

ABSTRACT

Title of Dissertation: GENETIC MANAGEMENT OF GROUPS

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Genetic diversity is essential for the long- and short-term survival of populations and individuals. Some of the most intense genetic management occurs in captive populations where breeding programs involve specific breeding recommendations for every individual in the population. The current strategy used by captive breeding programs worldwide to minimize loss of genetic diversity pairs individuals according to a mean kinship (MK) value. MK requires both knowledge of the population's pedigree and control over which pairings are made. This strategy is practical for many of the large species managed in captivity, but is unrealistic for species for which there is insufficient information or over which I have less control. These include certain species of captive animals that are not maintained individually (e.g., herds of antelope) and populations in the wild. Populations such as these, where detailed pedigree information is unknown, ages and individuals are difficult to identify, and/or specific pairings cannot reliably be made, are referred to as "groups". I propose a strategy for managing groups that involves manipulating population structure, migration rates, and the tenure of breeding males. I found that group management does carry a genetic cost relative to MK-based

management, and that cost will need to be weighed against the financial costs of managing animals at the individual level as opposed to the population level. Group management is better than no management and may provide an option for genetic management of currently “unmanageable” captive populations (e.g., tanks of fish), global captive populations, and wild populations. I also tested the robustness of an MK-based management strategy. A kinship-based breeding strategy is modeled with all breeding recommendations being followed. However, this idealized scenario does not always occur. I found genetic diversity does decrease as breeding recommendations are not followed. This includes the breeding of overrepresented (High MK) animals that are recommended to not breed and the reduced success of Low MK animals that are recommended to breed. The robustness of MK is dependent upon the species being managed. These results should be factored into any cost/benefit analysis of individual and group management strategies.

GENETIC MANAGEMENT OF GROUPS

By

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Chapter 1: Genetic Management of Groups.

Introduction

Genetic management is critical to the survival of many species. Preserving genetic diversity directly impacts individual fitness (Allendorf & Leary, 1986; Hedrick, Brussard, Allendorf, Beardmore & Orzack, 1986; Lacy, Petric, & Warneke, 1993; Ralls, Ballou, & Templeton, 1995; Wildt, Bush & Goodrowe, 1987) and allows populations to adapt to changing environments (Allendorf, 1986; Lewontin, 1974; Reed & Frankham, 2003; Sealander, 1983). Small and fragmented populations are especially susceptible to loss of genetic variation through the process of genetic drift (Nei, Maruyama & Chakraborty, 1975). Small populations are becoming more common as many populations of wild animals are decreasing in size due to habitat loss and fragmentation and other human-induced threats. The World Conservation Union (IUCN) Red List of threatened species lists 5,966 species of threatened vertebrates (IUCN, 2008), almost one quarter of those evaluated. And almost half of the invertebrates evaluated were threatened (IUCN 2008).

Although increasing the amount of available habitat would be the most functional solution for preserving endangered populations, it is often not tenable. In an effort to curtail extinction, many threatened or endangered species are managed through reintroduction, translocation, culling and contraception. These actions are often based more on demographic considerations than genetic ones. This is because detailed genetic management is difficult in the wild where species are considered at the population level and individuals are difficult to identify and manipulate.

Some of the most intense genetic management occurs in captive populations where regional and international breeding programs involve specific breeding recommendations for every individual in a population. Hundreds of captive species are managed through cooperative breeding programs such as the Association of Zoos and Aquariums (AZA) Species Survival Plan (SSP[®]) or Population Management Plan (PMP) programs or the European Association of Zoos and Aquaria (EAZA) European Endangered Species Programme (EEP). These cooperative programs provide the essential framework of planning and support for long-term population sustainability.

The science of population management has been greatly advanced through work on captive populations (Ballou & Foose, 1996; Ballou & Lacy, 1995; Lacy, Ballou, Princee, Starfield & Thompson, 1995). Captive genetic management programs focus predominantly on maintaining prescribed levels of allelic diversity and heterozygosity over long periods of time (e.g., 90% gene diversity for 100 years). The current strategy used by cooperative captive breeding programs worldwide to minimize loss of genetic diversity pairs individuals according to a mean kinship (MK) value (Ballou & Lacy, 1995). The relationship between two individuals, or the probability that alleles drawn randomly from each of two individuals (i and j) are identical by descent, can be measured by the kinship coefficient (f_{ij}) (Falconer, 1981). The mean kinship of individual i (mk_i) is then defined as the average of the kinship coefficients between that individual and all living individuals (including itself and others of its sex) in the known pedigree:

$$mk_i = \frac{\sum_{j=1}^N f_{ij}}{N}$$

This also equals the average inbreeding coefficient of progeny of this individual if it were mated at random in the population (Crow & Kimura, 1970). Under this strategy, an individual's genetic importance can be determined based on the number and degree of relatives that individual has in the population.

When creating a genetic management plan, MK values are calculated for each individual in a managed population. Individuals with the lowest MK value are priority breeders. In addition, pairings of animals that would result in offspring with "high" levels of inbreeding are also avoided ("high" is a relative term dependent upon the population in question, but attempts are usually made to keep the inbreeding coefficient of a pair below that of the population's average MK). The disparity between MK values is also considered, so as not to create offspring with both rare and common alleles. If this were to happen, it could be difficult to perpetuate those rare alleles without the accompanying common ones.

Mean kinship is the accepted strategy for maintaining genetic diversity in captive populations and has been tested against alternatives in both a computer simulation (Ballou & Lacy, 1995) and on living organisms (Montgomery, Ballou, Nurthen, England, Brisco & Frankham, 1997). However, the key to MK is that it requires an understanding of the genetic constitution of the entire population (the pedigree) so that animal-by-animal breeding recommendations can be made. Individuals are introduced, contracepted or separated based on whether or not they have a recommendation of "breed" or "do not breed."

This strategy is practical for many species in captivity such as elephants (*Elephas maximus*, *Loxodonta africana*), komodo dragons (*Varanus komodoensis*), and vultures

(Falconiformes), but is unrealistic for species for which there is insufficient information or over which we have less control. These include certain species of captive animals that are not maintained individuals (e.g., herds of ungulates, troops of primates, flocks of birds, tanks of fish) and most populations in the wild. Populations such as these are called groups. The purpose of this paper is to define groups, discuss how they are relevant to the management of captive and wild populations, and to explore potential strategies for managing groups instead of individuals.

Defining Groups

With regards to population management, I define a group as a population for which detailed pedigree information is unknown, ages and individuals are difficult to identify, and/or specific pairings cannot be made reliably. The term “colony” is sometimes used to refer to a group, but I discourage this to avoid confusion with true colonial organisms, such as some corals or social insects.

Group management does not simply refer to managing populations in the absence of a pedigree, but instead is a continuum that represents a progressive loss of information and control. I define nine management categories along that continuum. These categories and definitions arose during two Groups Population Management Workshops held by the international zoo and aquarium community (Mace, Hall, & Vedmar 1998; Smith, 2002).

1. Individuals can be identified and parentage is known. Pairings can be controlled. Species in this category can be managed by MK. (great apes, doves, large reptiles)

2. Individuals can be identified and parentage is known. Pairings cannot be controlled. Species in this category are often controlled in such a way (e.g., contraception, physical separation) that they can be managed by MK.
(penguins, polygamous ungulates)
3. Individuals can be identified, but one parent most often is not known. Pairings cannot be controlled. MK is often used to plan genetic management for species in this category, but requires intensive management and numerous pedigree assumptions. (primate troops, large herds of ungulates)
4. Individuals can be identified, but typically both parents are not known. Pairings cannot be controlled (bats, aviary birds).
5. Individuals cannot be distinguished, but can be counted (or abundance estimated accurately) and classified into age/stage/size and sex classes. Pairings cannot be controlled (amphibians, large flocks of birds).
6. Individuals cannot be distinguished but can be counted (or abundance estimated accurately) and classified into age/stage/size groups. Sexes are unknown. Pairings cannot be controlled (amphibians, fishes, invertebrates).
7. Individuals cannot be distinguished, but can be counted. (or abundance accurately estimated) at the reproductive stage only. Pairings cannot be controlled. (insects)
8. Individuals cannot be distinguished, but a census of the population can be conducted. Life stages cannot be discerned. Pairings cannot be controlled.
(large tanks of fishes)

9. Individuals cannot be distinguished or counted at any life stage (or only at non-reproductive stages. Pairings cannot be controlled. (corals, eusocial insects)

Defining group categories is important, as it is unlikely that there will be one ideal management method for all types of groups. Examples are given of captive species that typically fit into each type of category, but the examples are generalizations and no one taxon is restricted to any single category. Species in category 1 are not groups, as I define them, as they can have their pedigree tracked and can be managed using mean kinship. Species in categories 2 and 3 are often managed using MK, though management takes additional husbandry efforts and often requires parentage assumptions in the pedigree. Species in category 4-9 are typically thought of as groups, for which new genetic management techniques are needed to make management decisions that adequately preserve and predict retention of genetic diversity. Wild populations mostly fall into these categories.

Not all species that have an incomplete pedigree are considered groups. Even some of the most manageable species have some unknown parentage information in their pedigree due to incomplete or inaccessible historical records. In a population with an otherwise complete pedigree, individuals with unknown ancestry can be excluded from management or assumptions can be made to allow their inclusion, while understanding the impacts of erroneous assumptions on the population (Willis, 2001; Willis, 1993). For example, assuming animals with unknown ancestries are unrelated could lead to an underestimation of inbreeding if they actually are related; however, assuming animals are related if they are not could lead to a loss of gene and allelic diversity. Decisions on

whether and how to use these animals are based on the genetic status of the population and the costs of the assumptions (Willis, 2001; Willis, 1993). Groups are distinctive because the excessive amount of unknown information in their pedigrees prohibits pedigree-based analyses.

Both captive and wild populations can benefit from group management, but for different reasons. As the number and variety of captive populations being managed increases, so does the need for more flexible management strategies. As more wild populations become more defined and controlled, more structured genetic management becomes possible.

Captive Groups

Traditionally, management efforts in zoos and aquariums have focused on charismatic keystone and endangered species, such as gorillas and elephants. As the conservation needs of all species in nature have increased, so has the scope of zoo and aquarium programs. Coordinated population management programs now exist for a variety of taxa including snails, fish, flamingos, toads, guenons, and gazelles. Although many species can be managed using MK, there is an ever-increasing number of groups in need of population management.

A survey conducted in 2008 (Smith 2008) surveyed all of AZA's SSPs and PMPs to evaluate the group management needs of cooperatively managed species. Program leaders were asked if group management was "Required" for their species (i.e., MK management was not possible), or "Preferable." "Required" was an option because some programs, such as the Straw Colored Fruit Bat (*Eidolon helvum*) PMP, might need group management because the sheer number of animals in the program make individuals

difficult to identify and manage. “Preferable” was an option because, for some species, it is possible to manage them using MK values, but it would be less resource intensive to manage them as a group. For example, many polygamous species might fall into category 1 (Table 1) through the use of contraceptives or by physically separating out specific breeding pairs; however, contracepting animals carries risks and costs (Chuei, Asa, Hall-Woods, Ballou & Taylor-Holzer, 2007; Patteon, Jöchle & Penfold, 2007; Wheaton, Joseph, Reid, Webster, Richards, Forde & Savage, 2007) and separating out animals is often difficult because of limited resources, a lack of holding space, and social concerns. Another example in which management is influenced by biology involves species that can be easily put into pairs but for which mate choice is a critical component of breeding success. As an example, African pygmy geese (*Nettapus auritus*) naturally form pairs, but pre-selected pairs rarely produce offspring. If the birds are allowed to select their own mate, the pair typically does produce offspring (Piekarz, D. personal communication, 2004). The significance of mate choice has been documented in many species (Andersson, 1994; Brown, 1997; Duraes, Loiselle, Parker & Blake, 2009; Edwards & Hedrick, 1998; Eizaguirre, Yeates, Lenz, Kalbe & Milinski, 2009; Milinski, 2006; Ryder, Tori, Blake, Loiselle & Parker, 2010) and it plays an increasing role in captive management decisions.

Response rate was high from both SSP (99%) and PMP (73%) program leaders. The survey revealed that it would be preferable for almost 30% of PMP species and almost 20% of SSP species to have some type of group management. Although only a small number (2%) of SSPs require group management, 18% of PMPs require group management.

Table 1. Population Management Categories

Category	Taxonomic Examples
1. Individuals can be identified and parentage is known. Pairings can be controlled. Populations can be managed using MK values.	great apes, doves, large reptiles
2. Individuals can be identified and parentage is known. Pairings cannot be controlled. Species in this category are often controlled in such a way (e.g., contraception, physical separation) that they can be managed using MK values.	penguins, polygamous ungulates
3. Individuals can be identified, but one parent most often is not known. Pairings cannot be controlled. Management using MK values is often used for species in this category, but requires extensive effort and numerous pedigree assumptions.	primate troops, large ungulate herds
4. Individuals can be identified, but both parents are most often not known. Pairings cannot be controlled.	bats, aviary birds
5. Individuals cannot be distinguished, but can be counted (or abundance accurately estimated) and classified into age/stage/size and sex classes. Pairings cannot be controlled.	amphibians, large flocks of birds
6. Individuals cannot be distinguished but can be counted (or abundance accurately estimated) and classified into age/stage/size groups. Sexes are unknown. Pairings cannot be controlled.	amphibians, fishes, invertebrates
7. Individuals cannot be distinguished, but can be counted (or abundance accurately estimated). Life stages cannot be discerned. Pairings cannot be controlled.	insects
8. Individuals cannot be distinguished, but a census of the population can be conducted. Life stages cannot be discerned. Pairings cannot be controlled.	large tanks of fishes
9. Individuals cannot be distinguished or counted at any life stage. Pairings cannot be controlled.	corals, eusocial insects

These figures are especially important because, out of all of the thousands of species in captivity in AZA institutions, only a few hundred have been given SSP or PMP status, and the majority of these programs focus on the more easily tracked larger vertebrates (for example, in 2008 there were only seven AZA management programs for amphibians, three for invertebrates, and two for fishes). If group genetic management techniques become available, the number of managed species in those and other taxonomic groups is likely to increase.

Equally important, group management has the potential to enhance animal welfare. Although the survey confirms what animal husbandry experts have long known – that it is possible change natural social structure through management so that breeding recommendations can be made – there is an intrinsic irony in this type of management. Modern zoos and aquariums expend extensive resources creating exhibits and enhancing care to allow animals to exhibit behaviors similar to those that would occur in the wild. Managing groups as individuals often requires that animals are managed in a way that minimizes natural social and breeding behaviors.

Wild Groups

Wild animals are usually thought of as free ranging and unmanaged. Unfortunately, habitat destruction has made the wild less so, forcing many populations of animals into parks and reserves. These protected areas have been called megazooos because they are not part of an independently functioning ecosystem but rather a place where animals are managed ecologically, behaviorally, genetically, and demographically (Conway, 1995). As an example, a study of mammals in eastern North American wildlife

reserves estimated that few reserves are large enough to avoid loss of mammal species without some type of active management of habitat or populations (Gurd, Nudds & Rivard, 2001).

Some wildlife management programs are very specific, focused on a particular species or even particular populations or metapopulations within a species.

Reintroduction and translocation programs are developed to enhance the survival of a species by restoring or invigorating wild populations. Genetic management techniques for groups would be ideal for these populations. For example, the black lion tamarin (*Leontopithecus chrysopygus*) population in the Atlantic forest of Brazil uses a metapopulation management system that includes reintroductions, translocations, and managed dispersals, as well as a captive reservoir population. The project entails actively moving animals as well as creating conditions for natural dispersal to occur (Valladares-Padua & Padua, 2000). Populations such as this could benefit from group genetic management techniques that direct animal movement to increase genetic diversity at the species level. A similar project, Operation Noah's Ark, run by The Kissama Foundation and the North-West Parks and Tourism Board, involves relocating elephants from South Africa to Angola by air. In September 2000, fifteen elephants were relocated from the Madikwe Game Reserve in the Northwest Province of South Africa to the Quicama National Park in Angola. This relocation was the first step to relocate elephants from other African countries to the park and is one of the Angolan government's plans to rejuvenate its economy through conservation-based tourism. Group genetic management techniques could be used in conjunction with information on herd social dynamics to

determine which animal moves would create the most genetically diverse new population, while minimizing genetic losses to existing herds.

In addition, group management techniques can also be used in deciding where corridors should be maintained or created to permit gene flow through natural dispersal. Corridors, linear landscape elements that reconnect patches of wildlife habitat (Soulé & Gilpin, 1991), could be prioritized by determining which populations would most benefit from genetic exchange. Although the effectiveness of corridors has been debated (Beier & Noss, 1998; Simberloff, Farr, Cox & Mehlman, 1992) many studies have been conducted to evaluate their usefulness and they are often recommended as a way to mitigate the negative effects of habitat fragmentation on population persistence and retention of genetic diversity.

Strategies for Group Genetic Management

In contrast with the use of MK for managing individuals in populations, it is unlikely that a single “group management” strategy will maximize retention of genetic diversity in all types of groups. The diversity of biological and physical factors will require development of individualized management plans tailored for each type of group.

