Florida Panther
Population and Habitat Viability Assessment and Genetics Workshop

Gainesville, Florida
8-11 June 1999

Final Report

Sponsored by
Florida Fish and Wildlife
Conservation Commission

Facilitated by
Conservation Breeding Specialist Group, IUCN/SSC

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Edited by
Susie Ellis, Robert C. Lacy, Suzanne Kennedy-Stoskopf, David E. Wildt, Jenny Shillcox, Onnie Byers and Ulysses S. Seal

Compiled by
Workshop Participants

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A contribution of the IUCN/SSC Conservation Breeding Specialist Group.

This report is a product of the workshop participants: Sonny Bass, Jane Comiskey, Patty Cramer, Jennifer Hackshaw, Phil Hedrick, Karen Howard, Deborah Jansen, Holly Jenson, Mike Jones, Suzanne Kennedy-Stoskopf, Jim Krakowski, Robert Lacy, Darrell Land, Shanna Land, Jerrie Lindsey, Tom Logan, David Maehr, Sumner Matthes, Roy McBride, Steve O'Brien, Forrest Penny, Jack Pons, Betsy Purdum, Larry Richardson, Melody Roelke, David Schindle, Sharon Taylor, David Wildt and Steve Williams.

The recommendations summarized in this report represent the individual contributions of working group participants. CBSG facilitated the working group discussions and compiled the working group reports, but did not attempt to reconcile conflicting recommendations nor to cross-check for scientific or factual accuracy. The result is an inclusive compendium of suggestions by interested, knowledgeable parties presented for consideration by agencies charged with the conservation of Florida panthers.

This report is the result of a project supported by the Florida Fish and Wildlife Conservation Commission (FWC). It has not received peer review, nor has it had substantive editing for clarity, style and typographical errors by the FWC. Therefore any errors, opinions or recommendations in the report are those of the workshop participants and do not represent the policy of the FWC.

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Section 1
Introduction and Summary

Florida Panther Population and Habitat Viability Assessment and Genetics Workshop: Introduction and Summary

An experimental plan to restore historic Florida panther genetic variation and health was implemented in March 1995. This plan involved the translocation of eight female West Texas cougars into selected areas of the current panther range in South Florida. The immediate objective of these releases was for these female cougars to survive, mate with resident males and produce at least two F_1 offspring recruited as breeders into the population. The long-range objective of this experimental management action is to achieve a significant level of genetic restoration in the population by the time F_2 offspring recruit as breeders (6-8 years). The effects of inbreeding related genetic depression will have begun reversing as historic variation is achieved. A thorough evaluation of this experimental action would serve as a basis for designing a "Genetic Management Plan" to continue management of the genetic health and recovery of the Florida panther.

Six of the original eight female cougars still survive, and it is confirmed that at least 15 F_1 kittens, in 9 litters, and 1 F_2 litter have now been produced. Sufficient data have been gathered during the monitoring of these animals, to date, to make it both possible and prudent to conduct an evaluation of current results as a planning tool for the final evaluation of this experimental management action. Therefore, a review Population and Habitat Viability Analysis (PHVA) was needed to assess the relative status of this endangered population and to evaluate the effectiveness of current efforts to prevent its extinction. The previous PHVA was completed in 1989. To address these and other concerns affecting the conservation of the Florida panther, a second PHVA workshop was convened 8-11 June 1999 in Gainesville, Florida, facilitated by the Conservation Breeding Specialist Group (CBSG). Thirty-one people (Appendix I) attended the workshop, which addressed specific issues:

1. Comparison of current PHVA results with those generated from the workshop conducted in 1989. Changes in calculated population viability and demographic values, data deficiencies and additional data needs will be identified and evaluated for final analysis of genetic restoration.

2. Evaluation of the original experimental genetic restoration objectives, the methods used to accomplish these objectives, other experimental methods used, parameters being measured and progress to date.

3. Identification and description of any changes in experimental design and/or management actions which may be appropriate to implement prior to final evaluation of the experimental genetic restoration plan. Management needs of the surviving female cougars will also be evaluated.

4. Preparation of a plan with a time-line that specifies the data and analyses that will be necessary for final evaluation of genetic restoration and development of a continuing “Genetic Management Plan” for the Florida panther.

5. Quantified recovery criteria that are based upon the above analyses will be recommended for inclusion in a revised recovery plan for the Florida panther.

The PHVA Process

Each PHVA workshop begins with an agreement among the participants that the general desired outcome is to prevent the extinction of the species and to maintain a viable population(s). The workshop process takes an in-depth look at the species' life history, population history, status, and dynamics, and assesses the threats putting the species at risk.

One crucial by-product of a PHVA workshop is that an enormous amount of information can be gathered and considered that, to date, has not been published. This information can be from many sources; the contributions of people with a wide variety of expertise as well as a stake in the future of the species are considered. Information contributed by wildlife officers, scientists, field biologists, private landowners and others all carry equal importance.

All the information that can be gathered is discussed by the workshop participants with the aim of first reaching agreement on the state of current information to obtain the entire picture concerning a species. These data then are incorporated into a computer simulation model to determine: (1) risk of local extinction under current conditions; (2) those factors that make the species vulnerable to extinction; and (3) which factors, if changed or manipulated, may have the greatest effect on preventing local extinction. In essence, these computer-modeling activities provide a neutral way to examine the current situation and what needs to be changed to prevent local extinction.

Complimentary to the modeling process is a communication process, or deliberation, that takes place throughout the workshop. Participants work together to identify the key issues affecting the conservation of the species and then work in small groups to discuss these issues, which can range from predator management, disease, human-animal interactions, or other emerging topics. Each working group produces a brief report on their topic, which is included in the document resulting from the meeting. A successful PHVA workshop depends on determining an outcome where all participants, coming to the workshop with different interests and needs, "win" in developing a management strategy for the species in question. Local solutions take priority. Workshop report recommendations are developed by, and are the property of, the local participants.

Process for the Present Workshop

The 31 participants worked together in the initial plenary to identify their own goals for the workshop. These centered around five main topics, which then became the focus of four topic-based working groups: Assessment of Wild Populations; Health; Genetics; Captive Populations; and Modeling.

Each working group was asked to:

- Brainstorm issues and problems related to the group's topic.
- Prioritize the identified issues.
- Identify and prioritize goals to address the most important issues/problems.
- Identify and prioritize actions to achieve each goal.
- Re-visit the top priority actions under each issue and indicate a group or individual(s) to take responsibility, either to carry the action out personally or to recruit others to help.
- Identify measurable outcomes for each action, including time lines.

Each group presented the results of their work in daily plenary sessions to ensure that everyone had an opportunity to contribute to the work of the other groups and to assure that each group's work was reviewed and discussed by all workshop participants. Recommendations coming from the workshop were accepted by all participants, thus representing a consensus. Working group reports can be found in Section 2 of this document.

Workshop goals identified by workshop participants: (Not prioritized)

1. Learn about progress of genetic restoration.
2. Progress re: Florida Panther – it's a grand experiment. Reproductive fitness.
3. Here to help.
4. Learn about recovery of FP – final and complete recovery
5. Assure awareness for need for retirement sanctuary – diverse population throughout state.
6. Next step processes needed and how to integrate with other recovery tasks – goal to achieve benign management.
7. Learn about issues – genetic restoration – help other managers with management and protection.
8. Help move beyond symptom-based management and see animal managed from a landscape/regional perspective.
9. Provide field perspective – landscape perspective – regional for full recovery – southeastern U.S. coastal plains.
10. Understand current progress and issues – make the model useful.
11. See what progress has taken place since 1992. Understand physiological responses to genetic restoration.
12. Learn. Participate. Achieve goal of benign management.
13. Learn how Florida cats will be utilized. Participate and help recovery process – reintroduction, genetic restoration, and habitat preservation.
14. Learn where project is going. What role will zoos play in the program? Like to see full recovery.
15. Role of zoos in recovery of panther. Learn.
16. Priorities for future steps to take. Responsibility of the National Parks Service for management.
17. Be "Leveling influence." Steps to achieve benign management.
18. Feedback on projects done from biomedical perspective.
19. Review with genetic restoration – expand population in number and area – healthy population in the southeast.
20. Provide scientific and self-evaluation of genetic restoration. Progress continues in recovery – achieve benign management.
21. Share and learn modeling techniques. More than one population landscape issue – move on people issues.
22. Learn more about program. Process continues with public support.
23. Evaluate and contribute to genetic aspects. Use genetics to evaluate success and make FP sustainable wild population.
24. Better focus research activities. Long-term plan to achieve hands-off management.
25. See what's going on and where to go.
26. Learn about status and use info in public programs at zoo. Explore public issues in recovery program.
27. Determine effective role for captive programs. Restore to historic range.

Overview of Results

The Conservation Breeding Specialist Group (CBSG) facilitated a Florida Panther Population and Habitat Viability Assessment and Genetics Workshop 8-11 June 1999 in Gainesville, Florida to address five specific issues. Below is a summary of recommendations related to these issues.

Issue 1. Comparison of current PHVA results with those generated from the workshop conducted in 1989. Changes in calculated population viability and demographic values, data deficiencies and additional data needs will be identified and evaluated for final analysis of genetic restoration.

The modeling working group compared data from the previous workshops with those used in this most recent evaluation. Participants reviewed the values used by Maehr et al. 1999 to describe the present population. The values used by Maehr et al. 1999 are summarized, and compared to values used in earlier PVA efforts for the taxon, in the table below.

Comparison of input parameters used in 1989, 1992, and Maehr et al. (1999) Population Viability Analyses (Primary estimates used are given first; other values tested are given in parentheses.)

