PUERTO   RICAN   PLAIN   PIGEON

Columba inornata wetmori

POPULATION VIABILITY ANALYSIS

and

RECOMMENDATIONS

Captive breeding Specialist Group

Species Survival Commission IUCN

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PUERTO RICAN PLAIN PIGEON

POPULATION VIABILITY ANALYSIS

Final Report

July 21, 1989

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PUERTO RICAN PARROT

AND

PUERTO RICAN PLAIN PIGEON

POPULATION VIABILITY ANALYSIS WORKSHOP

PROPOSAL

June 25-27, 1989

Problem:

The Puerto Rican Parrot (<u>Amazona</u> <u>vittata</u>) and Plain Pigeon
(<u>Columba</u> <u>inornata</u> <u>wetmori</u>) are endangered. They exist
in the wild as single small populations. Captive
populations have been established. The parrot
population numbers less than 40 birds and the pigeon
less than 150 birds in the wild. The parrot wild
population has increased slowly from a low of 13-17
birds and the captive population has a low rate of
increase with incomplete founder representation. The
basis for the limited recruitment in the wild and in
captivity is not understood. These conditions favor
continued loss of genetic diversity and potential
extinction in the wild from random environmental
events.

Goals:

(1) Conduct population viability analyses of the Puerto Rican
     Parrot and Puerto Rican Plain Pigeon.
(2) Formulate quantitative strategies with risk assessments to
     prevent extinction and achieve the Recovery Plan
     objective of developing viable, self-sustaining
     populations within the historic range of the birds.

Objectives:

   (1) Determine numbers of parrots and plain pigeons and
        subpopulations required for various probabilities of
        survival and preservation of genetic diversity for
        specified periods of time (i.e. 25, 50, 100, 200
        years).

   (2) Consider how possible interventions in the wild
        population might increase their rates of growth and
        decrease their loss of genetic diversity.

(3) Consider how possible interventions in the captive
        populations might increase their rates of growth and
        maximize their retention of genetic diversity.

(4) Develop goals for the captive populations to provide birds
        for release to the wild without compromising the
        genetic diversity and demographic stability of the
        captive population.

(5) Project the potential expansion or decline of parrot and
        pigeon population numbers under various management
        regimes.

(6) Outline metapopulation structure needed to establish viable
        populations of each species. Indicate management
        consequences of this approach.

(7) Formulate quantitatively and evaluate role of captive
        propagation as a component of the strategy for each
        species. In particular, consider how captive
        propagation can:

a)accelerate expansion of population

          b)enhance preservation of genetic diversity

c)protect population gene pool against fluctuations due to
                environmental vicissitudes in wild

          d)provide birds for reinforcement of wild
             populations or establishment of new
             populations

(8) Identify problems and issues that need continuing analysis
        and research.

(9) Recommend courses of action.

(10) Produce a document for each species presenting the results
        of the workshop.

II. 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 popula-
tions 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 survivor-
ship 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 scientifi- cally 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.

POPULATION VIABILITY ANALYSIS

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 Puerto Rican parrot, the only psittacine native to Puerto Rico, was formerly widespread on the island and numbered perhaps a million birds. By 1972 the species was reduced to just 20 birds (4 in captivity). Intensive efforts since have accomplished a steady recovery to 46 captive and 34 wild birds at the end of 1988. Both the captive and wild flocks are still too small to be assured of persistence over even short time spans.

When populations become small and isolated from any and all other conspecifics, they face a number of demographic and genetic risks to survival: in particular, chance events such as the occurrence and timing of disease outbreaks, random fluctuations in the sex ratio of offspring, and even the randomness of Mendelian gene transmission can become more important than whether the population has sufficient habitat to persist, is well adapted to that habitat, and has an average birth rate that exceeds the mean death rate. Unfortunately, the genetic and demographic processes that come into play when a population becomes small and isolated feed back on each other to create what has been aptly but depressingly described as an "extinction vortex". The genetic problems of inbreeding depression and lack of adaptability can cause a small population to become even smaller --which in turn worsens the uncertainty of finding a mate and reproducing -- leading to further decline in numbers and thus more inbreeding and loss of genetic diversity. The population spirals down toward extinction at an ever accelerated pace. The size below which a population is likely to get sucked into the extinction vortex has been called the Minimum Viable Population size (or MVP).

The final extinction of a population usually is probabilistic, resulting from one or a few years of bad luck, even if the causes of the original decline were quite deterministic processes such as over-hunting and habitat destruction. Recently, techniques have been developed to permit the systematic examination of many of the demographic and genetic processes that put small, isolated populations at risk. By a combination of analytic and simulation techniques, the probability of a population persisting a specified time into the future can be estimated: a process called Population Viability Analysis (PVA) (Soule 1987). Because we still do not incorporate all factors into the analytic and simulation models (and we do not know how important the factors we ignore may be), and because we rarely examine feedback among the factors, the results of PVAs

almost certainly underestimate the true probabilities of population extinction. The value of a PVA comes not from the crude estimates of extinction probability, however, but rather from identification of the relative importance of the factors that put a population at risk and assessment of the value (in terms of increased probability of population persistence) of various possible management actions. That few species recognized as Endangered have recovered adequately to be downlisted and some have gone extinct in spite of protection and recovery efforts attests to the acute risks faced by small populations and to the need for a more intensive, systematic approach to recovery planning utilizing whatever human, analytical, biological, and economic resources are available.

GENETIC PROCESSES IN SMALL AND FRAGMENTED POPULATIONS

Random events dominate genetic and evolutionary change when the size of an inter-breeding population is on the order of 10s or 100s (rather than 1000s or more). 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. For example, the prevalence of cryptorchidism (failure of one or both testicles to descend) in the Florida panthers (<u>Felis</u> <u>cconcolor</u> <u>coryi</u>) is probably the result of a strongly deleterious allele that has become common, by chance, in the population; and a kinked tail is probably a mildly deleterious (or at best neutral) trait that has become almost fixed within the Florida panthers. No deleterious trait in the Puerto Rican parrots or plain pigeons has yet been clearly demonstrated to have a genetic basis, but the poor breeding performance of many of the birds may have, in part, genetic causes.

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. As only four (or fewer) wild Puerto Rican parrot nests have been active for the past 20 years, it is possible that most or all of the currently breeding breeding birds are closely related, perhaps even full-siblings. 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.

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. Because of the long generation times of the Puerto Rican parrot, the present bottleneck has existed for just one or two generations, and could be exited (successfully, we hope) before another generation passes and further genetic decay occurs. The Puerto Rican plain pigeon may have been in a bottleneck for the past 50 years. 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 1 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 2, 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 1.

Figure 1. The average losses of genetic variation (measured by heterozygosity or additive genetic variation) due to genetic drift in 25 computer-simulated populations of 20, 50, 100, 250, and 500 randomly breeding individuals. 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 1-2% 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).

Figure 2. The losses of heterozygosity at a genetic locus in 25
populations of 120 randomly breeding individuals, simulated by
     computer. Figure from Lacy 1987.