Managing Biological Factors

One of the biological factors that impacts management, population size and effective population size is mating system (e.g., promiscuity, monogamy, polygamy). Wright (1931) introduced the concept of effective population size (N_e) as the number of individuals in an ideal population that would lose heterozygosity at the rate observed in the real population. Genetic diversity is lost at a rate of $1/2N_e$ per generation, so the smaller N_e , the faster genetic diversity is lost. In some mating systems such as harem

polygyny, in which females breed only with a dominant male, there is the potential for the effective size to be smaller than that of a monogamous species. This effect is exacerbated in species with short generation times (Nunney, 1993). Effective size increases with generation time, because more males are provided with opportunities to breed (Nunney 1993). In order to enhance the effective size of a population, one goal of management could be to minimize the time dominant animals were allowed to breed, turning them “off” after a certain number of breeding years and allowing more individuals a chance for breeding success. Turning an animal’s reproduction off could be temporary (contraception, housing with other post- or non-reproductive animals, sending outside of the managed population) or permanent (castration or euthanasia). This strategy is recommended for the Lake Victoria Cichlid SSP, in which fish are kept in large groups but dominant males are distinguishable and can be removed, allowing other males to reproduce (Fiumera, Parker & Fuerst, 2000; Hemdal, 2008).

Another factor that impacts mean kinship management is mate choice. The importance of mate choice has been documented in a number of species and can impact the genetic health of the population (Andersson, 1994; Brown, 1997; Duraes, Loiselle, Parker & Blake, 2009; Edwards & Hedrick, 1998; Eizaguirre, Yeates, Lenz, Kalbe & Milinski, 2009; Milinski, 2006; Ryder, Tori, Blake, Loiselle & Parker, 2010). In a managed population in which individuals are being paired, there is some evidence that a lack of choice leads to a decrease in reproductive success. By contrast, there is an increasing amount of data that show that if individual animals are allowed to select their own mate, they tend to make a genetically sound choice (Andersson, 1994; Brown, 1997; Duraes, Loiselle, Parker & Blake, 2009; Edwards & Hedrick, 1998; Eizaguirre, Yeates,

Lenz, Kalbe & Milinski, 2009; Milinski, 2006; Ryder, Tori, Blake, Loiselle & Parker, 2010). These data suggest that genetic prospects for group-managed populations may be better than predictions based on random breeding. However, if there is evidence that only one or a few animals are being selected for breeding, managers may increase the effective size by turning dominant individuals “off” (similar to above). In addition to individual pairings, sexual selection sometimes necessitates that species be housed in large groups instead of as individuals and so cannot be managed as such. The Allee effect is a negative density-dependent effect on reproductive success (Moller & Legendre, 2001). There is a lack of breeding and reproductive success of females at low population densities due to an absence of suitable males from which to choose in the population.

Population growth rate is another example of a biological factor that influences management. R-selected species tend to be highly fecund, with little parental investment; K-selected species tend to be long-lived, with few offspring that receive extensive parental investment (MacArthur & Wilson, 1967/2001). Although r-selected species tend to fall in the higher groups categories (Table 1), they may have an advantage in terms of management because of how they can be managed. These species may require fewer resources to house, so the carrying capacity can be increased. In addition, management disposition may mean that it's easier to breed more often and to manage offspring in a way to maximize effective size (e.g., euthanizing animals to equalize sex ratio, sending animals outside of the managed population to minimize variance in the number of offspring each individual produces).

Focusing on biological factors to guide genetic management will require a paradigm shift in captive genetic management. Genetic management guides how species breeding behavior is managed. Successful group management techniques will allow for the converse, in which species behavior guides genetic management.

Managing Physical Factors

There are many physical factors which impact the potential for group management, mostly because they impact the ability of an institution (or ranch or park or reserve) to control how groups of animals are subdivided into populations and how individuals can migrate between populations.

Instead of focusing on a single population of individuals, successful group management will require that populations are managed at the subpopulation level, creating what is essentially a management metapopulation. Metapopulations are discrete local breeding populations connected by migration (Hanski & Simberloff, 1977). Levins (1969) defined metapopulations as sets of discrete, local breeding populations that are small and extinction-prone, with migration occurring between populations and with asynchronous dynamics. Group management could reflect this simple model, with “management” including a level of control over subpopulation structure and migration rates. Group management strategies will also have to give direction on how populations are configured, either as a single large or several small subpopulations. Genetic diversity in the total population should be higher for several small populations than for a single large population of the same total size (Chesser, 1991; Kimura & Crow, 1963; Lande, 1995), because the random impact of drift works differently on each subpopulation, minimizing loss of alleles in the overall population. Data from an experiment using

Drosophila also offered support for the genetic benefits of several small populations, with pooled data having lower average inbreeding, higher genetic diversity, and higher fitness (Margan, Nurthen, Montgomery, Woodworth, Lowe, Brisco & Frankham, 1998). One genetic problem in small populations is inbreeding, as fewer individuals result in a faster increase in inbreeding over time. If inbreeding decreases fitness in the subpopulations, it could lead to subpopulation extinction(s), resulting in a loss of alleles from the subpopulation(s) and eliminating any benefit of population subdivision. A management strategy to address that risk is one that maintains distinct subpopulations, with occasional migration to prevent extensive inbreeding and extinctions (Lacy, 1987; Margan, Nurthen, Montgomery, Woodworth, Lowe, Brisco & Frankham, 1998; Caballero, Rodríguez-Ramilo, Ávila & Fernández, 2010).

The goal of group management is to provide a strategy that is biologically feasible for the species, but also logistically feasible for the managing institution(s). For example, if a zoo has the ability to hold a total of 60 sable antelope (*Hippotragus niger*), the group management strategy would have to consider if physical resources were adequate to allow separation of the animals into two groups of 30 individuals each, or three groups of 20 individuals, etc. The advantage of additional population subdivisions in a polygynous species is that more males would have a chance to be dominant and produce offspring. Even when considering physical factors, biological factors cannot be ignored. Groups would have to be of a large enough size to prevent rapid inbreeding and also to maintain appropriate behaviors necessary for reproduction. For example, flamingoes have demonstrated an Allee effect of negative density-dependent reproduction (Allee, 1931; Berec, Angulo & Courchamp, 2007; Pickering, Creighton & Stevens-Wood, 1992;

Stevens, 1991). This is likely due to elaborate breeding displays that bring the flock into reproductive synchrony (Stevens, 1991). A metapopulation management strategy would need to take into account the fact that without a flock, there is no reproduction. Also to be considered is that in captive situations, subpopulation carrying capacity can often be set by management; in wild populations, it is dependent upon available habitat.

Migration between populations provides gene flow to reduce differences among populations generated by selection and drift and to reduce inbreeding by introducing unrelated or less related individuals into the breeding pool. Management of migration involves consideration of (1) which individuals migrate, (2) to which populations they migrate, and (3) how often migration occurs.

Group management can be used to migrate individuals in a way that mimics natural behavior. Selecting individuals to migrate can be done by using natural dispersal patterns. For example, in a species in which males leave their natal group to find mates, males can be randomly selected to migrate between populations. Selecting the populations between which individuals migrate could also be done randomly. There are a number of potential strategies for migrating individuals that could enhance genetic diversity with only a little extra investment of resources. Wang (2004) proposed a method for migrating animals using F_{ST} , which is a comparison of the average heterozygosity of the subpopulations relative to the total population (Wright, 1931). Genetic distance could also be used. Nei's (1987) genetic distance is a measure of the genetic difference between allele frequencies in two populations or species. Whereas F_{ST} focuses on expected heterozygosity, genetic distance focuses on alleles. In either case, it would require some molecular sampling or some basic pedigree knowledge to establish

values for each of the subpopulations. Managers would have to establish migration rates that balance the need for population differentiation with the need to reduce inbreeding.

Molecular Information

Genetic markers have a strong role to play in group management. Microsatellite and, increasingly, SNP analyses are useful tools for assessing genetic diversity, including relatedness among individuals and populations, breeding behavior, migration rates, and hybridizations (Anderson & Garza, 2006; Russello & Amato, 2004; Slate, Gratten, Beraldi, Stapley, Hale & Pemberton, 2009; Jones & Wang, 2010). One way to use molecular markers in management is to fill in pedigree gaps so that a population can be managed by MK. This includes discerning relationships between population founders (Haig, Rhymer & Heckel, 2008; Jones, Glenn, Lacy, Pierce, Unruh, Mirande & Chavez-Ramirez, 2002; Russello & Amato, 2004; Rudnick & Lacy, 2008). Using molecular information to supplement the pedigree information works best when there are only a few gaps in the pedigree (Fernández, Villanueva, Pong-Wong & Toro, 2005).

The disadvantage of microsatellite and other molecular methods is that isolation and development is very resource intensive. In addition, molecular data must be continually maintained to fill in unknown information as births occur. It also is a less realistic solution for wild than for captive populations because of the need for biological samples from identifiable individuals. Molecular pedigree identification does not meet the need of being able to control breeding pairs, as necessitated by a MK Strategy.

Although the power of genetic markers may not be appropriate for turning groups into MK-managed individuals, it can facilitate management in other ways. Molecular analysis may be used to provide information to move groups into lower categories,

providing more tools for management. Molecular markers can also be used to characterize the breeding behaviors and subpopulation structures of a population. That information could be used to help guide migration patterns between subpopulations in a way that might enhance genetic diversity in the overall population. As mentioned above, the ideal management migration scheme has not been established, but some models have been proposed (Wang, 2004). The Indian tiger (*Panthera tigris tigris*) population provides a good example of how a broadly accepted strategy would be useful. In this population, molecular data revealed significant differences between the subpopulations (compared with zoo animals as a reference) (Sharma, Stuckas, Bhaskar, Rajput, Khan, Prakash Goyal & Tiedemann, 2009). Although the data indicate differences, there is still a need for recommendations on how to translocate tigers between the subpopulations.

Incorporating molecular data also provides a new level of information that opens up a wider array of management questions, especially in regard to the level of genetic diversity that should be preserved. For example, if it is possible to characterize the alleles in a population, is the goal to maximize gene diversity by decreasing the variance in those alleles, or is it to maintain the original allele frequencies as they exist or were sampled from the wild? There are methods for achieving both (Ballou & Lacy, 1995; Caballero & Toro, 2002; Saura, Perez-Figueroa, Fernandez, Toro & Caballero, 2008; Caballero, Rodríguez-Ramilo, Ávila & Fernández, 2010) and the management strategy will depend upon the goal of either preserving all the sampled alleles for the uncertainties of the future or upon perpetuating the population allelic structure as it currently exists. Or, if historical DNA analysis is possible, the question arises if those frequencies are the

ones that should be used to reconstruct a population before it was diminished or extirpated (Russello & Amato, 2007).

Cost of Group Management

There is a genetic cost to group management. Studies show that minimizing the overall kinship is more effective in reducing loss of genetic diversity than other proposed management methods (Ballou & Lacy, 1995; Montgomery, Ballou, Nurthen, England, Brisco & Frankham, 1997; Fernandez & Toro, 1999; Toro, Silio, Rodriguez, Rodriganez & Fernandez, 1999; Saura, Perez-Figueroa, Fernandez, Toro & Caballero, 2008). However, this cost must be compared to the benefits of group management. The most obvious benefits are reduced resource requirements. Keeping animals in a single group as opposed to separate enclosures reduces facilities and staff costs. Staff costs are reduced if, in species that are obligate group breeders (e.g., flamingoes), there is no longer a need to constantly monitor the group to record the breeding activities of individual animals. Costs of transport are decreased if there is no longer a need to move animals to create ideal breeding pairs. There are also demographic benefits to group management. Most notable is the potential to increase carrying capacity for some species if they can be housed in large groups rather than in individual enclosures. In addition, there may be welfare benefits of allowing animals to live and breed in more natural social groupings. The challenge for managers will be to balance these costs and benefits. At this point, most captive programs define success by genetic diversity, with the general accepted goal of maintaining 90 percent gene diversity for 100 years, while keeping inbreeding below that of the population's average mean kinship. What will happen if group management, as opposed to MK management, decreases retention of gene diversity by one percent?

Two percent? Five percent? And on. It will depend both upon the level of benefit (e.g., it's easier to provide separate containment for a partulid snail than a sable antelope) and the tolerance of the species or taxa in question to tolerate a genetic decline (Lacy, 1993; Ralls, Ballou, & Templeton, 1995)

There is also a cost to not having group management strategies. There are captive and wild populations in need of genetic management that cannot be managed by MK. Many of these populations would benefit immediately from group management.

Conclusion

Mean Kinship is the most widely accepted strategy to genetically manage animals in captivity. However, there are many species for which MK, an individual based model, cannot work. These are groups – populations for which pedigree information is missing and pairing cannot be controlled. These populations, both in captivity and in the wild, are in need of a genetic management plan that is an alternative to MK.

Group management is relevant to captive populations as there are a wide variety of species in need of propagation and long-term sustainability. More and more of these species have a conservation relevance and do not fit the charismatic megafauna mold, but rather are the intriguing media- and minifauna that exhibit and exist better in larger natural social groupings. Group management will be especially useful in managing wild populations, where it is virtually impossible to maintain a pedigree and control pairings. This is especially relevant in parks and reserves where populations are small, resources are limited, and animals are already being actively managed.

An example of a species that represents many of the complexities of group management is the scimitar horned oryx (*Oryx dammah*). This species is a large

ungulate, indigenous to arid lands in Northern Africa that lives in polygynous herds of 20 – 40 individuals. Although the dominant male is the most successful breeder, other males also have opportunities to breed. From the biological perspective, this species should be managed as a group, because, even in captivity, it is difficult to manage in an appropriate social structure and still select two specific individuals for breeding; there are also significant gaps in pedigree information. Although this species is listed by IUCN as extinct in the wild, there is a large global captive population, with hundreds of animals in zoos, hundreds of animals in a few fenced reintroduction sites, and thousands of animals on game ranches and in private herds. In zoos, which typically have limited space but sufficient facilities and resources, this species could fit into category 1 or 2 and be managed by MK. In larger zoological breeding parks, which have thousands of acres of land in addition to sufficient facilities and resources, this species fits more in a group category 3 and MK management becomes more difficult. In the private herds and game ranches and in the reintroduction sites, which have ample space and varying resources, this species cannot be managed by MK and ranges between categories 4-6. To compound the management issue, there are efforts to develop a world herd that maximizes genetic diversity and demographic stability in captive, reintroduced and, ideally some day in the future, wild populations. Because of the international cooperative efforts for this program, management for this species should not be broken up into several distinct pieces (North America, Europe, the Middle East, Africa, etc.). Instead, there should be one overarching group management strategy for this species that will address the management and movement of animals within and between all these very different entities.

Chapter 2: Group Genetic Management Strategies.

Introduction

Genetic variation is essential for the long- and short-term survival of populations and individuals. As the basis for evolution, genetic variation allows populations to adapt to changing environments (Allendorf, 1986; Lewontin, 1974; Sealander, 1983) and many studies have shown its direct impact on individual fitness (Allendorf & Leary, 1986; Hedrick, Brussard, Allendorf, Beardmore & Orzack, 1986; Lacy, Petric, & Warneke, 1993; Ralls, Ballou, & Templeton, 1995; Wildt, Bush & Goodrowe, 1987). Small populations are especially susceptible to loss of genetic variation through the process of genetic drift (Nei, Maruyama & Chakraborty, 1975). This random fluctuation in allele frequencies can greatly impact the genetic composition of small populations, hastening their demise.

Many populations of species are becoming endangered due to their shrinking size. The world's antelope are among them, with a quarter of all antelope species threatened with extinction (Shurter, 2009). The World Conservation Union's (IUCN's) Antelope Specialist Group conducted an assessment that showed out of 91 species of antelope, 25 are threatened with extinction as their populations decrease, mostly due to unsustainable harvesting and habitat loss (IUCN, 2008; Mallon & Kingswood, 2001; Shurter, 2009). Saving these species is not only a global conservation imperative, but also a local survival imperative for the communities that depend upon these animals for their sustenance (Mallon & Kingswood, 2001).

There are numerous antelope conservation programs, including several captive breeding and reintroduction programs for those that are most in need, like the Critically

Endangered addax (*Addax nasomaculatus*) and the Extinct in the Wild scimitar-horned oryx (*Oryx dammah*). The captive programs, such as the Association of Zoos and Aquariums' (AZA) Species Survival Plan (SSP[®]) and the European Association of Zoos and Aquaria (EAZA) European Endangered Species Programme (EEP) breed individuals to minimize inbreeding and maximize retention of gene diversity, with the general goal of maintaining 90 percent of gene diversity for 100 years (Soulé, Gilpin, Conway & Foose, 1986).

