FLORIDA PANTHER

Felis concolor coryi

POPULATION VIABILITY ANALYSIS

and

RECOMMENDATIONS

Captive breeding Specialist Group

Species Survival Commission IUCN

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FLORIDA PANTHER

POPULATION VIABILITY ANALYSIS

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I. RECOMMENDATIONS - FLORIDA PANTHER PVA

Interventions:

1. Establish a captive breeding population in 1989 with the objectives of collecting as full a representation of the available wild Florida panther genetic diversity as rapidly as possible and expanding the captive population to 250-350 animals as rapidly as possible.
2. The limited size of the wild Florida panther population in the Big Cypress and neighboring habitats, perhaps 50 adults, will require continuing monitoring, intensive management, intervention, and genetic supplementation for survival.
3. Establish a collaborative Recovery and SSP program in 1989 to provide the resources for the captive population including a masterplan for genetic and demographic management.
4. Initiate the search for sites in the panthers former range to establish new populations using animals from the captive propagation program.
5. Begin in 1989 the collection of genetic material (semen and embryos) from the wild population to preserve the wild gene pool and to use in developing the captive population.
6. Breed (naturally or artificially) in 1989 the two Everglades females in captivity with an unrelated Florida panther male. Retain the first surviving litters in the captive population. Return these females to the population pregnant. Capture and breed two of the remaining wild females in this population with an unrelated male during 1989.
7. Initiate in 1989 the genetic and reproductive research needed to implement and guide the recovery program.

Establishment of a captive population:

1. Capture and retain in 1989 at least 6 panthers less than 18 months old. Make a special effort to locate any litters born this year and retrieve cubs as young as possible. The female is likely to rebreed.
2. Capture a young healthy pair (2-6 years) in 1989 for study of the reproductive cycle and captive propagation.
3. Collect and cryopreserve semen from all wild males. Capture unbred adult females for collection of genetic material, breeding, and release pregnant.

Research priorities:

1. Conduct the genetic studies necessary to establish the subpopulation structure of the species and the relationship of the Florida population to the rest of the species. Determine the kinship patterns among the current Florida panthers. Determine the population relationships of the Everglades animals.
2. Conduct the reproductive biology studies necessary to develop the technology to allow reliable enhancement of panther reproduction and cryopreservation of semen and embryos.
3. Continue development and testing of population and simulation models as guide to selection of the most effective management actions.

II. EXECUTIVE SUMMARY - FLORIDA PANTHER PVA

Goal and Premises of the Population Viability Aanalysis:
Recommend actions and schedule needed to secure the Florida panther against extinction and assure a 95% probability for survival in the wild for 100 years with retention of 90% of the currently available heterozygosity. Outline population sizes and distribution needed to provide a wild Florida panther population of sufficient size to allow continuing evolution by selection and accumulation of genetic variation.

The PVA was conducted on the basis that the gene pool of the present population of Florida panthers is to be preserved with no additions or replacements with animals from other geographically distant populations. The conclusions regarding population viability are linked to the size and fragmented character of the available habitat (Big Cypress and surrounding patches) which appear to limit any likely population size to about 50 adult animals.

Status of present panther population:
The demographic projections for the Florida panthers over a range of values for the life history parameters based upon conservative or realistic estimates from the field data, indicate a declining panther population with an 85% probability of extinction in 25 years and a mean time to extinction of 20 years. The genetic projections indicate a continuing erosion of genetic diversity in the wild population even if it were stable. These projections do not include a factor for environmental variance or catastrophe which can only reduce the time to extinction. If the population were stable at 30 adults, its effective size would be 8-15, and it would lose heterozygosity at 3-7% per generation and hence lose 50-75% of its heterozygosity in 100 years. A reduction in fitness may already have occurred as reflected in the high incidence of cryptorchidism and sperm abnormalities.

Effects of *status quo* and current interventions:
The current and planned interventions in management of the wild population (treatment of injured animals, vaccination in the wild, local expansion of habitat to increase K to 45 or 80 adults, reduction of adult mortality to 25%), still yield 99% to 75% probabilities of extinction within 100 years. The mean times to extinction range from 18 to 50 years. The most optimistic scenarios yield 12-40% probabilities of extinction within 100 years.
Metapopulation:

Survival of the Florida panther in the wild will require establishment of a captive and multiple wild populations. The surplus from the captive population would provide the animals to establish 3 to 10 new geographically separate wild populations of at least 30-50 adults each. These populations will require monitoring, periodic exchange of animals (about 1 every 5 years), and replacement in the event of local extinction.

Effects of a captive population:
Establishment of a captive population is the only management intervention that can assure survival of the Florida panther for 100 years with a 95% probability, and retention of 90% of the

available heterozygosity. A captive population can provide stock for establishment of new wild populations. It would be expected to grow at 15% per year and have a zero probability of extinction during the next 100 years for adult population sizes of 25-100 or more. The population could be expanded more rapidly with annual litters and a reduction in infant mortality.

Recommended actions for establishment of a captive population:

1. Seek representation from each of the 25-30 animals presently known to be in the wild population.
2. Bring in this year at least 6 animals selected from all young of the year and all animals less than 24 months old. (Females are likely to rebreed if a young litter is removed.)
3. A pair of young animals (3-7 years) should be obtained this year for the reproductive biology characterization and to initiate the captive breeding program.
4. Collect and cryopreserve semen from any free ranging males.
5. Breed the two captive Everglades females as soon as clinically feasible and retain their litters in captivity. Rebreed them and return them pregnant to the Park.
6. Plan to rotate into captivity any adult wild females without litters for breeding (natural or artificial) in captivity. The females could be returned to the wild after they have produced a surviving litter to be retained in captivity and returned to the wild pregnant.
7. Initiate an SSP program in the next 6 months with the 4 Florida zoos that have indicated an interest in the breeding program. The SSP program can be expanded to include zoos in the historic range of the Florida panther.

Everglades animals:

This population has less than a 10% probability of survival for 25 years, has an effective size of 3, and is losing heterozygosity at the rate of 16% per panther generation or 5 years. The projected mean time to extinction is 5-11 years depending upon whether the 2 females are returned and another unknown pair is present.

The genes present in the Everglades animals can be saved by captive breeding. Retain in captivity the two females from the Everglades and breed them either naturally or using reproductive technology (possibly embryo transfer). Obtain a minimum of one surviving litter from each female. Use a male or sperm from the other Florida population. Do not use the male currently in the Everglades. Retain the litters produced in the captive population. If these females then are returned to the wild, two of the other females should be captured and bred in a similar fashion. Two pregnant females might be returned to the population for natural rearing of replacement males. Addition of a new male to the population might be considered. Reestablishment of a natural corridor between the populations might reduce the need for management intervention in the future.

Research priorities:

There are immediate problems important to management of the Florida Panthers for recovery that are amenable to resolution by current research methodologies if supported.

<u>Genetic</u>: 1. Establish relationship of the Florida panthers to other geographic populations

(subspecies) of panthers throughout range of panthers. 2. Determine the relationship of the Everglades animals to the other Florida panthers. Evaluate in the context of population substructure information from 1 above. 3. Measure the relatedness or kinship within the population outside the Everglades. This information would provide guidance to the intensive breeding program that will be required if the Florida panthers are maintained as a genetically distinct population.

Reproduction: 1. Characterize the reproductive cycle of the female panther and males including seasonality. 2. Develop techniques for reproductive enhancement including artificial insemination, embryo transfer, and *in vitro* fertilization. 3. Develop techniques for cryopreservation of semen and embryos. 4. Evaluate possible effects of inbreeding on fertility and reproductive performance, particularly consequences of cryptorchidism.

Field: 1. Continue monitoring of current status of population. 2. Continue development of translocation methodology. 3. Initiate plans for release studies of captive bred animals. 4. Assess habitat availability including current range, new sites in Florida, and new sites in Southeast region. Need K evaluation, landscape analysis, effects of human populations and uses.

PVA and SSP: 1. Support continued modeling and PVA of population as part of evaluation of responses to management interventions. 2. Establish a collaborative Recovery and SSP Program with zoos as soon as a decision is made to establish a captive population.

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III. SPECIES SURVIVAL PLANS AND COLLABORATIVE MANAGEMENT APPROACHES FOR SMALL POPULATIONS (T. J. Foose).

Abstract

A conservation strategy or recovery plan based on viable populations for a taxon like the Florida panther should:

(1) Expand the population in numbers (100's to 1000's) and in range (multiple populations of 50-100 each) all managed as a metapopulation).

(2) Develop a vigorous program of captive propagation to reinforce the wild populations.

(3) Intervene in wild populations to ameliorate genetic, demographic, and environmental problems.

(4) Conduct an extensive and continuing population viability analysis as situations change, knowledge increases, and science advances.

Introduction

Conservation strategies for endangered species must be based on viable populations. While it is necessary, it is no longer sufficient merely to protect endangered species *in situ*. They must also be managed.

The reason management will be necessary is that the populations that can be maintained of many species under the pressures of habitat degradation and unsustainable exploitation will be small, i.e. a few tens to a few hundreds (in some cases, even a few thousands) depending on the species. As such, these populations are endangered by a number of environmental, demographic, and genetic problems that are stochastic in nature and that can cause extinction.

Environmentally, small populations can be devastated by catastrophe (disasters and epidemics) as exemplified by the case of the black footed-ferret, or decimated by even less drastic fluctuations in the environment. Demographically, small populations can be disrupted by random fluctuations in survivorship and fertility. Genetically, small populations lose diversity needed for fitness and adaptability.

Minimum Viable Populations

For all of these problems, it is the case that the smaller the population is and the longer the period of time it remains so, the greater these risks will be and the more likely extinction is to occur. As a consequence, conservation strategies for species which are reduced in number, and which most probably will remain that way for a long time, must be based on maintaining certain minimum viable populations (MVP's), i.e. populations large enough to permit long-term persistence despite the genetic, demographic and environmental problems.

There is no single magic number that constitutes an MVP for all species, or for any one species all the time. Rather, an MVP depends on both the genetic and demographic objectives for the program and the biological characteristics of the taxon or population of concern. A further complication is that currently genetic and demographic and environmental factors must be considered separately in determining MVP's, although there certainly are interactions between the genetic and demographic factors. Moreover, the scientific models for assessing risks in relation to population size are still in the early stages of evolution. Nevertheless, by considering both the genetic and demographic objectives of the program and the biological characteristics pertaining to the population, scientific analyses can suggest ranges of population sizes that will provide calculated protection against the stochastic problems.

Genetic and demographic objectives of importance for MVP

The *probability of survival* (e.g., 50% or 95%) desired for the population;

The *kind of genetic variation* to be preserved (e.g., allelic diversity or average heterozygosity);

The *percentage of the genetic diversity* to be preserved (90%, 95%, etc.);

The *period of time* over which the demographic security and genetic diversity are to be sustained (e.g., 50 years, 200 years).

In terms of demographic and environmental problems, for example, the desire may be for 95% probability of survival for 200 years. Models are emerging to predict persistence times for populations of various sizes under these threats. Or in terms of genetic problems, the desire may be to preserve 95% of average heterozygosity for 200 years. Again models are available. However, it is essential to realize that such terms as viability, recovery, self-sustainment, and persistence can be defined only when quantitative genetic and demographic objectives have been established, including the period of time for which the program (and population) is expected to continue.

Biological characteristics of importance for MVP

Generation time: Genetic diversity is lost generation by generation, not year by year. Hence, species with longer generation times will have fewer opportunities to lose genetic diversity within the given period of time selected for the program. As a consequence, to achieve the same genetic objectives, MVP's can be smaller for species with longer generation times. Generation time is qualitatively the average age at which animals produce their offspring; quantitatively, it is a function of the age-specific survivorships and fertilities of the population which will vary naturally and which can be modified by management, e.g. to extend generation time.