	1989	**1992**	**Maehr et al.**
Inbreeding depression (lethal equivalents)	3.4 (0,1.0,1.7)	3.0 (0,1.0)	3.14
Female breeding age	3 (2)	2 (3)	2
Male breeding age	3 (2)	2 (3)	4
Maximum age	15	12	12
Females breeding / yr	50	50	50
Mean litter size	3.0 (2.5)	2.0	2.175
% males breeding	100	50	50
1st yr mort	50	50 (20)	20
2nd yr mort (M/F)	30	20	20/30
3rd yr mort	25 (20)	20	17/30
4th + yr mort	25 (20)	20	17/15
Catastrophes	none	none	0.5% probability 5% repro. decline & mort.
N(0)	45	50 (30)	60
K	45 (30,60,80)	50	70
Change in K	0 (-10,-20,-50%)	-25% (0,-50%)	0 (-25%)
Removals	0 (6,12)	none	none (6 f)
Releases	none	none	2 f / 10 y (none)
Mean growth			
deterministic	-0.057	-0.018	0.120
simulation	not reported	-0.069	0.083
Prob. Persistence	0	0	100%
N			66
Final Heterozygosity			76%

The Modeling Working Group felt that the values used by Maehr et al. were based on reasonable interpretations of the currently available data, but that some parameters were only poorly known and alternative characterizations of the population were possible. The rationale for the shifts in values from the PVA models assessed in 1989 and 1992 to those used by Maehr et al. in 1999 was presented to the workshop plenary (see abstract on page 59 of this report). Some participants at the workshop expressed concern that the first year mortality might be much greater than had been estimated by Maehr et al. Given the uncertainty regarding this critical demographic variable, the Modeling Working Group conducted sensitivity tests to explore the effects of higher levels of first-year mortality (while using the other values proposed by Maehr et al.). They also projected the effects of various possible future conservation and management actions: including varying rates of release of additional Texas cougars; provision of additional habitat, either to allow expansion of the existing population or to create a second, largely independent population; and possible losses of existing habitat.

The modeling group also identified a number of types of information needed to produce the most realistic analysis of genetic restoration. Specifically, intensive and detailed monitoring of the fates and pedigrees of panthers and especially the intercross descendants is a prerequisite for determining the consequences of genetic changes to demographic performance, genetic diversity and the probability of persistence of the population. Other data needs include past, present and future landscape/habitat factors; social, cultural, economic and political factors; and metapopulation factors. The following actions were developed to address these issues. It was recommended that progress reports on efforts to achieve each of these goals should be presented in conjunction with the workshop proposed for early next year.

1. Dave Maehr and colleagues will complete a retrospective analysis of landscape changes over the past two decades. The trajectory from the past can provide a rate and direction of change, but should be supplemented with projections of landscape changes10, 20 and 50 years into the future.
2. Provide more support for the radio-telemetry efforts that provide needed data to better quantify demographic characteristics of the panther population which serve as input parameters for simulation models. Better estimation of parameters which drive VORTEX and other models depends on a high percentage of kittens being radio-collared before dispersal.
3. Conduct more intensive ongoing monitoring of kittens before dispersal from the natal area, with the goal of obtaining more complete records and recording them in the SPARKS database provided for that purpose. This will improve the reliability of determining whether kittens have survived or perished.
4. Apply mark-recapture methodologies developed over the past decade to existing capture data, field notes and photo-records from trail and underpass cameras to derive unbiased estimates of survival rates. David Shindle, wildlife biologist with the Panther Capture Team, is currently conducting a project to gather additional photo-records using trail cameras within panther ranges.

5. Assess habitat characteristics of the current range of panthers in South Florida and apply measures of habitat suitability derived from this analysis to potential new areas of panther habitat.
6. Rank the suitability of potential sites identified for population expansion or reintroduction.
7. Use the population viability model to evaluate potential effects on overall metapopulation stability in terms of genetic diversity, population growth and effectiveness of repopulating potentially suitable sites.

Issue 2. Evaluation of the original experimental genetic restoration objectives, the methods used to accomplish these objectives, other experimental methods used, parameters being measured and progress to date.

The genetics working group had as one of their goals to "determine whether or not our original design premise is still sound in light of what we now know". They concluded that it appears that the plan is currently on track. The Group agreed that two of the Texas cougars appear to have met their restoration objective which was for each female to produce at least 2 kittens recruited as breeders. There is concern about the potential for their overrepresentation. Therefore, it was proposed that Texas cougar females should be removed (physical removal is preferred, but contraception is an option) when, at least, two of their kittens have established territories and, at most, when an individual female has four independent kittens.

In addition, it was recognized that in order to adequately evaluate progress, molecular genetic and relatedness analyses on Florida panthers, Texas cougars and F_1's must be conducted. The group outlined steps to be taken in order to make a complete assessment of progress to date:

1. Continue monitoring to ensure that desired/target rate of restoration continues.
2. Determine the extent of Texas cougar genetic contribution to the Florida panther population.
3. Determine whether females have made their contribution as planned and is a contribution that would exceed their individual goals problematic to the population.
4. Develop guidelines for when/if animals should be removed. There is a concern that the controls originally intended have not been implemented (i.e., removing females once target contribution made). Identify humane and equitable disposition of Texas cougars (according to Florida Fish and Wildlife Conservation Commission protocol) as each female reaches its predetermined genetic contribution to the recovery effort.
5. Address the concern that there are individuals in the captive population that represent lineages not represented in the wild and whether or not these animals should be incorporated into the wild population.
6. Systematically organize, evaluate and disseminate biomedical data in order to document health problems in the population and determine whether genetic restoration have been beneficial to the population.

Issue 3. Identification and description of any changes in experimental design and/or management actions which may be appropriate to implement prior to final evaluation of the experimental genetic restoration plan. Management needs of the surviving female cougars will also be evaluated.

Many of the recommendations made by workshop participants involved the continuation of experimental design and management actions but some changes were identified.

1. Analyze current data, which already have been collected, including telemetry data, current pedigree information and genetic analysis to monitor the genetics of Florida panther population and track the geographic infusion of restored genes.
2. Collect samples from the remaining seven F_1 offspring of the Texas females (blood and tissue).
3. Continue collecting data on future backcross offspring to allow complete lineage identification.
4. Identify historic, present and potential available habitat for the Florida Panther. This information is needed for: 1) improving population modeling; 2) providing a better understanding of rate of habitat losses; 3) projecting future management/protection actions including dispersal and reintroduction; and 4) improving the estimates of accurate panther numbers.
5. Monitor the Florida panther population with sufficient intensity to determine population trends and to assess the effectiveness of genetic restoration.
6. Gross and histological post-mortem evaluations should be conducted on all recovered panther carcasses to evaluate the effectiveness of genetic restoration.
7. Continue banking biological samples for future analyses on all animals handled in an attempt to approach 100% representation.
8. Determine the consequence of genetic restoration in terms of identified fitness parameters (namely cryptorchidism, kinked tail, cowlicks, sperm quality, atrial septal defects, disease, size, weight and other physical characteristics) in F_1 animals and other animals with Texas ancestry.
9. Identify components of fitness which are specific to the Florida panther and monitor their incidence in the entire restored population, including the potential and current presence of adaptations specific to their habitat as a result of adaptive gene combinations.
10. Better quantify demographic characteristics of the panther population which serve as input parameters for simulation models, specifically kitten/juvenile mortality rates, percentage of females breeding each year and initial population size.

Issue 4. Preparation of a plan with a time-line that specifies the data and analyses that will be necessary for final evaluation of genetic restoration and development of a continuing "Genetic Management Plan" for the Florida panther.

It was recommended that agency level meetings be held annually to review the data and assure that the program is on-track. All recommended actions outlined in this report should be implemented and the results prepared for review at this annual meeting. In addition, participants at this workshop were given responsibility for identifying dates for a workshop to provide "final" analysis of genetic restoration and development of a management plan. This time frame must be made known to all involved as soon as possible so that the data gaps identified in this document can be filled as recommended and the data analyzed in preparation for this workshop.

The following specific information must be gathered and analyzed prior to the first annual agency level meeting:

1. Molecular genetic and relatedness analyses on Florida panthers, Texas cougars and F_1's including a determination of the extent of Texas cougar genetic contribution to the Florida panther population;
2. Monitoring of the fates and pedigrees of panthers and especially the intercross descendants to determine the consequences of genetic changes to demographic performance, genetic diversity and the probability of persistence of the population; and
3. The most accurate demographic characteristics of the panther population which serve as input parameters for simulation models, specifically kitten/juvenile mortality rates, percentage of females breeding each year and initial population size.

Issue 5. Quantified recovery criteria that are based upon the above analyses will be recommended for inclusion in a revised recovery plan for the Florida panther.

The genetics working group covered the issues surrounding recovery criteria but the specific requirements of Issue 5 were not addressed during the workshop. There was no text developed that could be used by the Recovery Team for inclusion as a qualified recovery objective (s) for the south Florida population in revision of the Recovery Plan. This issue could not be addressed in detail because the necessary data were not available for the analyzes at the time of the workshop.

Summary of Working Group Reports

Summaries of the issues and goals identified by each of the five Working Groups follow. Recommendations for actions, along with persons responsible and timelines can be found in the Working Group Reports in Section 2.

ASSESSMENT OF WILD POPULATIONS WORKING GROUP

The Assessment of Wild Populations Working Group identified four high priority issues, listed in order below:

1. Assessment of the wild population at the landscape level.
2. Reproductive fitness.
3. Health.
4. Genetic restoration.

Keeping the above issues in mind, the Group established goals, objectives and recommended concrete actions to reach said goals. Goals and objectives are listed below; specific actions can be found in the Working Group report in Section 2.

GOAL 1: Continue to monitor the genetics of the Florida panther population with sufficient intensity to determine population trends, assess the effectiveness of genetic restoration and track the geographic infusion of restored genes.