Captive breeding programs around the world currently use a mean kinship (MK) value to select optimal breeding pairs (Ballou & Lacy, 1995). The relationship between two individuals, or the probability that alleles drawn randomly from each of two individuals (i and j) are identical by descent, can be measured by the kinship coefficient (f_{ij}) (Falconer, 1981). The mean kinship of individual i (mk_i) is then defined as the average of the kinship coefficients between that individual and all living individuals (including itself and others of its sex) in the known pedigree. This also equals the average inbreeding coefficient of progeny of this individual if it were mated at random in the population (Crow & Kimura, 1970). Under this strategy, an individual's genetic importance can be determined based on the number and degree of relatedness of all relatives that individual has in the population. Individuals with the lowest mean kinship are priority breeders. Studies show that minimizing the overall kinship is more effective in reducing loss of genetic diversity than other proposed management methods (Ballou & Lacy, 1995; Montgomery, Ballou, Nurthen, England, Brisco & Frankham, 1997; Fernandez & Toro, 1999; Toro, Silio, Rodriguez, Rodriganez & Fernandez, 1999; Saura,

Perez-Figueroa, Fernandez, Toro & Caballero, 2008). A strategy based on MK is the benchmark against which all other strategies are compared.

A MK strategy has only been shown to be effective when the entire pedigree of the population is known and pairings can be controlled. For this reason, many species which do not naturally breed in pairs are managed in atypical social groupings so that the parentage is known and offspring can be identified. Using polygynous antelope as an example, instead of allowing dominant males breeding large groups of females, managers use MK values to structure small, artificial harems in which a chosen male has access to one or a few select females to breed with each year. Non-breeding males often live alone, off exhibit in individual enclosures or, if space is available, in bachelor herds.

Although it is possible, with enough resources and control, to manage antelope using MK values, this and other taxa with polygamous and promiscuous breeding systems would benefit greatly from management techniques that more closely approximate mating systems typically found *in situ*. In the context of population management, I define a “group” as a population for which detailed pedigree information is unknown and/or specific pairings cannot reliably be made (Chapter 1). I identified nine categories for genetic management (Table 1). Polygynous hoofstock tend to fit in the category in which individuals can be identified, parentage is known but pairings cannot be controlled, or in the category in which individuals can be identified, one parent often is not known and pairings cannot be controlled. Populations of these species in smaller institutions can be easily and often preferably managed using MK values. However, populations in larger captive facilities (including zoos, conservation breeding centers, and game ranches) and in the wild cannot be managed using MK values and need

some alternative. Focusing on management at the population level as well as the individual level allows for global programs that include hundreds of captive animals in smaller populations along with the thousands of animals that live in large private herds and in the wild. A population-level management system is especially important in many of the desert ungulate species whose populations are so endangered that intensive captive breeding and reintroduction programs have been implemented at the global level.

Group management techniques that meet genetic goals while allowing animals to live in larger groupings would also reduce management costs and improve the social environment relative to a pair-based management system using MK values. Rather than focus on manipulating individual pairings, as in MK, group management techniques would focus on other factors that influence genetic diversity. These factors include population subdivision, migration rates, and length of time a dominant individual is allowed to breed (Chapter 1).

Manipulating the number of populations impacts both gene diversity and inbreeding levels in a population. Genetic theory predicts that several small populations have a higher collective genetic diversity than a single large population of the same total size (Kimura & Crow, 1963; Chesser, 1991; Lande, 1995). This is because the random impact of drift works independently in each subpopulation, minimizing loss of alleles in the overall population. Experimental data also support the benefits of several small populations (Caballero, Rodríguez-Ramilo, Ávila & Fernández, 2010; Margan, Nurthen, Montgomery, Woodworth, Lowe, Brisco & Frankham, 1998), although one risk of small subpopulations is inbreeding depression and heightened risk of extinction, as fewer individuals mean a faster increase in inbreeding over time.

Controlling migration between subpopulations is a way to reduce inbreeding by introducing un- or less related individuals into the subpopulations (Caballero, Rodríguez-Ramilo, Ávila & Fernández, 2010; Margan, Nurthen, Montgomery, Woodworth, Lowe, Brisco & Frankham, 1998). Management of migration involves consideration of: (1) which individuals migrate; (2) to which subpopulations they migrate; and (3) how often migration occurs. Migrating or moving animals carries a financial cost to the institutions and a physical cost to the animals, so the most efficient management strategy would be one that keeps movement between subpopulations to a minimum. Group management can be used to migrate individuals in a way that mimics natural behavior. Selecting individuals to migrate can be done by using natural dispersal patterns. For example, in a species in which males leave their natal group to find mates, males can be randomly selected to migrate between subpopulations.

The tenure of a dominant male can impact the effective size of the population. Small populations are more susceptible to loss of genetic diversity than are large populations. Due to demographic conditions such as sex ratio, the number of breeders and the mean and variance in numbers of offspring, the genetically effective size of a population is often smaller than the census size. Wright (1931) introduced the concept of effective population size (N_e) as the number of individuals in an ideal population that would lose heterozygosity at the rate observed in the real population. Genetic diversity is lost at a rate of $1/2N_e$ per generation, so the smaller N_e , the faster genetic diversity is lost. Maximizing the number of breeders, equalizing the sex ratio, minimizing variance in the number of offspring among breeders and equalizing population sizes across generations can all increase N_e (Lande & Barrowclough, 1987; Wright, 1931).

Although each of these factors has been shown to affect retention of genetic diversity, they have not been manipulated and tested as a management strategy against one based on MK values. In contrast with management by MK, there are no commonly accepted strategies for group management.

In this paper I use computer simulations to compare the success of various group management strategies in retaining gene diversity and controlling inbreeding. I ran 489 scenarios that varied the number of subpopulations, migration rates, and the length of time males were used as herd sires. I also varied the percentage of the population that was managed using MK. A blended management strategy – in which a portion of the population is managed using MK values – might be appropriate for species that are managed in a variety of facilities that range from housing small groups to large herds. The computer simulations allowed us to compare the strategies and identify those factors that performed best at retaining gene diversity and controlling inbreeding.

I chose to use the addax (*Addax nasomaculatus*) studbook as a dataset representative of and applicable to other polygamous species. Like other captive populations, addax are distributed across the country and around the world in herds ranging in size from a few individuals in smaller zoos to dozens of animals in the larger conservation centers. In the case of the Addax SSP program, two facilities hold half of the population. Fossil Rim Wildlife Center (FRWC), a site of approximately 1,700 acres in Texas, has a carrying capacity of 60 animals and San Diego Wild Animal Park (SDWAP), an 1,800 acre site in California, can hold 40. Amongst the other zoos, there are a few facilities that have the potential to hold small herds of animals (15-20 individuals) and others that can hold only a few individuals.

The goals were to determine (1) whether group management could be considered as an alternative to MK management, (2) whether there was a group management strategy that could be recommended for the Addax SSP population, and (3) whether general recommendations could be made on how to manipulate the management variables for use in group management of other polygynous species.

Methods

I developed a stochastic simulation model (Figure 1) (Ivy, 2010) in C++, for which code is available upon request. I used the simulation to compare the effects of different group management strategies (Table 2) on retention of genetic diversity in a population after 100 years of managed breeding. Specifically, I evaluated the strategies based on their effectiveness in retaining gene diversity while keeping inbreeding to a minimum in the overall population.

I imported data from the addax studbook for my analyses. Studbooks are species-specific records that contain information on captive populations, including animal identities, sexes, parentage, locations, and event dates such as births, deaths, and transfers. Many ungulates have a long captive history and studbook data are used as a starting point to look at the effects of management on an actual population instead of a hypothetical, more idealized one.

Although one of the reasons to develop group management strategies is to minimize or eliminate the need for studbook data, this pedigree information is necessary in the simulation to calculate demographic parameters for the model as well as values for gene diversity and inbreeding which allows us to compare the effects of different strategies against MK management. In addition, group management for some of the

Figure 1. Primary Components of the Stochastic Simulation Model. Parameters include studbook data such as population size, sex, parentage, age, location, kinship, age of first and last reproduction and stage-based mortalities; they also include direction on breeding strategy, subpopulation structure, carrying capacities, migration rates, and harem male tenure.

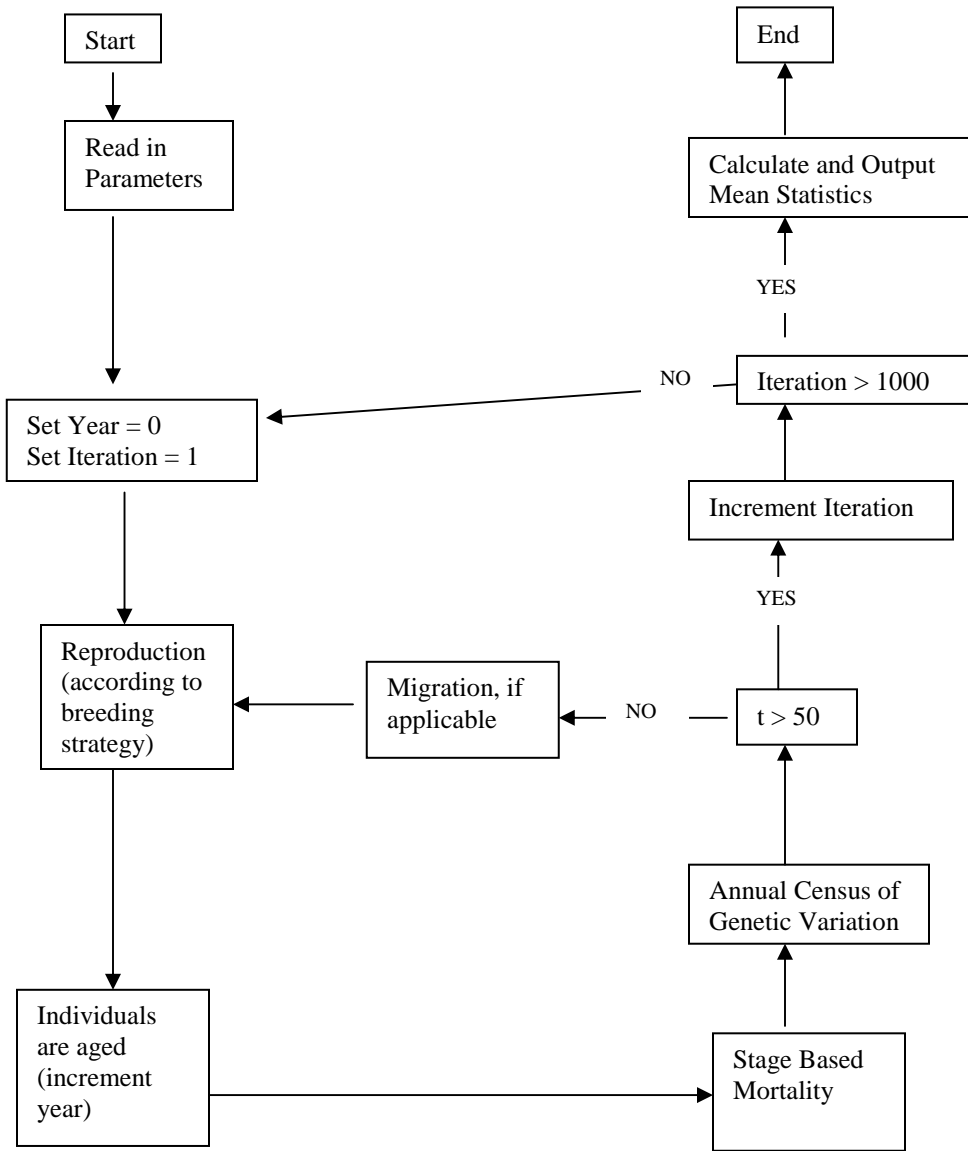


Table 2. Management Strategies Tested. In MK breeding, individuals are selected to breed according to their kinship value. In non-MK breeding, breeding individuals are selected randomly from the population. In all strategies, migrants are selected randomly as are the populations between which migrating individuals are exchanged. Migrants are selected as pairs to be exchanged in order to keep populations sizes stable.

Number of Subpops	Subpop size	Breeding Scheme ¹	Male Tenure ²	Migrants / Year
1	200	MK 100%; MK 0%; Random 100%	2, 5, 10, 18	NA
3	Subpop 1 = 60 Subpop 2 = 40 Subpop 3 = 100	MK 100%; MK 70%; MK 50%; MK 30%; MK 0%	2, 5, 10, 18	0, .2, .5, 1, 2, 4, 10, 20
5	Subpop 1 = 30 Subpop 2 = 30 Subpop 3 = 20 Subpop 4 = 20 Subpop 5 = 100	MK 100%; MK 70%; MK 50%; MK 30%; MK 0%	2, 5, 10, 18	0, .2, .5, 1, 2, 4, 10, 20
8	Subpop 1 = 30 Subpop 2 = 30 Subpop 3 = 20 Subpop 4 = 20 Subpop 5 = 50 Subpop 6 = 20 Subpop 7 = 15 Subpop 8 = 15	MK 100%; MK 70%; MK 50%; MK 30%; MK 0%	2, 5, 10, 18	0, .2, .5, 1, 2, 4, 10, 20

1. MK 70% indicates the proportion of individuals in population managed under an MK strategy, with 30% managed under the Group strategy.
2. Number of years the breeding male is used in each subpopulation.

lower group categories may involve a combination of group and MK management that will require that some individuals be identified.

I chose addax as the model species as the management and life history characteristics of this species are representative of a number of polygynous antelope. Addax herds are led by a dominant male that breeds year round with multiple females. Females produce a single offspring each year. Individuals become reproductively viable at around 3 years of age and reproductively senescent in their late teens. Addax were also chosen because they are a Critically Endangered species (IUCN 2008) with an active captive breeding, conservation, and reintroduction program (Newby & Wachter, 2008; Woodfine, Gilbert & Engel, 2004). The wild population in northern Africa is estimated at fewer than 300 individuals (Newby and Wachter, 2008); however, there are hundreds of individuals in zoos throughout the world and thousands more in private reserves (Gilbert, T., personal communication, 2009).

I imported data for an initial population of 186 individuals into the model (Figure 1). This number comprised all the managed addax in the AZA SSP program. Data were taken from the 2008 Addax Analytical Studbook (Spevak, 2009) and included information on each individual, including sex, parentage, age, location, and a kinship matrix of living animals created using PM2000 (Pollak, Lacy & Ballou, 2005). Inputs also included demographic information for both males and females, including age of first and last reproduction and juvenile, adult, and geriatric mortalities (Table 3). Carrying capacity for the total population was set at 200 individuals, the goal set by the AZA Antelope and Giraffe Taxon Advisory Group (TAG) (Fischer, 2009).

Table 3. Demographic parameters used in the simulation. Demographic data were calculated from the analytical studbook (Spevak, 2009). Although animals can live beyond 18 years, that age was treated as the cutoff because that is the age at which managers consider an animal too old to move or recommend for breeding.

	Males	Females
Age of First Reproduction	3	3
Age of Last Reproduction	18	16
Annual Infant Mortality (age 0-1)	.25	.25
Annual Adult Mortality (Age 1-16)	.08	.08
Annual Geriatric Mortality (age 16+)	.25	.25
Maximum Age	18	18

After importing the data, the population was modeled either as a single large population, or divided into several subpopulations (Table 2). Each year enough animals were bred to produce the offspring needed to maintain the population or subpopulations at carrying capacity. The number of offspring necessary to keep the population at carrying capacity was determined by subtracting the current population or subpopulation size from the carrying capacity, and then adding the number of currently living animals that are expected to experience mortality during the time-step. Individuals were paired according to a specified breeding scheme (defined below) and produced a single offspring per pairing. Offspring had a 50% chance of being either male or female. The kinship matrix was updated after offspring were produced, animals were aged one time-step (one year), and experienced stage-based mortality (rates shown in Table 3). The following genetic parameters were then calculated: Inbreeding was calculated as the average inbreeding coefficient (F); genetic variation was calculated as the proportional gene diversity (GD), which was $1 - \bar{m}k$, where $\bar{m}k$ was the average mean kinship in the population (Ballou & Lacy, 1995). If specified as part of the strategy, migration between subpopulations then occurred at the prescribed rate. Each simulation was run 1000 times using a different random number seed to select breeders and migration patterns. I did not include selection, mutation, or immigration into or emigration out of the total population in the models.

To examine the effect of different group management strategies on genetic diversity, I designed 489 scenarios based on combinations of the following four variables: the breeding scheme (percent of the population managed by MK vs. “group management” – see below), population structure (number and size of subpopulations),

migration rates, and the length of time a single male was kept as the dominant breeder (male tenure).

Breeding Scheme

One of the variables that affect the success of a management strategy is the breeding scheme. I compared a 100% MK breeding scheme, a 100% group breeding scheme, and combinations of MK and group management (e.g., 50% animals managed using MK, 50% with “group management”). I also compared these results with those from a single, randomly breeding population.

To simulate MK management, MK values were calculated each year for all individuals in the population. The two individuals with the lowest MK values were paired, without replacement (each animal could be paired only once each time-step), and produced a single offspring. MK values were recalculated and the next pair was selected. This process was repeated until the target number of pairs was reached. Although all pairs reproduced, not all offspring survived to the next time-step due to infant mortality. In order to minimize inbreeding, couples with a kinship value greater than the average MK were not paired and the next best pairing was chosen (as is done in practice).

