PUERTO RICAN PARROT

Amazona vittata

POPULATION VIABILITY ANALYSIS

and

RECOMMENDATIONS

Captive Breeding Specialist Group

Species Survival Commission IUCN

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POPULATION VIABILITY ANALYSIS

Final Report

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Contents Page

RECOMMENDATIONS - PUERTO RICAN PARROT PVA

1.Establish a collaborative Recovery and Captive Masterplan program in 1989.

2.Establish a captive population on the mainland as soon as possible to protect against catastrophic loss of the species and to assist in analysis of the reproductive problems.

3.Provide further support for the field program at Luquillo.

4.Establish a captive population of Puerto Rican parrots at Rio Abajo in the summer of 1990.

5.Develop long range plans to establish 5 independent wild populations of the Puerto Rican parrot in Puerto Rico.

6.Initiate a vigorous program to investigate the causes of breeding failure and to capture the founder contributions of the Puerto Rican parrot stock.

7.Do not initiate any timber removal operations in the areas of the Rio Abajo forest intended for maintenance or release of Puerto Rican parrots until an adequate review of impact has been done.

8.Begin planning a release and monitoring program for the wild population at Rio Abajo now.

9.Establish an 'external' independent review group for the parrot programs.

10.Do not use captive production for supplementation of the Luquillo wild population until the net increase in the captive population is more than 6 birds per year. Then use no more than half of the number above 6.

11.Conduct a literature search and review of all available information on diseases of free-ranging birds, reptiles, and mammals in Puerto Rico.

12.Do further molecular genetic work for estimation of possible past losses in diversity and close kin relationships in the wild and captive populations.

13.Tighten restrictions on visitors to the Luquillo aviary.

14.Do not selectively cull birds or lineages with presumed genetic defects. Detailed recommendations for the captive colony are provided in a separate analysis and plan.

15.There are multiple management needs for the captive flock (see the commentary on recommendations) and the facility itself is in serious need of maintenance.

COMMENTARY ON RECOMMENDATIONS - PUERTO RICAN PARROT PVA

1.Establish a collaborative Recovery and Captive Masterplan program in 1989.

This program should provide the analysis, planning, and management, to produce birds for (a) support and enhancement of the wild population in Luquillo Forest, (b) expansion of the captive population at Luquillo, (c) establishment of two new captive populations including the one at Rio Abajo and one on the mainland, and (d) establishment of a second wild population at Rio Abajo. This analysis and masterplan should provide guidelines and animal by animal recommendations for each of these objectives to assure security of the species and maximum retention of founder representation and of genetic diversity.

2.Establish a captive population on the mainland as soon as possible to protect against catastrophic loss of the species and to assist in analysis of the reproductive problems.

We recommend that the 7 older non-reproductive wild caught birds and 5 selected non-reproductive offspring of the breeders be used for this purpose. The site chosen should provide skilled management of parrots, maximum security for the species from catastrophic loss (disease, hurricanes, theft), and the immediate resources for a strong program to investigate the causes of reproductive failure. Do not remove breeders (producing chicks) from the Luquillo facility which should continue to focus on the effort to be a production facility.

3.Provide further support for the field program at Luquillo.

The experienced wild population can foster captive produced eggs and chicks into the wild population and will play a vital role in reintroduction programs at other sites. It is our impression that survival of the wild population continues to be dependent upon the intensive management provided particularly at nest sites. New nesting pairs may be appearing. They need to be located, monitored, and perhaps supported. This process is likely to need to continue until nests can be shown to be successful without intervention.

4.Establish a captive population of Puerto Rican parrots at Rio Abajo in the summer of 1990.

This should be done after a trial period with Hispaniolan parrots to monitor for disease and to carry them through a breeding season as a testing and learning period for the facility and husbandry resources.

The performance and needs of the Rio Abajo facility with Hispaniolan parrots should be reviewed after the 1990 breeding season. If satisfactory, then 12 or more Puerto Rican parrots should be moved to the facility at the end of the summer of 1990. This facility should plan to be another production facility to support a release program and provide security for the species.

5.Develop long range plans to establish 5 independent viable wild populations of the Puerto Rican parrot in Puerto Rico.

6.Initiate a vigorous program to investigate the causes of breeding failure and to capture the founder contributions of this stock.

7.Do not initiate any timber removal operations in the Rio Abajo forest intended for maintenance or release of Puerto Rican parrots.

The failure of this species to survive in any of the disturbed habitats it once occupied, the uncertainties concerning its long term decline with disturbances in Luquillo, and its very slow recovery in Luquillo despite intensive management argue strongly against disturbance of Rio Abajo prior to or during a reintroduction program.

8.Begin planning a release and monitoring program for the wild population at Rio Abajo now.

Much more detailed thought and preparation needs to be given to the reintroduction program. Consideration should be given to translocations from Luquillo when that population is deemed able to sustain removals as well as releases of prepared birds captive bred at Rio Abajo. Much of this will be experimentation and should be conducted with birds that can be lost without damage to the genetic and demographic security of the species. A goal of both production aviaries will be to produce birds for support, enhancement, and establishment of the wild populations as well as to provide continued security for the species.

9.Establish an 'external' independent review group for the parrot programs.

Members of this group should not be employees of the agencies responsible for the recovery of the parrot. This group might include a population biologist, field parrot biologist, veterinarian, reproductive biologist, and captive parrot biologist to review, discuss, and make recommendations on the captive and field programs for the Puerto Rican Parrot. This group should convene yearly with the biologists conducting the field and captive population programs and prepare a report to the responsible agencies. This group should serve as a peer review panel for management and research programs and proposals with the obligation to provide objective commentary and recommendations to the responsible agencies.

10.Do not use captive production for supplementation of the Luquillo wild population until the net increase in the captive population is more than 6 birds per year. Then use no more than half of the number above 6. Plan to establish and maintain a dispersed (10 sites or more), captive population which is cooperatively managed (SSP) for at least 50 years.

Exceptions to the supplementation policy would occur (1) in the case of a reduction in the wild population to prevent its loss and (2) if, as likely, captive production accelerates rapidly assuring rapid captive population growth. Exchanges would be made individually on the merits of each case.

11.Conduct a literature search and review of all available information on diseases of free-ranging birds, reptiles, and mammals in Puerto Rico.

There is a significant probability that the sharp declines (50-90%) in the adult Puerto Rican parrot population in 1966-1968 may have been due to disease. Species present in Luquillo and Rio Abajo should be surveyed for infectious diseases and surveillance should be maintained until both populations reach recovery goals. Serology studies of free ranging parrot species in Rio Abajo may provide useful information.

12.Do further molecular genetic work (electrophoresis, mitochondrial DNA, and DNA fingerprinting) for estimation of possible past losses in diversity, measurement of divergence from other species of Amazona, and identifying close kin relationships in the wild and captive populations.

13. We recommend further tightening of procedures at Luquillo.

This includes removal of domestic birds, exclusions of visitors with recent domestic or captive avian contacts, and greater precautions against disease. The movement of the Luquillo breeding facility to a site connected with a visitors center during the next 5-10 years should give special attention to the problems of disease, security, and potential visitor traffic in and near the facility. The Puerto Rican parrot is regarded as 'nervous'; it was vulnerable to unknown challenges in the wild, and it is not secure either in captivity or in the wild. Disease is of special concern both from possible neighboring domestic fowl operations and 'flyins' of wild species that can act as carriers.

14. Do not selectively cull birds with presumed genetic defects unless a firm genetic basis can be demonstrated and a demographic cost to breeding the birds with the trait can be shown. Plan pairings in the captive colonies to avoid inbreeding.

The masterplan should plan to manage the wild and captive populations as a single genetic population with interchanges to provide the broadest genetic base for both. It is likely that neither population has all of the diversity present in the other. Careful pedigree records are essential. The DNA data may be useful for identifying relationships.

15. Management needs of the Luquillo and future colonies include:

a. Sex determination on all birds at an early age. Adult birds that have not produced fertile eggs should have sex determination by laparoscopy (bring in a parrot-experienced expert) as soon as possible.

b. All eggs and birds should be reliably marked and assigned a single unique ID or Studbook number.

c. Remotely operated video cameras with time lapse capability for monitoring and learning about behavior and breeding of the parrots. Additional hatchers and incubators are needed.

d. Reformulation of diets according to details provided in nutrition section of report. Note problems of Ca/P ratio, adverse effects of food selection by parrots, and need for detailed composition information from manufacturers.

e. Organize and where possible computerize the record system. Use of ARKS, SPARKS, and MEDARKS is recommended since they are in use by more than 200 zoos and provide data standards and a large pool of information to draw upon.

f. Veterinary oversight is needed to assist in establishment of protocols for routine veterinary care, a preventative health program, nursery and incubator room protocols, diagnostic and post-mortem resources, and medical records.

g. A scientific program and protocols for analysis of the poor reproductive performance of parrots in the captive colony needs to be established. This program needs to involve an expert reproductive biologist with adequate facilities for the studies required. The Hispaniolan Parrots will be a valuable surrogate for the Puerto Rican Parrots for these preliminary studies.

h. The use and location of the diesel generator at Luquillo needs to be assessed in terms of human and animal toxicity for replacement or relocation. The peeling paint and water supply should be assayed for lead as a possible hazard to people and the parrots.