OBJECTIVES:

1. Improve kitten survivorship.
2. Improve recruitment of offspring.
3. Continue monitoring biomedical status (that includes genetics), especially for the purpose of assessing the overall impact of the genetic restoration.

GOAL 2: Identify historic, present and potential available habitat for the Florida panther to improve population modeling, provide better understanding of rate of habitat losses, project future management/protection actions and improve the estimates of accurate panther numbers.

OBJECTIVES:

1. Assemble a succinct set of visuals and text that details changes in Florida panther habitat over time throughout the state of Florida (old range, new, improved range).
2. Develop a document that provides accessible information to the public.
3. Glean information from the following existing documents:
   a. Cox, J., R. Kautz, M. MacLaughlin and T. Gilbert. 1994. Closing the Gaps in Florida's Wildlife Habitat Conservation System. Florida Game and Fresh Water Fish Commission.
   b. Logan, T. A. C. Eller, Jr., R. Morrell, D. Ruffner and J. Sewell. 1993. Florida Panther Habitat Preservation Plan.

   c. Mazzotti, F. J., L. A. Brandt L. G. Pearlstine, W. M. Kitchens, T. A. Obreza, F. C. Depkin, N. E. Morris and C. E. Arnold. 1993. An Evaluation of the Regional Effects of New Citrus Development on the Ecological Integrity of Wildlife Resources in Southwest Florida. Institute of Food and Agricultural Services, University of Florida.
   d. Data from Water Management District Report
   e. GAP Analysis
4. Produce a document that will be of diverse use, including helping to improve infrastructure relevant to enhanced management (wildlife crossings, speed zones, etc.).

GOAL 3: Maintain current population of Florida panthers.

GOAL 4: Expand the Florida panther population.

HEALTH WORKING GROUP

Veterinarians have been a part of the Florida panther field team nearly since the inception of the Florida panther recovery. A tremendous amount of data has been generated related to physical examinations, anesthesia, clinical pathology, and serology by veterinarians in the field. The Working Group emphasized that these data need to be systematically organized, evaluated, and disseminated in order to document health problems in the population and determine whether biomedical intervention and genetic restoration have been beneficial to the population. Furthermore, thoughtful analysis of data is necessary to determine future directions of biomedical research.

The Group identified five priority issues, established goals and objectives and recommended concrete actions to reach said objectives. Goals and objectives are listed below; specific actions can be found in the Working Group report in Section 2.

GOAL 1: Continue complete physical examinations of individual Florida panthers to maintain and augment health parameter databases in order to assess trends within the population.

OBJECTIVES:

1. Minimize risks associated with immobilization. Keep a complete anesthetic record for each immobilization.
2. Establish guidelines for a complete physical exam on adult and neonatal animals. Maintain individual medical records. Identify parameters that will be useful for assessing the effectiveness of genetic restoration.
3. Identify parameters that will be useful for assessing reproductive fitness and fecundity.
4. Establish health assessment guidelines for translocation of free-ranging panthers in southern Florida and introduction of additional animals for genetic restoration.
5. Establish health protocol recommendations for translocation of captive Florida panthers between institutions.

GOAL 2: Establish protocols for sample collection, distribution, and archiving.

OBJECTIVES:
1. Maximize the utilization of samples obtained from each animal.
2. Prioritize sample collection and utilization.
3. Assure adequate archiving of collected samples.

GOAL 3: Facilitate and prioritize research initiatives.

OBJECTIVES:
1. Standardize protocol for request of samples for research outside the agency.
2. Prioritize research initiatives.
3. Create an ad hoc advisory board of specialists to assist the veterinarian in the development of biomedical research priorities.

GOAL 4: Manage biomedical data.

OBJECTIVES:
1. Biomedical data and samples should be readily retrievable.
2. Biomedical data should be periodically reviewed to assess trends in overall health status of the population and provide useful biomedical parameters to assist in demographic modeling.
3. Biomedical data should be evaluated in a timely fashion and the results made known.

GOAL 5: Gross and histological post-mortem evaluations should be conducted on all recovered panther carcasses to evaluate the effectiveness of biomedical intervention and genetic restoration.

OBJECTIVE:
1. Necropsies will be conducted on all panther carcasses.

GENETICS WORKING GROUP

The Genetics Working Group identified five priority issues and listed goals and actions for each, including persons responsible and timelines. Goals and objectives are listed below; specific actions can be found in the Working Group Report in Section 2.

GOAL 1: Perform molecular genetic analyses including individual genotyping of Florida panthers, Texas cougars, and F_1 animals and assessment of parentage.

OBJECTIVE 1: Conduct molecular genetic and related analyses on Florida panthers, Texas cougars and F_1's to obtain baseline information on Florida panthers and Texas cougars to evaluate progress.

OBJECTIVE 2: Continue banking biological samples for future analyses on all animals handled in an attempt to approach 100% representation.

GOAL 2: Determine the consequence of genetic restoration in terms of identified fitness parameters (namely cryptorchidism, kinked tail, cowlicks, sperm quality, atrial septal defects, disease weight, size and other physical characteristics) in F_1 animals and other animals with Texas ancestry.

OBJECTIVE 1: Develop a profile of correlates to measure the effects/impacts of genetic restoration on the physical manifestations of inbreeding.

OBJECTIVE 2: Determine presence/absence/degree of physical manifestation of inbreeding.

GOAL 3: Identify components of fitness which are specific to the Florida panther and monitor their incidence in the entire restored population, including the potential and current presence of adaptations specific to their habitat as a result of adaptive gene combinations

OBJECTIVE 1: Investigate measurable characteristics that may be adaptive including:

- Skull morphometrics.
- Pelage characteristics.
- A behavioral "style" inventory including characteristics such as:
    - Tolerance to people.
    - Behavior at capture (e.g., F_1 panthers may leave trees a lot more than Florida panthers, drug dosage needed to sedate them).

GOAL 4: Determine whether or not our original design premise is still sound in light of what we know now.

OBJECTIVE 1: Continue monitoring to ensure that desired/target rate of restoration/refreshment continues.

GOAL 5 Part 1: Determine the extent of Texas cougar genetic contribution to the restoration of Florida panther population genetics and evaluate if and when any of the released Texas cougar females should be physically or reproductively removed from the population.

OBJECTIVE 1: Determine whether females have made their contribution as planned and is a contribution that would exceed their individual goals problematic to the population.

GOAL 5 Part 2: Identify humane and equitable disposition of Texas cougars as each female reaches its predetermined genetic contribution to the recovery effort.

OBJECTIVE 1: Examine options/range of flexibility for disposition according to Florida Fish and Wildlife Conservation Commission (FFWCC) protocol.

OBJECTIVE 2: Develop guidelines for when/if animals should be removed.

To address the above goal in a more immediate sense, according to the 1999 Genetic Restoration and Management Report by FFFWCCC, there are:

- 55 pure Florida panthers
- 5 pure Texas cougars (one died)
- 11 F_1 kittens
- 3 kittens 75% TX
- 1 kitten 25% TX

Based on these numbers, we can estimate that there are 18% TX genes in the population. If we remove all 6 Texas females, there will be 11% TX genes in the population. (This assumes that one Texas female is equivalent to 2 kittens genetically.)

If 12 more F_1 kittens are produced, then the Texas females pulled, then we would essentially be in the same place we are now. This assumes that Texas cougars are as likely to breed as the Florida panthers (i.e., all animals are equally likely to breed)

The Group agreed that:

- We want to meet the designed genetic objective.
- Genetic swamping is a potential problem.
- There is a problem with the lag-time/recruitment cycle for each female.
- There are four females, TX101, TX105, TX107, TX108, that are at a point of needing a management decision (e.g. physical removal or contraception).
- We want input from geneticists in decision-making process.
- The need for a decision is urgent.

The Group agreed that two of the Texas cougars appear to have met their restoration objectives. There is concern about the potential for their overrepresentation. Therefore, we propose that Texas cougar females should be removed (physical removal is preferred, but contraception is an option) when, at least, two of their kittens have established territories and, at most, when an individual female has four independent kittens.

GOAL 6: Address the concern that there are individuals in the captive population that represent lineages not represented in the wild and whether or not these animals should be incorporated into the wild population.

OBJECTIVE 1: Include genetic contribution of these animals, in some form, to wild population. One side-benefit of this approach is that it counters some of the swamping issues.

OBJECTIVE 2: Breed said animals and rear female offspring so as to maximize the probability of survival following reintroduction. Reintroduce into South Florida to restore those lineages that no longer exist in the wild.

There also was a discussion about an ad-hoc genetic issue after the initial prioritization had taken place:

Given the new information about the "cougars" that may be interacting with Florida panthers in and around the Big Cypress Seminole Indian Reservation, and given that the genetic backgrounds of those animals are unknown, and given that any genetic contribution of these animals into the south Florida panther population may alter the planned process of genetic restoration, we believe that this is a serious problem that requires immediate attention. A series of possible actions was recommended, including:

1. With the concurrence of the Seminole Indian tribe, capture each animal.
   Options to Address the Above Concerns:
   a. Radiocollar, transpond, and collect tissue samples for genetic analysis from all animals if possible (with emphasis on males).
   b. Prevent future reproduction, either permanently by sterilizing each animal, or temporarily by contracepting, or a combination of both.

2. Cooperate with Big Cypress Seminole Indian Reservation to retrofit existing "enclosure" to prevent future transgression of BCSIR "cougars" into the wild.

3. Develop a cooperative program with the BCSIR that targets Florida panther conservation.

4. Include representatives of the BCSIR in future Florida panther PHVAs, FPIC meeting, and other technical and policy meetings that involve Florida panther recovery.

5. Determine how this affects the other recommendations for action made by the group.

CAPTIVE BREEDING WORKING GROUP

The Captive Breeding Working Group began by identifying key problems and issues related to Florida panther captive breeding: that there is an aging group of Florida panthers in captivity, and that the value of captive population for recovery can be expanded.