     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 timescale of 100 years or more, for
a medium-sized vertebrate 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 breeding randomly. 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 animal, 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 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
timescale 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 3. 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 3). 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 4). 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 5). Because of the effectiveness of even low
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.

Figure 4. 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 5. 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.

<u>Genetic</u> <u>Considerations</u> <u>in</u> <u>Puerto</u> <u>Rican</u> <u>Parrot</u> <u>Management</u>

Effective Population Size:
     The wild flock of parrots has had about 4 breeding pairs
during the past two decades, with 6 - 10 known breeders each
year. The variance in family size (number fledged) is greater
than expected by chance (Poisson distribution would give a
variance equal to the mean brood size: data from Snyder et al.
1987 and information provided at the PVA workshop yield mean =
1.39 and variance = 1.92 for the past decade), depressing the
effective population size. Applying the methods of Crow and
Morton (1955), with the optimistic assumption that post-fledging
mortality is random with respect to brood, yields an effective
population size of 5.9 for the 8 breeding pairs. Annual
fluctuations in the number of breeders would depress this
slightly more. (The sex ratio of breeders will be exactly 1:1
because Puerto Rican parrots are monogamous.)

     This effective population size would result in a loss of
genic diversity or heterozygosity of about 8.5% per generation
(about 12-14 years). Thus perhaps 10-15% of genic diversity
would have been lost since the rapid decline in numbers of Puerto
Rican parrots. While this loss is not likely to cause immediate
problems (nor is it sufficiently depressed to allow detection by
molecular analysis of protein or DNA variation in small samples),
the long-term genetic prognosis would not be good if the
population were to remain at this low effective population size.
 Inbreeding would be inevitable after three generations. (Even
with maximal avoidance of inbreeding, each animal would have the
same 8 great-grandparents in the third generation descendants,
and the minimum inbreeding coefficient possible in fourth
generation progeny would be F=.0625.)

     Enough wild-caught Puerto Rican parrots have been brought
into the captive colony to provide a sufficient genetic base for
a long-term propagation program. Twenty birds, if all breed
equally, would capture 97.5% of the genic variation present in
the wild. Additional wild-caught Puerto Rican parrots have not
yet bred in captivity, and production from breeders has been
unequal. As a result, the living descendant population in
captivity is expected to contain about 94% of the genetic
variation that is present in the wild flock. If the as yet
unproductive wild-caught Puerto Rican parrots can be successfully
bred, the gene pool of the captive flock could closely
approximate that of the wild flock.

<u>Genetic</u> <u>Recommendations</u> <u>--</u> <u>Puerto</u> <u>Rican</u> <u>Parrots</u>

     The molecular genetic analyses that have begun should be
supported, encouraged, and further developed. At the same time,
caution should be used in drawing conclusions or making

management decisions from preliminary results.

The allozyme data presented at the PVA workshop held in San Juan are insufficient (10 loci examined, 2 of which are variable) to permit conclusions about the level of genetic variation or past inbreeding in the remnant population. The genic variation observed thus far in the Puerto Rican parrots (about 2.5% heterozygosity over the captive and wild flocks) is somewhat lower than the mean for bird populations studied (Corbin 1987) by electrophoresis, and lower than was observed in Hispaniolan parrots (about 7%), but is not unusually low for even abundant bird species (Corbin 1987). The values obtained in the preliminary study have very large standard errors, and the reduced variation observed in the captive flocks of Hispaniolan and Puerto Rican parrots could be due to sampling error. It should be noted that the present population bottleneck (about 1 or 2 generations at effective population size of less than 8) is not narrow enough to cause a loss in diversity that could be measured with few samples. Data on 25 to 35 allozymes should be obtainable, and comparisons to other Amazona parrots would allow assessment of possible past losses in diversity, continued monitoring of future losses of variation, and measurement of the genetic divergence of the Puerto Rican parrot from related species on nearby islands. We recommend that arrangements be made with geneticists at the University of Puerto Rico or elsewhere to obtain further electrophoretic analysis of protein variation.

The DNA fingerprinting begun by Kelly Brock can provide valuable insight into genetic relationships among the wild and wild-caught birds (though it is unlikely that relatives more distant than half-siblings could be identified by this or other techniques). The DNA fingerprinting work should continue to focus on determination of the number of independent loci assessed by the Jeffrey's probe and analysis of the statistical resolving power of that technique for identifying individuals, and close kinship relationships. Other probes of hypervariable DNA should be tried, with further attempts to identify genetic relationships among the remnant parrots.

Analysis of restriction fragment length polymorphisms of mitochondrial DNA could provide further evidence of relationships among the Puerto Rican parrots, and genetic divergence from related species.

It is essential for any breeding program (or even the monitoring of a wild population) that the sex of each animal be known with certainty. Many of the Puerto Rican parrots have been sexed by chromosomal analysis, and this should be done for all birds with the sex not yet confirmed by breeding.

As with any endangered species, each specimen is potentially a very valuable source of information. Whenever a Puerto Rican parrot dies in captivity or is found dead in the wild, tissues

should be removed within hours, if at all possible. The tissues should be stored below -60 C for later genetic analysis. The best tissue for genetic analysis is generally liver, but opening the body cavity should be avoided until a most mortem examination is performed to determine the cause of death. If a post mortem examination cannot be performed within a day, a small amount of breast muscle could be removed without compromising later medical diagnoses. (The veterinarian performing the post mortem examination should be informed that the muscle tissue was removed.) Following the post mortem examination, the carcass of the bird should be preserved for possible later examination (e.g., of morphology, breeding condition, or gut contents).

To date, no pairings of Puerto Rican parrots in the Luquillo aviary have been between birds of known genetic relationship. This avoidance of inbreeding in the aviary should be continued so long as it is possible and does not reduce the number of pairings that can be made. (Inbred offspring are better than no offspring: if only related birds are available for pairing they should not be kept separate.) If inbreeding does become inevitable, or can be confirmed to be occurring in the wild flock (by DNA analyses and/or pedigree tracking of banded birds), careful records should be kept to allow later comparison of mortality, fecundity, and growth of inbred vs. non-inbred birds. The genetic base of the captive flock could be improved, and inbreeding in captivity therefore further postponed, if exchanges of captive and wild nestlings can be made without risk to the chicks in order to bring genes from unrepresented wild breeders into captivity.

As the captive population reaches a size that forces decisions about which birds to breed, pairings should be planned to minimize the losses of genetic contributions from founder birds. Selective culling of birds with presumed genetic defects should be avoided unless the trait can be clearly demonstrated to have a genetic basis, and a demographic cost of allowing birds with the trait to breed can be shown (i.e., removing affected birds from breeding would allow enhancement of breeding by others). Deleterious traits have been noted in the progeny of some parrots (thin egg shells, nestlings that become weak and die), but have not been determined to have a genetic basis. Even if these traits are in part genetically determined, the value of the limited genetic material in each of the remnant parrots is such that we would not recommend the selective removal of any birds (each of which almost certainly harbors both beneficial and deleterious genes). The causes of breeding failures should be vigorously investigated, not so much to demonstrate any genetic base (which would be interesting but of relatively little importance to management), but rather to allow correction of problems stemming from environmental causes.