The number of founders. A founder is defined as an animal from a source population (the wild for example) that establishes a derivative population (in captivity, for translocation to a new site, or at the inception of a program of intensive management). To be effective, a founder must reproduce and be represented by descendants in the existing population. Technically, to constitute a full founder, an animal should also be unrelated to any other representative of the source population and non-inbred.

Basically, the more founders, the better, i.e. the more representative the sample of the source gene pool and the smaller the MVP required for genetic objectives. There is also a demographic founder effect; the larger the number of founders, the less likely is extinction due to demographic stochasticity. However, for larger vertebrates, there is a point of diminishing returns (Figure 1), at least in genetic terms. Hence a common objective is to obtain 20-30 effective founders to establish a population. If this objective can't be achieved, then the program must do the best with what is available. If a pregnant female woolly mammoth were discovered wandering the tundra of Alaska, it would certainly be worth trying to develop a recovery plan for the species even though the probability of success would be low. By aspiring to the optima, a program is really improving the probability of success.

The number of effective founders available for a recovery program for Florida panther can be estimated at between 5 and 30, depending on whether every surviving animal is accepted as the starting point or whether kinships among the panthers are also considered.

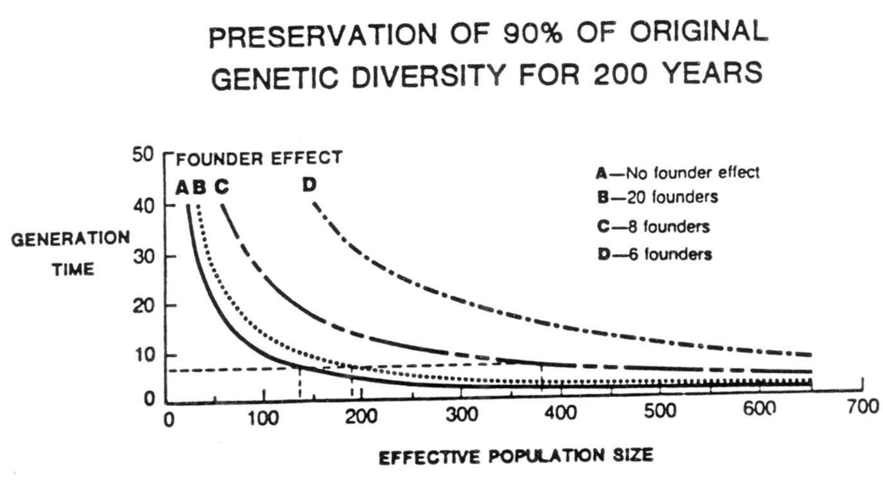

Figure 1. Interaction of number of founders, generation time of the species, and effective population size required for preserving 90% of the starting genetic diversity for 200 years.

Effective Population Size. Another very important consideration is the effective size of the population, designated N_e. N_e is not the same as N. Rather, N_e is a measure of the way the members of the population are reproducing with one another to transmit genes to the next generation. N_e is usually much less than N. For example in the grizzly bear, N_e/N ratios of about .25 have been estimated (Harris and Allendorf, 1989). As a consequence, if the genetic models prescribe an N_e of 500 to achieve some set of genetic objectives; the MVP might have to be 2000.

Growth Rate. The higher the growth rate, the faster a population can recovery from small size thereby outgrowing much of the demographic risk and limiting the amount of genetic diversity lost during the so-called "bottleneck". It is important to distinguish MVP's from bottleneck sizes.

Population viability analysis

The process of deriving MVP's by considering various factors, i.e. sets of objectives and characteristics, is known as Population Viability (sometimes Vulnerability) Analysis (PVA). Deriving really applicable results in PVA requires interactive efforts of population biology specialists with managers and researchers. PVA has already been applied more or less to about 30 species (Parker and Smith; Seal 1989).

As mentioned earlier, PVA currently must be performed separately with respect to genetic, demographic, and environmental problems or uncertainty. Considering genetics, PVA in general indicates it will be necessary to maintain populations in hundreds or thousands to preserve a high percentage of the gene pool for several centuries.

MVP's to contend with demographic and environmental stochasticity may be even higher than to preserve genetic diversity especially if a high probability of survival for an appreciable period of time is desired. For example, a 95% probability of survival may entail actually maintaining a much larger population whose persistence time is 20 times greater than required for 50% (i.e., average) probability of survival; 90%, 10 times greater. From another perspective, it can be expected that 50% of actual populations will become extinct before 70% of the average persistence time elapses.

Species of larger vertebrates will almost certainly need population sizes of several hundreds or perhaps thousands to be viable. In terms of the stochastic problems, more is always better.

Metapopulations and Minimum Areas

MVP's of course imply minimum critical areas of natural habitat, that will be vast for large carnivores like the Florida panther. Consequently, it will be difficult or impossible to maintain single, contiguous populations of the hundreds or thousands required for viability.

However, it is possible for smaller populations and sanctuaries to be viable if they are managed as a single larger population (a so-called metapopulation) whose collective size is equivalent to the MVP (Figure 2). Actually, distributing animals over multiple "subpopulations" will increase the effective size of the total number maintained in terms of the capacity to tolerate the stochastic problems. Any one subpopulation may become extinct or nearly so due to these causes; but through recolonization or reinforcement from other subpopulations, the metapopulation will survive. Metapopulations are evidently frequent in nature with much local extinction and re-colonization of constituent subpopulations occurring.

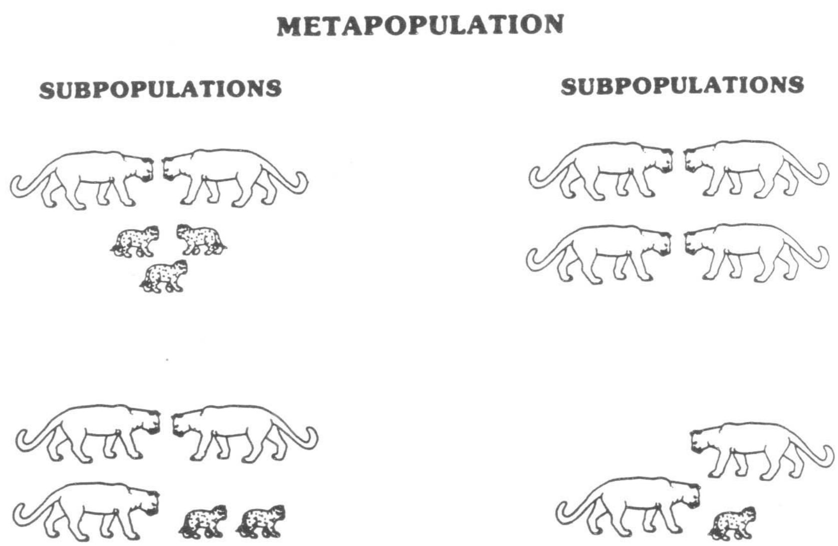

Figure 2. Multiple subpopulations as a basis for management of a metapopulation for survival of a species in the wild.

Unfortunately, as wild populations become fragmented, natural migration for re-colonization may become impossible. Hence, metapopulation management will entail moving animals around to correct genetic and demographic problems (Figure 3).
For migration to be effective, the migrants must reproduce in the new area. Hence, in case of managed migration it will be important to monitor the genetic and demographic performance of migrants

Managed migration is merely one example of the kinds of intensive management and protection that will be desirable and necessary for viability of populations in the wild. MVP's strictly imply benign neglect. It is possible to reduce the MVP required for some set of objectives, or considered from an alternative perspective, extend the persistence time for a given size population, through management intervention to correct genetic and demographic problems as they are detected. In essence, many of these measures will increase the N_e of the actual number of animals maintained.

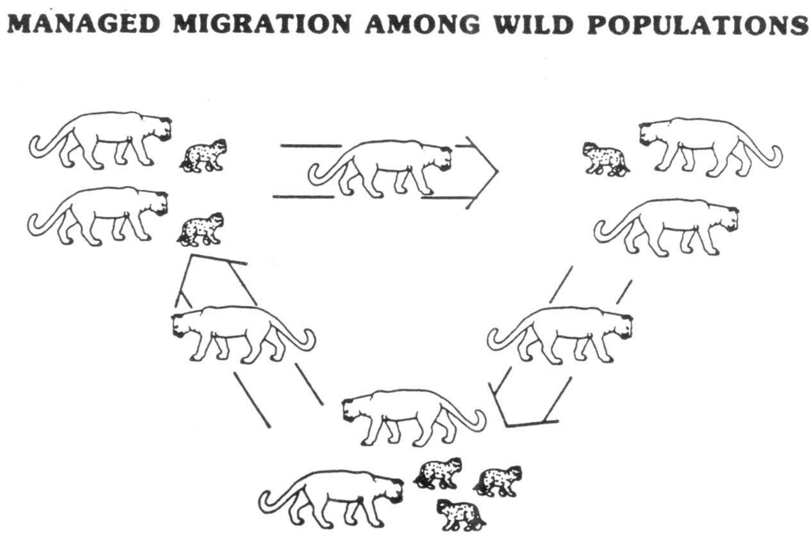

Figure 3. Managed migration among subpopulations to sustain gene flow in a metapopulation.

There are numerous examples of management intervention that would be applicable to the Florida panther case: action to improve juvenile survival, e.g. translocation of otherwise doomed dispersing young animals to available habitat to which they could not migrate naturally; introducing more breeding-age females to an area depauperate in this sex because of random biases toward males in a local area; accelerating turnover in dominant males that might be monopolizing breeding of multiple females and thereby causing distortion of sex ratios and family sizes with consequent depression of N_e; relocation of animals to prevent reproduction by close relatives.

Such interventions are manifestations of the fact that as natural sanctuaries and their resident populations become smaller, they are in effect transforming into megazoos that will require much the same kind of intensive genetic and demographic management as species in captivity.

Captive Propagation

Another way to enhance viability is to reinforce wild populations with captive propagation. More specifically, there are a number of advantages to captive propagation: protection from unsustainable exploitation, e.g. poaching; moderation of environmental vicissitudes for at least part of the population (e.g., it will keep the panthers off the roads); more genetic management and hence enhance preservation of the gene pool; accelerated expansion of the population to move toward the desired MVP and to provide animals more rapidly for introduction into new areas; increase in the total number of animals maintained.

It must be emphasized that the purpose of captive propagation is to reinforce, not replace, wild populations. Zoos must serve as reservoirs of genetic and demographic material that can periodically be transfused into natural habitats to re-establish species that have been extirpated or to revitalize populations that have been debilitated by genetic and demographic problems.

The survival of a great and growing number of endangered species will depend on assistance from captive propagation. Indeed, what appears optimal and inevitable are conservation strategies for the species incorporating both captive and wild populations interactively managed for mutual support and survival (Figure 4). The captive population can serve as a vital reservoir of genetic and demographic material; the wild population, if large enough, can continue to subject the species to natural selection. This general strategy has been adopted by the IUCN which now recommends that captive propagation be invoked anytime a taxon's wild population declines below 1000 (IUCN 1988).

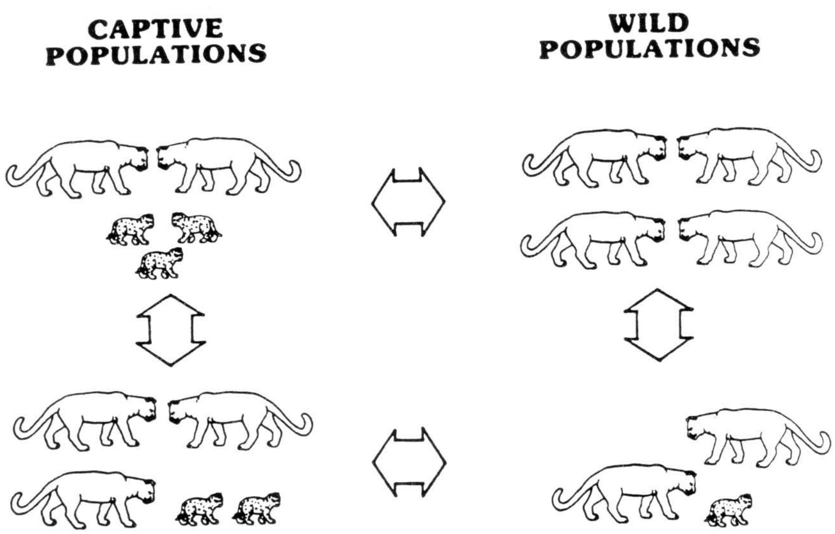

Figure 4. The use of captive populations as part of a metapopulation to expand and protect the gene pool of a species.