In group management, breeding was simulated by randomly selecting one male to breed with randomly selected females in that subpopulation. Each female produced one offspring per year. Offspring were produced until carrying capacity for the subpopulation was reached. Once a given male was selected for breeding, he continued to be the breeding male until he either (1) reached the maximum number of breeding years specified or died. If a male bred for the maximum number of years specified and remained alive, that male was not selected again for breeding.

I examined a mix of MK and group breeding populations as part of a blended management scheme. This scheme simulated a realistic management strategy by which smaller institutions with less space and fewer animals could manage their animals using MK while larger facilities and managers working in situ could allow animals to breed naturally in polygynous herds. Mixed breeding strategies included subpopulations with 70% group management/30% MK management, 50% group management/50% MK management, and 30% group management/70% MK (Table 2)

The final breeding scheme in the comparison was a single, randomly breeding population. During the random breeding process, a male and a female were randomly selected to pair, without replacement each year, to produce one offspring. Random breeding pairs were selected until carrying capacity was reached. As with the random breeding option in group breeding, some individuals never reproduced and others reproduced multiple times with the same or different partners over their lifetime.

Population Structure

To test the impact of subpopulation division, I modeled addax as: (1) one population; (2) three subpopulations, in which the SDWAP and FRWC each managed a large herd, while the rest of the population was managed by MK; (3) five subpopulations, allowing SDWAP and FRWC to split their large herds into two subpopulations each; and (4) as eight subpopulations, in which SDWAP and FRWC each had two subpopulations, three breeding centers were created with carrying capacities of 20, 15, and 15 individuals each, and the remaining 50 animals were managed as a single subpopulation (Table 2).

Migration

Subpopulations between which migration occurred were selected randomly. In order to maintain relatively constant subpopulation sizes, pairs of individuals were traded between subpopulations. In a single migration event, two subpopulations were randomly selected, with replacement, between which the pair of male migrants was exchanged. Migrants were selected randomly without replacement (a given male could not move more than once during a given time-step) and traded between subpopulations. This process was repeated until the total number of migration events specified each time-step was reached.

In this simulation, reproductive males were randomly selected to migrate, as that is how it would most likely occur in managed and wild populations. I compared eight migration strategies (Table 2) ranging from no migration to twenty migrants per year (ten migrant pairs exchanged). In this simulation, the act of migration has no impact on fecundity or mortality.

Male Tenure

In a polygamous mating system, in which a dominant individual monopolizes mates, breeding opportunities for others are lost, reducing the total number of breeders and N_e . I reduced variance in male breeding success by reducing the time a dominant animal was allowed to breed. Breeding males were turned “off” after a specified number of breeding years thus allowing more individuals to breed. In reality, turning an animal off could be temporary (contraception, housing with other post- or non-reproductive animals, sending outside of the managed population) or permanent (castration or euthanasia). In the model, a single male in a harem subpopulation is randomly selected

to pair with all randomly selected females. Once a given male is selected for breeding, he continues to be the breeding male until he reaches the maximum number of breeding years specified or dies. If a male breeds for the maximum number of years specified and remains alive, he is not selected again for breeding. I tested male dominance durations of 2 years, 5 years, 10 years, and 18 years (the duration of a male's reproductive life).

For each scenario, I calculated the mean GD and F based on 1000 iterations after each of 100 years. I present the most effective strategies in three ways: (1) the ten best scenarios of all simulations, (2) the ten best scenarios for a 50/50 group/MK blended management strategy, which is relevant for addax and other managed polygynous ungulates, and (3) the ten best scenarios for 100% group (0% MK) management strategy, which are relevant for a variety of polygynous species in captivity and in the wild.

I used regression analyses to examine the impacts of the independent variables – percent MK management, male tenure, number of subpopulations, migration (Table 2) – on the dependent variables of GD and inbreeding (INB) after 100 years of breeding. Data were transformed by squaring the independent variables to achieve a more linear scatterplot. I added an interaction term to test the relationship between % MK and the other independent variables.

Results

I found that, out of the 489 breeding schemes tested, 100% MK management did better than any of the less controlled breeding schemes at maintaining gene diversity (GD) and minimizing inbreeding (INB) (Figure 2, Figure 3, Figure 4, Table 4). The most effective strategy was a single population managed using MK. The average GD after 100 years of

Figure 2. Ten most effective scenarios for average Gene Diversity over the 100 years of the simulation. All are 100% MK, 0% group management. Included for comparison is a single, MK managed population and a single, randomly breeding population. In the key, the first number is the number of subpopulations, the second is the number of migrants, the third is the number of years that the harem male can breed.

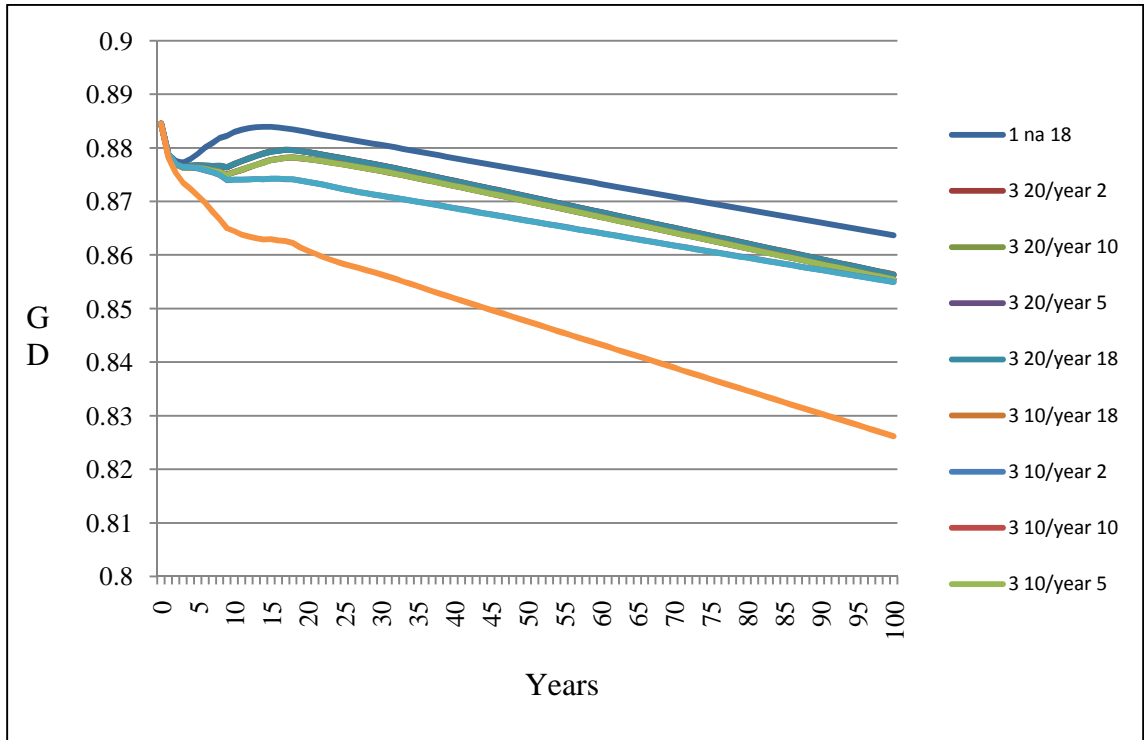


Figure 3. Top 10 scenarios for average Inbreeding over the 100 years of the simulation. All are 100% MK, 0% Group management. Included for comparison is a single, MK managed population and a single, randomly breeding population. In the key, the first number is the number of subpopulations, the second is the number of migrants, the third is the number of years for which a harem male can breed.

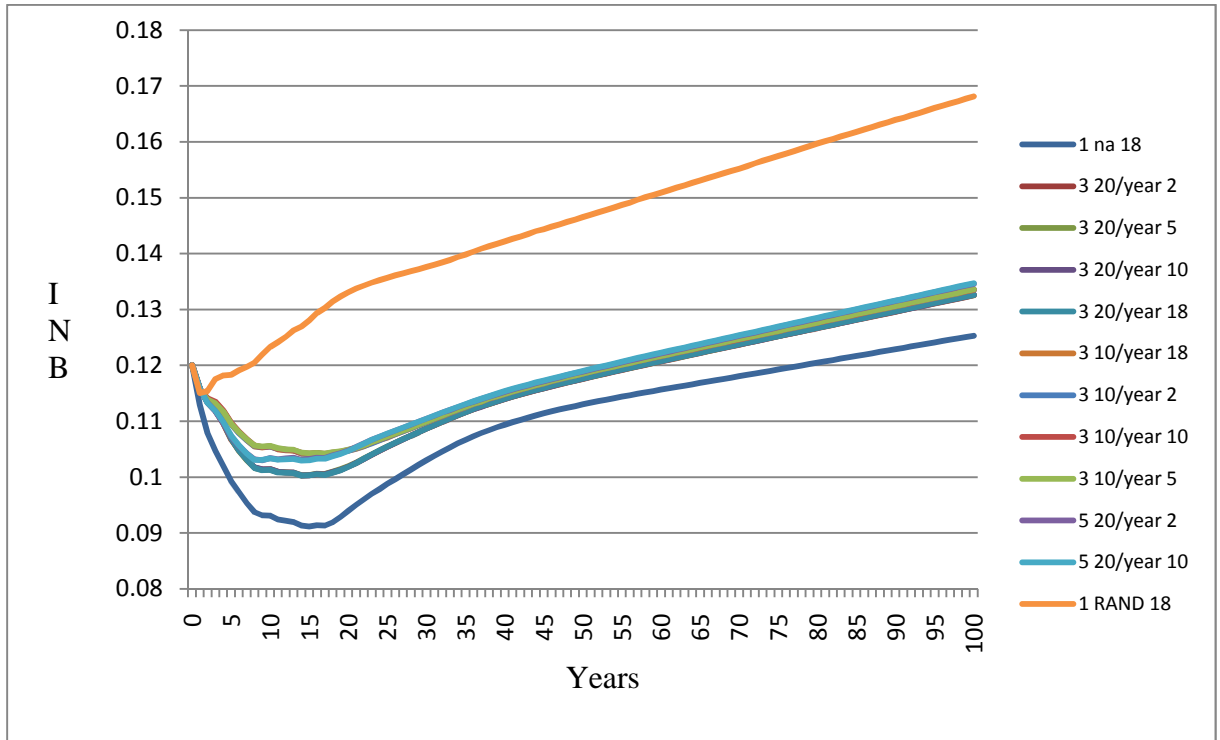
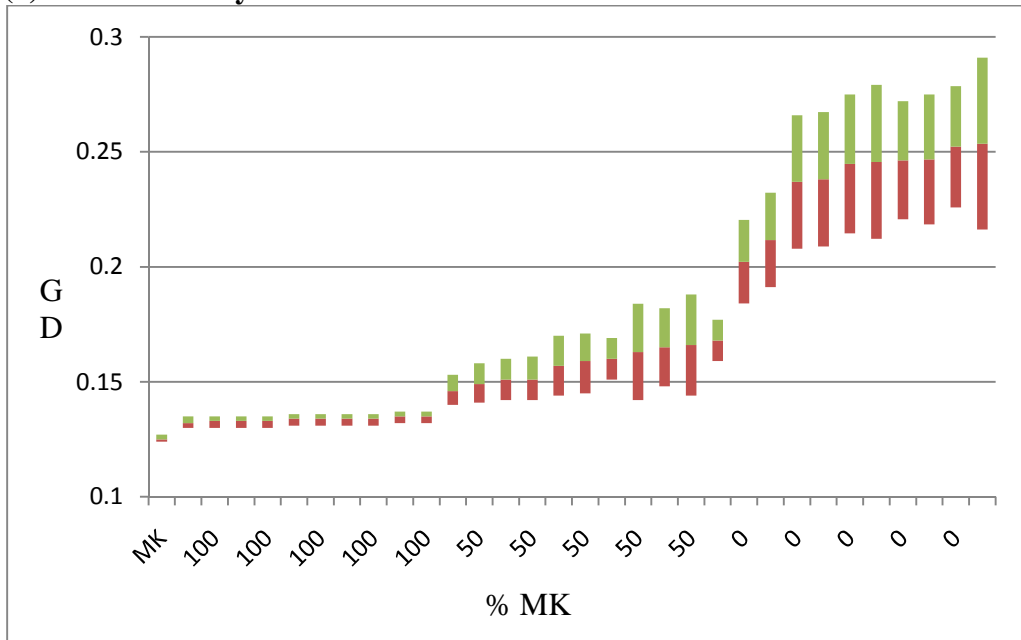


FIGURE 4. Averages and 95% confidence intervals for all strategies tested. Values are based on the averages over 100 simulations after 100 years.

(a) Gene Diversity



(b) Inbreeding

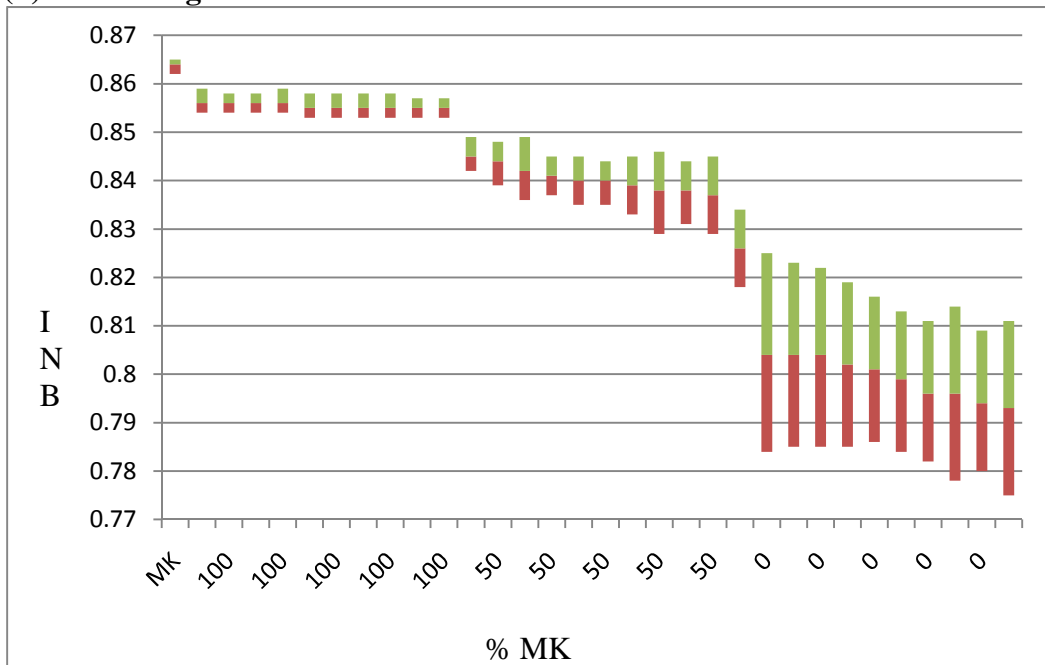


TABLE 4. Comparison of the top scenarios in minimizing inbreeding (a) and maintaining gene diversity (b). All are 100% MK, 0% Group management. Included for comparison is a single, MK managed population and a single, randomly breeding population. Values are based on the averages over 100 simulations after 100 years. Highlighted scenarios are the same in both INB and GD.

(a)

AVERAGE INBREEDING TOP STRATEGIES and RANDOM							
POPS	MK	MIGRATION	HM	AveF100	STDEV	2 stdev below	2 stdev above
1	100	na	18	0.125	0.001	0.124	0.127
3	100	20/year	2	0.132	0.001	0.130	0.135
3	100	20/year	5	0.133	0.001	0.130	0.135
3	100	20/year	10	0.133	0.001	0.130	0.135
3	100	20/year	18	0.133	0.001	0.130	0.135
3	100	10/year	18	0.134	0.001	0.131	0.136
3	100	10/year	2	0.134	0.001	0.131	0.136
3	100	10/year	10	0.134	0.001	0.131	0.136
3	100	10/year	5	0.134	0.001	0.131	0.136
5	100	20/year	2	0.135	0.001	0.132	0.137
5	100	20/year	10	0.135	0.001	0.132	0.137
1	Rand	na	18	0.168	0.004	0.159	0.177

(b)

AVERAGE GENE DIVERSITY TOP STRATEGIES and RANDOM							
POPS	MK	MIGRATION	HM	GD Ave100	STDEV	2 stdev below	2 stdev above
1	100	na	18	0.864	0.001	0.862	0.865
3	100	20/year	2	0.856	0.001	0.854	0.859
3	100	20/year	10	0.856	0.001	0.854	0.858
3	100	20/year	5	0.856	0.001	0.854	0.858
3	100	20/year	18	0.856	0.001	0.854	0.859
3	100	10/year	18	0.855	0.001	0.853	0.858
3	100	10/year	2	0.855	0.001	0.853	0.858
3	100	10/year	10	0.855	0.001	0.853	0.858
3	100	10/year	5	0.855	0.001	0.853	0.858
3	100	0	2	0.855	0.001	0.853	0.857
3	100	0	10	0.855	0.001	0.853	0.857
1	RAND	Na	18	0.826	0.004	0.818	0.834

MK management is .864 and the average INB is .125. In managing one population using MK, the resultant values of GD and INB were the same regardless of male tenure, so only a single value for 1 population, 100% MK management is shown. In the ten next-best strategies, GD after 100 years ranges from .856 to .855 and INB ranges from .132 to .135. None are significantly different from each other, but they are all significantly different from a single population managed using MK (Figure 4, Table 4). In GD, the difference between the MK strategy and the next best strategy is .009, in INB it is .007. All 10 of the best-managed populations did significantly better than a single, randomly breeding population.