Genetic Considerations in Puerto Rican Plain Pigeon Management

Accurate and complete censuses of the wild population of

Puerto Rican ParrotPs do not exist. Based on incomplete censuses over the past few years, the known population numbers between 150 and 200 birds, with about 24-30 active nests. Unless reproductive success is highly skewed, with a only a few nests producing most of the young each year, the effective population size is likely large enough so that loss of genetic variation by random drift will be small over the next decade (unless, of course, the population declines substantially). If the effective population size is about 50, the rate of genetic loss would be 1% per generation. Nest site fidelity and fragmentation of the population into smaller units may lead to local inbreeding and greater genetic loss within some isolates, but only if migration between subunits is virtually non-existent (fewer than a few birds per year).

Enough wild-caught birds have been brought into the captive colony to provide a sufficient genetic base for a long-term propagation program. Twenty birds, if all breed, would capture 97.5% of the genic variation present in the wild. Seven of the wild-caught Puerto Rican ParrotPs have not yet bred in captivity, and production from breeders has been unequal. As a result, the living descendant population in captivity has lost about twice as much variation (5%) as would be the case with optimal breeding success.

Genetic Recommendations -- Puerto Rican Plain Pigeons

The Puerto Rican plain pigeon (Columba inornata wetmorei) is distinct from other plain pigeons only at the subspecific taxonomic rank, and even that subspecific distinction has been questioned in a recent reevaluation (Banks 1986). Banks also questioned whether the extant population of plain pigeons on Puerto Rico (rediscovered in 1958 after not being seen since the 1920s) belong to the endemic subspecies or population, or whether it was the result of a recent introduction from Hispaniola or Cuba. To clarify better the validity of the plain pigeon subspecies and to characterize the present population on Puerto Rico, molecular genetic studies should be undertaken to examine the genetic divergence among plain pigeons on Puerto Rico and the other islands. Subspecies level differences often can be identified easily and relatively quickly by analysis of protein variation (blood and/or feather pulp samples could be used), or by analysis of mitochondrial DNA. We recommend that arrangements be made with geneticists at the University of Puerto Rico or elsewhere to begin such studies soon.

Because of the nest site fidelity of plain pigeons, it is quite possible that some of the birds brought into captivity to initiate the captive propagation program were closely related genetically. DNA analyses (both fingerprinting of hypervariable regions and restriction fragment length analyses of mitochondrial DNA) should be undertaken to identify such relationships.

Attempts should be made to obtain offspring from as yet

unproductive wild-caught Puerto RicanPPs in captivity. If this fails, five to ten new birds should be added to the captive colony to better represent the Puerto RicanPP gene pool in the captive flock. One of the breeding pairs of pigeons (male 56 and female 53) is a half-sib pairing and is therefore producing inbred offspring. If possible, such pairings should be avoided. Recommendations made for the Puerto Rican parrots regarding the monitoring of production by any inbred pairing that do take place apply also to the pigeons. (Developmental problems in inbred chicks have been noted already.)

Comments made above (in the Puerto Rican parrot section) regarding the need to preserve material from parrots that die, the recommendation not to cull birds suspected of having genetic defects, and the need to chromosomally sex all birds apply equally to the pigeons.
[i.e., ...

As the captive population reaches a size that forces decisions about which birds to breed, pairings should be planned to minimize the losses of genetic contributions from founder birds. Selective culling of birds with presumed genetic defects should be avoided unless the trait can be clearly demonstrated to have a genetic basis and a demographic cost of allowing birds with the trait to breed can be shown (i.e., removing affected birds from breeding would allow enhancement of breeding by others). Deleterious traits have been noted in some pigeons, but have not been determined conclusively to have a genetic basis. Even if these traits are in part genetically determined, the value of the limited genetic material in each of the remnant pigeons is such that we would not recommend the selective removal of any birds (each of which almost certainly harbors both beneficial and deleterious genes). The causes of breeding failures should be vigorously investigated, not so much to demonstrate any genetic base (which would be interesting but of relatively little importance to management), but rather to allow correction of problems stemming from environmental causes.

It is essential for any breeding program (or even the monitoring of a wild population) that the sex of each animal be known with certainty. All Puerto RicanPPs in captivity should be sexed by chromosomal analysis, unless the sex has already been confirmed by successful breeding.

As with any endangered species, each specimen is potentially a very valuable source of information. Whenever a plain pigeon dies in captivity or is found dead in the wild, tissues should be removed within hours, if at all possible, and stored below -60 C. The best tissue for genetic analysis is generally liver, but opening the body cavity should be avoided until a most mortem examination is performed to determine the cause of death. If a post mortem examination cannot be performed within a day, a small amount of breast muscle could be removed without compromising later medical diagnoses. (The veterinarian performing the post

mortem examination should be informed that the muscle tissue was removed.) Following the post mortem examination, the carcass of the bird should be preserved for possible later examination (e.g., of morphology, breeding condition, or gut contents).]

DEMOGRAPHIC PROCESSES IN SMALL AND FRAGMENTED POPULATIONS

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 1 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.

Figure 1. 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 2). Over
time the population becomes increasingly smaller and more
susceptible to extinction (Gilpin, 1986).

Figure 2. 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:

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

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 3. 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 3. 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 4. 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 4. 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 3, we can estimate the probability of extinction at different time periods (Figure 5). 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 5. 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).

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. (See above intro material -- to be written by someone.) 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 (Grier 1980a, 1980b, Grier and Barclay 1988), to simulate the Puerto Rican parrot [and plain pigeon?] populations. The computer model simulates the birth and death processes of a population by generating random numbers to determine whether each animal lives or dies, and whether each female reproduces broods of size 0, 1, 2, 3, or ... during each year. Mortality and reproduction probabilities are the same for each sex, and fecundity is assumed to be independent of age (after an animal reaches reproductive age). Mortality rates are specified for each pre-reproductive age class and for reproductive-age animals. 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. The computer program simulates and tracks the fate of each population, and outputs summary statistics on the probability of population extinction over a specified time span and the mean time to extinction of those simulated populations that went extinct. By using constant probabilities of birth and death processes, the basic Grier model simulates demographic (individual) stochasticity, but does not allow for environmental variation that imposes greater or lesser birth and death probabilities across the population in subsequent years, nor does it allow for catastrophic impacts (e.g., severe storms, disease epidemics) on reproduction and mortality. (Grier is developing further his program to accommodate some of these factors.)