Species Survival Plans

Zoos in many regions of the world are organizing scientifically managed and highly coordinated programs for captive propagation to reinforce natural populations. In North America, these efforts are being developed under the auspices of the AAZPA, in coordination with the IUCN SSC Captive Breeding Specialist Group (CBSG), and are known as the Species Survival Plan (SSP).

Captive propagation can help but only if the captive populations themselves are based on concepts of viable populations. This will require obtaining as many founders as possible, rapidly expanding the population normally to several hundreds of animals, and managing the population closely genetically and demographically. This is the purpose of SSP Masterplans. Captive programs can also conduct research to facilitate management in the wild as well as in captivity, and for interactions between the two.

A prime example of such a captive/wild strategy is the red wolf program in North America. In fact, there is now a combined USFWS Recovery Plan/SSP Masterplan for this species (Parker and Smith 1988). Much of the captive propagation of red wolves has occurred at a special facility in Washington state. But there are also a growing number of zoos providing captive habitat, especially institutions within the historical range of the red wolf.

For the Florida panther, there are approximately 37 zoos in the 9 states comprised within the historical range. Currently, there are about 40 cougars maintained by these zoos; only 3 are coryi. There are at least another 25 zoos in contiguous states where the historic subspecies of cougar have long been extinct. Some preliminary explorations indicates many of these zoos would eagerly participate in an SSP-type program if organized.

Another eminent example of a conservation/recovery strategy incorporating both captive and wild populations is the black-footed ferret. Here the species now evidently survives only in captivity. Because the decision to establish a captive population was delayed, the situation became so critical that moving all the animals into captivity seemed the only option, circumstances that also applied to the California condor. Another option may have been available if action to establish a captive population had occurred earlier. Consideration of the survivorship pattern, which exhibited high juvenile mortality for ferrets, as it does also for cougars, suggested that young animals destined to die in the wild anyway might be removed with little or no impact.

In general, AAZPA and CBSG have become involved in these kinds of strategies and program worldwide.

It should be emphasized that the kind of conservation strategy that has been delineated would apply regardless of how taxonomic problems of defining what constitutes separate entities to be preserved (i.e., evolutionary significant units or esu's) are resolved. The goal has to be to develop viable populations of each of the esu's. ESU's are based on a variety of biological and frequently biopolitical considerations. But in the case of the panther, viable populations for each esu should be developed, whether those esu's are: the entire population of cougar now inhabiting Florida; the Everglades population separately from the Big Cyprus population; some reconstituted population consisting of Florida animals and imports from populations elsewhere; or some other defined entities.

IV. OVERVIEW: DEMOGRAPHIC CHALLENGES AND PERSISTENCE TIME OF SMALL POPULATIONS. (J. Ballou)

Abstract

Extinction rates (persistence times) of populations are determined by the population size, growth rate, susceptibility to demographic challenges (sometimes measured as variation in growth rate), and its spatial distribution. In turn, growth rate, and population's susceptibility to demographic challenges is determined by the population's life history characteristics, and such random factors as the severity of demographic, environmental, genetic, disease and catastrophic events affecting the population.

Preliminary models are available for estimating persistence times for specific populations providing data are available on the demographic characteristics of the population. These model have been most useful for developing conservation strategies for small populations.

While the mean (expected) persistence time can be roughly estimated, these models show that persistence time is distributed as an approximate exponential distribution. Hence there is a high probability that the population will go extinct well before its calculated mean time. Model results that indicate long mean persistence times are therefore misleading since more than 50% of the time populations will go extinct before the indicated mean time period.

To protect against this, very large populations or a number of different populations will be needed to assure high certainty of population survival for significant periods of time. Furthermore, management decisions need to specify both time frame for management and degree of certainty as specific management goals (e.g. 95% certainty of surviving for 100 years) in order to accurately evaluate available management options and develop Minimum Viable Population Size ranges for populations.

Introduction

Goals of single-species conservation programs are, in general, specifically directed towards mitigating the risks of extinction for those species of interest. This is best accomplished by understanding, identifying and redressing those factors that increase the probability of the population going extinct.

Small populations, even if stable in the demographic sense, are particularly susceptible to a discouraging array of challenges that could potentially have a significant impact on their probability of survival (Soule, 1987). Among these challenges are Demographic Variation, Environmental Variation, Disease Epidemics, Catastrophes and Inbreeding Depression.

Challenges to Small Populations

Demographic Variation: This is the variation in the population's overall (average) birth and death rates caused by random differences among individuals in the population. The population can experience 'good' or 'bad' years in terms of population growth simply due to random (stochastic) variation at the individual level. This can have consequences of the population's survival. For example, one concern in captive propagation is the possibility that all individuals born into a small population during one generation are of one sex, resulting in the population going extinct. Figure 5 illustrates the probability of this occurring over a 100 generation period in populations of different size. There is a 50% chance of extinction due to biased sex ratio in a population of size 8 sometime during this time period. However, these risks are practically negligible in populations of much large size. Similar consequences could result from the coincidental but random effects of high death rates or low birth rates.

In general, the effect of any one individual on the overall population's trend is significantly less in large populations than small populations. As a result, Demographic Variation is a minor demographic challenge in all but very small populations.

Florida Panther PVA Report

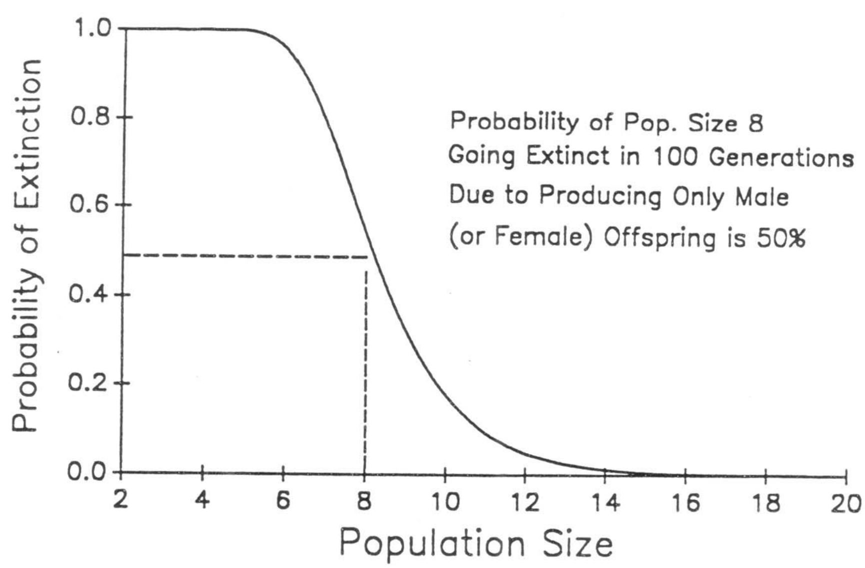

Figure 5. Example of Demographic Variation: Probability of extinction sometime during a 100 generation period due solely to producing only one sex of offspring.

Environmental Variation: Variation in environmental conditions clearly impact the ability of a population to reproduce and survive. As a result, populations susceptible to environmental variation vary in size more than less susceptible populations, increasing the danger of extinction. For example, reproductive success of the endangered Florida snail kite (Rostrhamus sociabilis) is directly affected by water levels, which determines prey (snail) densities: nesting success rates decrease by 80% during years of low water levels. Snail kite populations, as a result, are extremely unstable (Beissinger, 1986).

Disease Epidemics: Disease epidemics and catastrophes are similar to other forms of environmental variation in the sense that they are external to the population. However, they are listed separately because they are not within the realm of the normal environmental pressures exerted on a population. They can be thought of more appropriately as rare events that can have devastating consequences on the survival of a large proportion of the population.

Epidemics can have a direct or indirect effect. For example, in 1985 the sylvatic plague had a severe indirect effect on the last remaining black-footed ferret population by affecting the ferrets prey base, the prairie dog. Later that same year, the direct effect of distemper killed all of the 6 ferrets that had been brought into captivity (Thorne and Belitsky, in press).

Catastrophes: From a demographic perspective, catastrophes are one-time disasters capable of totally decimating a population. Catastrophic events include natural events (floods, fires, hurricanes) or human induced events (deforestation or other habitat destruction). Large and small populations are susceptible to catastrophic events. Tropical deforestation is the single most devastating 'catastrophe' affecting present rates of species extinction. Estimates of tropical species' extinction rates vary between 20 and 50% by the turn of the century (Lugo, 1988).

Inbreeding Depression: In small closed populations, mate choice is soon limited to close relatives, resulting in increased rates of inbreeding. The deleterious effects of inbreeding are well documented in a large variety of taxa. Although inbreeding depression has a genetic mechanism, its effects are demographic. Most data on exotic species come from studies of inbreeding effects on juvenile mortality in captive populations (Ralls, Ballou and Templeton; 1983). These studies show an average effect of approximately 10% decrease in juvenile survival with every 10% increase in inbreeding. Data on the effects of inbreeding on reproductive rates in exotics is limited (lions; Wildt et al, 1987); however, domestic animal sciences recognize that inbreeding effects on reproduction are likely to be more severe than effects on survival. Inbreeding also may reduce a population's disease resistance, and ability to adapt to rapidly changing environments (O'Brien et al, 1988).

Interacting Effects: Clearly, demographic challenges do not act independently in small populations. As a small population becomes more inbred, reduced survival and reproduction are likely; the population decreases. Inbreeding rates increase and because the population is smaller and more inbred, it is more susceptible to demographic variation as well as disease and severe environmental variation. Each challenge exacerbates the others resulting in a negative feedback effect (Figure 6). Over time the population becomes increasingly smaller and more susceptible to extinction (Gilpin, 1986).

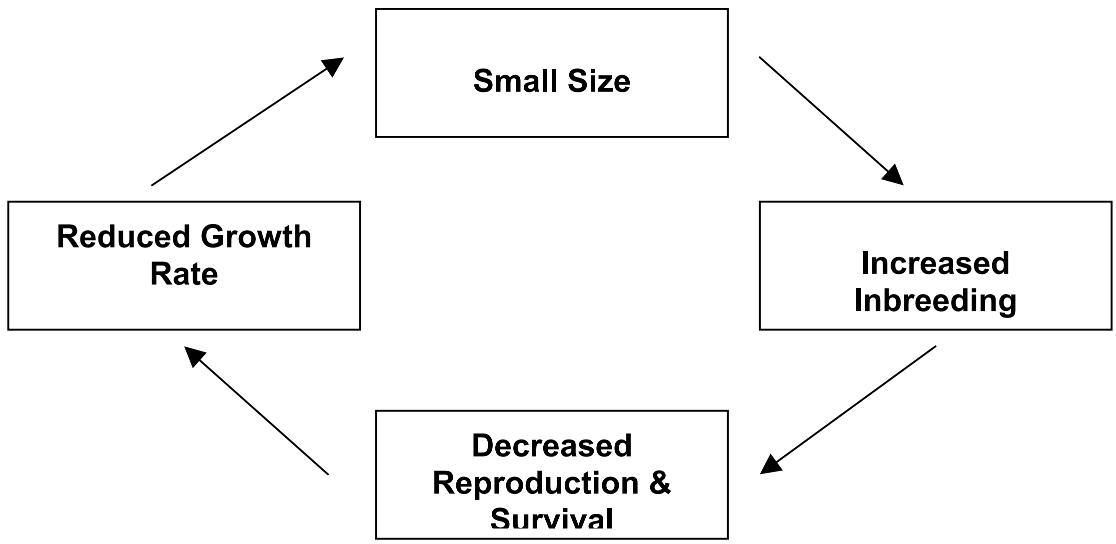

Figure 6. Negative feedback effects of inbreeding on small populations.

