARKS, SPARKS and MedARKs	Will be available to staff of ISIS member zoos. ZIMS (2007).

15 APPENDIX B: Demographic definitions.

SYMBOL	TERM	DEFINITION
x	Age Class	The time interval that includes an individual's age. Age class 0 includes all animals between 0 and 0.999 year of age, age class 1 includes those between 1 and 1.999, etc. Age is denoted by an *x* in other terms.
	Age Pyramid (or Distribution)	A histogram showing the structure of the population, in the form of the numbers or percentages of individuals in various age and sex classes.
SAD	Stable Age Distribution	The age distribution at which the relative proportions of each age class remain stable (change at the same rate) and the population growth rate remains constant.
M_x	Age- and Sex - Specific Fecundity	The average number of same-sexed young born to animals in an age class. Fecundity rates provide information on the age of first, last, and maximum reproduction.
Q_x	Age- and Sex - Specific Mortality Rate	The probability that an individual of age *x* will die during that age class. $Q_x = 1 - P_x$
P_x	Age- and Sex - Specific Survival Rate	The probability that an individual of age *x* will survive to the beginning of the next age class (age x + 1). $P_x = 1 - Q_x$
l_x	Age- and Sex - Specific Survivorship	The probability that a newborn individual (e.g., age 0) will be alive at the beginning of age *x*. Survivorship is a cumulative measure -- for example, the survivorship of age class 10 is influenced by all of the survival rates in all age classes from birth until 10. $l_x = \prod_{i=0}^{x-1} p_i$
r	Instantaneous Rate of Change	The rate of change in population size at any instant in time. If $r > 0$, the population is increasing; if $r = 0$, the population is stable; if $r < 0$, the population is declining.
λ	Lambda or Population Growth Rate	The proportional change in population size from one year to the next. λ can be based on life table calculations (expected λ) or from observed changes in population size from year to year. If $\lambda > 1$, the population is increasing; if $\lambda = 1.0$, the population is stable or sustaining; if $\lambda < 1.0$, the population is declining. A λ of 1.11 means an 11% per year increase; lambda of .97 means a 3% decline in size per year.
E_x	Sex-Specific Life Expectancy	Average years of further life for an animal in age class *x*.

	Median Life Expectancy/ Median Survivorship	The age where $l_x = 0.5$; half of the individuals in the dataset died before this age and half of the individuals survived. This is commonly used to describe a population's survival pattern.
	Maximum Longevity	The age of the oldest known individual in an analysis; the individual can be living or dead. Note that this value may change frequently and that it is inaccurate to assume that the majority of specimens will survive to this age (e.g., it should not be used as the sole summary parameter for survival patterns).
T	Mean Generation Time	The average time elapsing from reproduction in one generation to the time the next generation reproduces. Also, the average age at which a female (or male) produces offspring. It is not the age of first reproduction. Males and females often have different generation times.
V_x	Sex-Specific Reproductive Value	The expected number of same-sex offspring produced this year and in future years by an animal of age *x*.
	Risk (for Q_x, M_x, or any age- or sex-specific rate)	The number of individuals that have lived during an age class. The number at risk is used to calculate M_x and Q_x by dividing the number of births to and deaths of individuals in age class *x* by the number of animals at risk of dying and reproducing during that age class.

16 APPENDIX C: Genetic definitions.

Term	Symbol	Definition
Heterozygosity	H_o, H_e	Observed Heterozygosity (H_o): The proportion of individuals in a population that are heterozygous (have two different alleles) for a particular trait or genetic marker. Expected Heterozygosity (H_e): The proportion of individuals in a population that would be expected to be heterozygous if the population were bred at random.
Allele diversity	A	The average number of alleles existing in a population for a set of traits or markers.
Gene diversity	GD or H_t	Another term for H_e. In genetic management, often refers to the proportion of the wild or source population heterozygosity that is retained in the analyzed population.
Founder genome equivalent	f_g or FGE	The number of equally represented founders with no loss of alleles (retention = 1) that would produce the same gene diversity as that observed in the living, descendant population. Equivalently, the number of animals from the source population that contain the same gene diversity as does the descendant population. The gene diversity of a population is $1 - [1 / (2 \times f_g)]$.
Founder retention	r_i	Proportion of a founder's genome surviving in the analyzed population.
Mean kinship	mk_i	Mean kinship: The mean kinship coefficient between an animal and all animals (including itself) in the living, captive-born population.
Average mean kinship	$\bar{mk}$	Average of mean kinships of individuals in the population. The average mean kinship of a population is equal to the proportional loss of gene diversity of the descendant (captive-born) population relative to the founders and is also the mean inbreeding coefficient of progeny produced by random mating. Average mean kinship is $[1 / (2 \times f_g)$. Proportion GD retained = $1 - \bar{mk}$.
Inbreeding coefficient	f	Probability that the two alleles at a genetic locus are identical by descent from a common ancestor to both parents.
Average inbreeding		Average of the inbreeding coefficients of all individuals in a population. The average inbreeding coefficient of a population will be the proportional decrease in observed heterozygosity relative to the expected heterozygosity of the founder population.