GOAL 1: Maintain the current captive population through an approved breeding program for:

1. Genetics – to preserve and enhance current genetic material.

2. Education – implement a uniform, coordinated education program to support panther recovery, taking advantage of the fact that participating zoos currently reach more than 1 million visitors with the potential to reach more than 3 million visitors annually on issues related to the Florida panther recovery program.

3. Research – should be carried out with animals available as needs are identified, including: reproductive research, vaccine development, immunological function, genetic anomalies, and serving as contaminant control group.

RECOMMENDED ACTION 1: Obtain agency authorization to initiate program.

The group also listed the individuals currently in captivity and made several recommendations for captive pairings and moves.

Facility	Specimen number	Rank	Lineage
White Oak	202 (male)	Critical blood line	Sire- 37 (prob.) Dam- 9
White Oak	204 (female)	Important blood line	Sire- 12 Dam- 31
Jacksonville	210 (male)	Important blood line	Sire- 42 Dam- 23
Jacksonville	209 (female)	Important blood line	Sire- 42 Dam- 23
Lowry Park	207 (male)	Bilaterally cryptorchid	Sire- 26 Dam- 36
Lowry Park	208 (female)	Critical blood line	Sire- 12 Dam- 32

Initial breeding recommendations (made with consideration to leave breeding females at current facilities):
202 and 204
210 and 208

Moves to support breeding recommendations:
210 from Jacksonville Zoo to Lowry Park Zoo
207 from Lowry Park Zoo to Tallahassee Zoo

MODELING WORKING GROUP

The Modeling Working Group began its discussion by listing issues related to PVA modeling. Paired ranking was then used to list the issues from highest to lowest priority:

1. Inclusion of landscape/habitat features in models to assess probability of panther survival so that land use, changes in landscape which produce changes in carrying capacity, habitat fragmentation, and connectivity issues can be addressed.
2. Determine whether there is a consensus on the Maehr et al. model.
3. Inclusion of cultural/social/economic/regulatory/legal aspects in future models.
4. Metapopulation/reintroduction/expanded population models.
5. Facilitate data gathering and sharing for spatial models.
6. Determine implications of results from current PVA models for needed actions.

7. Develop a “world map” of threats and impacts on Florida panther viability.
8. Inclusion of political analysis in modeling efforts.
9. Cost/benefit of various recovery actions.
10. Compare the panther situation to lessons learned from other species being recovered.

While it was determined that all of the above issues need further exploration within the Florida panther recovery program, the Modeling Group focused on addressing the first six priority issues at the workshop. These analyses are presented in Section 2. The following goals and proposed actions were formulated to address the remaining issues:

GOAL 1: Quantify potential/likely loss and change of Florida Panther habitat in South Florida. This would provide better estimates of habitat loss to feed into panther viability simulations.

RECOMMENDED ACTIONS:

1. Complete a retrospective analysis of landscape changes over the past two decades.

2. Forecast/project future landscape changes using the trajectory from the past supplemented with projections into the future.

3. Increase communication and coordination among various modeling approaches and efforts to coordinate spatial and temporal scales, formats, units, and methodologies.

GOAL 2: Better quantify demographic characteristics of the panther population which serve as input parameters for simulation models, specifically kitten/juvenile mortality rates, percentage of females breeding each year, and initial population size.

RECOMMENDED ACTIONS:

1. More support for the radio-telemetry efforts which provide needed data. Better estimation of parameters which drive VORTEX and other models depends on a high percentage of kittens being radio-collared before dispersal. The extended 1999 capture season covered about 120 days, but captures only occurred on half those days due to unavailability of veterinary support and inadequate water levels and temperatures. Suggestions also were made as to how best to increase the intensity of radio-collaring efforts.

2. More intensive ongoing monitoring of kittens before dispersal from the natal area, with the goal of obtaining more complete records and recording them in the SPARKS database provided for that purpose, so that more reliable determinations may be made as to whether kittens have survived or perished.

3. Apply mark-recapture methodologies developed over the past decade to existing capture data, field notes, and photo-records from trail and underpass cameras to derive unbiased estimates of survival rates.

4. Compile and review all data (from various sources) on kitten/juvenile survival, female breeding percentages and population size.

GOAL 3: Gain a better understanding of potential Florida Panther habitat in terms of what is currently available and what is projected to be available in the future for dispersal or reintroduction.

RECOMMENDED ACTIONS:

1. Assess habitat characteristics of the current range of panthers in South Florida, minimum size of patches of suitable panther habitat based on current range sizes, availability of resting and denning areas and stalking cover, support for prey productivity, and human land use.

2. Apply measures of habitat suitability derived from this analysis to potential new areas of panther habitat.

3. Rank the suitability of potential sites identified for population expansion or reintroduction.

4. Use the population viability model to evaluate potential effects on overall metapopulation stability in terms of genetic diversity, population growth, and effectiveness of modes of repopulating those sites.

The Working Group recommended that progress reports on efforts to meet each of these goals should be presented in conjunction with the next PHVA workshop that is proposed by other working groups for early next year.

Florida Panther Population and Habitat Viability Assessment and Genetics Workshop

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8-11 June 1999
Gainesville, Florida

Final Report

Section 2
Working Group Reports

Assessment of Wild Populations Working Group Report

Participants: Darrell Land, Sonny Bass, Deborah Jansen, Larry Richardson, Roy McBride, Betsy Pudum, Jerrie Lindsey, David Shindle
Facilitator: Dave Wildt

Initially, a working group formed to identify all issues pertinent to wild population data, diseases and biomedical issues. This larger group then divided into two groups, one focusing on wild population issues, and the other focusing on health-related issues. First, however, a brainstorming session identified the larger group's areas of interest in random order:

- Kitten survivorship.
- Non-reproducing females.
- Future of the Texas female cougars that have been released.
- Determining the completion of the role of these Texas cougars.
- Intraspecific aggression.
- Impact of pseudorabies.
- Dispersal patterns related to juvenile survivorship.
- Percentage of F1's requiring monitoring to evaluate restoration effectiveness.
- Monitoring overall Florida panther population.
- Inbreeding in panthers within the Everglades.
- Males participating/contributing to the population.
- Guidelines for monitoring Texas cougar.
- Monitoring Florida panthers on private lands.
- Role of environmental toxins.
- Impact of physical barriers on blocking cat movements.
- Assessment of immune function.
- Collecting the right data to address most pertinent questions.
- Role of assisted breeding.
- Samples collected and prioritization of use, including having standardized protocols.
- Issues related to reintroduction of captive animals.
- Incidental releases of generic panthers.
- Semen evaluations of authentic Florida panthers, F1's and backcrosses.
- The need for completing physical examinations.
- Manipulating wild populations to address demographic issues (moving animals using protocols).
- Protocol for introgression of more Texas animals into Florida.
- Disease monitoring and its effects.
- Effects of biomedical intervention on survival.
- Feasibility of developing monitoring techniques for kittens.

The group then collapsed the above issues into four more generalized categories and refined the individual areas of interest within each:

Reproductive Fitness and Fecundity

- Kitten survivorship.
- Non-reproducing females.
- Inbreeding in the Everglades panther population.
- Males contributing to the population.
- Role of assisted breeding.
- Semen evaluations of authentic Florida panthers, F1's and backcrosses.
- Feasibility of developing a technique for monitoring kittens.

Assessment of Wild Populations at the Landscape Level:

- Dispersal patterns/recruitment.
- Intraspecific aggression.
- Impact of pseudorabies.
- Monitoring the overall Florida panther population.
- Monitoring Florida panthers on private lands.
- Physical barriers blocking cat movements.
- Methods of data collection to answer the most pertinent questions.
- Manipulating wild populations to address demographic issues (moving animals).

Role of Genetic Restoration

- A plan for Texas females.
- Percentage of F1's to monitor for determining if restoration is successful.
- Guidelines for monitoring Texas cougar females.
- Protocol for introgressing more Texas animals into Florida.
- Use of captive animals for reintroduction.
- Incidental releases of generic cougars.

Health

- Role of toxins in the environment.
- Assessment of immune function.
- Standardization of sample collection and priority of use.
- Continue complete physical examinations.
- Continue monitoring diseases and effects.
- Assessing effects of biomedical intervention on survival.

These four generalized issues then were pair-ranked by the entire group, with the order of priority being calculated as: 1): assessment of the wild population at the landscape level; 2) reproductive fitness; 3) health; and 4) genetic restoration. However, subsequent discussion revealed that one of the highest priorities of this workshop was to assess the impact of the ongoing genetic restoration. There also was concern that there may be insufficient time for this group to address all issues within these four general categories, especially given that several participants were scheduled to leave the meeting early. Thus, it was decided to form two working groups, one on Assessing the Wild Population and another on Health. The Health Working Group report can be found on pages 35 – 40 in this document. Further, it was decided that every attempt would be made to address all identified issues under those two primary categories.

GOAL 1: Continue to monitor the genetics of Florida panther populations and track the geographic infusion of restored genes.

RECOMMENDED ACTIONS:

1. Analyze current data, which already have been collected, including:
   a. Telemetry data.
      Persons Responsible: Darrell Land, Deborah Jansen and Sonny Bass
      Timeline: September 1999.)
   b. Further analysis and maintenance of current pedigree information.
      Persons Responsible and Timeline: Darrell Land, Deborah Jansen and Sonny Bass as well as the FFWCC veterinarian [including participation of Sharon Taylor] in providing the raw data to Ulie Seal by August 1999; Dr. Seal to complete within 4 weeks and return to Darrell Land.)
   c. Completing genetic analysis of already collected samples. Samples already have been forwarded to Dr. O'Brien's laboratory for analysis.
      Persons Responsible: Darrell Land and Sharon Taylor in collaboration with Stephen O'Brien and his staff
      Timeline: for completing interpretation of all current data, December 1999.