Susceptibility to Demographic Challenges

Populations differ in their susceptibility to demographic challenges. As mentioned above, population size clearly effects vulnerability. Large populations are relatively unaffected by demographic variation and are less apt to be totally devastated by environmental variation than small populations.

The severity of the demographic challenge is also important. A population in a fairly stable environment is less likely to go extinct than a population in a highly variable environment or an environment vulnerable to catastrophes.

A third important factor is a population's potential for recovering from these demographic challenges, in other words, the population's growth rate. A population at carrying capacity experiences normal fluctuation in population size; the degree of fluctuation depending on the severity of demographic challenge. Populations with low growth rates remain small longer than populations with rapid growth potential and therefore are more vulnerable to future size fluctuations.

A fourth important consideration is the population's spatial distribution. A population that is dispersed across several 'metapopulations,' or patches, is significantly less vulnerable to catastrophic extinctions than a same-sized population localized in a single patch. Extinction of one patch among many does not extinguish the entire population and colonization between patches could reconstitute extinct patches (Gilpin, 1987).

Populations dispersed over a wide geographic range are also unlikely to experience the same environment over the entire range. While part of a population's range may suffer from extreme environmental stress (or catastrophes), other areas may act as a buffer against such effects.

Estimating Susceptibility with Persistence Time Models

A population's susceptibility to demographic challenges can be measured in terms of the amount of time it takes a population to go extinct. This is often referred to as the persistence time of the population. Ideally, persistence time should be estimated from data on all the variables discussed above. Persistence times are usually estimated from mathematical models that either simulate the population over a period of time (stochastic models) or estimate the population's expected (mean) persistence time (deterministic models).

Unfortunately, methods are not (yet) available to simultaneously consider the effect of all the above variables on persistence time. Usually, persistence times are estimated by considering the effects of only one or two variables. The effects of spatial distribution are the most important; however, they are also the most difficult and consequently are not considered (or only rudimentarily considered) in most persistence time models. These models assume a single, geographically localized population.

Goodman(1987) presents an example of a deterministic persistence time model. This model estimates the mean persistence time of a population given its size, growth rate and its susceptibility to environmental and demographic challenges.

In Goodman's model, susceptibility to demographic challenges is represented by the variance in the population's growth rate. A population that is very susceptible to environmental perturbations will vary drastically in size from year to year, which, in turn, will be reflected as a high variance in the population's growth rate. Goodman's model is:

$$\textit{Mean Extinction Time} = \sum_{x=1}^{N} \sum_{y=x}^{N} \frac{2}{y(yV - r)} \qquad \sum_{z=x}^{Y-1} \frac{zV + r}{zV - r}$$

where: r = exponential annual growth of the population
V = variance in r
N = Maximum (ceiling) population size

The mean persistence times for populations of size 30 and 50 (ranges of estimates for the Florida panther population) with low growth potentials (.5% and 2% per year) are shown in Figure 7. These graphs are provided simply to introduce the concept of persistence time models and are not suggested as realistic models of the Florida panther population. More realistic models, based on life history data collected from the field, are provided below.

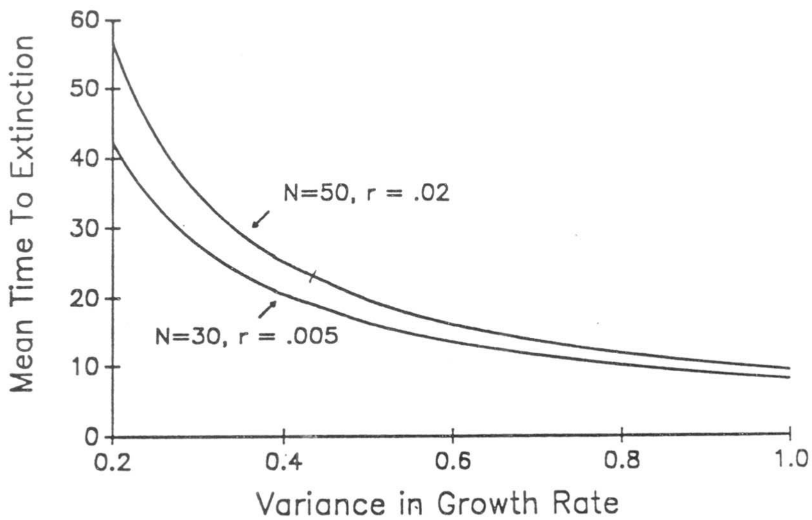

Figure 7. Mean time to extinction (persistence time) for a population of 50 animals with exponential growth rate of .02 (approx. 2% per year) and population of 30 animals with exponential growth rate of .005 (approx. 0.5% per year) under different levels of variation on growth rate. Variation in growth rate is a measure of the population's susceptibility to demographic challenges.

The mean time to extinction is inversely related to the variation in the growth rate: if variance is extremely high, regardless of the population sizes or potential growth rates, the mean persistence time (time to extinction) is approximately 10 years. However, with variances of .2, mean persistence time varies from 42 to 57 years.

To provide perspective on the meaning of variance in r, if the growth rate is distributed as a normal random variable, a variance of .2 would mean that 75% of the growth rates experienced by the population would fall within the range of 50% increase per year and 50% population decline per year.

Persistence Time is Exponentially Distributed

An important characteristic of persistence time is that it has an approximately exponential distribution. The models provide the mean, or expected time to extinction; however, there is significant variation around this mean. Many population go extinct well before the mean time; a few go extinct long after.

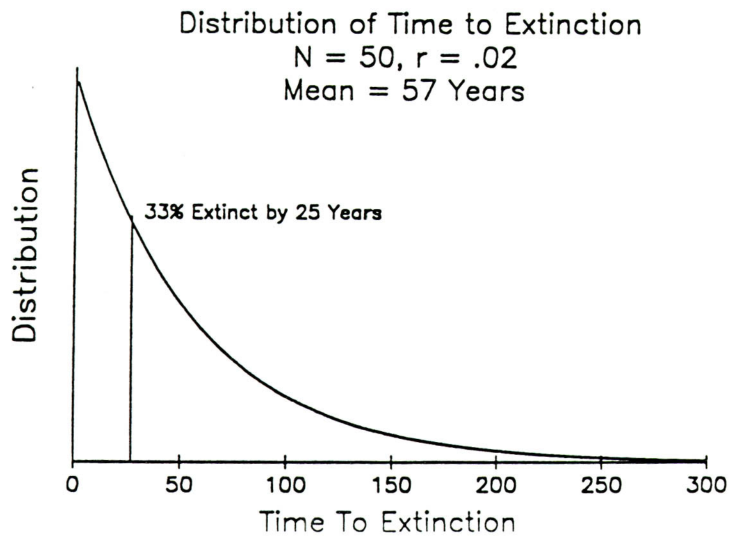

Figure 8. Exponentially distributed persistence time for a population of 50 animals growing at an exponential rate of .02 with a variation in growth rate of 0.2. While the mean (expected) persistence time is 57 years, the exponential characteristic of the distribution shows that there is a high probability of extinction before this period (33% chance by 25 years).

The exponential distribution of persistence time for a population of 50 individuals with a growth potential of 2% and growth variance of .2 is shown in Figure 8. The mean persistence time is 57 years. However, since the distribution is exponential, there is a high probability that the time to extinction will occur before 57 years. In fact, there is a 33% chance that the time of extinction will be before 25 years.

Given that persistence times are approximately exponentially distributed, times to extinction can be estimated with various degrees of certainty. Again for the same population described in Figure 7, we can estimate the probability of extinction at different time periods (Figure 9). With growth rate variation at .2, mean time to extinction is 57 years; however, there is a 50% chance that the population will survive only to 40 years, only a 75% chance that the population will survive at least to 15 years, and a 95% chance that the population will survive at least to 4 years. In other words, there is a 5% chance that the population will go extinct in 4 years.

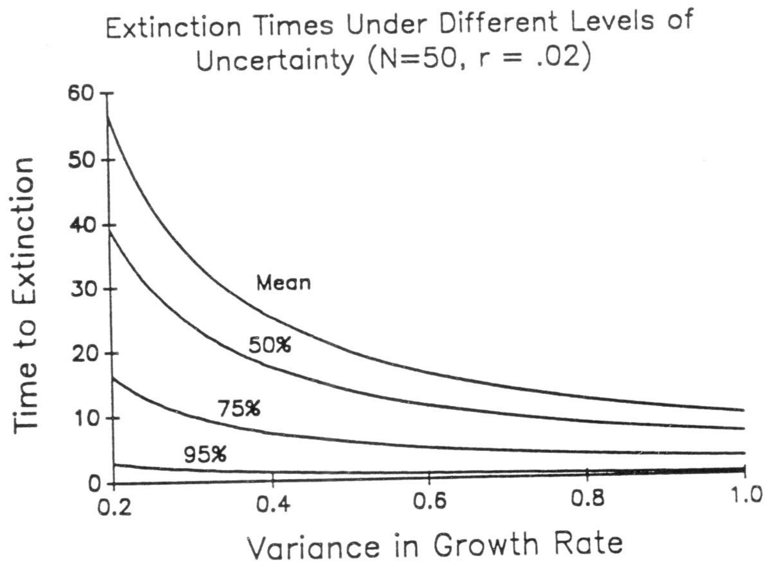

Figure 9. Extinction times under different levels of uncertainty. See text.

The Minimum Viable Population (MVP) Size concept is based on the premise that persistence times can only be defined with reference to degrees of certainty. Ideally, given a population's life history characteristics and management goal (a desired persistence time under a specified degree of certainty, e.g. 95% chance of surviving for 200 years), we could estimate the population size required to achieve the goal. This would be a Minimum Viable Population Size (MVP size) for the program (Shaffer, 1981). However, since MVP size is a function of the specific management goals of the population, there is no one "magical" MVP size for any given population in any given circumstance.

Management Implications

The implication of exponentially distributed persistence time is that management strategies can not be based on the mean persistence time if a high degree of certainty is desirable. Although the mean persistence time of the modeled panther population is 57 years, management strategies should recognize that to be 95% certain that the population survives even 50 years would require a population size whose mean persistence time is 975 years. This would require well over 1000 individuals.

A second implication is that management strategies can only be fully evaluated if both degree of certainty and time frame for management are specified. For example, programs may be evaluated in terms of their potential for assuring a 95% chance of the managed population surviving for 200 years. It is critical that the management decision making process recognize that the process of extinction is a matter of probabilities, as are all its components (environmental and demographic variation, probability of catastrophe, etc.; Shaffer, 1987).

V. GENETIC PROCESSES IN SMALL AND FRAGMENTED POPULATIONS
(R. C. Lacy).

Many wildlife populations that were once large, continuous, and diverse have been reduced to small, fragmented isolates in remaining natural areas, nature preserves, or even zoos. For example, black rhinos once numbered in the 100s of thousands, occupying much of Africa south of the Sahara; now a few thousand survive in a handful of parks and reserves, each supporting a few to at most a few hundred animals. Similarly, the range of the Florida panther has been reduced from most of the southeastern United States to just the southwestern part of the Florida peninsula. Moreover, even that remnant population of panthers seems to be fragmented into a population of about 30 animals in the Big Cypress area and an isolated Everglades population of perhaps only 4-6 animals.

On top of the demographic risks, small populations also face genetic risks -- which exacerbate and in turn are exacerbated by the demographic problems. When the size of an inter-breeding population is only on the order of 10s or 100s (rather than 1000s or more), random (stochastic) events predominate and population survival becomes more or less a lottery. In the absence of selection, each generation is random genetic sample of the previous generation. When this sample is small, the frequencies of genetic variants (alleles) can shift markedly from one generation to the next by chance, and variants can be lost entirely from the population -- a process referred to as "genetic drift". Genetic drift is cumulative. There is no tendency for allele frequencies to return to earlier states (though they may do so by chance), and a lost variant cannot be recovered, except by the reintroduction of the variant to the population through mutation or immigration from another population. Mutation is such a rare event (on the order of one in a million for any given gene) that it plays virtually no role in small populations over time scales of human concern (Lacy 1987). The restoration of variation by immigration is only possible if other populations exist to serve as sources of genetic material.