Modifications by R. Lacy of the basic Grier program include a translation of the program language from interpreted BASIC to compiled C, calculation of mean (deterministic) population growth rates and the stable age distribution, and the addition to the simulation of population carrying capacities, environmental variation in reproduction, mortality, and the carrying capacity, and catastrophes. A population carrying capacity is imposed by truncation of each age class (after breeding) if the population size exceeds the specified carrying capacity. The carrying capacity is not taken to be a fixed number, rather the carrying capacity each generation is drawn from a Poisson distribution with mean (and variance) equal to the specified limit. Each year in the simulation (during which age-specific probabilities of birth and death are constant), the number of animals surviving, as well as the number reproducing, would be expected to follow binomial distributions with means equal to the specified probabilities. Environmental variation in reproduction, survival, and the carrying capacity is incorporated into the model by increasing the binomial or Poisson variances in these

parameters by an amount specified by the user. The frequency and severity of breeding and survival catastrophes are also specified by the user. A catastrophe is determined to occur if a randomly generated number between 0 and 1 is less than the probability of occurrence (i.e., a binomial process is simulated). If a breeding catastrophe occurs, the probability of breeding is multiplied by a severity factor that is drawn from a binomial distribution with mean equal to the severity specified by the user. Similarly, if a survival catastrophe occurs, the probability of surviving each age class is multiplied by a severity factor that is drawn from a binomial distribution with mean equal to the severity specified by the user. Thus, not all catastrophes are of equal magnitude, rather they are distributed around a mean specified by the user. Catastrophes impacting mortality and breeding are independent, and the severity of a catastrophe varies around the mean value specified.

Overall, the computer program simulates many of the complex levels of stochasticity that can impact a population. Some of its artificialities are the absence of trends across years (e.g., no long-term changes in the environment, no multi-year environmental perturbations or catastrophes), the independence of environmental fluctuation in birth and death rates, and the lack of density dependence of birth and death rates except when the population exceeds the carrying capacity. The first two of these simplifications will likely lead to underestimates of extinction rates, while the third may cause overestimation of extinction. A sample output from the program (for the "basic scenario" below) is given as Table 1.

[Note to Ulie: I have included a diskette with the program as I have used it for these analyses, with a brief description of its use. We can provide it to the Puerto Rican parrot and Puerto Rican plain pigeon groups for further exploration.]

COMPUTER SIMULATION OF THE WILD PUERTO RICAN PARROT POPULATION

The parameters used in the "baseline" scenario were chosen to represent, as best as could be determined, the current state of the wild population of Puerto Rican parrots. Data on the wild flock from 1979, the year that intensive management and predator control was started, to the present were used. The captive population was not modelled because management (e.g., double clutching, pulling eggs, placing nestlings into wild nests, other manipulations) has been sufficiently varied that it seemed impossible to determine accurately the population parameters for the captive flock, and because those parameters are likely changing rapidly with improved management. The observed population growth rate (about 13% mean annual growth [by regression analysis] from 1979 through 1988) of the captive population compares favorably with the growth rate of the wild flock (6% annual growth over the past decade). Note also that these growth rates incorporate 20 captive hatched birds that have been fostered into wild nests, while 12 eggs or nestlings from the wild have been added to the captive colony since 1979.

For the purposes of the demographic simulations, the start of life for a bird can be considered to be the egg at laying, the fertile egg, the hatchling, or the fledgling, so long as both the fecundity measurements and the first year mortality used in the model are based on the same starting point. (For examination of the causes of breeding failure, it is useful to examine mortality at each stage from egg through fledging.) Because data on brood sizes at fledging are more reliable than eggs laid or hatched, we chose to consider fecundity as the number of fledglings per nest, and first year mortality of post-fledging birds.

To explore other demographic parameters that may represent either the present conditions or future conditions, we examined a number of alternative scenarios with varied population sizes, carrying capacities, mortality rates, degrees of environmental fluctuations, and frequencies and severities of catastrophe.

Population Biology Parameters: Puerto Rican Parrot

Accurate estimates of a number of population parameters are essential to population viability assessment. The PVA presented here proceeds directly from the considerable body of data collected by biologists working with the Puerto Rican parrot and made available in the recent book by Snyder, Wiley, and Kepler (1987) as well as by direct communication from researchers working with the project. Citations to the book below are given simply by reference to the appendices from which data were taken.

[Ulie: insert PVA form here?]

Initial population size:
The demographic simulation begins just before the breeding season, i.e., breeding occurs prior to any mortality. In the

basic simulations, we started the population with 36 birds
distributed as six 1-year birds, six 2-year birds, four 3-year
birds, and 20 breeding age (4+ year) birds. In each age class an
equal sex ratio was assumed. This number (36) matches the number
of birds present at the beginning of the 1988 breeding season,
and is two more than the number of birds present just prior to
the 1989 breeding season. The age distribution (6:6:4:20)
approximates stable age distributions obtained from life history
table analysis, and gives the 1:5 ratio of fledglings to older
birds that has been observed during the 1987-1989 breeding
seasons (21:103, reported at the workshop). To examine the
viability of smaller or larger starting populations, we used 18
birds (4:2:2:10) and 72 birds (12:10:10:40) in alternative
scenarios.

Carrying Capacity:
     We do not know how many Puerto Rican parrots could live in
the Luquillo forest. Population estimates were in the hundreds
prior to and during the rapid decline from 1955 to 1965, perhaps
indicating that the carrying capacity of the habitat is well over
200. It is also possible that many parrots were forced into the
forest during the first half of the century by habitat
destruction elsewhere and that numbers were temporarily much
above the long-term capacity of the forest. The field biologists
do not see evidence of food stress (birds do not spend most of
the day actively foraging, malnourished birds have not been
observed, food seems plentiful, nestling mortalities have been
due to predation, warble flies, and flooding of nest cavities
rather than brood reduction related to food stress) and large
areas of the forest remain unoccupied, suggesting that the
present population of about 40 birds is well below the carrying
capacity of the Luquillo forest. We modelled carrying capacities
of 100, 250, and 500.

Fecundity:
     Fecundity was measured as the number of wild pairs producing
0, 1, 2, 3, and 4 fledglings each year, obtained from Appendix 33
for 1979-1985 and from data provided at the PVA workshop for
1986-1989 breeding seasons. Captive hatched nestlings that were
fostered into wild nests were excluded from the "basic scenario"
calculations, unless a captive hatched bird was substituted for a
wild-hatched nestling that was removed into captivity. Although
the number of non-nesting adult parrots has never been known
precisely (because not all birds are of known age), it has been
estimated that approximately one-half of the adult birds in the
population nest each year. This estimate was used in determining
the number of breeding-age birds producing no young each year.
From these data, we estimate that on average 69.3% of adults
produce no young (50% do not nest, 19.3% nest but fail to fledge
offspring), 9.1% produce one fledgling, 8.0% produce two, 11.4%
produce three, 1.1% produce four, and 1.1% produce five
fledglings each year. In alternative scenarios, we used
fecundities of: 66% no fledglings, 8% one, 8% two, 14% three, and
4% four for a more rapid growth rate that matches that observed

from 1978-1985 (from Appendix 33) if captive-hatched chicks
fostered into wild nests are counted as recruitment into the wild
population; and 72% no fledglings, 10% one, 8% two, 8% three, and
2% four for a slower population growth rate (not based on any
observed data).

Mortality:
     The only age-specific mortality data readily available,
based on the years 1973-1979, yield estimates of 32.5% first-year
mortality (after fledging), 15.2% annual mortality of subadult
age classes, and 8.7% mortality of nesting adults. We assumed
that mortality of non-breeding adults is the same as that of
breeding adults. Mortality of captive birds seems to be lower
(see life table analyses from studbook) than in the wild, but the
paucity of data and changing management make accurate estimation
difficult.