It has been extraordinary good fortune that the Puerto Rican Parrot has been tended by such a dedicated and capable small band of people over the past 20-25 years. The species clearly would not have survived with simple protection, study, and benign neglect. We thank each of you. All of the above recommendations are intended in the spirit of helping to build upon the contribution these people have made and are making.

U. S. Seal R. C. Lacy N. R. Flesness

EXECUTIVE SUMMARY - PUERTO RICAN PARROT PVA

GOALS of the Population Viability Analysis:

Recommend actions and schedule needed to secure the Puerto Rican parrot against extinction and assure at least 95% probability for survival for 100 years with retention of at least 90% of the currently available heterozygosity. Outline population sizes and distribution needed to provide a wild parrot population of sufficient size to allow accumulation of genetic variation and continuing evolution by natural selection.

STATUS of Present Parrot Population:

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 wild parrot population has increased from about 16 birds in 1972 to 34 at the end of 1988 with an annual rate of increase of about 6%. There have been both removals of eggs from the wild (with double clutching obviating a net loss to the wild) for the captive population and return of chicks to the wild to fledge as a supplement to the wild population. Captive bred chicks returned to the wild have come from only 2 of the captive pairs (9 from one pair and 3 from the other) a bias which should not be continued. However for the past 20 years there have been only about 4 breeding pairs in the wild each year. The effective population size during this time may be estimated at 5.9 which would result in a loss of genic diversity or heterozygosity of about 8.5% per generation. Given a 10-12 year generation time, perhaps 10-15% of genic diversity has been lost to date but inbreeding will be unavoidable in the third generation at the same nesting rate.

The captive population numbers 54 birds including this years fledglings. The net rate of increase from captive breeding of captive reared birds is about 6% (griwth has been 13% if wild laid eggs hatched in captivity are included). The captive egg fertility rate is about 25% as compared to a wild rate of perhaps 80%. The basis of the lower fertility needs to determined and corrected. There are 20 potential founders for this population of which 14 have descendants in the population. Breeding, by natural or artificial means, of the living unrepresented founders is a very high priority. This represents a significant fraction of the available genetic diversity.

EFFECTS of *Status Quo* and Current Interventions:

The wild and captive populations are growing in numbers at rates of about 5 - 6% per year which will produce a doubling in size in 12-14 years.

This rate is not sufficient to protect against catastrophic loss with a hurricane or disease. The current interventions including individual nest management and protection from predation have been essential for survival of the species in the wild. The formation and growth of the captive population has provided greater security against extinction and has allowed a far more rapid expansion of numbers than achievable with the wild population alone and retention of more genetic diversity. However, the close location of the wild population and the aviary and the exchange of chicks and eggs between the two significantly increases the risk of simultaneous catastrophic loss from either hurricanes or disease.

METAPOPULATION Needed:

The need for multiple wild populations of the parrot as a recovery objective is emphasized by the details of its history of decline and the vulnerability of populations to major hurricanes. The possible role of disease in the past decline and the continuous threat from highly mobile domestic human and animal sources further increases the risk of catastrophic loss of single populations. Survival of the Puerto Rican parrot in the wild will require in the short term establishment of 3 captive colonies to support survival and establishment, in the long term of 5 or more separated wild populations. These populations will require monitoring, periodic exchange of birds (for example cross foster about 3 - 5 chicks every 10 years) to maintain genetic exchange, and reestablishment in the event of local extinction.

CAPTIVE Population:

The captive population is absolutely essential for preservation of available genetic diversity of this species. Expansion of the captive population to at least 3 sites, one on the mainland, is the only management intervention that can assure survival of the Puerto Rican parrot for 100 years with a 95% probability, and retention of 90% of the available heterozygosity. A captive population can provide stock to assist establishment of new wild populations. It would be expected to grow at 15% per year and have a zero probability of extinction during the next 100 years for adult population sizes of 25-100 or more. The population could be expanded more rapidly with an increase in fertility and recruitment of additional breeders from the captive population.

ACTIONS Recommended for Additional Wild and Captive Populations:

Work is nearing completion on a second aviary at Rio Abajo. Hispaniolan Parrots (12 pairs) will be used as surrogates to test this facility with plans to move Puerto Rican parrots there in the early fall of 1990 if all goes well. It should be possible to take advantage of the 1991 breeding season. This state forest is also the planned site for the second wild population. Development of techniques for reintroduction will be done at Rio Abajo.

A second captive colony should be established on the mainland as soon as possible (preferably in 1989) to protect against possible catastrophic loss from a major hurricane or an epidemic and to study the causes of the low fertility rates and failure of many birds to breed.

It is necessary to do a genetic, demographic, and management analysis of the current captive population and develop a masterplan. This includes a bird by bird analysis with recommendations for individual parrots to move to the other colonies. No currently breeding birds should be removed from Luquillo. The mainland colony should include state of the art expertise in reproductive biology to study the low fertility and reproductive activity in many birds.

PRIORITIES:

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

Field: 1. Continue monitoring of current status of population, supporting individual nest sites as located, and development of lifetime individual identification methods. 2. Continue development of reproductive and survival enhancement methodology. 3. Initiate plans for release studies in Rio Abajo of captive bred and translocated birds. 4. Assess habitat availability including current range, new sites in Luquillo, and sites in Rio Abajo. Need K evaluation, landscape analysis, and effects of human populations and uses.

Reproduction: 1. Characterize the reproductive cycle of the female parrots and males and identify the reasons for low fertility in the captive population. 2. Develop techniques for reproductive enhancement including artificial insemination. 3. Develop techniques for cryopreservation of semen and embryos. 4. Evaluate possible effects of inbreeding on fertility and reproductive performance.

Genetic: 1. Expand the measurement of the heterozygosity of the captive population. 2. Measure the relatedness or kinship within the captive population and the wild population. This information would provide guidance to the intensive breeding program that will be required to expand the captive and wild populations. 3. Establish relationship of Amazona vittata to other Amazona species.

PVA and SSP: 1. Support continued modeling and PVA of population as part of evaluation of responses to management interventions. 2. Establish a combined Recovery and SSP Program and Masterplan. 3. Establish an 'external' advisory group to provide continuing review and recommendations on the programs and research projects.

U. S. Seal R. C. Lacy N. R. Flesness

INTRODUCTION: POPULATION VIABILITY ANALYSIS

An endangered species, such as the Puerto Rican Parrot, is (by definition) at risk of extinction. The dominant objective in the recovery of such a species is to reduce its risk of extinction to some acceptable level - as close as possible to the background, "normal" extinction risk all species face.

The concept of risk is used to define the targets for recovery, and is used to define recovery itself. Risk, not surprisingly, is a central issue in endangered species management. Unfortunately, there's ample reason to suppose that we (as humans) are not "naturally" good at risk assessment. Recovery will be more often successful if we could do this better. There's a strong need for tools that would help managers deal with risk. We need to improve estimation of risk, to better rank order the risk due to different potential management options, to improve objectivity in assessing risk, and add quality control to the process (through internal consistency checks). Among the risks to be evaluated are those of extinction, and loss of genetic diversity.

In the last several years such tools have been developing. The applied science of Conservation Biology has grown into some of the space between Wildlife Management and Population Biology. A set of approaches, loosely known as "Population Viability Analysis" has appeared.

These techniques are already powerful enough to improve recognition of risk, rank relative risks, and evaluate options. They have the further benefit of changing part of the decision making process from unchallengeable internal intuition to explicit (and hence challengeable) quantitative rationales.

In the following sections, Tom Foose, Bob Lacy, and Jon Ballou each describe aspects of Population Viability Analysis (PVA). Each approaches the subject from their own expertise and experience, so the contributions differ somewhat in perspective and content. There is some overlap, which may help the newcomer by occasionally repeating a point in different language. After these general reviews, the genetics of the Puerto Rican Parrot population are discussed beginning on page 32, and the demographics from the point of view of PVA begin with page 47.

Later sections, beginning on page 71, describe recommendations on husbandry, nutrition, veterinary care, and reproductive biology studies. Last are insights and comments submitted by Noel Snyder following his active and very valuable contributions during the meeting itself.

INTERACTIVE MANAGEMENT OF SMALL WILD AND CAPTIVE POPULATIONS
(T. J. Foose)

Introduction

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

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

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

Minimum Viable Populations

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

There is no single magic number that constitutes an MVP for all species, or for any one species all the time. Rather, an MVP depends on both the genetic and demographic objectives for the program and the biological characteristics of the taxon or population of concern. A further complication is that currently genetic and demographic 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 *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 Puerto Rican parrots can be estimated at between 10 and 20, depending on whether every surviving wild caught bird is accepted as the starting point or whether kinships among the parrots 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 applicable results in PVA requires an interactive process between population biologists, managers and researchers. PVA has been applied to about 7 species (Parker and Smith 1989; Seal 1989).