Genetic drift, being a random process, is also non-adaptive. In populations of less than 100 breeders, drift overwhelms the effects of all but the strongest selection: Adaptive alleles can be lost by drift, with the fixation of deleterious variants (genetic defects) in the population. The prevalence of cryptorchidism in the Florida panthers is probably the result of a strongly deleterious allele that has become common, by chance, in the population; and the kinked tail is probably a mildly deleterious (or at best neutral) trait that has become almost fixed within the Florida panthers.

A concomitant of genetic drift in small populations is inbreeding -- mating between genetic relatives. When numbers of breeding animals become very low, inbreeding becomes inevitable and common. Inbreeding has been documented in the Everglades subpopulation of panthers (where it will continue unless additional genetic material is introduced), and is likely occurring, if less frequently, in the larger Big Cypress population. Inbred animals often have a higher rate of birth defects, slower growth, higher mortality, and lower fecundity ("inbreeding depression"). Inbreeding depression has been well documented in laboratory and domesticated stocks (Falconer 1981), zoo populations (Ralls, et al. 1979; Ralls and Ballou 1983), and a few wild populations. Inbreeding depression probably results primarily from the expression of rare, deleterious alleles. Most populations contain a number of recessive deleterious alleles (the "genetic load" of the population) whose affects are usually masked because few individuals in a randomly breeding population would receive two copies of (are "homozygous" for) a harmful allele. Because their parents are related and share genes in common, inbred animals have much higher probabilities of being homozygous for rare alleles. If selection were efficient at removing deleterious traits from small populations, progressively inbred populations would become purged of their genetic load and further inbreeding would be of little consequence. Because random drift is so much stronger than selection in very small populations, even decidedly harmful traits can become common (e.g., cryptorchidism in the Florida panther) and inbreeding depression can drive a population to extinction.

The loss of genetic diversity that occurs as variants are lost through genetic drift has other, long-term consequences. As a population becomes increasingly homogeneous, it becomes increasingly susceptible to disease, new predators, changing climate, or any environmental change. Selection cannot favor the more adaptive types when all are identical and none are sufficiently adaptive. Every extinction is, in a sense, the failure of a population to adapt quickly enough to a changing environment.

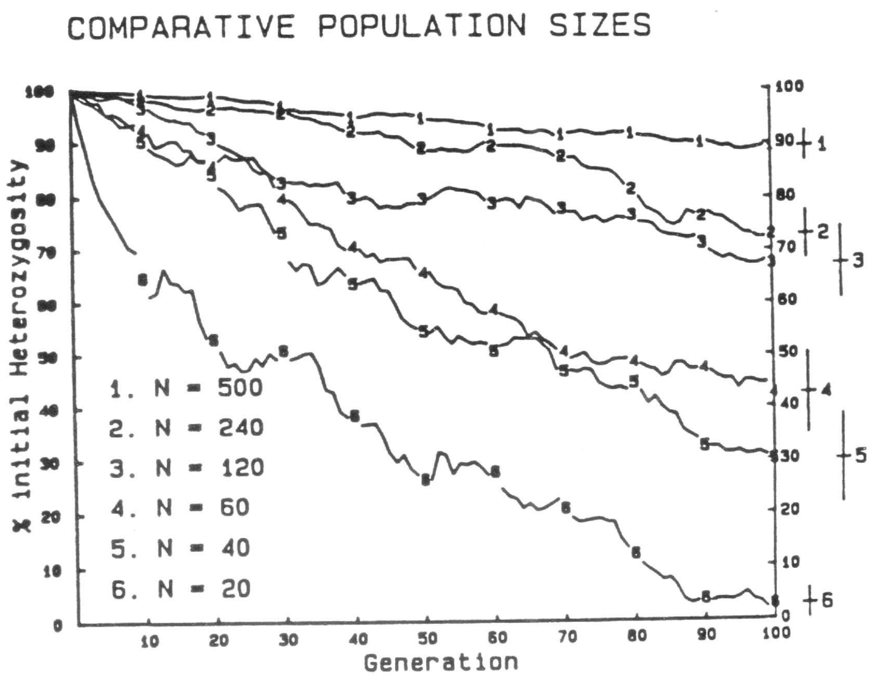

Figure 10. The average losses of genetic variation (measured by heterozygosity or additive genetic variation) due to genetic drift in 25 computer-simulated populations of 20, 40, 60, 120, 240, and 500 randomly breeding individuals. Figure from Lacy 1987.

To avoid the immediate effects of inbreeding and the long-term losses of genetic variability a population must remain large, or at least pass through phases of small numbers ("bottlenecks") in just one or a few generations. How many animals are sufficient to prevent substantial and threatening genetic losses? Although we cannot predict which genetic variants will be lost from any given population (that is the nature of random drift), we can specify the expected average rate of loss. Figure 10 shows the mean fate of genetic variation in randomly breeding populations of various sizes. The average rate of loss of genetic variance (when measured by heterozygosity, additive variance in quantitative traits, or the binomial variance in allelic frequencies) declines by drift according to:

$$V_g(t) = V_g(0) \times (1 - 1/(2N_e))^t,$$

in which V_g is the genetic variance at generation t, and N_e is the effective population size (see below) or approximately the number of breeders in a randomly breeding population. As shown in Figure 11, the variance in the rate of loss among genes and among different populations is quite large; some populations may (by chance) do considerably better or worse than the averages shown the Figure 10.

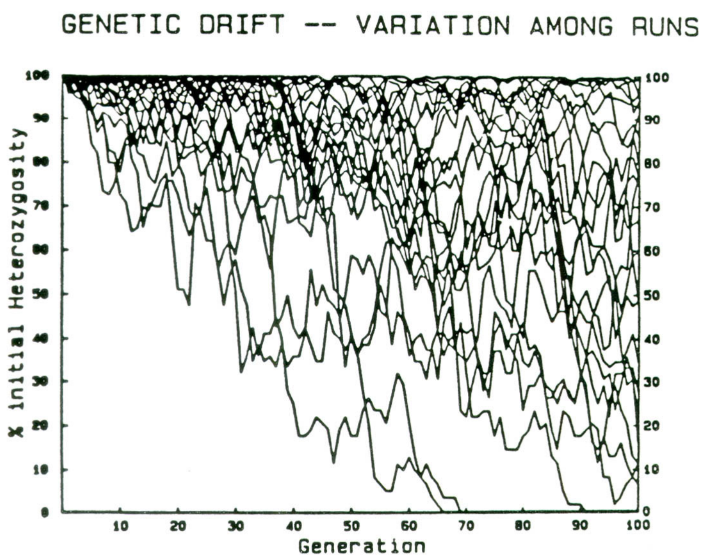

Figure 11. The losses of heterozygosity at a genetic locus in 25 populations of 120 randomly breeding individuals, simulated by computer. Figure from Lacy 1987.

The rate of loss of genetic variation considered acceptable for a population of concern depends on the relationship between fitness and genetic variation in the population, the decrease in fitness considered to be acceptable, and the value placed by humans on the conservation of natural variation within wildlife populations. Over the short-term, a 1% decrease in genetic variance (or heterozygosity), which corresponds to a 1% increment in the inbreeding coefficient, has been observed to cause about a 1% decrease in aspects of fitness (fecundity, survival) measured in a variety of animal populations (Falconer 1981). Appropriately, domesticated animal breeders usually accept inbreeding of less than 1% per generation as unlikely to cause serious detriment. The relationship between fitness and inbreeding is highly variable among species and even among populations of a species, however. A few highly inbred populations survive and reproduce well (e.g., northern elephant seals, Pere David's deer, European bison), while attempts to inbreed many other populations have resulted in the extinction of most or all inbred lines (Falconer 1981).

Concern over the loss of genetic adaptability has led to a recommendation that management programs for endangered taxa aim for the retention of at least 90% of the genetic variance present in ancestral populations (Foose, et al. 1986). The adaptive response of a population to selection is proportional to the genetic variance in the traits selected, so the 90% goal would conserve a population capable of adapting at 90% the rate of the ancestral population. Over a time scale of 100 years or more, and for a medium-sized mammal with a generation time of 5 years, such a goal would imply an average loss of 0.5% of the genetic variation per generation, or a randomly breeding population of about 100 breeding age individuals.

Most populations, whether natural, reintroduced, or captive, are founded by a small number of individuals, usually many fewer than the ultimate carrying capacity. Genetic drift can be especially rapid during this initial bottleneck (the "founder effect"), as it is whenever a population is at very low size. To minimize the genetic losses from the founder effect, managed populations should be started with 20 to 30 founders, and the population should be expanded to carrying capacity as rapidly as possible (Foose, et al. 1986; Lacy 1988, 1989). With twenty reproductive founders, the initial population would contain approximately 97.5% of the genetic variance present in the source population from which the founders came. The rate of further loss would decline from 2.5% per generation as the population increased in numbers. Because of the rapid losses of variability during the founding bottleneck, the ultimate carrying capacity of a managed population may have to be set substantially higher than the 100 breeding individuals given above in order to keep the total genetic losses below 90% (or whatever goal is chosen).

The above equations, graphs, and calculations all assume that the population is randomly breeding. Yet breeding is random in few if any natural populations. The "effective population size" is defined as that size of a randomly breeding population (one in which gamete union is at random) which would lose genetic variation by drift at the same rate as does the population of concern. An unequal sex ratio of breeding animals, greater than random variance in lifetime reproduction, and fluctuating population sizes all cause more rapid loss of variation than would occur in a randomly breeding population, and thus depress the effective population size. If the appropriate variables can be measured then the impact of each factor on N_e can be calculated from standard population genetic formulae (Crow and Kimura 1970; Lande and Barrowclough 1987).

For many vertebrates, breeding is approximately at random among those animals that reach reproductive age and enter the breeding population. To a first approximation, therefore, the effective population size can be estimated as the number of breeders each generation. In managed captive populations (with relatively low mortality rates, and stable numbers), effective population sizes are often 1/4 to 1/2 the census population. In wild populations (in which many animals die before they reach reproductive age), Ne/N probably rarely exceeds this range and often is an order of magnitude less.

The population size required to minimize genetic losses in a medium sized mammal, therefore, might be estimated to be on the order of $N_e = 100$, as described above, with N = 200 to 400. More precise estimates can, and should, of course be determined for any population of management concern from the life history characteristics of the population, the expected losses during the founding bottleneck, the genetic goals of the management plan, and the time scale of management.

Although the fate of any one small population is likely to be extinction within a moderate number of generations, populations are not necessarily completely isolated from conspecifics. Most species distributions can be described as "metapopulations", consisting of a number of partially isolated populations, within each of which mating is nearly random. Dispersal between populations can slow genetic losses due to drift, can augment numbers following population decline, and ultimately can recolonize habitat vacant after local extinction.