     It may be noted that fecundity and mortality rates estimated
from the wild population lead to a calculated long-term mean
annual population growth rate of 4.7% when supplementation from
captivity is included into recruitment (see Table 3), whereas the
wild flock has been increasing at an average rate of 6% over the
past decade. This modest discrepancy could result from
underestimated fecundities (unlikely given the intensity of
observation of wild nests), overestimated mortality rates
(possible), or from a temporary string of better than average
years for reproduction due to the age structure of the
population. (I.e., an abundance of breeding age birds relative
to subadults could cause a temporary "baby boom".)

Environmental Variation:
     If reproduction were wholly at random, the fledglings per
nest would have the same variance as mean (following a Poisson
distribution). Although the brood sizes at fledging show more
variation among nests than expected by chance (the numbers of
fledglings per nest, from Appendix 33 and similar data for recent
years, have a variance that is 1.38 times the mean number
fledging over the 1979-1989 breeding seasons), the annual
variation in mean brood size does not seem to vary more than
expected (the variance in mean number fledged per year is almost
exactly one-fourth the mean number fledged per year, as expected
for four breeding pairs if year to year fluctuations in breeding
success are due solely to random variation). Thus, for the past
11 years there is no evidence for annual fluctuations in the
probability of breeding success in the Puerto Rican parrot
population at Luquillo. The variance in the number of deaths per
year since 1979 has been 19% above the mean number of deaths per
year, suggesting slightly more than random annual fluctuations in
mortality. Confirming the lack of significant annual variation
in demographic parameters (over the past ten years) is the
similarity observed between the variance in population numbers
over the first ten years in the simulated populations when
environmental variances were set to zero (V = 30.7 for
simulations starting with 18 birds) and the annual variation

observed in the size of the wild flock over the past 10 years (V
= 32.5). It is unlikely that birth and death rates are
absolutely constant over time (even though we have no evidence
that they have fluctuated over the past ten years), and for our
base simulation we assumed that environmental variations in the
birth rate, in death rates, and in the population carrying
capacity are equal to the expected (binomial or Poisson)
demographic variation. In alternative scenarios, we examined
cases with no annual variation in fecundity, mortality, and
carrying capacity and scenarios with environmentally imposed
variation in birth and death rates and carrying capacity equal to
twice the expected demographic variation.

Catastrophes:
     Biologists managing the remnant flock of Puerto Rican
parrots recognize that the risk of a catastrophe largely or
wholly eliminating the species is not trivial (nor, fortunately,
unavoidable). Hurricanes earlier in this century are believed to
have reduced the Puerto Rican parrot populations, perhaps being a
major cause of decline. A 1899 hurricane apparently decimated
populations of a previously abundant bird, the troupial Icterus
icterus (which has subsequently recovered), a 1928 hurricane
almost eliminated the Puerto Rican flycatcher, Myiarchus
antillarum, and these storms devastated parrot habitat in Rio
Abajo and Luquillo (see Appendix 1). Puerto Rico has not been
directly hit by a major hurricane in the past 55 years, but 3
major hurricanes did strike the island in the previous 33 years
(1899, 1928, and 1932) and the long-term average seems to be that
a severe hurricane directly hits the island about three times
each century. The probability and effect of a major disease
epidemic is even more difficult to predict, although possibly is
no less likely to cause the demise of the Puerto Rican parrot.
The recent history of the black-footed ferret makes clear the
potential for disease to eliminate a small, remnant population.
The wild flock of Puerto Rican parrots is vulnerable to
hurricanes, and the tight flocking behavior of foraging parrots
may make them highly vulnerable to epidemics as well. The
captive flock could probably be protected from a severe storm (if
basic support services for humans and captive wildlife were not
severely compromised), but may be much more vulnerable to a
disease outbreak. The extreme (but not unwarranted) precautions
taken in the black-footed ferret breeding facility in Wyoming
(very restricted entry to the building, wash-down rooms prior to
entry, strict quarantine procedures [Ulie: ammend these if you
have better information than do I]) contrast with the fewer
precautions in the Puerto Rican parrot breeding facility. The
frequent exchange of eggs and nestlings between the captive and
wild flocks of Puerto Rican parrots also makes possible cross-
contamination during an epidemic.

     For the basic PVA, we assumed that the probability of a
major hurricane strike (or other catastrophe of similar effect)
is 3% annually and that such a storm would kill about 50% of the
subadult and adult birds and would cause total failure of

reproduction for one year. We also modelled scenarios with (a)
no catastrophic impacts, (b) with 6% probabilities of occurrence
(with the above effects), and (c) with 3% probability and 50%
decline in reproduction and 25% decline in survival.

Results of demographic simulations

     Table 2 shows the results from 1,000 computer simulations of
the wild flock of Puerto Rican parrots at Luquillo, under various
assumptions about the demography and sources of variation and
risk. The table gives, for each set of input parameters, the
mean annual population growth (lambda) and mean generation time
calculated from the life table of birth and death rates, the
proportion of simulated populations that survived 100 years, and
the mean size at 100 years of those populations that persisted.
The "basic scenario", representing the best guess as to the
demography of the Luquillo flock as is exists now (see above), is
shown in the middle of the table. Given the calculated birth and
death rates, a year-to-year environmental variation in birth and
death rates that is comparable to the (binomial) variation
between individuals, and the predicted frequency and severity of
hurricanes, the simulations suggest that the present wild flock
at Luquillo has about a two-thirds chance of persisting 100
years. The standard errors of survival probabilities in Table 2
(given by P x [1 - P] / sqrt[1000]) are typically about .01, and
standard errors around the number of parrots in surviving
populations ranged from about 1 to 5. In all cases examined in
Table 2, the asymptotic stable age distribution just prior to
each breeding season was 18% 1-year old birds: 29% sub-adults
between 1 and 4: 54% breeding-age birds. This distribution is
close to that observed at Luquillo (e.g., fledglings comprised
about 20% of the flock in the past 3 years).

     Comparison of lines within Table 2 demonstrates that neither
the carrying capacity of the Luquillo forest nor modest annual
environmental variation have much impact on the probability that
the population will survive (though both do affect the sizes of
the persisting populations). With the observed positive mean
growth rate, moderate environmental variation was not sufficient
to cause extinction.

     The predominant factor controlling extinction rates in Table
2 is the frequency of catastrophic mortality and failures of
reproduction as might be caused by a hurricane or a severe
disease epidemic. The modest growth rate of the Luquillo
population is apparently insufficient to assure that the
population will recover from one catastrophe before the next one
occurs. The mean time to extinction (of those simulated
populations that go extinct within 100 years) for almost all
scenarios was approximately 50 years, with extinctions fairly
even dispersed throughout the 100 years. It was not the case
that simulated populations regularly declined and increasingly
many went extinct as years progressed; rather, populations
fluctuated in size and extinctions followed quickly at almost any

time when a few bad years occurred by chance in close succession. The effect of catastrophes depended almost not at all on the carrying capacity of the population. If catastrophes are as frequent as has been estimated, then the population often does not reach the carrying capacity before being decimated again. The effect of catastrophes on population survival is highly dependent upon the growth rate of the population, with more slowly growing populations being especially vulnerable (presumably because they rarely recover from a catastrophe before another strikes the population).