As mentioned earlier, PVA modelling currently must be performed separately with respect to genetic and demographic events. Recent models allow simultaneous consideration of environmental uncertainty and demography. Genetic models indicate it will be necessary to maintain populations of 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 more than 50% of actual populations will become extinct before the calculated mean 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 are being applied to the Puerto Rican parrotse: improvement of nests, provision of alternate nests for pearly-eyed thrashers, removal of birds from the wild for treatment, removal of egss from the wild for hatching and then return for fledging, supplementation with captive produced eggs, predator control, and provision of surrogates to maintain use of nest sites.

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; 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; and 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. Captive colonies and 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.

Figure 4. The use of captive populations as part of a metapopulation to expand and protect the gene pool of a species. 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 (the world umbrella conservation organization) which now recommends that captive propagation be invoked anytime a taxon's wild population declines below 1000 (IUCN 1988).

Species Survival Plans

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

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

Prime examples of such a captive/wild strategy are the red wolf and Puerto Rican crested toad programs. In fact, there is now a combined USFWS Recovery Plan/SSP Masterplan for the red wolf and one is being developed for the toad. 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.

Another eminent example of a conservation and recovery strategy incorporating both captive and wild populations is the black-footed ferret. This 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 as was done with the Puerto Rican parrot and plain pigeon. Consideration of the survivorship pattern, which exhibited high juvenile mortality for ferrets, as it does also for parrots, suggested that young animals destined to die in the wild might be removed with little or no impact on the population. The AAZPA and CBSG/SSC/IUCN are involved in these kinds of strategies and program worldwide.

POPULATION VIABILITY ANALYSIS
(R. C. Lacy)

Many wildlife populations that were once large, continuous, and diverse have been reduced to small, fragmented isolates in remaining natural areas, nature preserves, or even zoos. For example, black rhinos once numbered in the 100s of thousands, occupying much of Africa south of the Sahara; now a few thousand survive in a handful of parks and reserves, each supporting a few to at most a few hundred animals. Similarly, the 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 a 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 (Felis concolor coryi) 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 effects 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 5 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 6, 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 5.

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

Figure 5. 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.

Figure 6. The losses of heterozygosity at a genetic locus in 25 populations of 120 randomly breeding individuals, simulated by computer. Figure from Lacy 1987.

inbreed many other populations have resulted in the extinction of most or all inbred lines (Falconer 1981).

Concern over the loss of genetic adaptability has led to a recommendation that management programs for endangered taxa aim for the retention of at least 90% of the genetic variance present in ancestral populations (Foose, et al. 1986). The adaptive response of a population to selection is proportional to the genetic variance in the traits selected, so the 90% goal would conserve a population capable of adapting at 90% the rate of the ancestral population. Over a 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.

Figure 7. 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.

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.

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 7). 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 8). 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 9). 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.

Genetic Considerations in Puerto Rican Parrot Management

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.)

Figure 8. 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 9. 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.

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.

Genetic Recommendations -- Puerto Rican Parrots

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 egg fertility and hatchability, 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.

DEMOGRAPHIC PROCESSES IN SMALL AND FRAGMENTED POPULATIONS

(J. Ballou)

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.

Goals

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 for 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 10 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 larger 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 10. 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 we are just beginning to appreciate their role as recurrent but difficult to predict environmental pressures exerted on a population. They can be thought of as relatively rare events that can have devastating consequences on the survival of a large proportion of the population. Less devastating diseases and parasites are a natural accompaniment of all species and populations which may act to decrease reproductive rates and increase mortality rates.

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 most of the wild population and all of the 6 ferrets that had been brought into captivity (Thorne and Belitsky, in Seal et al. 1989).

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 free ranging wild species 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 11). Over time the population becomes increasingly smaller and more susceptible to extinction (Gilpin, 1986).

Figure 11. 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 (which bracket estimates for the Puerto Rican parrot population) with low growth potentials (.5% and 2% per year) are shown in Figure 12. These graphs are provided simply to introduce the concept of persistence time models and are not suggested as realistic models of the parrot population. More realistic models, based on life history data collected from the field, are provided below.

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.

Figure 12. 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.

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.

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 13. 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 12, we can estimate the probability of extinction at different time periods (Figure 14). 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.

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 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).

Figure 13. 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).

Figure 14. Extinction times under different levels of uncertainty. See text.

Stochastic simulation of population extinction
(R. C. Lacy)

Life table analyses yield average long-term projections of population growth (or decline), but do not reveal the fluctuations in population size that would result from the variability in demographic processes. To begin an examination of the probabilities of population persistence under various scenarios, we used a modified version of the SPGPC computer model, developed by James Grier of North Dakota State University (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.

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 12 captive hatched birds that have been fostered into wild nests, while 20 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.

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

POPULATION VIABILITY ANALYSIS DATA FORM - BIRDS

Species: Amazona vittata

Species distribution: Luquillo Forest, Puerto Rico.
Formerly over whole island - perhaps numbering a million.

Study taxon (subspecies): No subspecies have been named. It has not been suggested to be a subspecies of any other form.

Study population location: Luquillo Forest and a captive population in an aviary at Luquillo.

Metapopulation - are there other separate populations? Are maps available?:
(Separation by distance, geographic barriers?)
This is the only remaining wild population. Others are planned.

Specialized requirements (Trophic, ecological):
Nesting sites are traditional. Eats fruits and plant parts.

Age of first reproduction for each sex (proportion breeding): 4 years.

a)Earliest: 2 years

b)Mean: 4 years

Clutch size (N, mean, SD, range): Up to 5.

Number fertile: 80% in one study.

Number hatched:

Number fledged: 80% of fertile.

Laying Season: February - May

Laying frequency (interclutch interval): Annual - usually in spring

Are multiple clutches possible? Yes - in wild and captivity.

Duration of incubation: 24-26 days

Hatchling sex ratio: 1:1

Egg weights:

Hatchling weights (male and female):

Age(s) at fledging: 60 days

Adult sex ratio: 1:1

Adult body weight of males and females: About 275 g.

Reproductive life-span (Male & Female, Range):
Perhaps 10-15 years.

Life time reproduction (Mean, Male & Female):
Could be 20 - 50 fledged birds.

Social structure in terms of breeding (random, pair-bonded, polygyny, polyandry, etc; breeding male and female turnover each year?):

Monogamous. Will remate with loss of one of pair.

Proportion of adult males and females breeding each year:
About 50% nest each year.

Dispersal distance (mean, sexes): Could easily be kilometers.

Migrations (months, destinations):
No.

Territoriality (home range, season):
Especially during breeding season. Nest site fidelity.

Age of dispersal:

Maximum longevity: Probably greater than 20 years in captivity.

Population census - most recent. Date of last census. Reliability estimate.: 34 >1 year and 9 fledglings

Projected population (5, 10, 50 years).:
Goal of 2000 in the population.

Past population census (5, 10, 20 years - dates, reliability estimates):
See book by Snyder et al.

Population sex and age structure (young, juvenile, & adults) - time of year.:

3.3	1 year
3.3	2 "
2.2	3 "
10.10	Adults

Fecundity rates (by sex and age class):

Clutch size: 0	69.3%		3	11.4
1	9.1		4	1.1
2	8.0		5	1.1

Mortality rates and distribution (by sex and age) (neonatal, juvenile, adult); 0 - 1 32.5%

1 - 2	15.2
2 - 3	15.2
3 - 4	15.2
Adult	8.7

Population density estimate. Area of population. Attach marked map.:

Forest stated historically able to accomodate 2000 birds.

We have map of forest available.

Sources of mortality-% (natural, poaching, harvest, accidental, seasonal?).:

Unknown for present population. No obvious poaching or harvest. Natural losses observed around breeding season with conflict between nesting pairs and pairs seeking to use the same site. Pearly-eyed predation and perhaps owl and hawk predation.

Habitat capacity estimate (Has capacity changed in past 20, 50 years?).:

This forest was not clear cut - it is last remanant of primitive forest on island which was 99% cut but the early part of the century. However the population declined very steeply in the mid 1960,s and dropped to a low of 16 birds in 1969 - 1972. Recovery has required intensive management of the wild habitat, predators, nest sites, and birds.

Present habitat protection status.:

National Forest. Fully protected by state and federal law.

Projected habitat protection status (5, 10, 50 years).:

Will remain protected. Puerto Rico has requested return of forest to commonwealth if their is a change in status.

Environmental variance affecting reproduction and mortality (rainfall, prey, predators, disease, snow cover ?).:

Disease a major uncertainty. Major hurricanes about 3 times per century with perhaps 50% mortality and complete loss of reproduction for one year. Lesser hurricanes about once per 10 years.

Is pedigree information available?:

Birds are now being banded in wild. No certain historical data.

Attach Life Table if available.