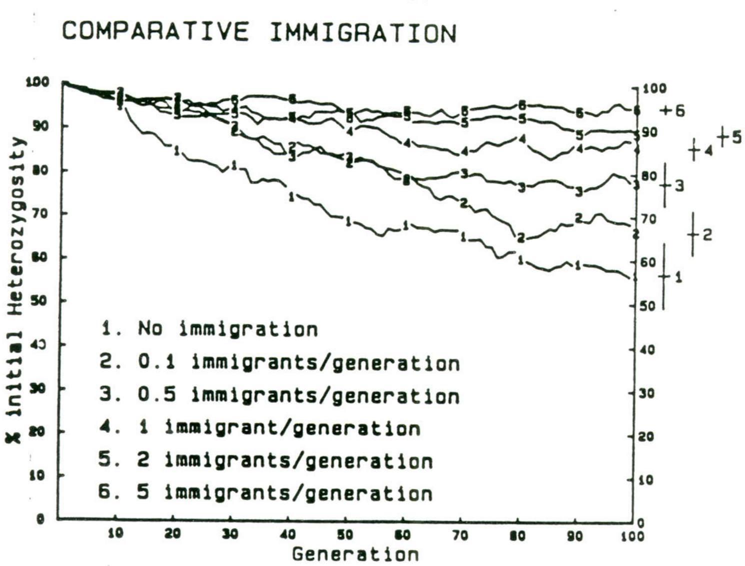

Figure 12. The effect of immigration from a large source population into a population of 120 breeding individuals. Each line represents the mean heterozygosity of 25 computer-simulated populations (or, alternatively, the mean heterozygosity across 25 genetic loci in a single population). Standard error bars for the final levels of heterozygosity are given at the right. Figure from Lacy 1987.

If a very large population exists that can serve as a continued source of genetic material for a small isolate, even very occasional immigration (on the order of 1 per generation) can prevent the isolated subpopulation from losing substantial genetic variation (Figure 12). Often no source population exists of sufficient size to escape the effects of drift, but rather the metapopulation is divided into a number of small isolates with each subjected to considerable stochastic forces. Genetic variability is lost from within each subpopulation, but as different variants are lost by chance from different subpopulations the metapopulation can retain much of the initial genetic variability (Figure 13). Even a little genetic interchange between the subpopulations (on the order of 1 migrant per generation) will maintain variability within each subpopulation, by reintroducing genetic variants that are lost by drift (Figure 14). Because of the effectiveness of even low

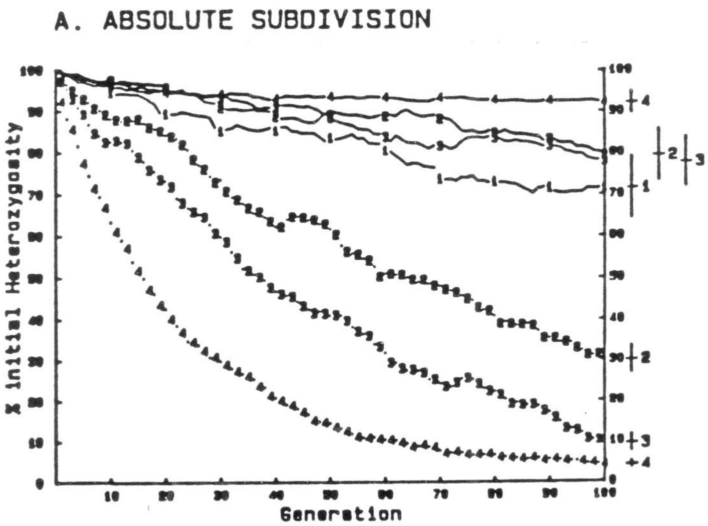

Figure 13. The effect of division of a population of 120 breeders into 1, 3, 5, or 10 isolated subpopulations. Dotted lines (numbers) indicate the mean within-subpopulation heterozygosities from 25 computer simulations. Lines represent the total gene diversity within the simulated metapopulation. Figure from Lacy 1987.

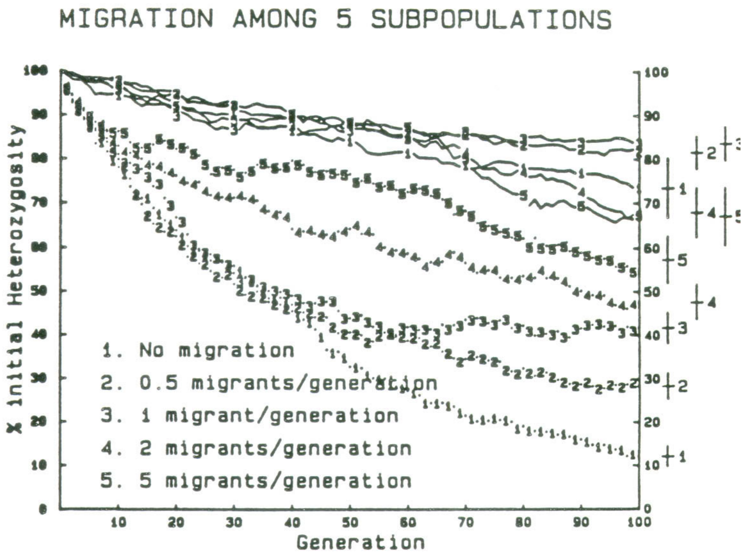

Figure 14. The effect of migration among 5 subpopulations of a population of 120 breeders. Dotted lines (numbers) indicate the mean within-subpopulation heterozygosities from 25 simulations. Lines represent the total gene diversity within the metapopulation. Figure from Lacy 1987.

Levels of migration at countering the effects of drift, the absolute isolation of a small population would have a very major impact on its genetic viability (and also, likely, its demographic stability). Population genetic theory makes it clear that no small, totally isolated population is likely to persist for long.

VI. POPULATION BIOLOGY PARAMETERS

Current population size

Because of the secretive nature of panthers, field biologists have been unable to make precise estimates of the present population size. The population seems to be distributed around three primary centers in southern Florida: Big Cypress, Raccoon Point, and the Everglades. Eight panthers are presently collared in the Big Cypress, and field biologists estimate perhaps as many as 10 uncollared animals in that area. The Raccoon Point population (contiguous with Big Cypress?) was stated to have from 2 to 6 panthers (none collared), though concern was expressed that the subpopulation may be declining or gone. Four collared animals are in the Everglades (and 2 Everglades panthers are in captivity), and the optimistic guess was made that perhaps a few more animals may be in the Everglades (though no signs of additional animals have been seen). Thus, the primary population of Florida panthers is estimated at 24 to 32 animals in the wild. Sporadic sign has been noted along the St. John's River, though no panthers have been sighted. Any panthers in that area are likely few and scattered, and are unlikely to constitute a viable, breeding population. Based on these data, we considered 30 adult panthers to be a moderately optimistic estimate of the Florida population to be used in our calculations. Note that the above counts of panthers includes some sub-adults (e.g., 3 of 11 collared animals).

Not all potential panther habitat has been thoroughly searched (e.g., the area around Highlands Co., north of the Big Cypress population), and some field biologists believe that another 10 adult panthers could live outside of the primary study areas. As an upper estimate on the present population size we used 40 adult panthers in the models.

The number of juvenile and sub-adult panthers (< 3 years of age) in the population is even harder to estimate than the adults. Only three litters are presently known in the wild, though others probably exist with uncollared females. Three of 11 collared animals in the wild are sub-adults, as are 2 of 4 panthers in captivity. Based on assumed biannual breeding, mean litter size of 3, and 44% annual mortality over the first three years of life (see below), it can be calculated that the average adult female would have 2.8 living juvenile or subadult offspring just after the birthing season (prior to any mortality of that year's cubs, females would have either 3 newborns and .94 2-year old offspring or 1.68 1-year old offspring). Just prior to the breeding season, the average adult female would have 1.6 living juvenile or sub-adult offspring (either 1.68 cubs from the previous year and .53 almost 3-year old sub-adults or .94 2-year old cubs). Thus, the expected ratio of juvenile + sub-adult to adult panthers may be estimated as between 0.8 and 1.4 (.67 to 1.17, if mean litter sizes are only 2.5), depending on when the animals are counted (see also Table 1). We examined two scenarios in our modelling of the population: a 1:1 sub-adult to adult ratio (roughly as above), and a 1:2 ratio, as would occur if only half of the adult population were in the breeding pool.

Carrying capacity

The population sustainable in the available habitat might, to a first approximation, be assumed to be equal to the present population size (30 to 40 adults, 15 to 40 juveniles and sub-adults). The dispersal of juveniles to the limits of apparently suitable habitat, the observed aggression (leading to death in 4 cases) among panthers, and the poor nutritional and health status of many panthers all suggest that all suitable habitat is occupied. Some field biologists noted that reproduction seems to have ceased in some subsets of the population (e.g., Fakahatchee Strand), and that the population may now exceed the carrying capacity and may be declining. It was also noted that areas of good panther habitat are in private ownership and are likely to be developed further for agriculture in the near future. It is also possible that management practices (e.g., leading to increased prey availability, decreased road kills) could raise the carrying capacity of the acreage currently supporting panthers. We examined scenarios with carrying capacities of 30, 45, and 80 panthers, representing pessimistic or declining, moderate, and optimistic or improving estimates of habitat availability.

Reproduction

The earliest age of reproduction observed in female Florida panthers was 18 months (at conception) and another female bred between 18 and 24 months, but it is thought that 30-36 months may be more typical. A 14-18 month male was found to have good semen, but the earliest known breeding by a male was at 2.5 years of age. To encompass the range of possible values of mean age of first reproduction, we analyzed three cases: reproduction at 24 months, 30 months, and 36 months. It is likely that the onset of reproduction would be toward the lower end of this range when unoccupied, good habitat was available for sub-adults; whereas reproduction would be delayed if available habitat was suboptimal or already occupied by breeding adults.

Of eight litters were observed at approximately 6 months of age (5 captured, 3 otherwise observed), the mean size was 2.0 (variance 1.14). Assuming a 25% mortality in the first 6 months (see below), we could estimate litter sizes at birth to be 2.67. We examined two scenarios with respect to litter sizes: a mean of 2.5, distributed as 20% litters of 1, 30% of 2, 30% of 3, and 20% of 4; and a mean of 3.0, distributed as 10% of 1, 20% of 2, 40% of 3, 20% of 4, and 10% of 5. Larger mean litter sizes (at birth) are conceivable, but would have to be accompanied by offsetting higher infant mortality rates to yield the 6-month litter sizes observed.

Most collared adult females have bred every other year, and we perhaps optimistically assumed in all scenarios examined that every reproductive-age female breeds biannually (has a 50% probability of producing a litter in any given year). Panthers were assumed to remain reproductive (without declining fecundity) throughout their life spans. No Florida panther has been observed to breed beyond the age of 11 years, but as few animals would be expected to live that long (see mortality estimates below) any error introduced by the assumption of no reproductive senescence would be minimal.

Mortality

Based on mortality of radio-collared panthers (12 deaths in 465 radio collar-months of tracking adult panthers, 2 deaths in 54 radio collar-months for sub-adults first observed at age 6 months) we estimate 31% and 44% annual mortality rates for adults and sub-adults (less than three years of age), respectively. The latter estimate is very crude (based on only 2 deaths and 4 animals). For our modelling, we assumed a somewhat more optimistic 50% first-year mortality (as observed in some western populations of panthers), followed by mortality no different from that of adults (i.e., 31%) subsequent to the first year. These first, second, and third year mortality rates of 50%, 31%, and 31% yield a total pre-reproductive mortality (76%) similar to that observed among radio-collared animals between 6 months and 3 years of age (44% annual mortality, yielding 76% mortality between 6 months and 3 years). If habitat is saturated, then mortality, especially of dispersing sub-adults, may be substantially higher. Such higher levels of mortality imposed by limited habitat were modelled with carrying capacities (see above) that impose random mortality across the population to limit numbers to no more than the set capacity each generation.

To give an end to the life table, we assumed a zero probability of survival from 18 to 19 years. Because the probability of an animal reaching 18 years of age is so small (< 0.1%), this truncation of the life table has no effect on the results presented.

Effective Population Size

The effective size of the wild population can be roughly estimated from the number of different adults breeding over a period of one generation. Data from collared panthers are available for such an estimate. A total of 29 animals have been collared since 1981, a period of 7 years. While this corresponds to slightly more than one panther generation, it was treated as one generation since not all animals were followed for the entire period. Fourteen of the 29 (48%) adults bred during this period. Additionally, given adult mortality rates (estimated at 31% per year), 47% of adults survive to mean breeding age (5 years). These data suggest that the effective of the population size is approximately 50% the number of adults. Since any variation in the number of offspring produced by these adults reduces the effective size, we used 25% as the lower bounds and 50% as the upper bounds for the estimates of the ratio of effective size to the number of adults.