2. Collect additional information and then analyze as per Action 1.
   a. Continue telemetry collection.
      Persons Responsible: Darrell Land, Deborah Jansen and Sonny Bass
      Timeline: Ongoing
   b. Collect samples from the remaining seven F_1 offspring of the Texas females (blood and tissue).
      Persons Responsible: Darrell Land, Deborah Jansen and Sonny Bass
      Timeline: Ongoing
   c. Continue collecting data on future backcross offspring to allow complete lineage identification.
      Persons Responsible: Darrell Land, Deborah Jansen and Sonny Bass
      Timeline: Ongoing

3. Provide all existing and future skin and blood samples to Stephen O'Brien for genetic analysis.
   Persons Responsible: Darrell Land, Deborah Jansen and Sonny Bass
   Timeline: Ongoing

4. Obtain guidance from geneticists about technical methods to improve data collection. For example, there is a need to explore alternative sampling from kittens to minimize the size of the biological sample (i.e., minimal amount of blood, skin as well as assessing the potential of analysis via hair samples).
   Persons Responsible: Darrell Land, Deborah Jansen and Sonny Bass in cooperation with Stephen O'Brien and his staff.

GOAL 2: Identify historic, present and potential available habitat for the Florida Panther. This information is needed for: 1) improving population modeling; 2) providing a better understanding of rate of habitat losses; 3) projecting future management/protection actions; and 4) improving the estimates of accurate panther numbers.

OBJECTIVES:

1. Assemble a succinct set of visual and text that details changes in Florida panther habitat over time throughout the state of Florida (old range, new, improved range).
2. Develop a document that provides accessible information to the public.
3. Glean information from the following existing documents:
   a. Cox, J., R. Kautz, M. MacLaughlin and T. Gilbert. 1994. Closing the Gaps in Florida's Wildlife Habitat Conservation System. Florida Game and Fresh Water Fish Commission.
   b. Logan, T. A. C. Eller, Jr., R. Morrell, D. Ruffner and J. Sewell. 1993. Florida Panther Habitat Preservation Plan.
   c. Mazzotti, F. J., L. A. Brandt L. G. Pearlstine, W. M. Kitchens, T. A. Obreza, F. C. Depkin, N. E. Morris and C. E. Arnold. 1993. An Evaluation of the Regional Effects of New Citrus Development on the Ecological Integrity of Wildlife Resources in Southwest Florida. Institute of Food and Agricultural Services, University of Florida.
   d. Data from Water Management District Report
   e. GAP Analysis
4. Produce a document that will be of diverse use, including helping to improve infrastructure relevant to enhanced management (wildlife crossings, speed zones, etc.).

RECOMMENDED ACTIONS:

1. Complete current analysis being done on contemporary habitat (in collaboration with the University of Florida). This study is examining trends over at least the last 30 years. This is a peer-reviewed article in preparation by Darrell Land, Dave Maehr, Tom Hoctor and Kathy Kantaras.
   Persons Responsible: these authors
   Timeline: October 1999

2. Prepare a formal proposal to generate information on habitat relevant to the Florida panther. This should be considered for funding from the Florida Panther Trust Fund.
   Person Responsible and Timeline: Darrell Land to prepare Request for Proposal guidelines that will be advertised by October 1999. Eventual contractor will generate a compiled document to meet the goal with the document including information on:

   a. maps
   b. trends
   c. summary of telemetry data (unified)

GOAL 3: Monitor the Florida panther population with sufficient intensity to determine population trends and to assess the effectiveness of genetic restoration.

OBJECTIVES:

1. Improve kitten survivorship.
2. Improve recruitment of offspring.
3. Continue monitoring biomedical status (that includes genetics), especially for the purpose of assessing the overall impact of the genetic restoration.

RECOMMENDED ACTIONS:

1. Ensure that all kittens of radiocollared cats are permanently marked and that tissue samples are collected from every kitten at den sites (from birth through 30 days of age).
   Persons Responsible: the field crew, Darrell Land, Deborah Jansen and Sonny Bass
   Timeline: Ongoing

2. Identify highest priorities for biomedical assessment (i.e., what is absolutely necessary to meet the goal by the veterinarians and the researchers).
   Persons Responsible: the veterinarians and various biomedical researchers working in cooperation with Darrell Land, Deborah Jansen and Sonny Bass
   Timeline: September 1999

3. Maintain overall flexibility in capture protocol to maximize opportunities and capitalize on unplanned opportunities. If necessary, expand or shorten capture season.
   Timeline: Ongoing

The group also identified a capture priority list. The first priority is the F_1 individuals (from birth through dispersal). The second priority is the backcross individuals (from birth through dispersal). The third priority is Florida panther individuals (from birth through dispersal). Regardless of priority, whenever necessary and there is opportunity, it is important that adult cats that require re-collaring are captured, especially those animals that require biomedical assessment (i.e., sperm assessments for evaluating the impact of genetic restoration). All cats that require re-collaring shall be re-collared. Special emphasis should be given for capture opportunities on private lands.
Persons Responsible: field staff, including Darrell Land, Deborah Jansen and Sonny Bass, working in collaboration with the field veterinarian and with JoGayle Howard of the National Zoological Park [for semen assessments].)

On Day 2, the group returned to the originally identified Goal #4 (identify criteria for manipulating the population to achieve demographic goals). Initially, two objectives were identified to meet this goal: 1) maintain the current Florida panther population; and 2) facilitate population expansion. This then provoked much discussion on the factors that would influence the success of meeting these objectives, to include: minimizing inbreeding, maximizing breeding opportunities for most genetically valuable cats; improving the pedigree; minimizing the disruption of social groups; understanding habitat; describing the role of the Texas cougars already in the field; role of assisted breeding; translocation and disease/health status. Following this exercise, there were several hours of discussion on next approach. Eventually, it was determined that the role of assisted breeding and translocation were tools to reach the objective, not factors influencing success. The group then consolidated factors under habitat, genetics, disease, role of Texas individuals and resource issues categories. These were paired ranked to meet the two objectives:

1. **To maintaining the population:**
   Priorities in order: habitat, genetics, sources of animals, disease/health and role of Texas individuals.

2. **To expanding the population:**
   Priorities in order: habitat, genetics, disease/health, source of animals and role of the Texas individuals.

The working group then decided that maintaining and the expanding of the population should be goals, not objectives. Thus, the next goal is to:

GOAL 4: Maintain current population of Florida panthers.

RECOMMENDED ACTIONS (NONPRIORITIZED):

1. Meet the actions of Goal # 2 (involving habitat assessment) as well as determine rates of habitat loss. (See above for responsibility assignment.)

2. Distribute habitat information widely, including technical publication, electronic/digital (CD).
   Responsibility to be the agency's [FFWCC] technical publication department;
   Timeline: late 2000

3. Identify 'empty', suitable spaces within existing habitat that can be used to establish breeding units, including examining prey, cover, space, human/livestock conflicts and using GIS.
   Persons Responsible: NPS and Sonny Bass
   Timeline: , December 1999

4. Establish baseline for population census and demographic parameters (requiring confidence limits and power analysis) using multi-faceted monitoring (especially remote cameras).

Persons Responsible and Timelines: David Shindle, with support by Sonny Bass, will complete a proposal by July 1999 with project onset in 2000 and first estimates to be obtained in 2001. Preliminary explorations (feasibility trial) to be conducted by David Shindle and Larry Richardson beginning in July 1999.

5. Then continuously monitor the population using the same above technology, plus current methods, to establish trends.
   Timeline: Ongoing

6. Evaluate non-reproductive animals by pedigree analysis followed by appropriate animal-by-animal biomedical and behavioral analysis, etc. There are substantial data available on biomedical, pedigree and individual situations to explore problems, such as reproductive failure and differential fecundity failure. One can conduct animal-by-animal specific evaluations. Persons Responsible and Timelines:
   Pedigree by Darrell Land and Ulie Seal to be completed in August 1999.
   Biomedical correlation with the pedigree information to be coordinated by Darrell Land with the FFWCC veterinary staff and advisement of Sharon Taylor
   Timeline: throughout 2000

7. Follow the recommendations of the genetics working group formed at this workshop. Additionally, there is the need to translocate new genetic material into the Everglades segment of the Florida panther population. This should be accomplished by translocating at least one male. But there also is the possibility of using artificial insemination of a wild caught female (involving short-term capture and holding of a female).
   Persons Responsible: FFWCC in collaboration with NPS for moving a male. Darrell Land, JoGayle Howard and Dave Wildt will have further discussions about developing a protocol for artificial insemination.
   Timeline: August 1999

8. Identify the conditions for translocation of an animal to establish a breeding unit. Like Action #3, use the substantial data already available and animal-by-animal specific evaluations. There is a need to evaluate prey availability, cover, space and human/livestock conflicts.
   Persons Responsible: National Park Service and Sonny Bass
   Timeline: December 1999

9. Identify elements of the current biomedical management program that are critical to the annual capture season.
   Persons Responsible: FFWCC, NPS and FWS staff in cooperation with veterinarians including Suzanne Kennedy-Stoskopf
   Timeline: working group session tentatively planned for August,1999

10. Continue rehabilitation and return of short-term captured Florida panthers as currently done.
    Timeline: Ongoing

GOAL 5: Expand the Florida panther population.