Note in Figures 2 and 3 that all strategies show an initial drop in genetic diversity which is due to the death of the oldest animals in the population. In these simulations I set the maximum age at 18 years, which reflected how the animals are managed, but resulted in the oldest animals, several of which were genetically valuable, to be removed from the population at the beginning of the simulation.

The top ten breeding strategies using 50% Group/50% MK management are shown in Figures 4, 5, and 6 and Table 5. This 50/50 strategy is shown because it is a likely management option for addax, where half the population is managed in smaller zoos and the other half is located in two large herds at FRWC and SDWAP. A comparison of average values of GD and INB after 100 years of management is also shown in Table 5. The best overall strategies are those that maximize migration and minimize harem male tenure. Although group management did not do as well as MK management, it did better than a single, randomly breeding population (Figure 4, Table 5). The average INB in MK management is .125 and the GD is .864. In the ten next best

Figure 5. Average Gene Diversity over the 100 years of the simulation. Top 10 scenarios using a mixed management strategy of 50% group management, 50% MK management. Included as part of the comparison is a single, MK managed population and a single, randomly breeding population. In the key, the first number is the number of subpopulations, the second is the number of migrants, the third is the number of years for which a harem male can breed.

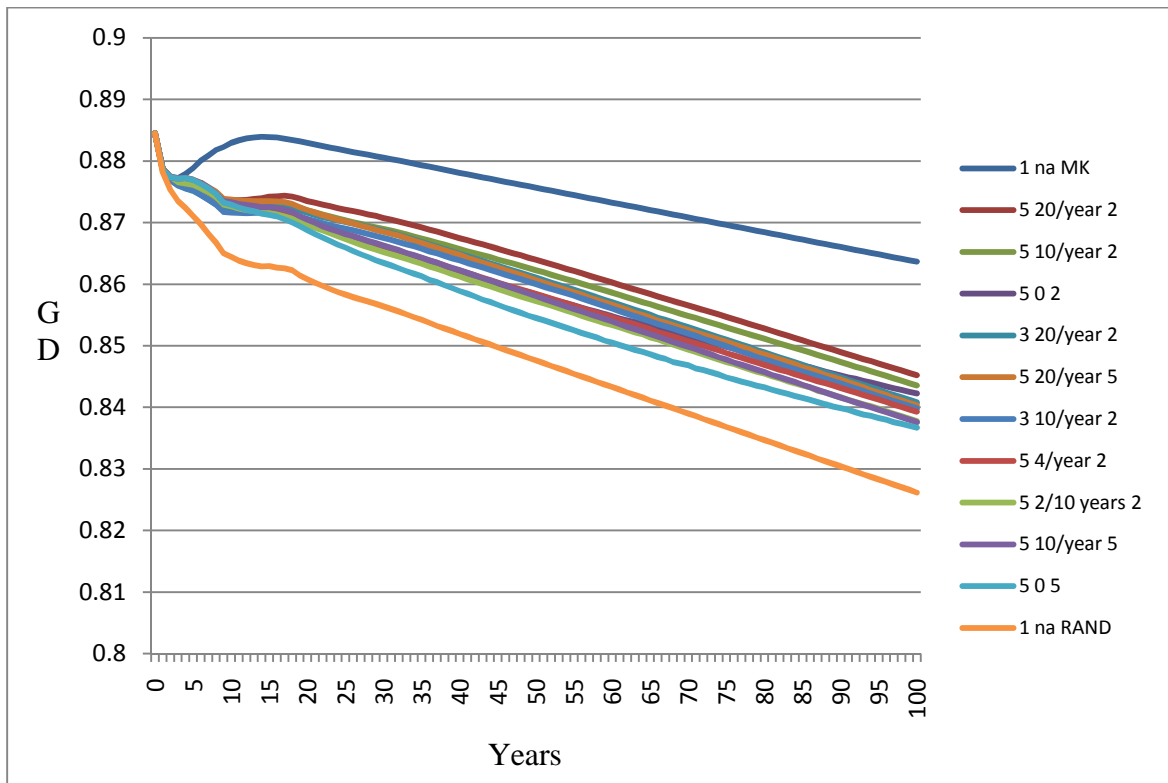


Figure 6. Average Inbreeding over the 100 years of the simulation. Top 10 scenarios using a mixed management strategy of 50% group management, 50% MK management. Included as part of the comparison is a single, MK managed population and a single, randomly breeding population. In the key, the first number is the number of subpopulations, the second is the number of migrants, the third is the number of years for which a harem male can breed.

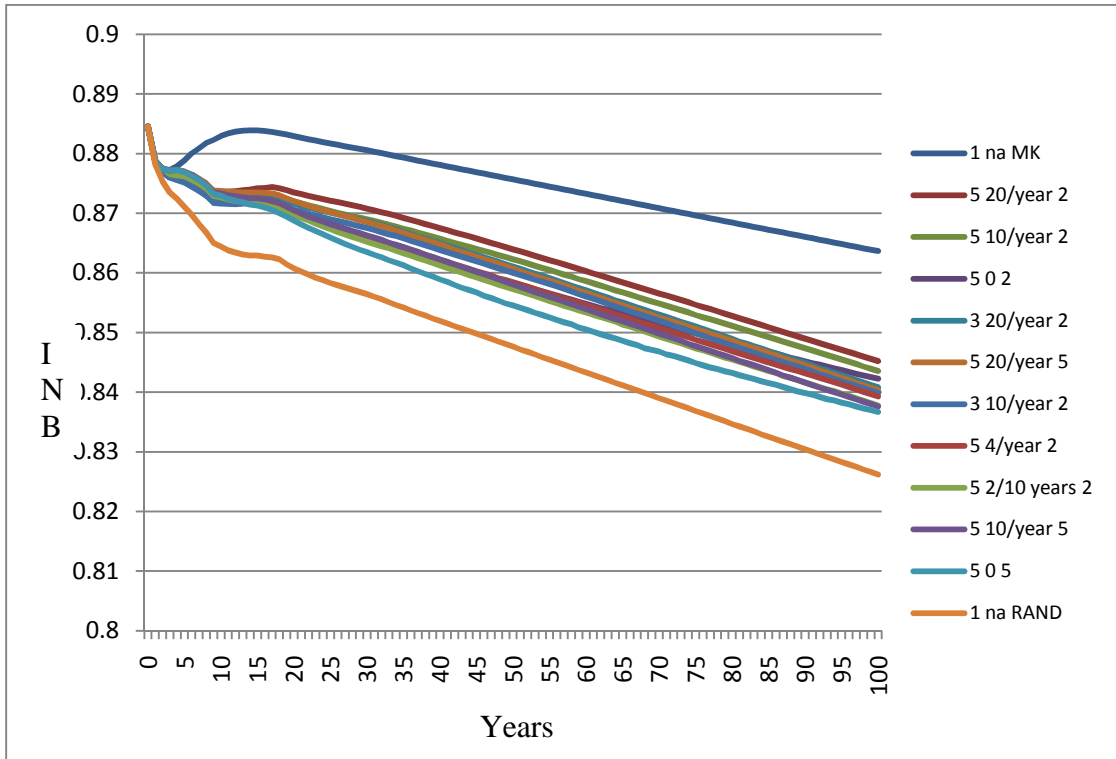


TABLE 5. Comparison of the top scenarios in minimizing inbreeding and maintaining gene diversity. All are 50% group management, 50% MK management. Included for comparison is a single, MK managed population and a single, randomly breeding population. Values are based on the averages over 100 simulations after 100 years. Highlighted scenarios are the same in both INB and GD.

AVERAGE INBREEDING 50%MK							
POPS	MK	MIGRATION	HM	AveF100	STDEV	2 stdev below	2 stdev above
1	100	na	18	0.125	0.001	0.124	0.127
5	50	20/year	2	0.146	0.003	0.140	0.153
3	50	20/year	2	0.149	0.004	0.141	0.158
3	50	10/year	2	0.151	0.005	0.142	0.160
5	50	10/year	2	0.151	0.005	0.142	0.161
5	50	20/year	5	0.157	0.006	0.144	0.170
3	50	4/year	2	0.159	0.007	0.145	0.171
8	50	20/year	2	0.160	0.004	0.151	0.169
3	50	20/year	5	0.163	0.0105	0.142	0.184
5	50	10/year	5	0.165	0.008	0.148	0.182
3	50	10/year	5	0.166	0.011	0.144	0.188
1	RAND	na	18	0.168	0.004	0.159	0.177

AVERAGE GENE DIVERSITY 50% MK							
POPS	MK	MIGRATION	HM	GD Ave100	STDEV	2 stdev below	2 stdev above
1	100	na	18	0.864	0.001	0.862	0.865
5	50	20/year	2	0.845	0.002	0.842	0.849
5	50	10/year	2	0.844	0.002	0.839	0.848
5	50	0	2	0.842	0.003	0.836	0.849
3	50	20/year	2	0.841	0.002	0.837	0.845
5	50	20/year	5	0.840	0.002	0.835	0.845
3	50	10/year	2	0.840	0.002	0.835	0.844
5	50	4/year	2	0.839	0.003	0.833	0.845
5	50	2/10 years	2	0.838	0.004	0.829	0.846
5	50	10/year	5	0.838	0.003	0.831	0.844
5	50	0	5	0.837	0.004	0.829	0.845
1	RAND	na	18	0.826	0.004	0.818	0.834

strategies, average INB ranges from .146 - .166. There are some significant differences between these strategies, and all result in a higher inbreeding level than MK. The results are similar with GD, for which the ten next best strategies range from .845 - .837.

Although there are some differences between the ten strategies, all result in less GD than MK. In INB, the difference between the MK strategy and the next best strategy after 100 years is .021, in GD, it is .018. Managed populations did significantly better at retaining genetic diversity than a single, randomly breeding population.

In many cases of group management, it will not be possible to manage any populations using MK. The top ten breeding strategies are shown for 100% group management (0% MK) in Figures 7 and 8 as well as a comparison of average values of GD and INB after 100 years of management (Table 6). Using MK management, average GD and INB are .125 and .864, respectively. In the ten next best strategies, average INB ranges from .202 - .254. There are some significant differences between these strategies, and all are significantly greater than MK. The results are similar for GD; the ten next best strategies range from .804 - .793, with some significant differences between strategies, and all are less effective than management using MK. In INB, the difference between the MK strategy and the next best strategy is .077, in GD, it is .059. The top 10 managed populations did significantly worse than a single, randomly breeding population.

I performed multiple regression analyses to look at the impact of the management variables on the dependent variables of GD and INB (Figures 9 – 12). In all scenarios, as the percentage of the population managed by MK decreased, the ability to maintain genetic diversity (GD and INB) over the long term also decreased. An interaction term

Figure 7. Average Gene Diversity over the 100 years of the simulation. Top 10 scenarios using a management strategy of 100% group management. Included as part of the comparison is a single, MK managed population and a single, randomly breeding population. In the key, the first number is the number of subpopulations, the second is the number of migrants, the third is the number of years for which a harem male can breed.

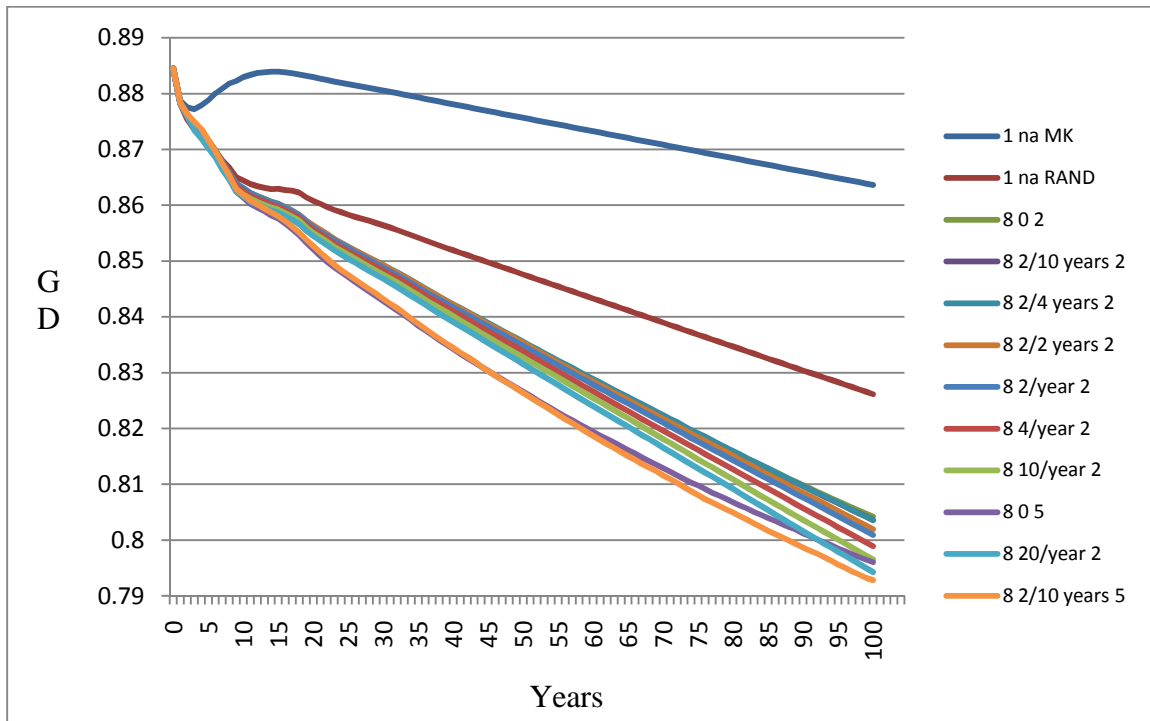


Figure 8. Average Inbreeding over the 100 years of the simulation. Top 10 scenarios using a management strategy of 100% group management. Included as part of the comparison is a single, MK managed population and a single, randomly breeding population. In the key, the first number is the number of subpopulations, the second is the number of migrants, the third is the number of years for which a harem male can breed. Note, the scale of this is twice that of the others in order to display the top 10 strategies.

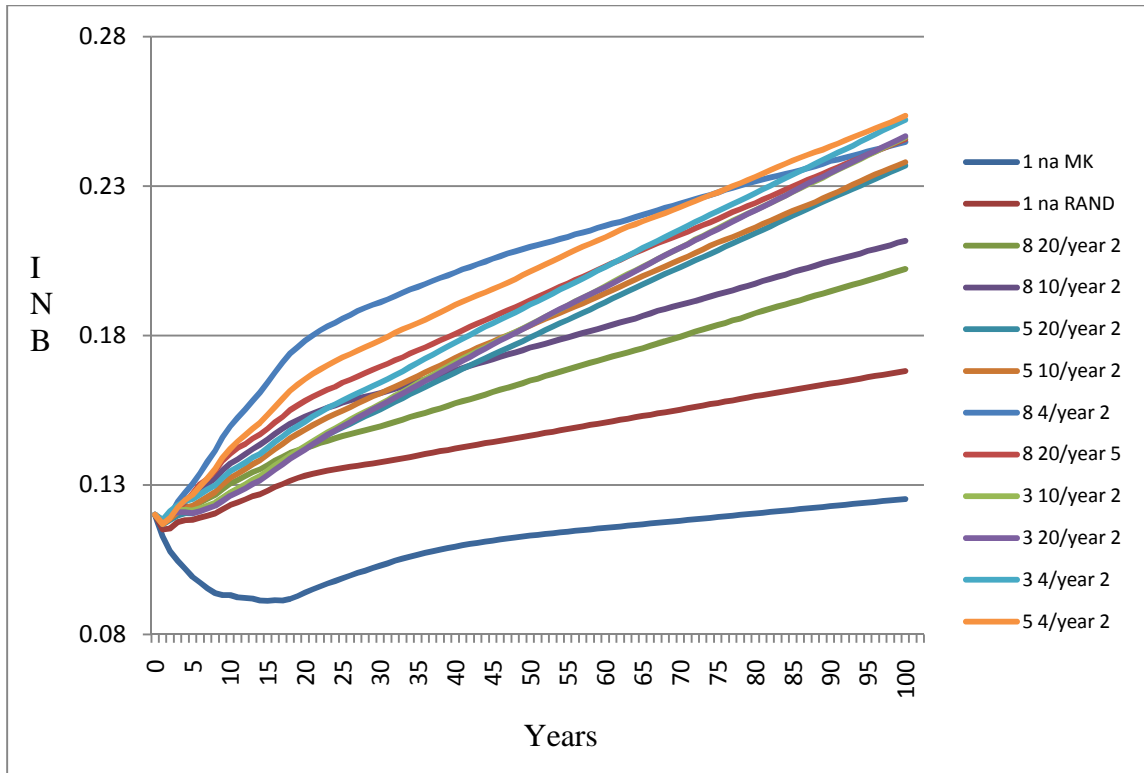


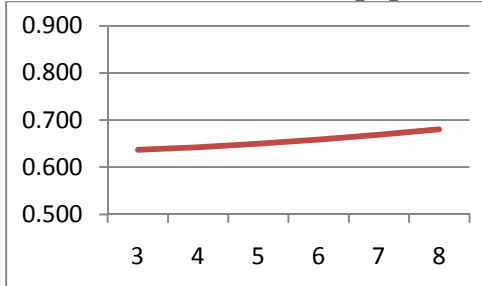
TABLE 6. Comparison of the top scenarios in minimizing inbreeding and maintaining gene diversity. All are 100% group management, 0% MK management. Included for comparison is a single, MK managed population and a single, randomly breeding population. Values are based on the averages over 100 simulations after 100 years. Highlighted scenarios are the same in both INB and GD.