If several flocks of Puerto Rican parrots existed at a sufficient distance to minimize the chance that a single catastrophe would decimate both, the probability that all would perish within 100 years would be equal to the product of the probabilities that each would go extinct, if no recolonization from extant populations followed local extinctions. (E.g., two populations following the basic scenario would both go extinct with a probability of about 11% [= 33% x 33%]; three such populations would vanish with probability 4%.) The probability of global extinction could be very much less if recolonization was affected after local catastrophes.

Table 3 shows results analogous to those in Table 2, except that fecundities were determined for wild flock from the years 1979-1985 with the inclusion of nestlings that had been added from the captive flock during the past decade. These scenarios therefore represent extinction probabilities for a supplemented wild flock (or, equivalently, a flock in which the number of fledglings per nest is increased about 18.5%). By comparing the results of Tables 2 and 3, it is apparent that the increased population growth achieved by supplementing the wild flock considerably lessens, though does not remove, the risk of extinction due to catastrophes.

Each of the demographic parameters used in the simulations had to be estimated from limited data. (It is difficult to obtain extensive data on an endangered species.) Table 4 examines simulation results in which the number of fledglings per nest was assumed to be about 15% lower than in the basic scenario. With this lower rate of recruitment into the population, the effects of 1-year catastrophes are even more dramatic, and the population is not assured of persistence even in the absence of catastrophes. It therefore seems unlikely that the wild flock at Luquillo could serve as a continued source of birds for captive programs or reintroduction efforts. Harvest from the population only when numbers are high, with cessation of harvest or even supplementation during recovery from catastrophes, may not jeopardize the population, however. Certainly harvest of surplus nestlings when the population is at a local carrying capacity would have no demographic impact.

Table 5 presents results for scenarios in which the initial wild flock is 72, rather than the present 36 birds. The greater

probabilities of population survival relative to Table 2 demonstrate that an immediate boost in numbers would considerably lessen the chance of catastrophe-caused extinction, to about the same extent as does the increase in annual production represented in Table 3. This also suggests that the next decade, during which the Luquillo flock would be expected to roughly double if no catastrophe strikes, may be critical to the long-term probability of persistence. Strategies that increase the number of birds at Luquillo more rapidly would shorten this window of high vulnerability.

Table 6 shows the extinction probabilities for a starting population of 18 -- about the size of the wild flock in the late 1970s, before intensive captive breeding efforts were coupled with an increased intensity of management of the wild flock. The very low probabilities of survival for those scenarios suggest that the progress made through intensive efforts in the past decade may have pulled the Puerto Rican parrot away from the brink of extinction.

Table 1. Sample output of the demographic simulation program for the best guess demographic parameters (the "basic scenario") for the wild flock of Puerto Rican parrots in the Luquillo forest.

Table 2. Results from 1,000 simulations of wild Puerto Rican parrots for 100 years, with
fecundities as estimated from 1979 – 1989 wild flock without supplementation from captive flock.
 Initial population size = 36. K = carrying capacity; EV = environmental variation as a multiple
of expected demographic variation in birth and death rates; catastrophes coded by frequency /
fraction breeding / fraction surviving. Lambda = mean annual growth rate; GT = generation time
in years. P[survival] = proportion of simulated populations surviving for 100 years; N = mean
population size at 100 years for those populations surviving. Omitted values are as in the
previous line.

Input parameters			Calculated mean growth		Population fates	
K	EV	Catastrophes	lambda	GT	P[survival]	N
100	0	0/1/1	1.035	14.4	1.00	97
250					1.00	243
500					1.00	455
100	1	0/1/1	1.035	14.4	1.00	86
250					.99	217
500					.99	393
100	2	0/1/1	1.035	14.4	.98	79
250					.99	207
500					.98	388
100	0	.03/0/.5	1.020	12.8	.67	54
250					.69	105
500					.69	138

********************** BASIC SCENARIO ******************************

Input parameters			Calculated mean growth		Population fates	
100	1	.03/0/.5	1.020	12.8	.65	48
250					.67	89
500					.68	144

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Input parameters			Calculated mean growth		Population fates	
100	2	.03/0/.5	1.020	12.8	.65	46
250					.65	99
500					.68	161
100	0	.06/0/.5	1.003	11.6	.22	32
250					.23	46
500					.24	44
100	1	.06/0/.5	1.003	11.6	.21	29
250					.22	51
500					.21	48
100	0	.03/.5/.75	1.028	13.6	.94	82
250					.95	173
500					.95	246
100	1	.03/.5/.75	1.028	13.6	.92	71
250					.94	158
500					.91	231

Table 3. Results from 1,000 simulations of wild Puerto Rican parrots for
100 years, with fecundities as estimated from 1979 - 1985 wild flock with supplementation from
        captive flock. Initial population size = 36.

Input parameters			Calculated mean growth		Population fates	
K	EV	Catastrophes	lambda	GT	P[survival]	N
100	0	0/1/1	1.047	14.4	1.00	99
250					1.00	250
500					1.00	499
100	1	0/1/1	1.047	14.4	1.00	90
250					1.00	237
500					1.00	477
100	2	0/1/1	1.047	14.4	1.00	85
250					1.00	226
500					1.00	457
100	0	.03/0/.5	1.034	12.8	.82	70
250					.87	170
500					.83	293
100	1	.03/0/.5	1.034	12.8	.81	62
250					.84	154
500					.83	271
100	2	.03/0/.5	1.034	12.8	.77	58
250					.81	147
500					.81	251
100	0	.06/0/.5	1.018	11.6	.42	43
250					.46	79
500					.46	121
100	1	.06/0/.5	1.018	11.6	.40	37
250					.44	80
500					.44	105
100	0	.03/.5/.75	1.041	13.6	.99	94
250					.99	234
500					.99	452
100	1	.03/.5/.75	1.041	13.6	.98	84
250					.98	216
500					.99	419

Table 4. Results from 1,000 simulations of wild Puerto Rican parrots for
100 years, with fecundities moderately lower than estimated from 1979 – 1989 for wild flock.
        Initial population size = 36.

Input parameters			Calculated mean growth		Population fates	
K	EV	Catastrophes	lambda	GT	P[survival]	N
100	0	0/1/1	1.022	14.4	.97	81
250					.96	141
500					.96	156
100	1	0/1/1	1.022	14.4	.92	68
250					.94	128
500					.94	164
100	2	0/1/1	1.022	14.4	.93	62
250					.93	140
500					.94	200
100	0	.03/0/.5	1.006	12.8	.45	34
250					.46	43
500					.46	43
100	1	.03/0/.5	1.006	12.8	.40	29
250					.39	46
500					.41	50
100	2	.03/0/.5	1.006	12.8	.44	29
250					.42	44
500					.40	61
100	0	.06/0/.5	0.988	11.6	.11	18
250					.09	18
500					.09	18
100	1	.06/0/.5	0.988	11.6	.10	19
250					.09	26
500					.09	26
100	0	.03/.5/.75	1.015	13.6	.79	51
250					.80	64
500					.76	68
100	1	.03/.5/.75	1.015	13.6	.75	45
250					.71	66
500					.73	74

Table 5. Results from 1,000 simulations of wild Puerto Rican parrots for
100 years, with fecundities as estimated from 1979 - 1989 wild flock without supplementation from
        the captive flock. Initial population size = 72.