RECOMMENDED ACTIONS (NONPRIORITIZED):

1. Meet the actions of Goal # 2 (involving habitat assessment). (See above for responsibility assignment.)

2. Using findings from Action #1, also identify suitable “empty” spaces within existing habitat that can be used to establish breeding units. Use GIS and other methods to examine prey, cover, space and human/livestock conflicts.
   Persons Responsible: National Park Service and Sonny Bass in partnership with Darrell Land
   Timeline: Winter 2000

3. Establish panthers in proposed space. Address prey, cover, space and human/livestock conflicts. This action will involve active stakeholder involvement. Persons Responsible: FFWCC, FWS and NPS
   Timeline: Ongoing as sites are determined

4. Follow the recommendations of the genetics working group formed at this workshop.
   Timeline: Ongoing

5. Use individual animal evaluation to select translocation candidates.
   Persons Responsible: FFWCC, NPS and FWS, as appropriate
   Timeline: Ongoing

6. Identify conditions for translocation, including examination of the IUCN guidelines for animal reintroduction/translocation.
   Responsibility FFWCC and NPS
   Timeline: As needed

7. Any translocated animal will be radiocollared and monitored at least at the level of the current monitoring level for Florida panthers (three times per week).
   Persons Responsible: FFWCC, NPS and translocation team
   Timeline: As needed

8. Identify elements of the current biomedical management program that are critical to future monitoring, including translocation.
   Persons Responsible: FFWCC, NPS and FWS staff in cooperation with veterinarians, including Suzanne Kennedy-Stoskopf.

9. Continue rehabilitation and return of short-term captured Florida panthers as currently carried out.

Another pair-ranking exercise was conducted to examine the relative importance of issues discussed within the above discussion. Priority rank was as follows:

1. Census status of the contemporary population.
2. Monitoring of the population.
3. Habitat loss.
4. Empty space suitability.
5. Maintaining biomedical program.
6. Genetics.
7. Animal-specific evaluation
8. Evaluation of non-reproductive individuals.

Health Working Group Report

Participants: Sharon Taylor, David Rotstein and Melody Roelke
Facilitator: Suzanne Kennedy-Stoskopf

Veterinarians have been a part of the Florida panther field team nearly since the inception of the Florida panther recovery. The historical basis for inclusion of a veterinarian related to one anesthetic death out of the first twelve field immobilizations and the concern that this related research mortality rate would be unsuitable for the endangered Florida panther population and unacceptable to the public. Since a veterinarian has been present in the field, there have been no anesthetic deaths with 186 immobilizations and only one capture-related death (cellulitis associated with dart site and subsequent septicemia). A tremendous amount of data has been generated related to physical examinations, anesthesia, clinical pathology, and serology by veterinarians in the field. This data needs to be systematically organized, evaluated, and disseminated in order to document health problems in the population and determine whether biomedical intervention and genetic restoration have been beneficial to the population. Furthermore, thoughtful analysis of data is necessary to determine future directions of biomedical research.

GOAL 1: Continue complete physical examinations of individual Florida panthers to maintain and augment health parameter databases in order to assess trends within the population.

OBJECTIVES:

1. Minimize risks associated with immobilization. Keep a complete anesthetic record for each immobilization.
2. Establish guidelines for a complete physical exam on adult and neonatal animals. Maintain individual medical records.
3. Identify parameters that will be useful for assessing the effectiveness of genetic restoration.
4. Identify parameters that will be useful for assessing reproductive fitness and fecundity.
5. Establish health assessment guidelines for translocation of free-ranging panthers in southern Florida and introduction of additional animals for genetic restoration.
6. Establish health protocol recommendations for translocation of captive Florida panthers between institutions.

RECOMMENDED ACTIONS:

1. A risk assessment that is based on accumulated anesthetic records needs to be done to determine percent of animals that had anesthetic complications requiring veterinary intervention in order to evaluate potential risks of field immobilizations.
   Person Responsible: Field Veterinarian
   Timeline: October 1999

2. Continued presence of a veterinarian in the field to monitor status of anesthetized animals and determine advisability of following guidelines as outlined for physical exam and sample collection below.

3. Create a procedures manual for physical examinations and current field anesthetic regimens. Include in the procedures manual existing instructions for contacting emergency facilities when injured animals are found. An annual review of protocols will be made prior to the start of each capture season to allow assessment of new and presumably safer immobilization drugs and effectiveness of physical exam protocols.
   Person Responsible: Field Veterinarian
   Timeline: October 1999

4. The veterinarian should have the ultimate responsibility to insure that complete anesthetic and medical records are maintained. The veterinarian will train field personnel in recording biomedical field data onto physical and anesthetic records. Part of the record will include the presence or absence of traits associated with inbreeding (i.e. kinked tails, cowlicks, cryptorchidism).

5. Address feasibility of conducting and recording ultrasound examinations in the field to evaluate cardiac defects to determine prevalence of atrial septal defects in the population. This data will be used to evaluate the effectiveness of genetic restoration. Determine feasibility by consulting with a board certified veterinary cardiologist by next capture season and implement if feasible that capture season (1999-2000).
   Responsibility: Field Veterinarian
   Timeline: 1999-2000

6. The veterinarian should develop protocols with the assistance of reproductive physiologists which can be conducted by field personnel to measure and record testicular morphometrics and other measurements of reproductive fitness by the start of next capture season.

7. Reproductive physiologists should identify procedures and techniques for assessing reproductive fitness and fecundity that will require their presence in the field to conduct. The field team and reproductive physiologists should coordinate schedules to optimize the number of animals for evaluation during the next capture season.

8. Develop health assessment guidelines for translocation of free-ranging panthers in southern Florida and introduction of additional animals for genetic restoration.
   Person Responsible: Field Veterinarian
   Timeline: October 2000

9. Compile and distribute health protocol recommendations for translocation of captive Florida panthers between institutions.
   Person Responsible: Field Veterinarian
   Timeline: October 2000

GOAL 2: Establish protocols for sample collection, distribution, and archiving.

OBJECTIVES:

1. Maximize the utilization of samples obtained from each animal.
2. Prioritize sample collection and utilization.
3. Assure adequate archiving of collected samples.

RECOMMENDED ACTIONS:

1. Biological samples collected and their proposed uses should be evaluated yearly by the veterinarian with input from field biologists.
   Person responsible: Field Veterinarian
   Timeline: Ongoing annually

2. The veterinarian should prioritize the relative importance of samples collected in the event that all samples cannot be collected from an individual during a single immobilization. Person Responsible: Field Veterinarian
   Timeline: To be completed prior to each capture season because it will vary.

3. Protocols for samples collected should be included in the physical exam procedures manual, and is the ultimate responsibility of the veterinarian. Protocols should include sample type, amount needed, sample handling and processing, shipping, and archiving to insure their usefulness to present and future investigations.

4. The veterinarian should train field personnel to collect and handle biological samples appropriately. Prior to each capture season, the veterinarian will assess if additional training is required to implement new sample protocols.
   Person Responsible: Field Veterinarian
   Timeline: Ongoing

GOAL 3: Facilitate and prioritize research initiatives.

OBJECTIVES:

1. Standardize protocol for request of samples for research outside the agency.
2. Prioritize research initiatives.
3. Create an ad hoc advisory board of specialists to assist the veterinarian in the development of biomedical research priorities.

RECOMMENDED ACTIONS:

1. The veterinarian should oversee the development of a request process for biological samples for research purposes. This will not exceed 2 pages but should include justification of the study for which samples are requested; types and amounts of requested samples; how samples are to be handled in the field; how samples are to be handled for shipment; what samples are to be used for and expected outcome; and expected date of completion of the study.
   Person Responsible: Field Veterinarian
   Timeline: September 1999

2. The veterinarian should oversee a review committee, which will include the south Florida panther coordinator and other appropriate scientists, to prioritize projects and determine applicability to current management, recovery, and research needs of the Florida panther project.
   Person Responsible: Field Veterinarian
   Timeline: 1999-2000

3. A panel of specialists should be organized by the veterinarian to meet yearly to evaluate current biomedical studies and make recommendations for future directions of biomedical research.
   Person Responsible and Timeline: The Field Veterinarian will determine the composition of this advisory board by September 1999.

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GOAL 4: Manage biomedical data.

OBJECTIVES:

1. Biomedical data and samples should be readily retrievable.
2. Biomedical data should be periodically reviewed to assess trends in overall health status of the population and provide useful biomedical parameters to assist in demographic modeling.
3. Biomedical data should be evaluated in a timely fashion and the results made known.

RECOMMENDED ACTIONS:

1. Databases for biomedical samples collected as part of a physical examination will be updated and maintained by the biomedical assistant. This will require a part-time staff position to enter backlogged data into the appropriate databases so they are current.
   Person Responsible: Biomedical Assistant, overseen by Field Veterinarian
   Timeline: August 2000

2. An accessible record keeping system should be available for the explicit purpose of logging and tracking collected samples that are distributed and archived. A temporary person should be hired to update the existing database (Microsoft Access) as quickly as possible in order to facilitate sample requests.

3. A consulting epidemiologist should be identified, who in conjunction with the veterinarian, will review databases to determine trends in the health of the population and assist in the development of future studies to address health issues. The epidemiologist should assist the veterinarian and demographers in identifying parameters that can be used for assessing the impact of biomedical intervention and genetic restoration on the population. This should be implemented as soon as databases are current.

4. A directory of current investigative studies involving the Florida panther should be established under the supervision of the veterinarian and the south Florida panther coordinator. A reasonable time line will be established for the completion of studies, reporting of results, and dissemination of findings. In some cases, results may dictate an expansion of time lines.
   Persons Responsible: Darrell Land and Field Veterinarian
   Timeline: October 1999

5. Results of biomedical studies should be published in peer-reviewed journals and commission reports. This is vital for dissemination of information and validation of sample collections. A current backlog of biomedical information exists and is in the process of being evaluated and prepared as manuscripts for submission to peer-reviewed journals.

6. A description of papers and their projected times of submission and acceptance currently exists.
   Timeline: This process should continue annually to insure that studies begin and end in a timely fashion.