Date form completed:

Correspondent/Investigator:

Name: U. S. Seal

Address:

Telephone:

Fax:

References:

Snyder, Wiley, & Kepler.

Comments:

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) contrast with the fewer strict precautions in the Puerto Rican parrot breeding facility. Similar precautions were exercised in the Arabian oryx, golden lion tamarin, and California programs. 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 (Wunderlie at workshop) 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 effected 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 ******************************						
100	1	.03/0/.5	1.020	12.8	.65	48
250					.67	89
500					.68	144
**						
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

~~Demographic Recommendations -- Puerto Rican Parrot~~

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 past 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 until the net annual production is greater than 6 birds. 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.

Puerto Rican Parrot HUSBANDRY and MANAGEMENT: (Don Bruning)

Housing

Larger cages should be used to allow more flexible management and to give the birds more security and seclusion. Cages should be no smaller than 4x4x8 feet but larger and more varied would be preferred.

Aviculturists should have more flexibility in sizes and shapes of caging. There should be introduction cages where groups of birds can be placed for mate selection. There should also be a series of adjacent cages that could be used for the same purpose, especially with aggressive individuals.

Shift cages should be available for separating birds or removing birds from one cage. This should include portable shifts for moving birds with minimal handling if necessary. These shifts would be used at the aviculturists discretion to minimize disturbance to other birds.

Cages should be able to provide a variety of perching and space as needed by individual pairs to stimulate reproduction.

Nesting

All pairs should be provided with at least two nest sites. Pairs that have not produced eggs or not produced fertile eggs should first be sexed by an independent method and then, if they are indeed pairs, should have access to several nest boxes including different sizes and designs to stimulate reproduction. In this way pairs can have a choice of nest sites and have the stimulation of investigating nest sites.

Special nest boxes should be used for aggressive or nervous birds to allow checking for eggs with minimal nest disturbance. This could be done with a viewing hole, one way glass, mirrors or other techniques. Ideally all nest boxes should be able to be monitored without disturbing them. Minimal disturbance to nest boxes will reduce disturbance of breeding birds and thereby should increase production. If nest boxes can be checked without disturbance then they can be monitored daily or at suitable intervals to be able to determine exact laying time for eggs.

Removal of eggs from the nest should be done as soon as possible or after completion of the clutch to increase production and to minimize the number of eggs moved and handled during the fragile first few days of incubation. Ideally eggs should be handled with surgical gloves, however, carefully scrubbed hands can be used if handling is minimized.

Eggs should be weighed before being placed in incubators and again before or at pipping. Weight loss during incubation is one of the best monitors of incubation conditions. Incubators should be disinfected regularly after each batch of eggs and should be serviced and inspected on a weekly basis during the breeding season.

Additional incubators and hatchers are needed so that there are always at least two incubators and hatchers in operation at all times. This is urgent so that eggs from the wild and from captivity can be kept separate to avoid any cross contamination. One hatcher should always be available for emergency needs. To allow for disinfection time a minimum of 3 or 4 incubators and 3 hatchers are needed. Incubators should be attached to an alarm system to alert aviculturists to any power failure or incubator malfunction. The alarm should be attached to a temperature probe so that any change in temperature will set off the alarm. It is suggested that the alarm should be set for a 1 degree rise or 5 degree (Fahrenheit) fall in temperature.

Bird Identification

Individual birds and eggs must be identifiable at all times. The current captive banding system should be reviewed and consideration given to differentially banding males and females. All birds must be sexed by karyotyping or laparoscopy. If a pair fail to produce fertile eggs for 2 years then the birds should be sexed again. Currently all young birds are close ring banded and therefore should always be individually identifiable; however, a review and improvement of the system for identifying chicks from egg hatching to fledging should be developed to prevent mixup of chicks or eggs in the process. Males and females should be visually distinguishable in each pair or group cage. Chicks should be sexed and individually identified as early as possible.

Remote video cameras should be installed so that problem pairs, aggressive birds, non productive pairs, and newly introduced birds can be remotely monitored. It would be useful to monitor behavior of breeding pairs and compare with non breeders. Video cameras with time lapse capability are extremely useful to monitor nest inspection behavior, nest construction, and during incubation. A one hour tape can be used to monitor a pair or nest for 24 to 48 hours, thereby establishing time on nest, copulation time, copulation frequency and intensity, and frequency of other behaviors.

Nutritional Care (See nutrition section also)

The diet should be analyzed carefully and a balanced diet maintained. A balanced pellet is preferred as a base for the diet unless cost or environmental conditions are prohibitive. However, all dietary items must be balanced to prevent individual selection of some dietary items and development of a nutritional deficiency. It is easiest to induce birds to eat the basic diet in the morning.

Record System

While complete and extremely valuable records are and have been maintained, there is a need to unify, organize, and computerize the records. Application should be made for official studbook status and the ARKS and SPARKS system should be used for the computer records. Fireproof files are needed for copies of all records and a complete set of hard copy and computer records should be kept off site for security. Computerization will greatly improve the usefulness of the records and help organize the collection of all data.

It was suggested that a permanent ID number (studbook number) be assigned to each egg. This would allow complete tracking of all eggs, chicks, and adults with one number.

Records of chick weight gains and a growth chart would be extremely helpful for monitoring health of chicks and discovering problems at an early stage. Deviations from the normal growth curve can be an early indicator of problems.

Veterinary Care (See section on veterinary program)

A regular protocol for veterinary care and routine parasite checks should be initiated to go with the clinical care provided. Necropsies must be done on all deaths and results reported quickly enough to be useful.

A more detailed analysis of management practices would only be possible by spending more time to inspect and discuss the details of the facility and procedures. In summary the avicultural team is doing a good job, but there are ways it can be improved. An essential element is to provide more flexibility to the aviculturists to allow them to do their jobs of maximizing captive production.

Puerto Rican Parrot **DIET REVIEW** (Ellen Dierenfeld):

Although nutrient requirements have not been specifically established for the parrot, estimates of dietary needs can be extrapolated from detailed studies on domestic poultry (National Research Council), cockatiels (Grau and Roudybush), and limited composition data of wild diets (Snyder et al.). Information from these primary sources was used in evaluating diets fed at the Loquillo aviary.

Maintenance Diet

The current diet fed consists of 3 primary portions: a rice/beans/corn mixture fortified with dicalcium phosphate and multivitamins (3 X per week), fruit (both seasonally available wild as well as domestic) and carrots, and a pelleted product produced by Avi-Sci, Inc. Two shelled peanuts are provided per pair as a treat item. All grain and produce items are consumed in total, and an estimated one-half to two-thirds of pellets are eaten daily (Sorenson, pers. comm.). Detailed information on complete feed intake, minerals and amino acids contained within the vitamin supplement, and the vitamin/mineral content of the pellets or wild fruits were unavailable for use in this analysis. Given these limitations, it must be recognized that the diet review is cursory; nonetheless, some evaluation is possible.

Using average adult body weights of 250 to 300 g for the Puerto Rican parrot, estimates of minimum daily metabolizable energy (ME) needs at 30 C range from approximately 35 to 40 Kcal [Kcal = (99.14)(body mass in $kg^{0.75}$].

Studies conducted on the Puerto Rican parrot captive colony (Avi-Sci, Inc.) reported intake amounts between 20 and 27 g dry matter per bird per day, with 33 to 95 Kcal ingested, depending upon the diet fed. Average caloric needs of an adult, non-reproducing healthy bird eating a balanced diet probably range between about 35 and 70 Kcal. Captive energy requirements are often higher than those estimated from standard body mass equations due to unknown (or unmeasurable) stress factors, including dietary imbalances of other nutrients.

Intake per pair of birds fed the current diet was recorded for all ingredients except pellets over a one-week period in late January, 1989; amounts are found in Table 1, with dry matter percentages and calorie concentrations based on literature values. Using data from the previous intake trials and estimates of calorie needs, it appears likely that pellet intake may have been overestimated in the current assessment.

Table 1. Average daily intake per pair of Puerto Rican parrots fed a mixed diet 22-28 January 1989.

Diet Ingredient	Feed Intake (g)		Calorie Intake
	As-Fed	Dry Matter[1]	(Kcal ME)
Corn/Rice/Beans Mix	78.9	23.7	67.8
Domestic Fruit	14.4	2.2	7.2
Native Fruit	10.0	0.3	1.1
Carrots	8.8	1.3	4.7
Pellets (intake estimated)	35.0	31.5	108.4
Total	147.1	58.6	189.2

[1]Moisture contents used to calculate dry matter intake: 70% beans mixture, 85% domestic fruit, 70% native fruit, 85% carrots, 10% pellets.

Energy estimates of 95 Kcal/bird/day were calculated from the data in Table 1, which are higher than those found through energetics equations. However, it must be recognized that energy intakes may vary seasonally (in this case, in preparation for the breeding season). Furthermore, calorie values were calculated, not measured directly and may differ substantially from what was actually being consumed. Finally, the pellet intake values were totally estimated, rather than measured. Even with all these manipulations, it is apparent that dietary energy needs are likely being met (or even over-compensated) on the current diet. More importantly, it may be possible that birds can meet their energy needs on the produce and grain portions of the diet without consumption of any pellets. This fact can have serious consequences upon overall nutrition of the parrot.