Genetic Variation and Inbreeding Depression

Preliminary research by Drs. Roelke and O'Brien on levels of genetic variation in Florida panthers as measured by protein electrophoresis indicate 27% polymorphism and 2% level of heterozygosity. Although low, this level of genetic variation is not low enough to fall outside the normal range of heterozygosity levels found in other mammals. Furthermore, these results are preliminary and potentially subject to chance with further analysis.There is no direct evidence of inbreeding depression in the population. However, the direct effects of inbreeding depression are very difficult to document since inbreeding does not directly cause reduced fitness (survival and reproduction). Rather it unmasks deleterious genes that are then responsible for the depression effects. Therefore, inbreeding depression may manifest itself as many unpredictable ways. Nevertheless, given the high incidence (40%) of cryptorchidism (a recessive trait that could increase in frequency in inbred populations) and the high rate of acrosomal deformities in the sperm (also associated with inbreeding in other carnivore populations), we can't rule out the possibility that inbreeding depression exists in the population.

Time period for population projections

We modelled the Florida panther population over a 100-year time span. The goal was to model the population to facilitate management decisions that would leave options for the future. As we learn more about the panthers, and as the status of the population changes, management will have to be a dynamic process. Reanalyses should lead to modified management. We do not, however, want to manage with goals that could leave us with no or a debilitated panther population in just a few decades. (Note that most Species Survival Plans of the American

Association of Zoological Parks and Aquariums use a 200 year goal for captive management.)

Demography of captive panthers

As no substantial effort (many animals, over many years, at multiple sites) has been made to breed Florida panthers in captivity, the demographic parameters of a captive population of Florida panthers can only be estimated from data available on other subspecies that are currently held in captivity. Clearly the Florida subspecies may breed less well in captivity or suffer higher mortality than do western pumas in captivity, especially if genetic (inbreeding) problems have already markedly decreased the fitness of Florida animals. On the other hand, the captive propagation of non-Florida panthers has never received intensive effort, both because there has been little conservation concern for the less threatened subspecies and because pumas have bred so well in captivity that there has been little demand for production of more animals. Thus, reproductive rates in particular could probably be several-fold greater in captivity than has historically been the case. The ultimate size of a captive population of Florida panthers depends on the commitment of resources made to the species, which in turn presumably would be driven by the perceived need and value. Therefore, stochastic modelling of possible captive populations focused on determination of the number of panthers necessary for a long-term, viable population.

From the ISIS (International Species Information System) computerized data set, it was determined that the captive population of *Felis concolor* (not usually designated to subspecies and almost certainly consisting of a mixture of multiple subspecies) in North American institutions contributing data to ISIS is presently at about 218 living pumas, 70% captive-born. Births out pace deaths, and the population is held stable by export to private (non-ISIS) holders. First year mortality is approximately 40-45%, second year mortality is 5-10%, and annual mortality of adults is approximately 2-3%. To model a potential captive Florida panther population conservatively, we used 50% juvenile mortality (as in the models of the wild population) and 10% annual adult mortality. If human-caused mortality (road kills and illegal hunting) was removed from the wild population of Florida panthers, adult mortality would be reduced to approximately 10%. Reproduction in captivity could probably be accelerated to two litters per year with reproductive technologies and hand-rearing of litters, but we have assumed conservatively that the captive population would be less intensively managed and that females would produce biannual litters of mean size 3, beginning at age 2. Thus, we modelled the scenario of lowered adult mortality in captivity, but reproduction and juvenile mortality as in the more optimistic scenarios for the wild population.

VII. POPULATION VIABILITY ANALYSES

Life table determinations of population growth rates

The demographic parameters above were analyzed by standard life-table analysis (using a LOTUS program developed by Jon Ballou and Laurie Bingaman of the National Zoo) to determine the expected long-term population growth rate under various scenarios of age of first reproduction, mean litter size, juvenile mortality, and adult mortality. Table 1 shows the results of these calculations, presenting growth rates both as r, the instantaneous or exponential growth rate, and as lambda, the annual growth rate of the population. Also shown are the generation times (approximately the mean age of reproduction) and the age structure resulting from the demographic parameters.

As can be readily seen in the table, only the most optimistic estimates of population parameters for the wild population (reproduction at age 2, 25% adult mortality, mean litter size of 3) lead to positive population growth; population decline is projected under all other scenarios. Under the parameters perhaps most closely matching the available field data (mean age of first reproduction of 2.5 years, 31% adult mortality, mean litter size of 2.5), we calculate that the Florida panther population will decline about 11% per year. A captive population is projected to grow at 12-15% per year.

Table 1. Average population growth rates under various scenarios for Florida panthers

Age of 1st reproduction Years	Adult mortality %	Mean litter size N	Growth rates r	Growth rates lambda	Generation time	Age distribution 0 yr:1 yr:2 yr:3+
2	25%	3.0	.023	1.023	4.87	36:17:13:35
2	25	2.5	-.015	.985	4.87	32:16:12:39
2	31	3.0	-.044	.957	4.20	35:18:13:34
2	31	2.5	-.087	.917	4.20	31:17:13:39
2.5	25	3.0	-.005	.995	5.29	33:17:13:38
2.5	25	2.5	-.039	.962	5.29	30:16:12:42
2.5	31	3.0	-.076	.926	4.60	32:17:13:37
2.5	31	2.5	-.116	.890	4.60	29:16:13:42
3	25	3.0	-.031	.970	5.84	31:16:12:41
3	25	2.5	-.062	.940	5.84	28:15:12:45
3	31	3.0	-.107	.899	5.18	30:16:13:41
3	31	2.5	-.142	.868	5.18	27:15:12:46
2	10	3.0	.136	1.146	7.60	33:15:11:41
2	10	2.5	.112	1.119	7.60	31:14:11:44

The generation times and age structures obtained from the analyses reveal a population that is perhaps younger than is indicated in the field data available. We calculate that about 40% would be more than 3 years of age (see Table 1), whereas 10 of 15 collared animals are adults and collared females presently have 3 litters of perhaps 6 offspring. The calculated generation times of 4.2 to 5.8 years are somewhat less than the observed mean age of conception for females of 6.2 years; and the presence of 5 of 15 collared animals over 7 years, with 2 over 10 years, is unexpected given the high estimated annual mortality of adults. Several factors could account for this discrepancy. First, young animals may be less likely to be observed than are breeding age adults and the actual age distribution may closely approximate those calculated. This is the justification for examining some stochastic models (below) with a 1:1 juvenile:adult ratio. Alternatively, the observed "top heavy" age distribution may reflect a more rapidly declining population than any scenarios examined (note that in Table 1 negative growth rates result in older age distributions), or a population in which reproduction has been less in recent years than in the past (i.e., recent deterioration of demography and an unstable age distribution). By comparing scenarios with 25% vs. 31% adult mortality, we can see that moderate changes in adult mortality have very little effect on the age distribution. Lower adult mortality leads to longer generation times, but also to more rapid population growth; and the juvenile age classes increase proportionately with the adult age classes.

Stochastic simulation of population extinction

Life table analyses yield average long-term projections of population growth (or decline), but do not reveal the fluctuations in population size that would result from the variability in demographic processes. To begin an examination of the probabilities of population persistence under various scenarios, we used a modified version of the SPGPC computer model, developed by James Grier of North Dakota State University, to simulate the Florida panther population. The computer model assumes constant probabilities of death over time (though first year and later year mortality rates can be specified independently), constant probabilities of reproduction, with set probabilities for each possible litter size. Thus, the simulation program models demographic stochasticity among individuals, but not environmental variation that impacts the entire population. Consideration of environmental variation (including catastrophic events) might lead to greater extinction probabilities and shorter population persistence times.

Each simulation is started with a specified number of males and females of each pre-reproductive age class, and a specified number of male and females of breeding age. A population carrying capacity can be imposed by truncation of each age class (after breeding) if the population size exceeds the specified carrying capacity. The computer program simulates and tracks the fate of each population, and outputs summary statistics on the probability of population extinction over 25, 50, and 100 year time spans and the mean time to extinction of those simulated populations that went extinct.

To model the wild population of Florida panthers, the age of first reproduction was set at either 2 or 3 (the computer program cannot handle fractional years), first year mortality was set at 50%, adult mortality was set at either 25% or 31%, biannual mean litter sizes were set at either 2.5 (distributed as 50% annual probability of no litter, 10% probability of a litter of one, 15% of litter size 2, 15% of size 3, and 10% of size 4) or 3.0 (50% probability of no litter, and 5%, 10%, 20%, 10% and 5% probabilities of litters of size 1, 2, 3, 4, and 5, respectively), and the population carrying capacity was set at 30, 45, or 80. The populations were started with 30 adults and 15 juveniles, with 30 adults and 30 juveniles, or with 40 adults and 40 juveniles.

The results of 1000 simulations for each set of parameters are shown in Table 2.

It is clear that if adult mortality is 31%, as indicated in the field data, there is virtually no probability that the present population of Florida panthers will persist for 100 years. Under most scenarios, persistence through 50 years is also unlikely, and extinction within 25 years is often the norm. Even if adult mortality is optimistically estimated at 25%, there is still a high probability that the extant Florida panther population would not survive 100 years in its present habitat, and the mean time to extinction is often about 50 years.

Comparing alternative scenarios in Table 2, the most dramatic improvement in population persistence results from a reduction of adult mortality from 31% to 25% per year. Comparing the mean times to extinction among scenarios with 31% adult mortality, we find that the simulated populations die out about 10 years more quickly if reproduction begins at age three rather than at age two, and the populations die out an average of 8 years sooner if mean litter size is 2.5 rather than 3.

Populations of initial size 80 (40 adults, 40 juveniles) persist an average of 4 years longer than do populations of initial size 45 (30 adults and 15 juveniles), and increasing the population carrying capacity from 30 to 80 only prolongs population persistence times by about a year.

Demographically, therefore, the age of first reproduction and the mean litter size (or, equivalently, the first year mortality rate) have much larger effects on population persistence times than do initial population size or population carrying capacity.

Genetically, however, the smaller population sizes would lose variability more rapidly, and this greater loss of genetic variability may speed demographic decline and extinction relative to the simulated populations (in which there was no genetic feedback on fecundity and viability).

Table 2A. Probabilities of extinction and mean times to extinction (of those populations that went extinct) populations with parameters plausible for the existing Florida panthers.

Age of first reproduction	Demographic Parameters Adult mortal.	Litter size	Initial Adults/Juv	Carrying capacity	Prob. of extinction 100 yr	50 yr	25 yr	Mean time to extinc. Years
3	31%	2.5	30/15	30	1.00	1.00	.88	18
			30/30		1.00	1.00	.88	18
			40/40		1.00	1.00	.84	20
			30/15	45	1.00	1.00	.88	18
			30/30		1.00	1.00	.83	19
			40/40		1.00	1.00	.77	21
			30/15	80	1.00	1.00	.88	18
			30/30		1.00	1.00	.85	19
			40/40		1.00	1.00	.79	21
3	31%	3.0	30/15	30	1.00	.99	.75	21
			30/30		1.00	.99	.72	22
			40/40		1.00	.99	.67	24
			30/15	45	1.00	.99	.76	21
			30/30		1.00	.99	.69	22
			40/40		1.00	.99	.61	24
			30/15	80	1.00	.99	.76	21
			30/30		1.00	.99	.71	22
			40/40		1.00	.99	.60	25
2	31%	2.5	30/15	30	1.00	.97	.66	24
			30/30		1.00	.97	.62	25
			40/40		1.00	.96	.57	26
			30/15	45	1.00	.97	.62	24
			30/30		1.00	.96	.57	26
			40/40		1.00	.95	.48	28
			30/15	80	1.00	.98	.66	23
			30/30		1.00	.97	.59	25
			40/40		1.00	.95	.45	29

Table 2A. Continued

Age of first reproduction	Demographic Parameters: Adult mortal.	Litter size	Initial Adults/Juv	Carrying capacity	Prob. of extinction: 100 yr	50 yr	25 yr	Mean time to extinc. Years
2	31%	3.0	30/15	30	.99	.83	.41	33
			30/30		.99	.82	.36	35
			40/40		.99	.77	.29	38
			30/15	45	.99	.81	.37	35
			30/30		.99	.78	.32	37
			40/40		.98	.71	.20	42
			30/15	80	.99	.83	.39	34
			30/30		.98	.74	.32	38
			40/40		.97	.65	.19	43
3	25%	2.5	30/30	30	1.00	.86	.29	35
				45	1.00	.84	.25	36
				80	1.00	.85	.26	36
		3.0	30/30	30	.95	.60	.17	46
				45	.91	.54	.12	50
				80	.91	.52	.11	50
2	25%	2.5	30/30	30	.86	.49	.14	50
				45	.75	.37	.09	54
				80	.72	.37	.09	52
		3.0	30/30	30	.40	.18	.04	57
				45	.22	.08	.03	58
				80	.12	.07	.02	50

Table 2B. Probabilities of extinction and mean times to extinction for 1,000 simulated populations with some demographic parameters plausible for the Everglades population.