Input parameters			Calculated mean growth		Population fates	
K	EV	Catastrophes	lambda	GT	P[survival]	N
100	0	0/1/1	1.035	14.4	1.00	98
250					1.00	249
500					1.00	499
100	1	0/1/1	1.035	14.4	1.00	88
250					1.00	237
500					1.00	480
100	2	0/1/1	1.035	14.4	1.00	81
250					1.00	224
500					1.00	460
100	0	.03/0/.5	1.020	12.8	.85	58
250					.87	136
500					.88	217
100	1	.03/0/.5	1.020	12.8	.80	51
250					.86	121
500					.85	209
100	2	.03/0/.5	1.020	12.8	.79	47
250					.85	117
500					.86	192
100	0	.06/0/.5	1.003	11.6	.38	34
250					.42	62
500					.42	81
100	1	.06/0/.5	1.003	11.6	.36	31
250					.43	53
500					.43	72
100	0	.03/.5/.75	1.028	13.6	1.00	90
250					1.00	224
500					1.00	411
100	1	.03/.5/.75	1.028	13.6	1.00	78
250					1.00	210
500					1.00	380

Table 6. Results from 1,000 simulations of wild Puerto Rican parrots for
100 years, with fecundities as estimated from 1979 - 1989 wild flock without supplementation from
        the captive flock. Initial population size = 18.

| Input parameters | | | Calculated mean growth | | Population fates | |
K	EV	Catastrophes	lambda	GT	P[survival]	N
100	0	0/1/1	1.035	14.4	.88	87
250					.89	182
500					.90	267
100	1	0/1/1	1.035	14.4	.87	75
250					.84	173
500					.85	270
100	2	0/1/1	1.035	14.4	.86	74
250					.87	183
500					.88	327
100	0	.03/0/.5	1.020	12.8	.43	48
250					.41	73
500					.38	76
100	1	.03/0/.5	1.020	12.8	.37	45
250					.40	80
500					.40	105
100	2	.03/0/.5	1.020	12.8	.46	46
250					.45	99
500					.45	137
100	0	.06/0/.5	1.003	11.6	.11	28
250					.11	30
500					.11	33
100	1	.06/0/.5	1.003	11.6	.11	28
250					.12	45
500					.12	58
100	0	.03/.5/.75	1.028	13.6	.71	67
250					.72	112
500					.69	137
100	1	.03/.5/.75	1.028	13.6	.66	60
250					.68	113
500					.69	158

<u>Demographic</u> <u>Recommendations</u> -- <u>Puerto</u> <u>Rican</u> <u>Parrot</u>

Additional sites:
     The primary risk to the Puerto Rican parrot at this time
seems to be the chance that a catastrophe will strike the
population. The wild population and probably also the captive
population seem sufficiently large so that, in the absence of a
sudden population decimation, the modest growth rate as
experienced over the past ten years will prevent random
fluctuations in birth and death rates (demographic and
environmental variability) from driving the population to
extinction. The probability that a hurricane, a disease
outbreak, or some other natural catastrophe will decimate the
population is very difficult to estimate. The perhaps
conservative guesses about the frequency and effect of hurricanes
made by participants in the PVA workshop were found to lead to
extinction probabilities that we find unacceptably high. The
simulation results support the view expressed in the recovery
plan that a primary and urgent goal of the program should be to
establish additional captive and wild populations of Puerto Rican
parrots.

     Given that no one population of parrots is likely to provide
sufficient security for the survival of the species (and that
there is perhaps a 1 in 30 chance that a devastating hurricane
will hit within a year; a 1 in 15 chance of catastrophe within 2
years), we would recommend that two additional aviaries for the
Puerto Rican parrot be established as soon as possible. One of
these could be the Rio Abajo aviary already under construction.
The Rio Abajo site should be viewed as a long-term commitment to
a propagation facility that allows a doubling (or more) of the
potential for breeding parrots for eventual release.

     The other new site for Puerto Rican parrots should be off
the island of Puerto Rico, so that it is outside of the likely
path of severe destruction of any storm that may hit the island.
 This off-island site should make use of existing facilities
(rather than waiting for new facilities to be constructed for the
purpose) and existing expertise. Efforts should begin
immediately to identify a captive breeding facility that has
experience and success breeding parrots, that has good quarantine
facilities, and that can house the Puerto Rican parrots separate
from other psittacines and give them intensive management. The
off-island facility will not likely be a major propagation center
for Puerto Rican parrot recovery, but it is essential that some
birds be moved from Luquillo soon.

     The breeding program at Luquillo should not be disrupted to
provide birds for either of the two additional sites. Six to
eight present non-breeders should be identified by the Luquillo
aviculturist for move to the off-island site. The 7 wild-caught
Puerto Rican parrots that have failed to breed for more than a
decade would be good candidates for this facility, as would one
female of the homosexual pair (which needs to be separated if

repairing is to be successful). We can hope that different
management practices or just the change in environment will
stimulate reproduction in some of these birds. The birds
destined for the Rio Abajo aviary could be subadults that hold
promise for reproducing within a year or two after the move.
Over time, the Rio Abajo aviary should receive representation
from all of the genetic lines represented in the Luquillo aviary.
 Joint management of these flocks could utilize occasional
exchange of individuals to bolster the genetic diversity of each
when necessary.

     The timetable for moving parrots to the Rio Abajo aviary is
constrained primarily by construction schedules and the need for
precautions to avoid a catastrophic disease outbreak at the new
aviary. The schedule for moving birds to Rio Abajo must be a
compromise between the urgent need for establishing flocks that
are isolated from Luquillo and the need to avoid placing a
substantial number of parrots in an untested facility that may
harbor unknown disease vectors or have other unforeseen
management problems. Discussion at the PVA workshop led to a
workable compromise: 24 Hispaniolan parrots would be moved to
Rio Abajo as soon as it is ready to receive them (no later than
October 1989). These birds would serve as sentinels for disease
and management difficulties and their move out of Luquillo would
free up resources needed there for Puerto Rican parrots. The
Hispaniolan parrots should be bled and tested for disease prior
to the move and again 120 days after the move. Serum from each
should be banked for later analysis if problems arise. After 120
days of successful operation of the Rio Abajo aviary, any further
Hispaniolan parrots in Luquillo that need to be moved to avoid
overcrowding there could be sent to Rio Abajo. Again, serum
samples and testing should be undertaken before and after the
move. Breeding of Hispaniolan parrots should be attempted in Rio
Abajo in early 1990. At the end of the breeding season, progress
at the Rio Abajo aviary should be evaluated. If no serious
medical or management problems arise, 12 or more Puerto Rican
parrots should be sent to Rio Abajo at the end of the summer
1990. (Movement of fewer than 12 birds would have little value:
a few birds would not be sufficient stock for recovery of the
species if a catastrophe hit the Luquillo flocks.) This schedule
gives the Rio Abajo aviary almost a full year of experience with
Hispaniolan parrots before Puerto Rican parrots are moved to the
site, providing considerable but not excessive opportunity for
evaluation of local disease risks. Although many of the Puerto
Rican parrots moved to Rio Abajo may be too young to breed in
1991, initial attempts at propagating Puerto Rican parrots at Rio
Abajo could begin in the 1991 breeding season. The Rio Abajo
aviary should have a full breeding program in place by the 1992
breeding season.