The macronutrient composition of various diet ingredients, as can best be approximated at this time, are found in Table 2. Although the total diet composition does not appear excessively imbalanced, mixed diets from which animals can self-select preferred food items must be considered separately.

Grain Mixture: The current staple diet consists of approximately 1 part (by weight) mixed beans, 1.5 parts field corn, 1.5 parts wheat or oats, and 2 parts brown rice, all cooked and mixed together with dicalcium phosphate (1.8 - 2.0% of mixture) and Nekton-S multivitamin supplement (about 0.3% of mixture). This mixture has a low energy and protein content; the energy concentration could easily be increased by adding vegetable oil to the mixture. A more striking feature, however, is the low calcium content, as well as imbalanced Ca:P ratio in the grain mix.

All grains and seeds contain considerably more phosphorus than calcium; grain-based diets must, therefore, be supplemented with this calcium. Recommended Ca levels for maintenance and growth in poultry species are approximately 1% of dry matter for maintenance and growth, with an increase up to a maximum of 2.5% (dry matter basis) for females during egg production. Additionally, Ca:P ratios should be a minimum of 1 - 1.5:1. Due to the high phosphorus content of grains, a concentrated form of calcium (such as $CaCO_3$, sans added phosphorus) should be used as a supplement. Ground limestone could be added to this grain mixture -- 2 g per 300 g cooked grains -- to bring the Ca level to about 1% of dry matter.

There is no way to accurately evaluate total minerals in the grain mixture at this time (including Ca), as information concerning the mineral concentrations in the Nekton-S is not provided in manufacturer's literature.

Vitamin concentrations in the commercial supplement were available; fat-soluble vitamins are found in Table 2. According to this analysis, vitamin A may be somewhat in excess (better levels 10-15 IU/g), while D_3 and E may be low (suggested levels 1.5 IU/g and [at least] 100 IU/kg for these nutrients, respectively). Vitamin D is integrally involved in Ca metabolism and may exacerbate any problems already inherent from the mineral imbalance previously described, whereas vitamin E is a biological antioxidant associated with most metabolic systems. Diets high in polyunsaturated fats, as are found in many grains, increase the need for vitamin E. Excess vitamin A can decrease absorption of the other two fat-soluble vitamins discussed.

Accurate quantification and balancing of supplements used in feeding programs is essential to overall understanding and diet evaluation. If the current multivitamin supplement is to be continued, it should be administered as recommended by the manufacturer -- 1 g per 454 g drinking water.

Table 2. Calculated nutrient composition of diets fed to Puerto Rican parrots at Loquillo aviary, January 1989.

Diet Ingredient	Water %	Energy (Kcal/g)	Crude Protein %	Fat %	Ash %
	<------- Dry Matter Basis ------->				
Corn/Rice/Beans Mix	70	2.86	13.1	3.0	6.1
Domestic Fruit	85	3.27	3.7	2.2	1.6
Native Fruit	70	3.69(calc)	10.0	15.0	5.0
Carrots	85	3.58	10.0	1.7	8.3
Pellets	10	3.44	17.0	NA	NA
Total Diet	38.5	3.21	14.8	>2.5	>5.0

Table 2. (Continued)

Diet Ingredient	Ca %	P %	Vit A IU/g	Vit D_3 IU/g	Vit E IU/kg
	<---------- Dry Matter Basis ----------->				
Corn/Rice/Beans Mix	0.31	1.20	23.9	0.5	24.5
Domestic Fruit	0.12	0.04	5.6	NA	50.0
Native Fruit	0.65	NA	NA	NA	NA
Carrots	0.42	0.33	>600.0	NA	58.3
Pellets	1.00	0.50	NA	NA	NA
Total Diet	0.62	0.54	NA	NA	NA

NA = Not available due to lack of specific information.

It is suggested that a properly Ca-supplemented grain mixture comprise no more than 40% (as-fed weight) of the diet, providing about 30% of total calories. For zoo feeding programs, a commercial pelleted ration should completely replace this more variable grain mixture; due to location and program goals, however, it may be appropriate for Loquillo at this time.

Produce: Both fruits and vegetables used in the current diet have low protein and calcium concentrations (Table 2). As such, they are probably more valuable behaviorally (as feeding stimulants) than nutritionally in a captive feeding situation. Provision of a variety of fruits (both native and domestic), vegetables, and greens in different sizes, shapes, and colors may be necessary in proper training for ultimate release programs. Frozen native fruit should not be stored for more than 1 to 2 months unless freezer temperatures are < -20 C.

In order to provide a more balanced captive diet, a minced mixture of **dark** leafy greens, fruit, and yellow/orange vegetables is suggested in the following rough proportions: 2 parts greens, 1 part fruit, 1 part vegetables by weight (50:25:25% of total mixed salad weight on an as-fed basis) The greens contain calcium and protein to balance the remaining ingredients, as well as good sources of vitamins A and E.

Total fruit and vegetable salad should comprise no more than 40% of the daily diet (as-fed weight), providing about 20% of calories.

Pellets: A commercially formulated, nutritionally complete pelleted ration should be considered the basis of the diet, rather than a supplement, for the Puerto Rican parrot. Although pellets should be available to birds ad libitum (as they currently are), a minimum of 50% of caloric needs should be met through pellet intake (20% of diet as-fed weight), which may require limit-feeding of other diet portions. Thus it is essential that current pellet intake be quantified.

Complete nutrient concentration information should be obtained from the manufacturer in order to properly evaluate the current diet, including mineral and vitamin levels. Energy, crude protein, Ca, P, and Se levels are currently available. From this limited information, Se, at 0.1 mg/kg, may be low, particularly if pellets are the only dietary source of this nutrient. Protein concentration in pellets may also need to be increased to provide a **minimum** dietary crude protein level of 15% (dry matter basis).

Breeding Diet

The current breeding diet includes an increase in native fruit (2 tablespoons sierra palm per day per pair) and, once chicks are born, a switch to Avi-Sci Starter/Grower pellets and added papaya. Although no data are available on pellet concentration, it is apparent from Table 2 that addition of fruit to diets may not add specific nutrients necessary during breeding -- particularly increased Ca (for egg shells), protein, and energy.

The maintenance diet should be modified over a 2-3 week period immediately prior to the breeding season by increasing overall nutrient concentration. This can be accomplished by switching to a more concentrated breeding pellet, coating the fruit/vegetable salad with crushed pellets, and doubling the Ca supplement in the grain mixture. Calcium supplementation should return to maintenance levels when parents are feeding chicks.
As currently practiced, maintain the provision of fresh browse to parents during breeding season.

General Recommendations

1. Supply diet containing approximately 150% of estimated calorie needs or about 100 Kcal ME per day per bird (during breeding, perhaps 60 Kcal during non-breeding season). A maximum of 30% of Kcal should be provided by the current (modified) grain mixture, 20% Kcal from a mixed salad portion, with the remainder (50%) supplied by nutritionally complete, commercial pellets.

2. Supplement grain portion of diet with $CaCO_3$ to provide 1% Ca (dry matter basis) for maintenance and chick-rearing periods; 2-2.5% of diet dry matter during egg production.

3. Add dark green leafy vegetables to the fruit/vegetable portion of the diet. Coat with crushed pellets during breeding season.

4. Obtain complete nutritional information on pellet composition from manufacturer; switch to a breeder pellet containing higher nutrient composition during breeding season, and eliminate starter/grower pellet. Consider economics of locating a local commercial supplier.

5. If the current multivitamin supplement is to be retained, administer in drinking water at concentration recommended by manufacturer.

6. A representative sample of adult birds should be weighed periodically (minimum of once per month), particularly following any diet change to quantify diet adequacy. Diet suitability should be assessed through weight and feed intake monitoring, as well as examination of overall health, and reproductive parameters.

Hand-Rearing Diet

The diet currently in use (dry ingredients: a mixture of 63% ground monkey biscuit, 29% Roudybush hand-rearing diet, 8% baby oatmeal cereal) is mixed with water and jarred baby foods (fruits/vegetables) to about 20% solids for chicks < 3 days of age, and about 25% solids for chicks > 3 days of age. These diets have been scientifically formulated and tested on numerous psittacine species, and appear adequate for the Puerto Rican parrot captive breeding program. A detailed nutrient composition of the hand-rearing diet used at Loquillo will be supplied for inclusion in permanent records.

In addition to an accurate record of the diet used, feeding protocols for hand-rearing chicks including schedule and amounts per meal should be documented. Environmental conditions such as incubator temperature, humidity, and light regimes should be recorded, along with any changes over time.