AVERAGE INBREEDING 0%MK							
POPS	MK	MIGRATION	HM	AveF100	STDEV	2 stdev below	2 stdev above
1	100	na	18	0.125	0.001	0.124	0.127
1	RAND	na	18	0.168	0.005	0.159	0.177
8	0	20/year	2	0.202	0.009	0.184	0.220
8	0	10/year	2	0.212	0.010	0.191	0.232
5	0	20/year	2	0.237	0.015	0.208	0.266
5	0	10/year	2	0.238	0.015	0.209	0.267
8	0	4/year	2	0.245	0.015	0.215	0.275
8	0	20/year	5	0.246	0.017	0.212	0.279
3	0	10/year	2	0.246	0.013	0.221	0.272
3	0	20/year	2	0.247	0.013	0.218	0.275
3	0	4/year	2	0.252	0.014	0.226	0.279
5	0	4/year	2	0.254	0.019	0.216	0.291

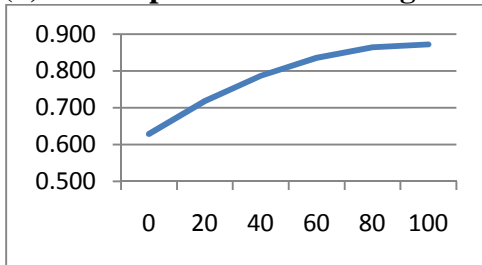
AVERAGE GENE DIVERSITY 0% MK							
POPS	MK	MIGRATION	HM	GD Ave100	STDEV	2 stdev below	2 stdev above
1	100	na	18	0.864	0.001	0.862	0.865
1	RAND	na	18	0.826	0.004	0.818	0.834
8	0	0	2	0.804	0.010	0.784	0.825
8	0	2/10 years	2	0.804	0.009	0.785	0.823
8	0	2/4 years	2	0.804	0.009	0.785	0.822
8	0	2/2 years	2	0.802	0.008	0.785	0.819
8	0	2/year	2	0.801	0.008	0.786	0.816
8	0	4/year	2	0.799	0.007	0.784	0.813
8	0	10/year	2	0.796	0.007	0.782	0.811
8	0	0	5	0.796	0.009	0.778	0.814
8	0	20/year	2	0.794	0.007	0.780	0.809
8	0	2/10 years	5	0.793	0.009	0.775	0.811

FIGURE 9. In populations that have some percentage of MK management, impact on GD ($R^2 = .831$) of (a) number of subpopulations, (b) percent MK management, (c) male tenure, and (d) number of migrants.

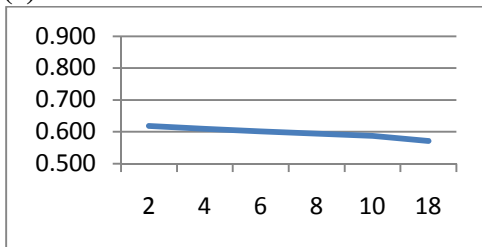
(a) GD vs. number of subpopulations



(b) GD vs. percent MK management



(c) GD vs. male tenure



(d) GD vs. number of migrants

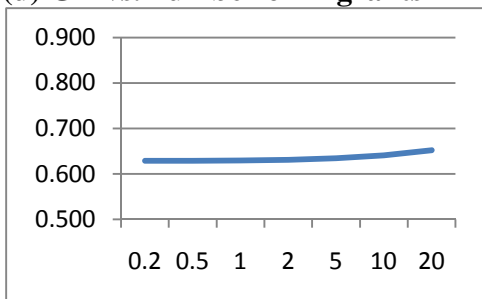
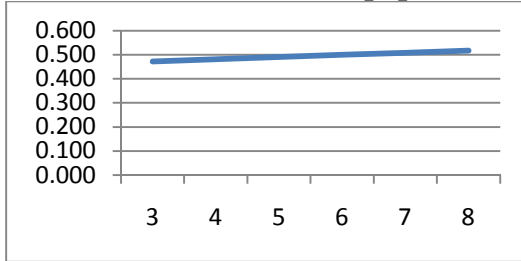
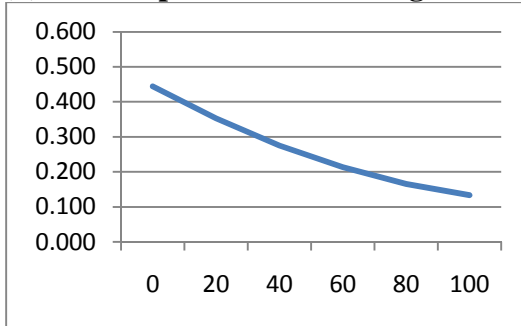


FIGURE 10. In populations that have some percentage of MK management, impact on INB ($R^2 = .836$) of (a) number of subpopulations, (b) percent MK management, (c) male tenure, and (d) number of migrants.

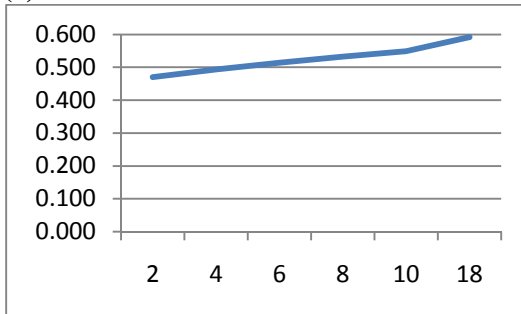
(a) INB vs. number of subpopulations



(b) INB vs. percent MK management



(c) INB vs. male tenure



(d) INB vs. number of migrants

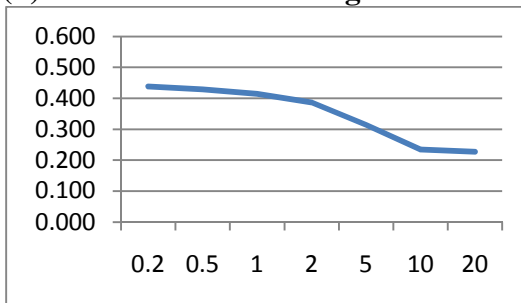
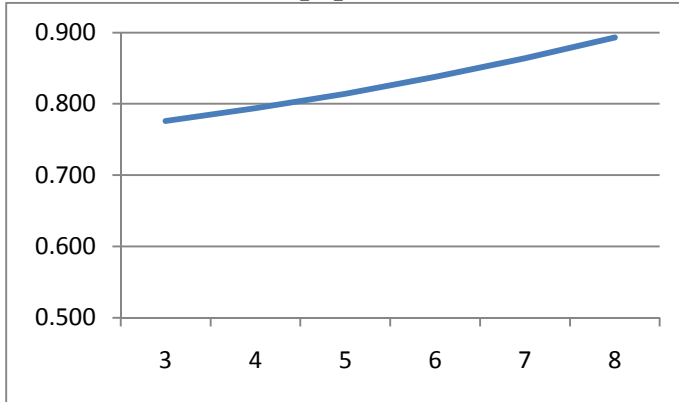
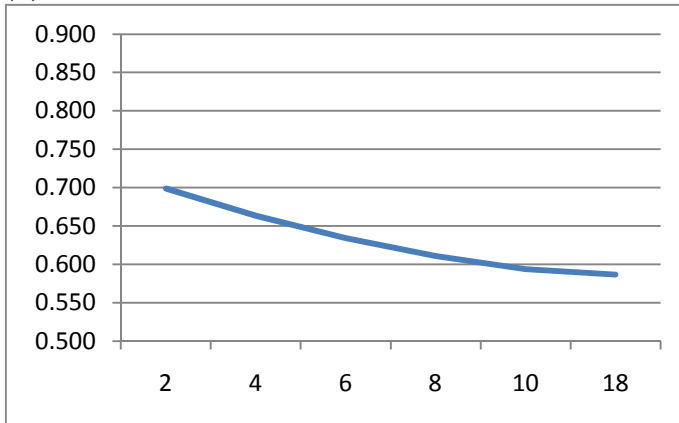


FIGURE 11. In populations that have some 100% group management (0% MK management), impact on GD ($R^2 = .902$) of (a) number of subpopulations, (b) male tenure, and (c) number of migrants.

(a) GD vs. number of populations



(b) GD vs. male tenure



(c) GD vs. number of migrants

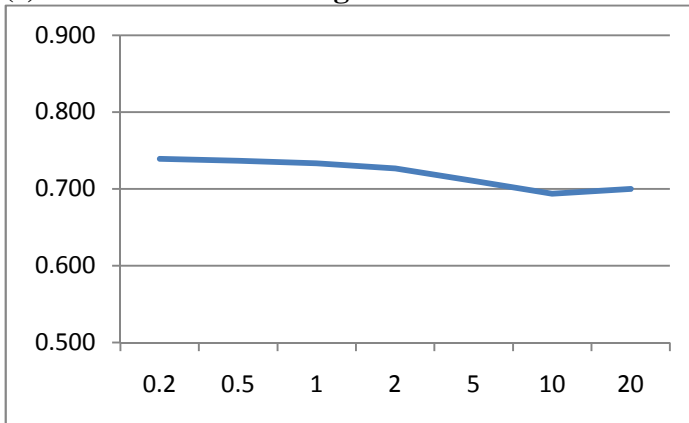
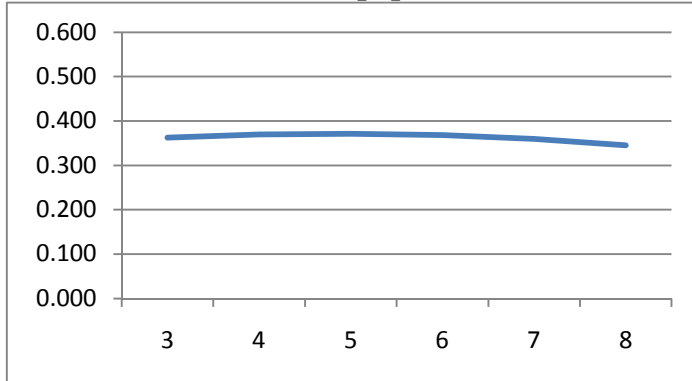
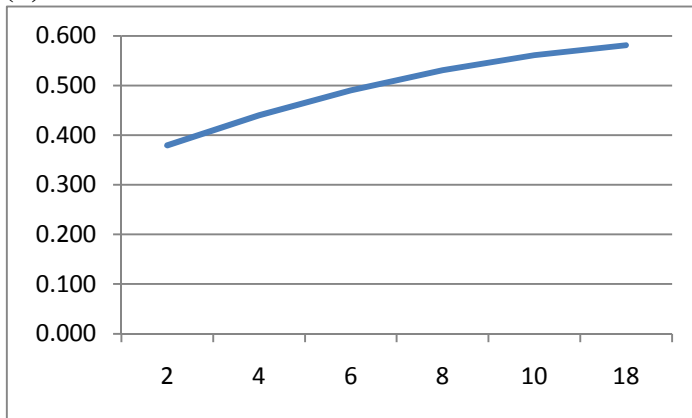


FIGURE 12. In populations that have some 100% group management (0% MK management), impact on GD ($R^2 = .756$) of (a) number of subpopulations, (b) male tenure, and (c) number of migrants.

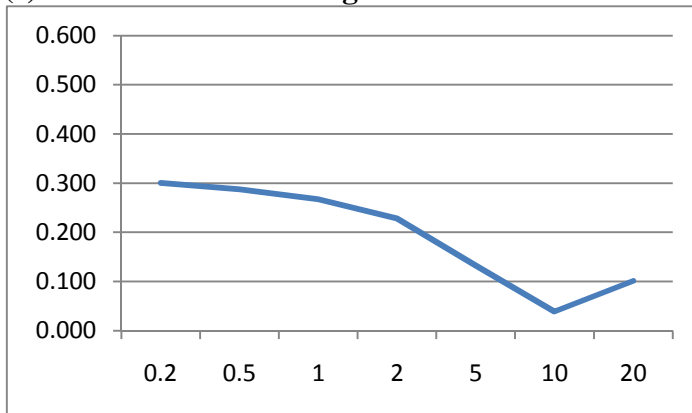
(a) INB vs. number of subpopulations



(b) INB vs. male tenure



(c) INB vs. number of migrants



was added to test the relationship between MK and the other independent variables. When there was no MK management, the impact of the independent variables was sometimes opposite that of MK management. The population was examined in two ways, (1) when there was some form of MK management (percent of MK managed subpopulations > 0) (Figures 9-10) and (2) when there was no MK management (group management only) (Figures 11-12).

Discussion

Mean Kinship is the most widely accepted strategy for genetically managing animals in captivity and my simulation results also show it to be the most successful in retaining gene diversity and minimizing inbreeding. I also found that, as percent of the population which is managed using MK values decreases, so does genetic diversity in the population. However, there are many species for which an individual-based model cannot be implemented. These are groups – populations for which pedigree information is missing and pairings cannot be controlled. These populations, both in captivity and in the wild, are in need of a genetic management plan that is an alternative to MK management.

Group Management versus MK

For those species for which MK management is not possible, group management can provide an alternative that is more effective than no management. With 100% group management – using no pedigree information, but relying on population subdivision, migration rates, and male tenure to manage the population – the decrease in genetic diversity (INB and GD) in the addax population after 100 years could be as little as 8 percent from that of the starting population. In comparison, MK management would

result in a decrease of about 2 percent. In the ten most effective breeding schemes using 100% group management, GD ranged from .804 - .793, and INB ranged from .202 - .254. In the ten worst strategies, GD ranged from .572 - .279 (with the lowest being the case of a single population with a single dominant male breeding for the duration of his life) and INB ranged from .680 - .749. These data suggest that, even with no knowledge of the pedigree, simple management recommendations regarding population and social structure can enhance retention of genetic diversity.

In simulations in which there was some MK management, increasing the number of migrants and decreasing the male tenure had a positive impact on genetic diversity (increasing GD and decreasing INB). Increasing the number of subpopulations increased GD, but it also increased INB.

In populations in which there was no MK management (i.e. 100% group management), decreasing male tenure also had a positive impact on genetic diversity. Increasing the number of migrants tended to decrease INB (with the exception of 20 migrants/year), but it also decreased GD. The slight rise in inbreeding at 20 migrants occurs because some subpopulations contain 20 individuals or less. Instead of infusing populations with new migrants, a large migration rate has the impact of simply moving most of the population from one location to the next, allowing related individuals to continue to interbreed. Increasing the number of subpopulations increased GD.

Group management does carry a genetic cost as compared to MK management. Costs are loss of gene diversity and an increase in inbreeding. These genetic costs and tolerance for risk should be considered within the framework of the species being managed and the goals of the program. Research has shown that a loss of genetic

diversity impacts species differently (Shields, 1993; Caro, 1994; Ralls, Brugger & Ballou, 1979; Keller & Waller, 2002). In addition, the conservation, research, and management goals for the population must be considered. The genetic standards for a captive group of American toads (*Bufo americanus*) meant for education and display purposes in zoos and aquariums will be lower than for a captive population of the Critically Endangered Panamanian golden frog (*Atelopus zeteki*) which is being managed as an assurance population because numbers in the wild have been decimated due to disease and habitat destruction. The benefits of genetic management should be weighed against resource availability and the financial costs of animal management. There are financial and welfare costs to moving animals, subdividing populations, contracepting or separating out individuals who are not recommended to breed, and artificially inseminating animals that need to breed. Molecular determination of individual and population relatedness does not impact welfare, but may carry the most significant financial cost to a management plan.

Group Management of Addax

In the addax case study, using a 50% group/50% MK management strategy, which approximates the current structure and management strategy for the captive population, the loss in genetic diversity after 100 years could be as little as 2 percent more than with 100% MK management. Achieving this level of genetic diversity retention would involve creating 5 subpopulations, decreasing male tenure to two years, and migrating 20 individuals each year (two facilities exchanging 10 animals each). If this level of management is financially impractical a less expensive alternative could be chosen, for example one with 5 subpopulations, a male tenure of 5 years, and a migration

rate of 10 individuals per year. The genetic cost of this management strategy over a MK strategy after 100 years is a 4% increase in INB and a 2.6% decrease in GD.