GOAL 5: Gross and histological post-mortem evaluations should be conducted on all recovered panther carcasses to evaluate the effectiveness of biomedical intervention and genetic restoration.

OBJECTIVES:

1. Necropsies will be conducted on all panther carcasses.

RECOMMENDED ACTIONS:

1. Identify facilities with board certified veterinary pathologists to which panther carcasses will be sent for complete necropsies. A protocol will be placed in the procedures manual for submission of dead animals.
   Person Responsible: Field Veterinarian
   Timeline: September 1999

2. Recognizing that field situations may not always be conducive to submitting carcasses to diagnostic facilities in a timely fashion, a protocol should be added to the procedures manual for how the field veterinarian will conduct these necropsies. The veterinarian will be trained by a pathologist(s) to conduct field necropsies.
   Person Responsible: Field Veterinarian
   Timeline: October 2000

3. The veterinarian should have the ultimate responsibility to insure that complete pathology reports are obtained and enter the permanent medical records. The veterinarian will generate a summarized report for distribution to the field and recovery teams.
   Person Responsible: Field Veterinarian
   Timeline: Beginning 1999 field season

Genetics Working Group Report

Participants: Phil Hedrick, Holly Jensen, Jim Krakowski, Shauna Land, Tom Logan, Dave Maehr, Sumner Mathes, Steve O'Brien, Jack Pons
Facilitator: Susie Ellis

The group began by identifying key problems and issues related to genetics of the Florida panther. These were:

- Need to determine paternity of F_1 cats.
- What to do with Texas cougars in Florida.
- Is our design premise (original) still sound in light of today's revelations?
- Should captive animals be incorporated into wild population?
- What has been consequence in terms of fitness parameters – e.g. markers of inbreeding (kinks, cowlicks, cryptorchidism, etc. in F_2s)?
- Does introgression or genetic restoration solve the problems we've seen?
- Concern about F_2's breeding with Texas cats and ending up .75 TX ancestry.
- Pedigree database hasn't been established.
- Loss of local adaptation in terms of fitness and adaptation to local south Florida environment.
- Need to develop a morphological profile/analysis for the panther.
- Determine the genetic identity for all Florida panthers and Texas cougars using molecular genetics techniques.
- Many F_1 cats not radio-collared—prevents adequate monitoring.
- How have evolutionary traits of population changed in terms of adaptation to the environment (e.g., landscape-influenced adaptations)?
- Is it appropriate to consider the Florida panther and previously identified subspecies as one interacting population?
- Is *stanleyana* the best choice for restoration? (Consensus was probably, since the North American population has sustained over a long period of time).

These then were collapsed into the following six issues and prioritized using paired ranking:

Priority Issue 1: We need to determine the paternity of F1 cats.

a. Need to determine paternity of F1 cats by molecular genetic techniques.
b. Need to develop a morphological profile/analysis.
c. Many F1 cats are not radio-collared.
d. Is it appropriate to consider the Florida panther and previously identified subspecies as one interacting population?

Priority Issue 2: We need to decide what to do with Texas cougars in Florida.

a. What has been the consequence in terms of fitness parameters, e.g. inbreeding markers?
b. Does introgression or genetic restoration solve problems we've seen?

Priority Issue 3: We need to determine whether there is a loss of local adaptation in terms of fitness and adaptation to local south Florida environment.

a. How have evolutionary traits of population changed in terms of adaptation to the environment?
b. Is it appropriate to consider the Florida panther and previously identified subspecies as one interacting population?

Priority Issue 4: We need to evaluate whether our original design premise is still sound in light of today's revelations.

a. Is our original design premise still sound in light of what we now know?
b. Is *P. c. stanleyana* still best choice for restoration?

Priority Issue 5: We need to determine the fate of *P.c. stanleyana* cougars.

a. What should be done with the *P.c. stanleyana* cougars?

Priority Issue 6: We need to determine whether or not captive animals should be incorporated into the wild population.

a. Should captive animals be incorporated into the wild population?

The group then worked together to tighten definitions of these issues into goals, to develop objectives to address these goals, and to recommend actions to achieve each objective, including assignment of an individual(s) or group(s) to take responsibility for each action, either by carrying it out personally or by recruiting others to help.

GOAL 1: Perform molecular genetic analysis, including individual genotyping of Florida panthers, Texas cougars, F1 animals and assess parentage.

OBJECTIVE 1: Conduct molecular genetic and related analyses on Florida panthers, Texas cougars and F_1's to obtain baseline information on Florida panthers and Texas cougars to evaluate progress.

RECOMMENDED ACTIONS:

1. Assemble extant SPARKS data sheets and send to Ulie Seal.
   Person Responsible: Sharon Taylor
   Timeline: July 1, 1999

2. Enter above data into SPARKS program.
   Person Responsible: Ulie Seal
   Timeline: July 15, 1999

3. Develop and maintain a mechanism for regular updating of SPARKS database.
   Person Responsible: Darrell Land, Sharon Taylor *et al.*
   Timeline: Ongoing after July 15, 1999

4. Construct pedigree and analyze representation from pedigree.
   Person Responsible: Bob Lacy
   Timeline: ASAP after December 1, 1999

5. Send biological samples already in hand to Steve O'Brien's laboratories at the National Cancer Institute as well as to an independent lab for confirmation of results.
   a. Determine what's in hand
   b. Arrange transport
   c. Who are paternal/maternal candidates?
   Person Responsible: Sharon Taylor
   Timeline: July 1, 1999

6. Complete the analysis of current blood and tissue samples and assess paternity.
   Person Responsible: Steve O'Brien
   Timeline: December 1, 1999 or three months after receiving samples

7. Collect and maintain biological specimens for future access.
   Person/Organization Responsible: Propose the National Cancer Institute
   Timeline: In perpetuity

OBJECTIVE 2: Continue banking biological samples for future analyses on all animals handled in an attempt to approach 100% representation.

RECOMMENDED ACTIONS:

1. Biological specimens (blood and skin biopsy) are collected from all animals handled, including neonates, beginning today.
   Responsible: FFWCC (Tom Logan and colleagues)
   Timeline: beginning June 9, 1999

2. Ship samples to repository at the National Cancer Institute as soon as possible, preferably within 24 hours.
   Responsible: FFWCC
   Timeline: beginning June 9, 1999

3. Review/revise handling protocol to ensure that needed samples are obtained from all handled animals including neonates/kittens.
   Responsible: FFWCC/USFWS, spearheaded by Tom Logan
   Timeline: October 1, 1999

4. Biological specimens held in the repository shall be available for research applications that apply to Florida panther conservation with advice and approval of FFWCC and USFWS.
   Organization Responsible: FFWCC/USFWS
   Timeline: Ongoing

5. Develop resources to pay for the costs of the repository.
   Organization Responsible: FFWCC
   Timeline: January 1, 2000

GOAL 2: Determine the consequence of genetic restoration in terms of identified fitness parameters (namely cryptorchidism, kinked tail, cowlicks, sperm quality, atrial septal defects, disease, size, weight and other physical characteristics) in F_1 animals and other animals with Texas ancestry.

OBJECTIVE 1: Develop a profile of correlates to measure the effects/impacts of genetic restoration on the physical manifestations of inbreeding.

RECOMMENDED ACTIONS:

1. Collect and record phenotypic trait for every animal handled.
   Person Responsible: Field Staff
   Timeline: Ongoing

2. Analyze above (pedigree analysis).
   Persons Responsible: Bob Lacy/Steve O'Brien, Field Crew, *et al.*
   Timeline: Ongoing

OBJECTIVE 2: Determine presence/absence/degree of physical manifestation of inbreeding.

RECOMMENDED ACTIONS:

1. Develop explicit descriptive criteria for assessing qualitatively and quantitatively the six manifestations of inbreeding (namely cryptorchidism, kinked tail, cowlicks, sperm quality, atrial septal defects, disease and other physical characteristics).
   Persons Responsible: Veterinary Supervisor and Reproductive People (Sharon Taylor, JoGayle Howard)

2. Determine presence/absence/degree of manifestation of selected, readily observable manifestations of inbreeding during field examinations using criteria developed in #1 above (e.g., cryptorchidism, kinked tail, cowlicks).
   Persons Responsible: Field Crew
   Timeline: Ongoing

GOAL 3: Identify components of fitness which are specific to the Florida panther and monitor their incidence in the entire restored population, including the potential and current presence of adaptations specific to their habitat as a result of adaptive gene combinations.

OBJECTIVE: Suggest measurable characteristics that may be adaptive. These might include:

- skull morphometrics
- pelage characteristics
- a behavioral "style" inventory including characteristics such as
  - tolerance to people
  - behavior at capture (e.g., F_1 panthers may leave trees a lot more than Florida panthers, higher drug dosage needed to sedate them).

RECOMMENDED ACTION:

1. Develop measurement protocol. Combine with morphological traits of inbreeding.
   Person Responsible: Dave Wildt to identify behaviorists and physiologists to develop the protocol.
   Timeline: October 1, 1999

GOAL 4: Determine whether or not our original design premise is still sound in light of what we know now.

OBJECTIVE 1: Continue monitoring to ensure that desired/target rate of restoration/refreshment continues.

RECOMMENDED ACTIONS:

1. Continue genotypic and phenotypic monitoring (numbers of animals, phenotypic appearance, genotype) as outlined in the restoration plan. (SEE ALSO ISSUE 1, GOAL 2 this report).

2. Implement adaptive management as needed to be sure restoration goals are met.
   Person Responsible: FFWCC

3. Annual reports from the field staff.
   Persons Responsible: Field Staff

4. Identify the appropriate timing of workshop(s) to review the plan/design/success.
   THREE TYPES OF MEETINGS:
   a. Agency level: a formal annual meeting to review accomplishments of the year and to review the data and assure on-track with the program.
   b. Identify/suggest date for workshop to provide "final" analysis of genetic restoration and development of a management plan.

c. Responsible: Participants in this meeting
d. Timeline: As soon as possible
e. Make a statement of need regarding appropriate time for a full PHVA.