Chicks should be weighed daily at the same time, and growth curves plotted for each individual. These weigh curves are an excellent indicator of diet utilization and/or animal health. If possible, growth curves of parent-reared (or foster parent - reared) chicks should be used as a comparative indicator.

Puerto Rican Parrot **VETERINARY CARE PROGRAM**:(G.V. Kollias DVM, PhD)

I. Free-ranging parrot population

a. Protocol for intervention for birds exhibiting problems

1. Should include quarantine and treatment area for birds brought into aviary area (adults and chicks)

2. Birds dying or found moribund in field
   a. Necropsy, when practical, of all birds 1) Literature search and review of all published information on diseases of free-ranging birds, reptiles, and mammals in Puerto Rico.

3. Surveillance of sympatric species for infectious diseases.

II. Captive Propagation Program (Puerto Rican & Hispaniolan Parrots)

1. Veterinary supervisor: oversee and ensure that the objectives of the veterinary program are implemented.

2. Emergency care

   a. Primary care veterinarian on call (contract)
      1) This is important for consistency and for the long term goals of the project.

   b. Secondary veterinarians with particular areas of expertise for consultation (follow-up with primary care veterinarian is critical for continuity and optimal case management).

   c. Emergency first aid by aviary personnel (protocol to be developed)

3. Routine veterinary care/colony disease surveillance
   a. Some responsibilities can be delegated to aviary personnel (implementation and follow-up critical)
   b. Visit aviary weekly or biweekly; telephone communications as needed.

   c. Physical examinations every 12 months (every 6 months would be optimal);include weights
      1) Blood drawn for complete blood counts and biochemical profiling.
      2) Blood drawn for serum banking
      3) Other samples collected for research projects or other studies.
      4) Disease surveillance
         a)First determine what has been done,tabulate available data and set up record systems.
         b)Considerations: fecal examinations for protozoa and nematode ova, serology for antibody titers to viral diseases, fecal bacterial cultures for potential pathogens.
            I. Selection of specialized laboratories sample submission.
         c)Evaluation of feeds and feed storage practices.

d)Review protocols for disinfection of aviaries,substrate, nest boxes

5) Establishment of an on site pharmacy and medical supplies stores.

6) Develop protocol for transport of seriously ill birds for further treatment and diagnostic work.

7) Protocol for night care/weekend-holiday care of ill birds.

4. Records Systems (ideally computerized)

a. Medical records

1) Compile and collate available medical records

2) Medical records need to be expanded (e.g. standard forms,observation sheets should be separate from medical entries, kept chrono-logical,written in black ink,etc.)

a. History summary should be a beginning of the record.

3) There should be copies of all records.

4) A dead animal record file should be kept.

b. Necropsy

l) Protocol for submission of all dead birds for necropsy (personnel and laboratories involved);include immediate sample collection by technicians,transport of samples,etc.

2) All past necropsy data and reports need to be centralized on site

3) Evaluation of mortality factors:

a) All necropsy data needs to be tabulated, collated,and assessed,identifying trends etc.

c. An annual report summarizing medical and necropsy data should be written and reviewed.

d. Copies of all records should be made.

5. Basic Components of the Preventive Health Program

a. Positive sex determination of all birds (tattoo, leg bands,and or other methods)

b. Disease surveillance of current colony (screening for infectious diseases e.g.papovavirus,reovirus, chlamydia,etc.); collate currently available material.

c. Routine cultures,fecal examinations,serum banking

d. Protocol development for quarantine of newly acquired and ill birds

l) As part of quarantine procedures include limit to contact with outside individuals,particularly if they have had contact with other birds within 48 hours of entering the aviary.

e. Evaluation of diets and nutritional requirements.

f. Remove chicken flock adjacent to aviary.

6. Nursery and Incubator Rooms-Protocols to Develop

a. Recognition of problems in chicks, handling, sample collection.

b. Disinfection before entering nursery/incubator room (include limited access,time of day,etc.)

c. Immigration and emigration of eggs and chicks from the nursery and incubator.

d. Feeding procedures,disinfection of feeding utensils, etc.; food storage procedures

e. Incubated eggs (e.g.quality control for humidity, temperature,mechanics of incubator)

l) Protocol for disinfecting incubator (e.g.timing,water holding reservoirs,substrate materials)

2)Protocol for insuring separation of eggs brought into the incubator room.

3)Protocol for exam of "dead in the egg" chicks

f. Incubator reared chicks-Protocols to develop:

l) Basic hygiene for nursing personnel

2) Development of critical care records

3) Routine data base collection (e.g.weights,dates of feather growth,photos at various ages)

4) Identification of hand-reared chicks

5) Routine health surveillance of incubator and substrate

6) Night/weekend/holiday care of chicks

7. Other considerations:

a. Vermin control in aviary and nursery/incubator room

1) Identify problems and pests

b. Toxicology studies

1) Water and watering systems in aviary and associated areas for lead, pesticide residues

2) Paint in aviary and associated areas (e.g.lead,cadmium,zinc,etc.

3) Evaluate disinfectants used in aviary and nursery.

4) Evaluation of new wire used in aviaries for zinc residue.

Puerto Rican Parrot **REPRODUCTIVE BIOLOGY** (David Wildt):

Reproduction

There is little doubt that the recovery program for the Puerto Rican parrot is severely compromised by a poor fertility rate. For example, 2 of 8, 5 of 7, 4 of 8, 6 of 11 and 5 of 8 pairs of adult birds during the years 1985 through 1989, respectively, were infertile (defined simply by the production of nonembryonic eggs). Overall, more than half of all sexually mature females chronically maintained with a conspecific male have never produced a fertile egg. This contrasts to the limited data available on wild Puerto Rican parrots; of 7 nests examined, all contained fertile eggs and only 1 of 22 eggs was infertile.

The lack of reproductive success in the captive Puerto Rican parrot may have a behavioral, dietary, physiological or other etiology. None of these causes can be unequivocally associated with the poor reproductive performance primarily because: 1) the population to-date has been small; and 2) breeding efforts have focused more on the random alteration of management factors rather than relying on an organized, scientific approach.

The primary recommendation is that a formal research plan be developed to determine the cause of poor reproductive performance of the Puerto Rican parrot. The current staff is doing an admirable job of assessing many management and behavioral problems, but the overall approach is neither organized nor formally prioritized. Most emphasis is oriented toward sexual compatibility and the identification of birds which appear nonaggressive toward each other. Behavioral incompatibility may or may not be a major cause of infertility in this specific population. Nonetheless, the examination of individual records and discussions with staff indicated that there were birds (specifically male 083 and female 032; male 111 and female 112) that demonstrate intra-pair aggression (or otherwise "abnormal behaviors") and also produce fertile eggs. Therefore, a detailed examination of other factors is warranted.

Overall, efforts should be directed at organizing research protocols designed to: 1) describe and characterize the fundamental biology of the species; and 2) explore approaches for enhancing reproduction by natural and artificial means. It should be emphasized that artificial breeding techniques are not considered as an immediate panacea to the current reproductive crisis. For example, artificial insemination (AI) will be useful only if preemptive data are available on the influence of other reproductive factors (i.e. the relative impact of season, sperm viability, number of sperm required for fertilization and time of inseminations). The practical benefits of AI only will become apparent if a better understanding of the basic reproductive biology of the Puerto Rican Parrot can be achieved first.

A logical approach is to extend, expand and exploit the existing resource of Hispaniolan parrots as a model species for the Puerto Rican parrot. Studies should be designed to study the reproductive behavior and physiology of the Hispaniolan parrot while simultaneously developing protocols and testing the potential of artificial breeding in this surrogate species. The Puerto Rican and Hispaniolan parrots are related taxonomically and appear to have a number of biological characteristics in common (similar seasonality trends, levels of intra-pair aggression, clutch size). The Hispaniolan parrot also is a valuable model because many birds already are on-site and available to the existing staff or potential scientific collaborators. Perhaps most importantly, some valuable research already has been conducted by K. Brock using the Hispaniolan parrot. These studies have demonstrated the effectiveness of semen collection and, to a much lessor extent, the possibility of successful AI. A recently prepared manuscript by Brock on this subject provides some exciting encouragement on the potential of enhancing psittacine reproduction via artificial breeding.

Specific recommendations:

1. Direct observations of gonadal sex should be made for all adult birds with a history of infertility (i.e. all birds maintained in pairs which never have produced a fertile egg). Past cytogenetic analyses should not be used as conclusive evidence that all infertile pairs are sexed correctly. Records indicate that some birds have been paired for extraordinarily long periods of time (years) without ever producing a single, fertile egg. Two actions are recommended:

a. the data and chromosomal photographs from the commercial sexing laboratory be obtained and examined by an independent cytogeneticist;

b. an expert immediately be contracted to laparoscopically examine all adult birds with unproven fertility for an unequivocal diagnosis of sex. Birds known to have participated in the production of at least 1 fertile egg should be excluded from this examination.