     While the Rio Abajo and off-island facilities will provide
emergency back-up in case of catastrophe (and allow more
opportunity for experimentation with varied management
approaches), longer-range recovery plans should address the need

for about 5 reasonably independent populations of parrots on Puerto Rico, as well as one or more off-island safeguard populations. Only after Puerto Rican parrots are well-established in multiple sites (5 or more) could the risk of extinction be considered low enough to permit easing of recovery efforts (the ultimate goal of any recovery planning).

Interactive demographic management of the wild and captive flocks at Luquillo:

     Neither the wild nor the captive flocks of Puerto Rican parrots in the Luquillo forest are at such low numbers that extinction is imminent (though both were a few years ago). Yet neither the captive nor the wild flock is sufficiently large to be safe from natural catastrophes. As the computer modelling demonstrates, the chance that a hurricane or other catastrophe will eliminate a parrot population is critically dependent on the rate of growth of that population and strongly dependent on the initial size of the population.

     Given the ease with which nestlings can be fostered into nests other than those of their parents, nestlings could be moved from captivity to the wild or the reverse to maximize the probability that the species will survive and recover. Both flocks need as rapid population growth as is possible, but obviously supplementation of one necessitates culling from the other. In the past, nestlings from the aviary have been fostered into nests to supplement the wild flock. This supplementation may have been an important component of the slow but steady increase in the wild flock, but we lack information on the fates of almost all the birds added to wild nests and evaluation of the benefit of that supplementation is impossible. There is no clear reason why the captive-hatched birds would not have suffered mortality at a rate comparable to birds with wild parents. Without the supplementation, the wild flock would still have had a positive, albeit lower, growth rate. The supplementation of the wild flock was halted after 1985, although a reciprocal exchange of wild and captive birds occurred in 1988.

     Many of the factors that impinge upon a decision to supplement or not the wild flock are easy to identify: relative mortality of captive and wild birds, later breeding success by captive-hatched birds fostered into wild nests, the importance of the numbers of Puerto Rican parrots in a flock to the breeding of all members of the flock (social facilitation of nesting behavior), and the relative risks to the captive and wild flocks of natural catastrophes. Even with a clearly stated commitment to maximizing the probability that Puerto Rican parrots will not go extinct as a species, experts disagree on whether supplementation of the wild flock should resume and, if so, at what rate. Given the lack of data on the ultimate fates of captive and wild fledglings, and the lack of information on the relative risks to the wild and captive flocks, our recommendations on supplementation rest perhaps more on what has

been learned from experiences with other endangered species than on analytical evaluation of Puerto Rican parrot demography and management successes.

First, it is recognized that a critical impediment to faster population growth both in the wild and in captivity is the failure of adult birds to nest and reproduce. Fostering of eggs or nestlings should not be done if it is likely to cause nest failure and abandonment. If fostering is likely to preserve an active nesting pair that may otherwise abandon reproductive attempts (e.g., after nest predation or damage by storm), it should be used as a management tactic. As in the pst few years, this can usually be accomplished by the transfer of chicks between nests in the wild or the exchange of nestlings in captivity with some in the wild (perhaps because the wild-hatched chicks need medical care). If the only chick available to foster into a wild nest is from captivity, that transfer should be made.

Beyond such rescue efforts for wild nests, we would recommend that priority be given to maintenance of a thriving captive colony. Wild populations of many species, endangered and otherwise, are subject to so many risks that any one has a relatively short expected duration. Black-footed ferrets, California condors, and whooping cranes are just a few of the better known examples of wild populations being decimated very quickly. Captive colonies do not always thrive, but they also rarely are exterminated quickly, especially if divided among multiple locations. Mortality is generally very low in captive facilities with experience in propagating a species (as is the case for Puerto Rican parrots in the Luquillo aviary). This low mortality can "buy time" while husbandry methods for enhancing reproduction are developed (hence the lower probability of sudden extinction). Although the captive Puerto Rican parrots at the Luquillo aviary have been increasing at a rate only modestly greater than the increase of the wild flock, we expect that continually refined management will lead to a faster growth rate of the captive flock, perhaps very much faster. Improvements in the management of the wild flock may also assist that population, but dramatic increases are unlikely to come soon. Given that highest priority should go toward increasing numbers of parrots by whatever means are available, we favor retaining most or all of captive-produced nestlings in the captive breeding program. If captive production is faster than production in the wild (as seems to be increasingly the case), the quickest route to a secure wild and captive population is to use the captive population as a short-term, high-investment production facility. Slowing growth of the captive flock will likely lead to costly delays in progress toward full recovery of the species.

Our recommendation to retain birds in captivity until the captive flock is large and secure has two qualifiers. First, in the event of disastrous events in the wild, the wild population should not be allowed to perish if that can be prevented without also sacrificing the captive colony. Unlike the case with condors and ferrets, the Puerto Rican parrot recovery program has

the very important advantage of having a wild population of experienced birds that will readily accept fostered young. The second qualifier relates to a more optimistic and probably more likely scenario: if production in the Luquillo aviary improves so markedly that rapid population growth seems almost assured, fostering some captive-produced nestlings into wild nests may achieve very rapid recovery in both facets of the Puerto Rican parrot program. The captive flock has been increasing at a mean rate of 3.2 birds per year since 1979 (growth estimated by least squares regression), and this has been achieved with an average of 4.7 fledglings per year. We recommend that fostering of captive-produced nestlings into wild nests be considered only if nestlings at the appropriate age are available for nests that could receive them, and only after the production of the captive flock in the breeding season is likely to exceed the captive bird mortality of the past 12 months by more than 6 (i.e., population growth is approximately doubled over the experience of he past decade). Because a decision about supplementation of the wild flock may have to be made before many of the captive nestlings have fledged, the aviculturists will have to assess whether ongoing production is likely to produce a net increase over the previous year of at least six birds. We recommend that the aviculturists be conservative in their assessment of still incomplete production, so that deaths of late-stage nestlings after supplementation is underway do not jeopardize the captive flock. Even after captive production assures a net increase of more than six birds, we recommend that no more than half of the production above this limit be used to supplement the wild flock.

The wild flock is recovering and has continued to do so after supplementation was halted, though not as fast as recent increases in the captive flock. If no catastrophe strikes, the wild flock is likely to recover, perhaps slowly, even if there is no further input from the captive flock. If a hurricane or disease does decimate the wild flock of parrots, a large captive flock as a source for replenishment or reestablishment will likely be far more important to the recovery of the wild flock than will additional birds in the pre-catastrophe wild flock.

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