The addax population is Critically Endangered (IUCN, 2008) and the populations in the wild are thought to be half as large as those in captivity (Spevak, Blumer & Corell, 1993; Shurter, 2009). If genetic diversity is lost in captivity, it is likely lost forever. There are several studies that show that inbreeding depression decreases ungulate survival and reproductive success (Ralls, Brugger & Ballou, 1979; Lacy, 1993; Cassinello, Montserrat & Roldan, 2002; Roldan, Gomendio, Garde, Espeso, Ledda, Berlinguer, Del Olmo, Soler, Arregui, Crespo & González, 2006). Tolerance for risk in the addax population is low and I recommend the continued use of MK management for the AZA Addax SSP population.

The information gleaned from the simulations in this study should also be used for an international captive breeding strategy for pedigreed populations. Although individual regions (e.g., North America, Europe and Australia) manage many of their populations using MK, they do so as separate entities. Captive plans could instead be developed around a single international population with regional subpopulations (e.g., SSP, EEP, Australasian Species Management Program) and then migration rates and male rotation could be altered accordingly while each region continued to manage their own population using MK. In addition to addax, this type of breeding scenario could be applied across many species in a number of taxonomic groups.

Group Management General Recommendations

The simulations in this study provide guidance for managers looking to implement group management:

1. MK management was the most effective strategy to maintain genetic diversity in a population. Increasing the percentage of the population managed by MK and increasing the number of individuals that migrated through MK-managed populations increased GD and decreased INB.
2. Decreasing the tenure of breeding males enhanced the genetic diversity in a population. Instead of allowing a single male and his genes to dominate the population, a decreased male tenure increased the effective size by reducing the variability in breeding success and giving more males an opportunity to breed. The duration of the tenure will depend upon the species and available resources to house non-reproductive males. The financial costs of limiting male tenure are minimal (except to the males, as the solution for turning them off would likely be castration or vasectomization); however the quickest rotation (every other year) could leave managers with the problem of finding housing for all their no-longer-viable males.
3. In this simulation, I compared the effectiveness of migration strategies (Table 2) ranging from no migration to twenty migrants per year (ten migrant pairs exchanged). Migration typically reduced the inbreeding in a population. In terms of maximizing retention of GD, the impact of migration depended on the level of MK management. If there was some MK management, increasing migration tended to increase GD. Migration increases the number of individuals that rotated through a MK-managed population, in which underrepresented individuals are bred preferentially. When there was no MK management, eliminating or minimizing migration was the best strategy.

Migration has a cost in managed populations. Costs include the actual transport of an animal from place to place as well as the staff resources involved in receiving an animal or preparing one for shipment (e.g., quarantine space and care, medical tests, crate training). Also, although in this simulation the act of migration has no impact on fecundity or mortality, in reality there is always a certain risk. Because of this, the benefits of migration will always have to be considered against the costs. In many scenarios, the benefit of moving from ten migrants per year to twenty was not a significant one. Given the costs and logistics of moving 20 individuals, managers might decide that the minor benefits of doubling migration are not worth it. However, this is focused on a population of addax, and migration would involve moving animals across the country. In a population of snails migrating between tanks in the same environmental chamber, the cost is negligible and even the tiniest benefit could be worth the effort.

4. Population subdivision tends to increase both INB and GD. The exception is in populations where there is no MK management and inbreeding arcs very slightly, increasing from 3 to 5 populations and decreasing from 5 to 8. Difficulties for managers arise in determining which factor is more important – maximizing GD or minimizing INB. The answer lies in the population and species and which measure of genetic diversity needs to be conserved.

Population subdivision is also the one factor which is most often difficult to control, given that captive populations are made up of discrete institutions with set facilities and carrying capacities. In the case of addax, subdivision would be most useful in situations of true group management, where large wildlife centers have

herds of antelope that can be separated in a variety of ways. Subdivision considerations can be very useful for other taxonomic groups, where the boundaries of space and carrying capacities are less rigid. For example, the Partulid spp. snail SSP has more flexibility with subpopulations, as they are tanks instead of zoos.

The term “group management” usually evokes images of attempting to manage massive colonies of bats, large flocks of birds, or indistinguishable tanks of invertebrates. Polygynous ungulates are a unique case, in that they straddle the world of individuals and groups and the solution may lie in a mixture of MK and group management. These simulations show that a single best group management scheme (something akin to MK) will not exist for all for species. Instead, population biologists should develop strategies based upon the species, the population (size, scope, and structure), and the management capabilities of the institutions and individuals involved. Instead of a single recommendation, this research provides a process, a set of components that any manager should take when considering a group for management. The stepping stones of variables to consider should include (1) group category, (2) genetic history (in this case, genetic history was contained in the studbook data used in the simulation), (3) % MK management possible, and (4) how the parameters of subpopulation structure, migration rates, and effective size can be combined with the other factors and manipulated to maximize gene diversity and minimize inbreeding. These guidelines can be used by managers looking to develop a comprehensive long-term management plan, and also by those just looking to answer a specific management question on a particular animal or population.

There is a strong need for Group management strategies for preserving genetic diversity. This type of group management (based on populations instead of individuals) can be applied to a wide variety of captive species in need of propagation and long-term sustainability. Group management will be especially useful in managing wild populations, where it is virtually impossible to maintain a pedigree and control pairings. For some species, there will be a cost of moving from individual to group management that must be considered and evaluated. For others, which are at present considered “unmanageable,” group management offers nothing but an enhancement of their genetic security.

Chapter 3: A Robustness Test of Mean Kinship.

Introduction

Zoos and aquariums around the world manage animals to maintain populations that are demographically stable and genetically diverse. Some of the most intense genetic management occurs in regional and international cooperative breeding programs that involve specific breeding recommendations for individual animals across hundreds of species. These programs provide the essential framework of planning and support for the intense genetic management needed for long-term population sustainability.

The goal of genetic management is to preserve the heritable diversity found in wild gene pools so the captive population has genetic variation for both individual fitness and population variability. Many programs – such as the Association of Zoos and Aquariums (AZA) Species Survival Plan (SSP[®]) or Population Management Plan (PMP) programs or the European Association of Zoos and Aquaria (EAZA) European Endangered Species Programme (EEP) – strive to minimize inbreeding and maximize retention of gene diversity, with the general goal of maintaining 90 percent gene diversity for 100 years (Soulé, Gilpin, Conway & Foose, 1986).

Mean Kinship (MK) (Ballou and Lacy 1995) is the genetic management strategy used worldwide in captive population management to maintain genetic diversity and is the benchmark against which all other strategies are compared. See Chapter 1 for a detailed description of how MK is calculated. Under this strategy, an individual's genetic importance can be determined based on the number and degree of relatives that individual has in the population: individuals with the lowest MK value are priority breeders and are selected to produce offspring. The optimal breeding plan is produced by

sequentially selecting breeding pairs with the lowest MK values to produce offspring, starting with the pair with the lowest MK values, adding the pair with the next lowest, and so on, until the recommended number of offspring are produced.

Studies show that minimizing the overall kinship is more effective in reducing loss of genetic diversity than other proposed management methods (Ballou & Lacy, 1995; Montgomery, Ballou, Nurthen, England, Brisco & Frankham, 1997; Fernandez & Toro, 1999; Toro, Silio, Rodriguez, Rodriganez & Fernandez, 1999; Saura, Perez-Figueroa, Fernandez, Toro & Caballero, 2008). A kinship-based breeding strategy is modeled with all MK breeding recommendations being followed. However, this idealized scenario does not always occur in the complicated reality of animal management.

The AZA Population Management Center conducted an analysis of breeding and transfer recommendations during the one-year period after the distribution of population management recommendations (Cronin et al 2006). The study looked at recommendations to “breed” and “not to breed” as well as recommendations to transfer or hold animals and found that, on average, programs were able to achieve 75% of their target number of births. Out of those, only two-thirds of those births resulted from recommended pairings, with the remaining one third coming from pairings that were specifically recommended against (e.g., those with High MK values). Breeding success for SSPs, where participation from all holding institutions is expected, was found to be higher than for PMPs, where participation is only encouraged. Although the study did not solicit specific reasons for the failure of institutions to breed or not breed animals as recommended, one potential reason given was that animals that have low MK values are

underrepresented because they are unsuccessful breeders (Cronin et al 2006). This could be due to physical limitations of the individual animals involved in a particular recommendation or it could be due to the fact that the reproductive biology of their species is not suited to a MK pair based management system. As an example, the AZA Cheetah (*Acinonyx jubatus*) SSP utilizes large breeding centers, where mate choice plays a role in the enhanced breeding success the population needs for sustainability (CBSG 2010). The significance of mate choice has been documented in many species (Andersson, 1994; Duraes, Loiselle, Parker & Blake, 2009; Edwards & Hedrick, 1998; Eizaguirre, Yeates, Lenz, Kalbe & Milinski, 2009; Milinski, 2006, Brown, 1997; Ryder, Tori, Blake, Loiselle & Parker, 2010) and it plays an increasing role in captive management decisions.

Conversely, animals that are prolific breeders tend to rise above the average MK of the population. If they are part of a managed program, they are recommended to stop breeding, but they sometimes continue to do what they do best – produce offspring – even if it is contrary to the genetic health of the population.

A study in Australasia found that Australian zoos were successful in implementing only 68% of breeding recommendations (Lees & Wilcken, 2009). The top reason listed for the lack of success was the failure of people, for a variety of reasons, to follow the recommendations. These reasons are often not deliberate. For example, a simple lack of communication was indicated as a major culprit in failed recommendations. The next cited reason was the failure of animals to breed when they were put together for that purpose. Reasons for this include biological factors such as pair incompatibility and unexpected morbidity and mortality in the population.

Managers are familiar with the reality of failed recommendations and factor imperfect success into their management plans by recommending a number of breeding pairs that exceed that needed to maintain the population at carrying capacity. For example, if ten pairs are needed to reach carrying capacity, but managers' experience with the population led them to estimate a success rate of only 50%, then 20 pairings would be recommended in a management plan. Thus, even if the absolute best genetic pairings were not successful (the ten pairings with the lowest MK values), all recommendations are still genetically beneficial to for the population (the ten pairings will come from the 20 lowest MK values). Managers must also factor in the reality that overrepresented animals that are recommended "not to breed" regularly produce offspring. When this happens, the management plan must be altered and the number of recommended pairings must be reduced so that the population does not exceed carrying capacity.

In this paper I used computer simulations to determine how well a MK-based management system was able to retain gene diversity in a more realistic environment, where not all pairings were based on the absolute lowest MK values. To model reality I looked at a variety of breeding situations involving combinations of different percentages of low MK success and high MK breedings. "Low MK" pairs are those additional pairs recommended by managers to ensure that demographic goals are met. Although not the absolute best pairings, they are still recommended as being beneficial. "High MK" pairs are those that are recommended against, but sometimes occur and must be considered because the offspring from these pairings take up valuable captive space, decreasing the number of Low MK pairs that can be made.

My goals are to determine: (1) how capable a mean kinship strategy is at retaining gene diversity when pairings include less-than-ideal genetic matches (i.e., how robust it is) and (2) where managers should direct their efforts to improve genetic management – at improving the success of the lowest MK pairings or preventing High MK pairings from occurring.

Methods

I developed a stochastic simulation model (Figure 13) (Ivy, J. 2010) in C++, for which code is available upon request. I used the simulation to assess the robustness of a MK-base strategy in a population to retain gene diversity after 100 years when not all breeding pairs were chosen on the bases of ideal MK management.

I used data from six different studbooks (Table 7). Studbooks are species-specific records that contain vital information on captive populations, including animal identities, sexes, parentage, locations, and event dates such as births, deaths, and transfers. Many managed species have a long captive history and studbook data are used as a starting point to look at the effects of management on actual populations instead of hypothetical, more idealized ones. I chose to use studbooks from: addax (*Addax nasomaculatus*) (Spevak, 2009), maned wolf (*Chrysocyon brachyurus*) (Holland, 2010), Humboldt penguin (*Spheniscus humboldti*) (Brandt, 2009), swift fox (*Vulpes velox*) (Shotola 2010), lesser flamingo (*Phoeniconaias minor*) (Conrad, 2009), and Przewalski's horse (*Equus ferus przewalskii*) (Powell, 2008).

I chose these six species because they had different levels of gene diversity as well as varied life-history and population level characteristics (Table 7). To calculate MK values, I also imported the kinship matrix of living animals created from the

Figure 13. Primary Components of the Simulation. Parameters include studbook data such as population size, sex, parentage, age, location, kinship, age of first and last reproduction and stage-based mortalities; they also include percentages of High MK and Low MK breeders.

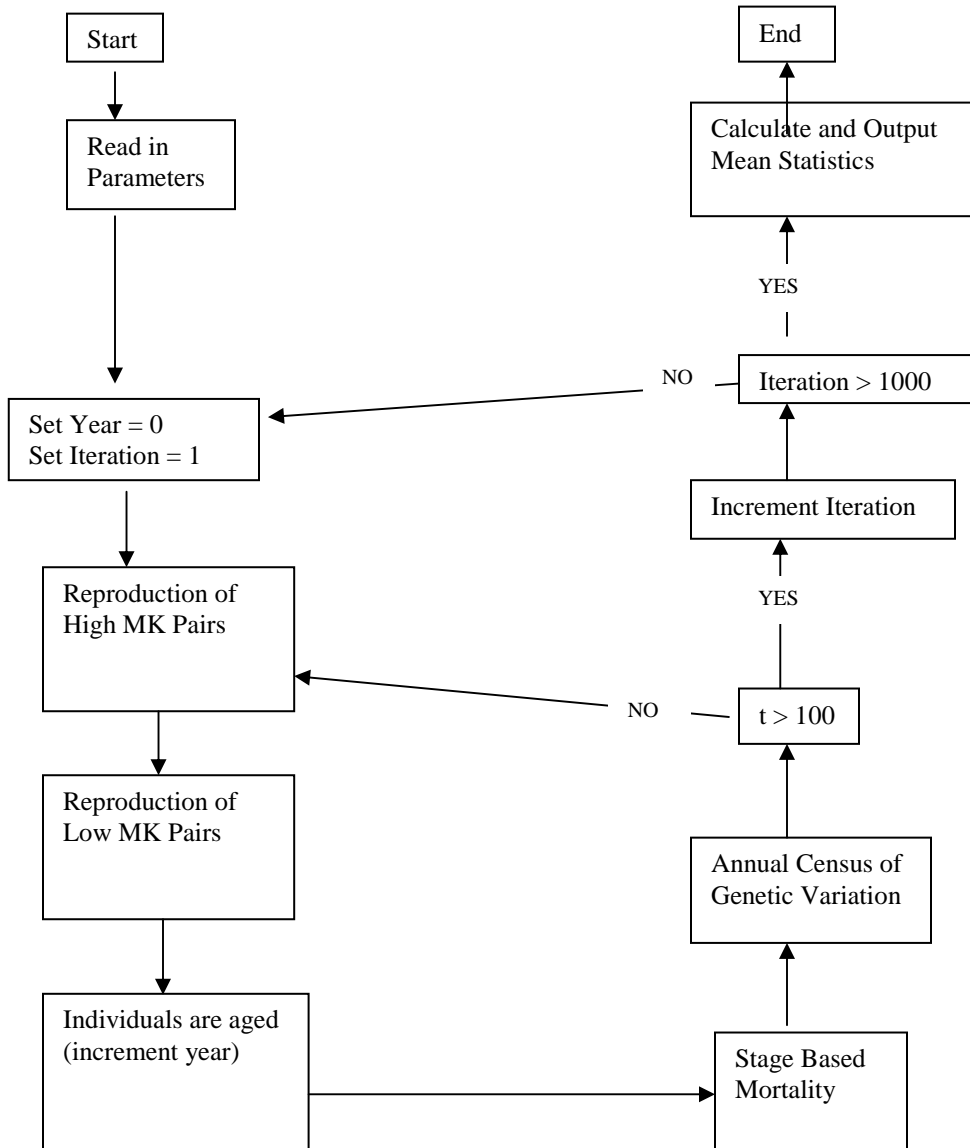


Table 7. Genetic and demographic parameters of studbooks used in the model. GD is the gene diversity

Species	Starting GD	Years Reproductive	Carrying Capacity	First Year Mortality	Annual Repro-Age Mortality	Annual Post-Repro Mortality
Addax	0.884	13	200	0.25	0.08	0.25
Maned Wolf	0.930	8	100	0.50	0.05	0.53
Humboldt Penguin	0.986	23	325	0.33	0.06	0.20
Swift Fox	0.940	6	80	0.20	0.04	0.15
Lesser Flamingo	0.999	37	525	0.40	0.08	0.30
Przewalski's Horse	0.785	19	125	0.15	0.06	0.22

studbook using PM2000 (Pollak, Lacy & Ballou, 2005). The simulation used annual sex and stage specific fecundity and mortality rates for each species calculated from life-table analyses of the studbooks also using PM2000 (Table 7). Because the number of offspring could affect the impact of breeding recommendations, I looked at low (1 offspring per pairing), medium (4 offspring per pairing) and high (8 offspring per pairing) clutch/litter sizes for each species. In actuality, addax, Humboldt penguins, lesser flamingoes, and Przewalski's horses would usually have one offspring, and maned wolves and swift fox would usually have four pups per litter. None of the species tested would have eight offspring, but this variable was included to help with comparisons for group-managed species which are often highly fecund.