2. An organized research plan should be developed for the existing populations of Hispaniolan and Puerto Rican parrots. The ultimate research goals within each species should be complimentary and directed at rapidly expanding the Puerto Rican parrot population while capturing the genes of all wild-caught founders. Detailed protocol development is beyond the present mandate of the CBSG, but general guidelines are outlined below. There is a need to emphasize the importance of data integration. Behavioral and physiological data should be collected and examined simultaneously. Likewise, it is important to realize that the benefits of certain manipulatory procedures go beyond immediate practical benefit. For example, semen collections over time provide information on fertility potential, seasonality, physiological synchrony with the female and even can serve as an indirect index of the level of inbreeding (i.e. loss of genetic diversity results in an increased incidence of structurally abnormal sperm). Such data eventually are useful in developing and applying artificial breeding techniques.

Hispaniolan parrots. This model species should be used initially to: 1) assess the impact of management and environmental factors on reproductive success; and 2) explore the potential of reproductive biotechnology (semen collection, analysis and artificial breeding). High priority should be given to research projects focusing on the influence of season, light, temperature, humidity, diet and various management factors (i.e. sight and vocal barriers, cage space, nesting box configuration) on reproductive success. Because there is evidence that semen can be collected routinely from this species, specific projects should be developed to assess the impact of semen collection frequency on bird behavior, semen characteristics and subsequent ability to naturally reproduce. Considerable emphasis should be placed on establishing semen characteristics from proven fertile as well as infertile males. Factors to evaluate include semen volume and sperm concentration, motility ratings and morphological integrity as well as seminal pH. A major factor dictating the utility of semen for AI will be the ability to support sperm viability in vitro. Therefore, semen samples collected from individual birds should be studied by comparatively testing the effectiveness of various seminal diluents. This basic information then should be applied to actual AI attempts. A number of factors will dictate the success of AI but studies should be designed to allow evaluating the impact of the number and timing of AIs needed and the sperm dosage and semen quality required to consistently produce fertile eggs.

A major strategy for sustaining genetic diversity over time would be the development of frozen semen technology. Germ plasm from existing founders could be stored indefinitely and re-infused into later generations. The ability to store frozen semen also would serve to protect the gene pool in the event of a natural catastrophe or alternatively could be used to transport genetic material between geographic locations in lieu of risking transport of live birds. Although not fully developed in domestic poultry species, rapid advances in cryobiology and the use of frozen fowl semen suggest that pilot studies should begin immediately in the surrogate Hispaniolan parrot. Areas of research effort should focus on developing semen cooling/freezing techniques and analyzing the effectiveness of various cryoprotectants, semen containers and thaw procedures. Particularly important will be the development of post-thaw viability assays and the timing protocols for AI.

Puerto Rican parrots. CBSG recommendations on management changes may improve fertility of the captive Puerto Rican parrot flock. Likewise, staff plans for creative aviculture may enhance reproduction performance. Nonetheless, more manipulative type approaches (including AI) will provide back-up technology to ensure that: 1) Puerto Rican parrots will continue to reproduce in captivity; and 2) all founder birds eventually can be represented in future generations.

The CBSG offers 2 recommendations. First, there are several adult, unpaired (excess) males which currently are not contributing to any aspect of the captive propagation program. These males should be considered as potential "research animals" and especially could be valuable for determining the effectiveness of semen collection in this species. These pilot efforts could be done concurrently with the Hispaniolan parrot semen studies described above. Optimal semen collection and processing procedures developed for the latter species could then be applied to Puerto Rican parrot ejaculates. Second, improvements of reproduction rate in the forthcoming (1990) Puerto Rican parrot breeding season should rely primarily on close adherence to the various CBSG management recommendations and not focus on extensive and random manipulations of other factors or artificial breeding. This strategy will permit developing a data base on the manipulative factors affecting reproductive efficiency and the efficacy of artificial breeding of the Hispaniolan parrot. Concepts and optimal techniques developed for the latter species then can be applied to the Puerto Rican parrot in subsequent years. If major species differences are apparent, it may be necessary to designate some of the Puerto Rican captive flock (including successfully breeding pairs) as "research stock" to more effectively identify those factors dictating captive breeding success.

3. Expert scientific advice and support in research planning and performance needs to be provided to the captive breeding program. Although the current staff appears talented in aviculture, none of the existing personnel are trained in the scientific method. Additionally, facilities and equipment are inadequate to conduct most of the scientific studies needed. Resources are mandatory either on-site or at a second institution to conduct the controlled studies necessary to determine those biological factors which: 1) impact most on natural breeding; and 2) would permit the use of artificial breeding and frozen semen technology, thereby allowing rapid population expansion and providing methods for sustaining genetic diversity. Serious consideration should be made to making Hispaniolan (and perhaps Puerto Rican) parrots readily available to institutions with existing experts, resources and documented evidence of research productivity.

Puerto Rican Parrot **CONSERVATION COMMENTS**: (N. Snyder)

The present wild population of PRP, standing at about 43 individuals post-fledging, is considerably larger that the wild population of 1972 (about 16 individuals post-fledging), a result that can be attributed primarily to enhanced productivity produced by (1) nest site provision and maintenance, (2) reduction of the impact of nest predators and parasites by various intensive procedures, and (3) bolstering of wild production by releases of captive progeny to the wild, primarily through fostering. At least under intensive management, the wild population appears to have had considerable intrinsic viability, and has been increasing at an average annual rate close to 5%.

The major resistance factor to a greater rate of population growth increase during the 1970's and 1980's has been a relatively low rate of formation of breeding pairs. On the order of half the territorial pairs observed during this period have not been egg-laying pairs. Causes of non-breeding have not been determined convincingly, but may include a relatively large number of young birds in the population, a reluctance of naive birds to assume the risks of breeding under conditions of low population density, a reluctance of birds to breed with close kin, compatibility problems and dearth of potential mates to choose from, a skewed sex ratio, and other factors. Regardless of cause, the low percentage of breeding pairs appears to be an abnormal situation, judging from comparisons with wild populations of other Caribbean Amazona (Hispaniolan and Bahamas Parrots), and there are grounds for hoping it may be a temporary situation that may recede in importance as the wild populations gains in size. In fact the several new breeding pairs documented in the past three years may be an indication that this resistance factor may finally be beginning to crumble at the present time.

Modelling of demographic factors during the CBSG conference indicated that in the absence of releases of captives into the wild population, the annual rate of increase would have been about 3.5%. Although this is still a positive rate of increase, it carries enhanced risks relative to a 5% rate, especially in the slower rate of achievement of a population size that might allow adequate security from disasters such as severe hurricanes. No severe hurricanes have hit Luquillo Forest in the past 50 years, although such storms can perhaps be expected to occur about 3 times per century. The present wild population is still quite vulnerable to such catastrophes, so the merits of bolstering the wild population to a level where it could be expected to survive catastrophes are considerable. Projections suggest that bolstering the wild population with captive releases at a level practiced in the past might reduce risk of extinction from hurricanes by a factor of almost 50% when compared with a non-bolstering situation. Even greater reductions would presumably result from greater levels of bolstering.

The existing wild population represents an extremely valuable resource, as it is made up of individuals with considerable sophistication with respect to survival in the wild. If this population is lost, replacing it from captivity may be quite difficult. Knowledge of locations of nesting areas, feeding areas, and relatively predation-free flight lines are aspects of this sophistication that presumably would have to be learned by a naive introduced population, and it is possible that such a process might be very slow and inefficient. The Luquillo Mountains represent by far the largest and best-protected block of native habitat in Puerto Rico and probably could support a larger population of parrots than any other region on the island. Loss of the parrots in this region would be a major setback in efforts to conserve the species. In terms of the ultimate goal of self-sustaining wild populations, the present wild individuals should be considered to have extraordinary value even if their survival rates may be lower than those of captive birds.

The existing wild population also may prove to be especially valuable as a source of birds for establishment of other wild populations by translocation. Results of our Thick-billed Parrot introduction program in Arizona suggest that wild-caught birds are way ahead with respect to their potentials for survival in unfamiliar terrain and that such birds may be by far the best birds to use in such programs. This is not to suggest that one cannot establish viable wild populations from captive sources alone, only that this appears to be a generally more difficult process.

Balanced against the values of bolstering the existing wild population are the values of establishing a larger captive population (in however many locations) and the values of establishing other wild populations. Risks of total loss of the species will presumably be minimized by creation of a number of populations that are relatively independent of one another in their susceptibility to factors such as disease and hurricanes. Presumably captive populations can be made more resistant to destruction by hurricanes than can wild populations, although they remain vulnerable, perhaps significantly more vulnerable than wild populations, to such threats as virulent diseases. Thus it is difficult to compare the intrinsic "safety" of wild versus captive populations, and the best approach is probably to attempt to achieve several of both sorts of populations. The splitting of the existing captive flock into a flock at the Luquillo aviary and a flock at some other existing institution probably in the states) with an established track record of success in breeding and maintaining psittacines seems a clear near-term priority, though I would argue for not moving the captive pairs that are presently breeding, and for high priority given to maintaining a Luquillo captive population that is large enough that it can serve to bolster the Luquillo wild population significantly in the near term. Since there are presently 52 birds in captivity, with more on the way this breeding season, meeting both these conditions while simultaneously establishing an off-island captive population would not seem to present insurmountable problems.