Demographic Parameters					Prob. of extinction			Mean time to extinc.
Age of first reproduction	Adult mortal.	Litter size	Initial Adults/Juv	Carrying capacity	100 yr	50 yr	25 yr	Years
2	31%	3.0	1M,3F/0	10	1.00	1.00	.98	5
			1M,5F/0	10	1.00	1.00	.96	7
			2M,6F/0	10	1.00	.99	.92	11

Table 2C. Probabilities of extinction and mean times to extinction for simulated populations with some demographic parameters plausible for a captive population of panthers.

Demographic Parameters					Prob. of extinction			Mean time to extinc.
Age of first reproduction	Adult mortal.	Litter size	Initial Adults/Juv	Carrying capacity	100 yr	50 yr	25 yr	Years
2	10%	3.0	20/0	100	.00	.00	.00	none
			20/0	50	.00	.00	.00	none
			20/0	25	.00	.00	.00	none
			0/20	100	.04	.04	.04	4
			0/20	50	.04	.04	.04	8
			0/20	25	.04	.04	.04	5
4 .04 4 years								
			0/20	50	.04	.04	.04	8
			0/20	25				

Loss of Heterozygosity

Loss of heterozygosity is a function of the population's effective size and how it changes over time. Heterozygosity loss in the Florida panthers was modeled using a number of different population scenarios.

Figure 15 shows the loss of heterzogosity in the population over time if the population remains at a constant size of 30 adults. The results from two different effective population sizes are shown: one assuming it is 50% of adult numbers, the other assuming it is 25% of adult numbers. This results in effective population between 8 and 15 animals. There is a 3 to 7% loss of genetic diversity per year and after 100 years (23 panther generation), only 25-50% of the genetic diversity will remain.

Note that this scenario is more optimistic than what is predicted by the most realistic demographic data, which indicate that the population is actually declining. If this is the case, models of long-term loss of heterozygosity are superfluous: mean extinction times in most cases are sooner than 25 years.

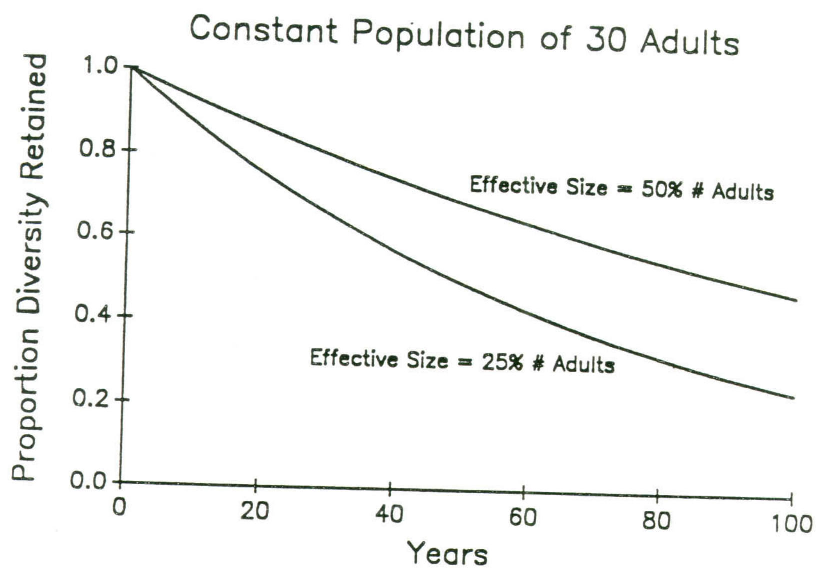

Figure 15. Loss of heterozygosity over time of a panther population of 30 adults with an effective population size (Ne) of 15 or 8.

Loss of heterozygosity is significant given even the most optimistic demographic scenario described (age first reproduction 2 years, 25% adult mortality, litter size of 3). This annual growth rate is 2.3% (r = 0.023, Table 1). When assuming a carrying capacity of 80 adults, the population still only retains between 50 and 70% of its current level of heterozygosity.

Loss of genetic diversity of this magnitude can have severe effects on both the short-term and long-term survival of the population. Inbreeding will increase rapidly. Regardless of the population's current susceptibility to inbreeding, future high levels of inbreeding are likely to have significant impact on the population's survival and reproductive rates. Data from captive and domestic populations indicate that, on the average, population fitness decreases at the same rate inbreeding increases: a 10% increase in inbreeding results in a 10% increase in mortality. Reduced fitness will result in even smaller population sizes and increased probability of extinction. Population's may become more susceptible to disease, further increasing their vulnerability. From a long-term perspective, extremely low levels of diversity may severely limit a population ability to adapt to changing environments. Natural selection acts on genetic diversity; without it the population will not evolve.

Everglades Population

Because the Everglades subpopulation seems to be isolated at present from the larger population in Big Cypress and contiguous habitat, it was desireable to investigate it as a special case (Table 2B). A population with 1 male and 5 females has an effective size of 3 and will lose genetic diversity at the rate of 16% per panther generation (4-5 years). The relationships of the animals in the population are already partially known. The only male is the son of one of the females and may be first cousin to two other females. Clearly very close inbreeding will occur in the immediate future if it has already not occurred.

Ignoring for now the genetic complications likely to face such a highly inbred population, the computer simulations project that the population in the Everglades has low (8%) probability of survival to 25 years and virtually no probability of survival to 50 years, even if the two females now in captivity are returned and an additional unknown pair of breeding adult panthers exist in the Everglades. The mean time to extinction in the simulations was just 7 years for the known population of 1 male and 5 females, 5 years if the 2 females now in captivity are not returned (leaving 1 male and 3 females), and 11 years for a population of 2 males and 6 females.

The Everglades population will have to be supplemented if it is to survive. Immediately, an unrelated male is needed, and periodic manipulation and supplementation will be needed unless a dispersal corridor is established between the Everglades and the Big Cypress area.

Metapopulation Management Options for the Florida Panther

Applying life table analysis and computer simulation of stochastic effects to the demographic variables estimated for the present Florida panther population makes it very clear that the population is not viable. Moreover, none of the demographic parameter estimates offered as possible upper bounds for the present population or projected as reasonably obtainable with intensified management yield a high probability of population persistence. To assure the future of the Florida panther, therefore, it seems imperative that additional populations be established. Multiple populations ('metapopulations') with managed frequent gene flow will retain significantly higher levels of genetic variation than the present single population.

If four additional populations of size equal to the present population (30 adults) could be established, with artificial migration between populations to assure good gene flow, 54% to 74% of the present genetic diversity could be retained. This is a 50% to 100% increase in the level of genetic diversity retained. Additionally, the likelihood of extinction is considerably decreased: the probability that multiple populations all go extinct at once would be equal to the product of the extinction probabilities of the individual populations, assuming no recolonization after local extinctions.

For example, the probability that five populations each with a extinction probability of .75 would all be lost is .24. Given the very high probabilities of extinction estimated for the present panther population, and the likelihood that additional, reintroduced populations will be not much larger nor individually more secure, it seems that either many (perhaps 10 or more) such populations will need to be established to assure the future of the Florida panther and continued intensive management will be necessary to re-establish temporarily extinct populations and to restore genetic variability to isolated subpopulations via artificial migration.

Given the precarious position and the probable ongoing decline of the existing panther population, it is very unlikely that the present wild population could serve as a sufficient source for a serious reintroduction program into other habitats. While the one-time removal of 10 to 20 young animals would seem to have little impact on population persistence (compare the scenarios with 45, 60, and 80 initial animals in Table 2), the population could not sustain a continued harvest (note that a 17% decrease in mean litter size -- 3.0 to 2.5 -- resulted in considerably shorter persistence times) and may be extinct before a prolonged translocation program could be completed.

Based on the history of other subspecies of *Felis concolor* in captivity, we expect that a viable captive population could be established. With the decreased adult mortality likely in captivity (10% vs. 31% in the wild), the life table analyses indicate that a captive population would grow at 12%-15% per year, providing an annual surplus that assures population stability (see below), and that could be used for reintroductions into additional habitats and augmentation of established wild populations. Stochastic simulations of a captive population (adult mortality 10%, first year mortality 50%, mean litter size 3, carrying capacity 25, 50, or 100) yielded no extinctions over 100 years when the captive population was founded with 20 adults (see Table 2C). When the population was started with 20 newborn panthers, the probability of extinction was .04. These extinctions all occurred in the very early years of the simulations, and were due to mortality of most or all founders prior to reproduction.

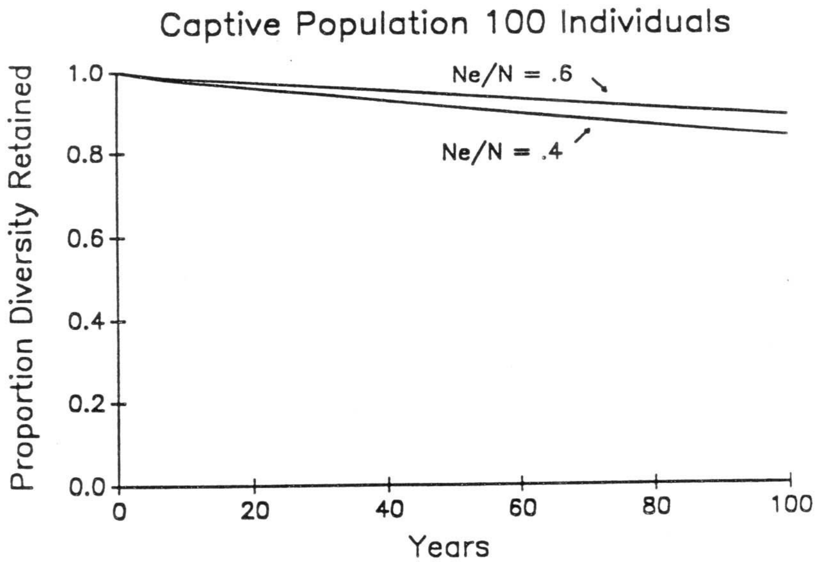

Figure 16. Enhanced retention of heterozygosity in captive populations with increase in effective population size. Together with the observation that the demographic fates of the simulated captive populations were the same whether carrying capacities were 25, 50, or 100, these results make it clear that a captive population, once established, would be very stable demographically (in striking contrast to the wild population).

The capability of intensive population management in captivity also allows substantial improvements in effective population size. Significantly higher levels of genetic variation can therefore be retained in captive populations. Figure 16 shows the percent retention of heterozygosity in a captive population of 100 individuals with an effective size ranging from 40% to 60% of the total population (Note effective sizes of panthers were defined in terms of proportions of adult populations). After 100 years, approximately 90% of the original levels of genetic diversity are retained. Establishing additional wild populations from captive surplus will further increase the level of genetic diversity retained.

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