Each population was modeled as a single, large population. Each year enough animals were bred to attempt to reach or maintain the population at carrying capacity (Table 7). The number of offspring needed was determined by subtracting the current population or subpopulation size from the carrying capacity, and then adding the number of currently living animals that were expected to experience mortality during the time-step. If an insufficient number of animals was available to make the number of pairs needed, the maximum number of pairs possible was used instead.

Individuals were paired according to a specified breeding scheme (Table 8) and produced a specified number of offspring per pairing (1, 4, or 8). Offspring had a 50% chance of being either male or female. The kinship matrix was updated after offspring were produced, animals were aged one time-step (one year), and experienced stage-based mortality (Table 7). MK values were calculated for all living animals at the beginning of each year from the kinship matrix. At year 100, gene diversity was calculated as the

proportional gene diversity (GD), which was $1 - \bar{m}k$, where $\bar{m}k$ was the average mean kinship in the population in year 100 (Ballou and Lacy 1995). Each simulation was run 1000 times using a different random number seed to select breeders. I did not include selection, mutation, immigration or emigration in the models.

The breeding schemes were based on two factors: 1) the percentage of pairs with High MK which were guaranteed breeding success; and 2) the likelihood of pairs with Low MK to be successful breeders. I varied the percentage of guaranteed successful breeding pairs from 0%, to 10%, 20% 30% and 40%, and the likelihood of successful Low MK pairs from 100% to 90%, 80% and 70% (Table 8). These ranges were chosen to correspond roughly with the rates that are seen of these kinds of pairings in actual breeding programs. These rates were used as follows. Once the number of offspring and pairs was determined (see above), the number of High MK guaranteed breeders to be used was calculated based on the percentage to be modeled in the particular scenario. This number of pairs was then randomly selected from animals with MK values above the average (High MK) to produce offspring. For example in a species with a litter size of 1, if 20 successful pairs were needed, and the proportion of High MK breeders being modeled was 0.10, then two High MK pairs were selected to produce offspring. If the scenario being modeled specified 0% probability of High MK breeding success, no High MK pairs were selected, and only Low MK pairs bred (see below). If there were not enough reproductive animals in the population to produce the recommended number of pairs, the 0.10 was applied to the number of pairs that was possible. In this example, the percentage results in a whole number; when it was not, the number was rounded up to the nearest whole. Once selected, a High MK pair was always successful.

After the High MK offspring were produced, the number of remaining pairs needed to reach carrying capacity was then selected using animals with the lowest MK values. Similar to the High MK pairs, the numbers of pairs needed were based on the size of the population (with the High MK births added) relative to its target population size. The likelihood of a Low MK pair successfully producing an offspring was based on the scenario being modeled (Table 8). For example, if a value of .9 was being modeled, the pair with the lowest MKs would be selected, but would have only a 90% chance of producing an offspring. If, by chance, they did not produce an offspring, the next lowest pair would be selected, and would have the same probability of success. This process was repeated until the number of desired offspring was produced. If there were not enough animals remaining to make the required number of Low MK pairs, the maximum number of pairs possible was made.

Overall the model ran 450 different scenarios. Each scenario differed with respect to the proportion of High MK pairings, the proportion of success of Low MK pairings, and the number of offspring produced per pair, for each of the six species included. The gene diversity for each of these scenarios was then calculated as the gene diversity at year 100 averaged across all 1000 simulations.

Multiple regression was used to determine the relative contribution of the different MK strategies, as well as the effect of different life-history characteristics, on the retention of genetic diversity. The dependent variables initially considered for inclusion in the model were: number of offspring produced per pair, the proportion of pairs that were overrepresented High MK pairs, the success rate for Low MK pairs, initial gene diversity (GD_0), first-year mortality, adult mortality, and number of years a species

Table 8. Variables for proportions of High MK pairings and success rates for Low MK pairings.

Proportion High MK Pairings	Proportion Low MK Success
0	1.0
.1	0.9
.2	0.8
.3	0.7
.4	0.6

was reproductive. In addition to these main effects, the biologically important interaction of mortality rates and number of offspring was considered, as well as the interaction between High and Low MK pairings.

The independent variable was gene diversity retained for any given scenario relative to that of the best (ideal) scenario for each species. I defined the ideal scenario as the scenario using 0% High MK pairings and 100% success rate for Low MK pairings, with one offspring per pairing. Thus, for my independent variable, I calculated the change in GD from that of the ideal:

$$\text{GD Change} = \text{GD}_{100, \text{Ideal Scenario}} - \text{GD}_{100, \text{Scenario } i}$$

where $\text{GD}_{100, \text{Ideal Scenario}}$ is the gene diversity after 100 years of breeding in the scenario where no High MK (above the population's average MK) pairs are selected and the Low MK pairings have a 100% breeding success rate and one offspring per pair, and $\text{GD}_{100, \text{Scenario } i}$ is the gene diversity after 100 years of breeding in each of the i scenarios where the proportion of High MK pairs selected for breeding is greater than 0 and the proportion of Low MK pairs breeding success is less than 100%, and the number of offspring per pair vary.

All independent variables were initially included in the model, then I used the regression analysis and stepwise selection to refine the model to include only those variables and interactions that were important. For the stepwise process, the p value for inclusion was 0.05 (all variables left in the model were significant at the 0.05 level). I used SAS Software (Version 9.2) for the multiple regression (SAS Institute Inc. 2002-2008).

Results

I examined the results of the stochastic simulation model by looking at the average GD value of 1,000 iterations of each breeding scenario after 100 years of management. The simulations varied as different random numbers were used to select breeders in each iteration. I found that, over the 450 simulations I tested, breeding over-represented (High MK) animals and decreasing the breeding success rate of Low MK animals both had negative impacts on GD in the population after 100 years. Although all populations showed this trend, the regression models that had the best fit were those developed by separating the data taxonomically, into non-canid and canid groups. Non-canid groups are comprised of data from the ungulate (addax, Przewalski's horse) and avian (flamingo, Humboldt penguin) populations. Canid groups are comprised of data from the maned wolf and swift fox populations. The canid species were demographically different from the others in that they have a very short reproductive tenure (8 years for maned wolf, 6 years for swift fox) combined with a small captive carrying capacity ($K = 100$ for maned wolf, 80 for swift fox) (Table 7).

The regression analysis of the ungulate and avian species had an R-squared value of .814 and adjusted R-squared of .809 (Table 9). My data showed that the impact on GD of overrepresented pairings (High MK) was almost four times that of decreasing the success of good pairings (Low MK). For every ten percent increase in overrepresented pairings, there was a .031 percent decrease in GD relative to that of the ideally managed population (Table 9). However, for every ten percent increase in the breeding success of Low MK pairs, there was only a .008 percent increase in GD (Table 9). The number is a

Table 9. Regression output for ungulate and avian populations. R-squared value is 0.814, adjusted R-squared value is 0.809.

	<i>Coefficients</i>	<i>Standard Error</i>	<i>P-value</i>
Intercept	0.023	0.013	0.057
# Offspring	0.005	0.000	0.000
Overrepresented	0.031	0.002	0.000
MK Success	-0.008	0.002	0.000
GD0	-0.033	0.018	0.071
Years Reproductive	0.000	0.000	0.917
1 st -Year Mortality	0.029	0.020	0.148
# Offspring*1 st -Year	-0.014	0.001	0.000

negative value because the dependent variable is GDCHANGE and, as breeding success increases, the difference from the ideal GD gets smaller. Increasing the number of offspring, the reproductive tenure, and the first-year mortality each decrease GD from that of the ideal. Increasing the GD of the starting population had a positive impact on GD, as did the interaction between number of offspring and first year mortality. The p-values for GD_0 , reproductive life-span, and first-year mortality were all above .05, suggesting that the difference can be explained by random variability at the 95% confidence level. The values for the reproductive life-span are both statistically large (.917) and practically small (.000) so the effect can be considered unimportant to management. GD_0 and first-year mortality have p-values of .071 and .148, respectively, but their practical impacts are of interest. Every additional percent of GD_0 results in a .033 increase in GD, and every additional percent in infant mortality results in a .029 decrease in GD.

A regression analysis of the canid species had an R-squared value of .914 and an adjusted R-squared value of .906 (Table 10). My data showed that the impact on GD Change of overrepresented pairings (High MK) was slightly less than the impact of a decrease in the percentage of low MK success. For every ten percent increase in overrepresented pairings (High MK), there was a .050 percent decrease in GD from that of the ideally managed population. As the breeding success of MK pairs increased by ten percent, there was a .090 percent increase in GD. Increasing the number of offspring negatively affected GD. We also tested the impact of the two different canid species, with the maned wolf having higher GD than the swift fox, as would be expected given the wolf's longer reproductive life-span and larger carrying capacity (Table 10).

Table 10. Regression output for canid populations. R-squared value is 0.914, adjusted R-squared value is .906.

	<i>Coefficients</i>	<i>Standard Error</i>	<i>P-value</i>
Intercept	0.053	0.033	0.112
Canid	0.019	0.027	0.491
# Offspring	0.016	0.005	0.001
Overrepresented	0.050	0.095	0.595
MK Success	-0.090	0.038	0.021
Canid*# Offspring	-0.019	0.001	0.000
Canid*Overrepresented	-0.092	0.024	0.000
Canid*MK Success	0.021	0.030	0.482
# Offspring*Overrepresented	0.018	0.004	0.000
# Offspring*MK Success	0.003	0.005	0.528
Overrepresented*MK Success	0.014	.108	0.894

In addition to looking at the regression analyses to determine the proportional and directional impact each of the variable had on the population, I also looked at the results from the model to determine the impact of overrepresented pairings and MK success on the studbook populations as they would be managed. Table 11 shows the change in GD for each population. Because my goal was to assess impact on each population, I include results where the number of offspring equals the number of offspring these species would actually have. Table 11 shows the results for the ungulate and avian species, which would have one offspring per clutch/litter, and for the canid species which would have a litter size of four.

Discussion

A genetic management strategy is robust if it is capable of retaining genetic diversity even when reproductive pairings include less-than-ideal genetic matches. In captive populations, these types of imperfect pairings include those of genetically overrepresented individuals who have High MK values, as well as those who have kinship values below the average MK, but not the absolute lowest. My results show that both of those realities impact GD over time and that the type of species being managed affects that impact as well as the robustness of an MK-based breeding strategy.

Ungulate and Avian Species

The ungulate and bird species I examined revealed that the proportion of High MK and Low MK breeding successes had an impact on GD. Overrepresented pairings (High MK) had a greater impact on GD than did a decrease in the breeding success of Low MK pairings. Overrepresented breeders help to reduce GD by contributing more of their already overrepresented alleles to the population. Their impact is magnified by the

TABLE 11. Maximum change in GD for each studbook species. Maximum change for all species occurred with 8 offspring. Change was that as compared to the ideal MK-based management (0% overrepresented pairs; 100% breeding success for Low MK recommended pairs).

Species	# Offspring per Litter/Clutch	Max GD Change (8 Offspring)	GD Change Actual Offspring
Addax	1	.036	.015
Humboldt Penguin	1	.017	.006
Lesser Flamingo	1	.009	.004
Przewalski's Horse	1	.045	.015
Swift Fox	4	.210	.104
Maned Wolf	4	.068	.031

set carrying capacity because the success of High MK pairings limits the number of Low MK pairings that can occur.

A breeding scheme using MK values is robust for these four studbook species. After 100 years, the maximum GD difference in the worst case scenario (40% of overrepresented pairings; 60% success rate low MK pairings; 8 offspring) is .04 for addax and Przewalski's horse. After 100 years, the maximum GD difference in the same worst case scenario for Humboldt penguin is .017, and for lesser flamingo it is .004 (Table 11). In a real management situation, these species would have only one offspring, and not eight. In this case, the biggest drop in GD would be .015 for addax and Przewalski's horse, .006 for Humboldt penguin, and .004 for flamingo (Table 11).

The model also shows that, although the number of offspring and first-year mortality both have a negative impact on GD as they increase, the interaction term of between the two has a positive impact. Increasing the number of offspring per clutch/litter gives fewer individuals an opportunity to breed. This keeps the population within the set carrying capacity. If the "wrong" individuals breeds (e.g., ones that are overrepresented), this limits the number of recommended pairings. If the first-year mortality rate is high, more births are needed to maintain the set population level, giving more individuals (who are randomly selected) an opportunity to breed. This increases the likelihood that their alleles will be passed on.

My advice to managers is that it is better to direct efforts into preventing overrepresented pairings. If these specific species are being managed using MK values, producing only one offspring per pairing, the population can withstand the vagaries of the animals and institutions. The detrimental effects of poor management increase with the

number of offspring per pairing. If a species with these population characteristics has a clutch/litter size of eight offspring, the impacts over 100 years would be more significant and managers would need to make more of an effort to address them.

Canid Species

The maned wolf and swift fox populations I examined had short reproductive lifespans (8 and 6 years respectively) and small population sizes (100 and 80 individuals respectively). The result of these population characteristics is a higher turnover in the breeding population and individuals with fewer reproductive years to rectify less than ideal pairings. An extreme example is a semelparous species where, if a founder did not breed in one year, its genes would be forever lost to the population. In these populations I could not analyze Low MK pairings with a .6 success rate. Because the number of breeding individuals was limited, this impact of the model given this factor was to reduce the population size to well below the carrying capacity. When this happened, the drop in GD was more influenced by a decrease in N rather than a decrease in management success.

In the canid populations, an MK-based strategy was less able to withstand the impacts of less rigorous management. Every ten percent increase in overrepresented (OVER) pairings with High MK resulted in a .055 percent decrease in GD from that of the ideal. Reducing the breeding success of Low MK pairs had a bigger impact on the population, with a .090% decrease in GD for every ten percent decrease in success. However, the p-value for OVER was .595, indicating that the slope of the regression line was close to 0. The impacts of both are greater than those in the non-canid population.

The class variable DOG was added to this population to discern the impacts of each species. This is different from the non-canid populations, where population variables such as GD0, YRSREPRO, and 1MORT helped determine the impacts of different populations. Using these variables for the canid data resulted in a model with a poor fit. The difference between maned wolf and swift fox was a decrease in GD of .019 percent. The p-value for this variable was high, at .491.

Increasing the number of offspring (NOFF) negatively affected GD. The direction of the impact is the same as in non-canid species, although it is three times larger (.005 in non-canids compared to .016 in canids). This is of special importance because small carnivore species such as this tend to have multiple offspring per litter. Interactions between variables had much more of an impact on this population (Table 10).

The ability of an MK-based breeding scheme can be compromised in these species if the top recommended pairings do not occur. After 100 years, the maximum GD difference in the worst case scenario (40% of overrepresented pairings; 70% success rate low MK pairings; 8 offspring) is a .068 for maned wolf. After 100 year, the maximum GD difference in the same worst case scenario for swift fox is .210. In a real management situation, these species would have four offspring, and not eight. In this case, the biggest drop in GD would be .031 for maned wolf and .104 for swift fox (Table 11).

My advice to managers is that it is important to direct efforts at both preventing overrepresented pairings and ensuring that the best recommended pairings (as determined by MK) occur. These types of small populations with higher turnover rate are more

impacted by these types of weak pairing than the non-canid populations I examined. Increasing the number of offspring per pairing increases the detrimental effect of poor management, which is especially important in species with large litter sizes.

Group Management

The captive populations of the species I examined are all programs that are nationally managed by the AZA. As such, each has a studbook and each is managed by using a MK value to recommend individual pairings. In a survey (Smith 2008) of all of AZA's SSPs and PMPs to evaluate the need for group management in captive programs, the program leaders for each of these species indicated that it would be preferable to have a group management option available to them. Group management was preferred because it would facilitate the ability of institutions to maintain species in large groups with a natural social structure (addax, Przewalski's horse, lesser flamingo) and/or to allow for mate choice to occur (addax, Przewalski's horse, lesser flamingo, swift fox, maned wolf, Humboldt penguin).

A study by Smith et al. (this paper) showed that there is a genetic impact to managing animals as groups instead of as individuals (using MK values to make specific breeding pairs on an animal by animal basis). The decision to manage a species as a group will be based on that cost, relative to other costs and benefits. In the case of Addax, I found that if I used a 50% MK/50% Group management strategy, then the decrease in GD would be 2.6 percent after 100 years. This is compared to an ideal MK-based management strategy where the best (lowest-MK) breeding recommendations occur and no overrepresented pairs produce offspring. If they are not breeding in this ideal fashion, the cost might be less, and allowing for some group management may be a

more feasible option. In this study, I found that weak management could drop GD by 1.5 percent. This reduces the cost by more than half. The AZA Population Management Center is currently studying the outcomes of breeding and transfer recommendations made through AZA SSPs and PMPs. I recommend that managers include breeding success levels as part of their cost/benefit analysis for group management.

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