Efforts to establish a captive population and a release effort in Rio Abajo also seem well advised. Though I would rank them as somewhat lower in priority than the above goals, they are nevertheless very important, and can probably be done simultaneously with the above processes. My principal concerns about proceeding quickly with the Rio Abajo efforts are that we are moving into an unknown security situation with respect to disease and vandalism, and as yet there has been no groundwork laid in educating local communities to the values of the effort and enlisting their support. The need for local support is not an optional or trivial matter. It needs to be met squarely and effectively, utilizing personnel skilled in such matters. Such personnel are not all that common, and the process could well fail in their absence. Here I am thinking of people like Paul Butler, but n to Paul himself, as it would be essential that the effort be made by native Puerto Ricans in the way that local communities really feel they are part of the program, and that it is not a program imposed by foreigners. ne cannot overemphasize the importance of this effort, and it is not clear how much time it will take and how effective it may be. It would be best to proceed with some caution in the process, and not by a rigid predetermined schedule. Rio Abajo is a very different situation from Luquillo with respect to a number of human social conditions and is a much more vulnerable region with respect to a number of potentially detrimental human impacts on the birds. While I am overall very positive about the Rio Abajo effort, especially since it can be combined with future efforts to reintroduce Plain Pigeons, White-necked Crows, and Limpkins, I see no reason for proceeding any faster here than can be sustained by actual development of physical and human resources. This effort will have to be monitored very closely. Failure here would be a very tragic development.

I am very concerned by the fact that understand there have been disagreements, as yet unresolved, about such things as various details as to how actual aviary construction should proceed in Rio Abajo--placement of quarantine facilities, cement vs dirt floors to cages, etc. The design of the Rio Abajo facility should undergo detailed review by avicultural experts before it is finished. Then testing by Hispaniolan Parrots should proceed and be done through at least a full year before Puerto Rican Parrots are brought in. There is no need for excessive speed in this process. There are too many unknowns here. n my experience such things, to be completed properly, always take longer than one anticipates.

Actual release of parrots to the wild in Rio Abajo should not be anticipated for several years. If such releases are made with captive-bred birds, one can expect relatively poor survival of birds until viable local traditions have been established, something that will likely be relatively difficult in the absence of an existing wild population in the area. Because of the relatively high losses that can be anticipated, birds available for wild releases in the near term should be released preferentially in Luquillo where they can be quickly integrated into a wild flock and can be expected to survive much better. Once a relatively secure wild population n size has been achieved in Luquillo (perhaps 70-100 birds), then direct translocations of trapped luquillo parrots may prove to be the best way to initiate releases in Rio Abajo, followed later by releases of captive-bred birds from both the Luquillo and Rio Abajo aviaries. Such a sequence of events could well prove to the quickest and most efficient way of establishing a viable Rio Abajo population.

I am alarmed by security aspects of the proposed move of the Luquillo aviary to Catalina. The existing aviary, minus most of the 90+ Hispaniolan Parrots currently housed there, would appear to be fully adequate in size for the goal of a viable captive population productive enough to sustain massive reintroduction efforts, so I am unconvinced there are any strong arguments that can be mounted that space will be inadequate in the future here. Further, the argument that climatic factors will significantly enhance reproduction in Catalina is based on little more than hope. Coupling an aviary with a visitor center in Catalina raises enhanced risks of spread of disease to the parrots. The birds would be living in close proximity to people with poultry on nearby private lands and would be placed in close proximity to whatever pathogens might be tracked in from all over the world by the million plus visitors that might be expected through the center during any year. The much higher human population in the Catalina area would also present increased risks of human vandalism. Finally, the move would be a very expensive proposition (more than a million dollars). I would much rather see monies go toward other aspects of the program that really need increased support. Renovation of the existing aviary in Luquillo could solve many of the existing aviary facilities problems (such as faulty plumbing and emergency power) at a much lower cost and with much greater safety.

My overall recommendation as to how the division of birds into various captive and wild populations should be prioritized is as follows. Genetically valuable individuals should be retained as captives. Thus progeny of as yet unrepresented "founders or near-founders" should not be considered for release until perhaps 5-6 sibs have been produced as permanent captives (exact numbers are negotiable). Given the availability of birds that meet release criteria, wild Luquillo broods should be augmented to 3 individuals per nest (4 in some experimental nests) assuming adequate synchrony of development can be achieved. The opportunities for fostering can be assumed to be relatively limited because most nests may already have 3 young and because of difficulties in achieving adequate synchrony between captivity and the wild. Thus it is reasonable to expect that numbers of birds of relatively low genetic value to the captive flock may soon be accumulating at the aviary. These are the birds that can be considered for direct release as free-flying birds into the wild population by methods developed by Jim Wiley and our Thick-billed Parrot program, or alternatively can be considered for initial stocking of a Rio Abajo aviary, once it is fully tested and functional. I would like to see some birds go in both of these directions. Since it will be impossible to predict just how many of such birds may be produced in the near future, I think it is impossible to specify in advance what numbers should go where. Decisions on such allocation, in my opinion should be a responsibility of the field project leader in consultation with the Luquillo aviculturist and cooperating geneticists, and should not be made at higher levels by people not in contact with the day to day field situation. Things change much too fast and unpredictably to allow a high probability of success if decisions are made at higher levels. Nevertheless there should be annual review of progress and decisions at higher levels, and especially by the CBSG.

With respect to establishment of a secure captive flock off island, I agree with the general view expressed at the conference that initial priority should be given to movement of genetically valuable birds that have proved refractory to breeding thus far. Other birds to be moved should be some F1 progeny of founders and near founders breeding at the Luquillo aviary. Decisions here should again be a responsibility of the field project leader in consultation with the aviculturist at the Luquillo aviary and cooperating geneticists. Birds to be moved to an off island facility would ultimately represent an adequate genetic cross-section of genetic lines in existence. I would prefer seeing birds move to such a facility in a phased manner, rather than all at once. We lost one bird in quarantine in moving it to the states in 1972, and it is essential that safe quarantine facilities be utilized in any future transfers.

In overview, I would view the primary purposes of various captive populations as follows:

Luquillo: Genetic security and releases of birds to the wild in the Luquillo region; once a Luquillo wild population is secure, releases in Rio Abajo and other Puerto Rico regions.
Off-island facility: Genetic security and transferring of birds to captive flocks in Luquillo and Rio Abajo.
Rio Abajo: Releases of birds to the wild in the Rio Abajo region, later releases to the wild in other Puerto Rico regions once the Rio Abajo wild population is secure.

My overall impressions of where the conservation program stands are very positive, and it was tremendous to see the level of concern and participation at the conference. Very significant progress has been made both in field studies and in captive breeding, and the people involved deserve commendation for their efforts. Though progress has not been as rapid as some had hoped, this is probably much more a reflection of the difficulties faced than of anything else. Both wild and captive populations are very clearly on the upswing and this is the important consideration.

After the conference I had an opportunity to visit the aviary and get out into the field for 3 days, and would like to emphasize the following. There are clearly many more birds now in the wild than when I was working with the species in the early 1970's, and they seem to be acting in a much more conspicuous and confident manner. Perhaps this "confidence" is in fact a reflection of "critical mass" considerations. The population has now grown to an extent that it is becoming more difficult to find all nesting pairs, and it is very probable that an egg-laying pair or two may have been missed in recent years because of manpower limitations. Finding such pairs is of extreme importance, as they may in general be expected to occupy sites vulnerable to thrashers and thus to be relatively unproductive. Getting their sites into a thrasher-proof condition is relatively straightforward process and could be expected to significantly increase the overall rate of population increase. Manpower for this effort is the principal need for the near term and is as important as any of the other concerns that were discussed at the conference.

In addition, I would like to see expanded field research into the phenomenon of non-breeding pairs. Who are these birds and what factors may correlate with onset of breeding? To this end development of good field marking techniques is needed along with an expanded field monitoring program. Intensive nest-guarding is still of great importance and will remain so until a more secure population level (perhaps 70-100 birds) is reached. After that point it may be wise to shift nest-monitoring to a less intensive intermittent checking basis. Other field research needs include more field testing of alternative parrot-nest structures for acceptance by parrots. Such experimentation could follow methodology similar to that used earlier to determine Pearly-eyed Thrasher nest-site preferences and tolerances.

As a final statement, I would like to see authority for decisions in the program kept as close to the field (and aviary) level as possible. We must rely on the competence of the people at the ground level, as they are closest to the situation and in the best position to evaluate what is happening. This is not to excuse these personnel from periodic review or from a crucial need for them to consult with outside specialists, but to give them the freedom and flexibility they need to make the decisions that are most likely to benefit the species. Too many endangered species programs have suffered greatly from micro-management at high administrative level.

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