GOAL 5 Part 1:. Determine the extent of Texas cougar genetic contribution to the restoration of Florida panther population genetics and evaluate if and when any of the released Texas cougar females should be physically or reproductively removed from the population.

OBJECTIVE 1: Determine whether females have made their contribution as planned and is a contribution that would exceed their individual goals problematic to the population.

RECOMMENDED ACTION:

1. Carry out an analysis to examine the level of complexity that 75% Texas back-crosses may or may not present. Ask/analyze whether increased contribution by females is a problem and if so, propose some suggested solutions. Consider: 1) potential for over-contribution of any female that is released; and 2) problems with back-crossed female F1's and male F1's.
   Person Responsible: Phil Hedrick to do analyses -- in light of typical panther demographics (including sex and age structure), social behavior (e.g., dispersal tendencies of the different sexes) and legal implications -- of having 75% back-crosses. Copy to all members of Genetics group. Susie Ellis to contact Phil Hedrick to determine his willingness to conduct the analysis and a time frame under which he can complete it.
   Timeline: In progress

GOAL 5 Part 2: Identify humane and equitable disposition of Texas cougars as each female reaches its predetermined genetic contribution to the recovery effort.

OBJECTIVE 1: Examine options/range of flexibility for disposition according to FFWCC protocol.

DISCUSSION STARTING POINT: There are two options: Leave or remove.
The Plan provides that they *may* be removed if needed. However, animals may be left if over-competition and over-contribution are NOT problems.
If Texas cougar females were contracepted, they would be removed if they were competing for space.
Options for Texas cougar females:

a. leave reproducing in wild
b. leave in wild contracepted→present problems in terms of taking up space and resources
c. remove. If they're removed, it's provided for in protocol. BUT, not all members of group agree on protocol directives.

There is a concern that the controls originally intended have not been implemented (i.e., removing females once target contribution made). Steps identified to determine when this should happen.

OBJECTIVE 2: Develop criteria to determine when/if animals should be removed.

RECOMMENDED ACTIONS:

1. Send the best data regarding animals on the ground to Phil Hedrick
   Responsible: Field Staff
   Timeline: June 20, 1999

2. Predict long-term trend based on current practices and those proposed at this meeting. Consider increasing diversity by removing Texas females that have contributed, replace with new females. This will be predicated on Hedrick's analysis.
   Person Responsible: Phil Hedrick and others to be determined

3. Examine the relative genetic contributions of all females (next evaluation?).

To address the above goal in a more immediate sense, Bob Lacy carried out an on-the-fly analysis that indicated, based on animals presently on the ground, there are:

- 55 pure Florida panthers (approximately)
- 5 pure Texas cougars (1 died)
- 11 F_1 kittens
- 3 kittens 75% TX
- 1 kitten 25% TX

Based on these numbers, we can estimate that there are 18% TX genes in the population. If we remove all 6 Texas females, there will be 11% TX genes in the population. (This assumes that one Texas female is equivalent to 2 kittens genetically.)

If 12 more F_1 kittens are produced, then the Texas females pulled, then we would essentially be in the same place we are now. This assumes that Texas cougars are as likely to breed as the Florida panthers (i.e., all animals are equally likely to breed).

Additional notes of import:

- TX101 already is contracepted but has not been pulled from the wild.
- TX 107 has five offspring on the ground, including three seen at the den this year.
- We need to consider removal of Texas females when they have made their full contribution, as planned, and then developing a mixed management strategy in the future.

4. Develop solutions based on Hedrick's analyses.
   Questions/issues to consider in the analyses and for the resulting recommendations:
   - At present, we do not have sites for placement/disposition.

- Is it possible that genetic goals have been met now, if so, do some females need to be removed immediately?
- What are follow-up actions?
- Reasons for removal may not be based on contribution but based on needing more management control.
- Need to determine the critical decision point for removal.
- Minimal criteria = when 2 F1's are recruited and breeding.

Organizations Ultimately Responsible: Decision/recommendations to be made by FFWCC/USFWS.

RELATED PROBLEMS DISCUSSED BY THE GROUP:

- There is a lag-time with other litters on the ground in the meantime. Is contraception before this juncture an option?
- Should the Texas females simply be removed once they've made their contribution? This precludes the potential for over-representation. We know that we can always add more Texas genes if needed.
- We may wish to be conservative in our recommendations, and also keep open the option of bringing in more Texas cougars if needed. This brings to a head more quickly the issue of disposition of females. The concern regarding swamping can be solved by removal of females.

The Group agreed that:

- we want to meet the genetic objective.
- there is a problem with the lag-time/recruitment cycle for each female.
- there are four females, TX101, TX105, TX107, TX108, that are at a point of needing a management decision (e.g. physical removal or contraception).
- we want input from geneticists in decision-making process.
- there is a need for a decision is urgent.

We agree that two of the Texas cougars appear to have met their restoration objectives. There is concern about the potential for their overrepresentation. Therefore, we propose that Texas cougar females should be removed (physical removal is preferred, but contraception is an option) when, at least, two of their kittens have established territories and, at most, when an individual female has four independent kittens.

QUESTIONS FOR PHIL HEDRICK:

1. Is there a need for .75 *stanleyana* males in the program?
2. Are .75 *stanleyanas*, regardless of sex, detrimental to the population?
3. Review our protocol/criteria for female Texas cougar removal.
4. Ask Phil to suggest follow-up actions and data needs we may have omitted.

GOAL 6: Address the concern that there are individuals in the captive population that represent lineages not represented in the wild and whether or not these animals should be incorporated into the wild population.

OBJECTIVE 1: Include genetic contribution of these animals, in some form, to wild population.
One side-benefit of this approach is that it counters some of the swamping issues.

OBJECTIVE 2: Breed said animals and rear female offspring so as to maximize the probability of survival following reintroduction. Reintroduced into South Florida to restore those lineages that no longer exist in the wild.

RECOMMENDED ACTIONS:
1. Select individuals from unrepresented lineages.
2. Select appropriate pairings to produce offspring suitable for release into the wild population.
3. Rear resulting offspring in a manner that prepares them for reintroduction.
4. Select appropriate site for reintroduction.
5. Release.
6. Monitor and evaluate.

AD HOC GENETIC ISSUE (POST PRIORITIZATION)

Given the new information about the “cougars” that may be interacting with Florida panthers in and around the Big Cypress Seminole Indian Reservation (BCSIR), and given the origin and parentage of those animals are unknown, and given that any genetic contribution of these animals into the south Florida panther population may alter the planned process of genetic restoration, we believe that this is a problem that requires immediate attention.

POSSIBLE ACTIONS:

1. With the concurrence of the BCSIR, capture each animal.
   Options to Address the Above Concerns:
   a. Radiocollar, transpond, and collect tissue samples for genetic analysis from all animals if possible (with emphasis on males).

    b. Prevent future reproduction, either permanently by sterilizing each animal, or temporarily by contracepting, or a combination of both.

2. Cooperate with BCSIR to retrofit existing “enclosure” to prevent future escape of BCSIR “cougars” into the wild.

3. Develop a cooperative program with the BCSIR that targets Florida panther conservation.
   Persons Responsible: FFWCC and USFWS, Phil Hedrick, Steve O’Brien
   Timeline: ASAP

4. Include representatives of the BCSIR in future Florida panther PHVAs, FPIC meeting and other technical and policy meetings that involve Florida panther recovery.

5. Determine how this affects the other recommendations for action made by the group?
   Persons Responsible: Phil Hedrick, Steve O’Brien
   Timeline: ASAP

Captive Breeding Working Group Report

Participants: Forrest Penny, Mike Jones, Jennifer Hackshaw

The group began by identifying key problems and issues related Florida panther captive breeding. These were:

- Aging group of Florida Panthers in captivity.
- Value of captive population for recovery can be expanded.

GOAL 1: Maintain the current captive population through an approved breeding program for:

1. **Genetics --** salvage and enhance current genetic material.
   a. Selective breeding of available animals to preserve existing captive animals (including breeding animals temporarily brought into captivity from the wild for rehabilitation)
   b. Introduction of genetic material from the wild population (i.e. artificial insemination)
   c. Assess lineage of captive animals to determine if introduction of genetic material from the captive population into the wild population is desirable

2. **Education –** zoos currently reach more than 1 million visitors with the potential to reach more than 3 million visitors annually on issues related to the Florida panther recovery program. There is a need to implement a uniform, coordinated education program to support panther recovery.

3. **Research –** should be carried out with animals available as needs are identified, including:
   a. Reproductive research (artificial insemination, embryo transfer, *in vitro* fertilization, sperm collection, cryopreservation technology)
   b. Vaccine development
   c. Immunological function
   d. Genetic anomalies
   e. Serving as contaminant control group

RECOMMENDED ACTION 1: Obtain agency authorization to initiate program.

Measurable outcomes.
- Current captive genetic diversity is enhanced.
- Captive source population is maintained to assist wild population management needs.
- Coordinated education program to assist recovery.

- Continue to provide facilities for emergency needs of the wild population.
- Serve research needs in a captive environment.
- Act as a potential repository for Texas cougars.

The group listed the individuals currently in captivity and made several recommendations for captive pairings and moves.

Current population

Facility	**Specimen number**	**Rank**	**Lineage**
White Oak	202 (male)	Critical blood line	Sire- 37 (prob.) Dam- 9
White Oak	204 (female)	Important blood line	Sire- 12 Dam- 31
Jacksonville	210 (male)	Important blood line	Sire- 42 Dam- 23
Jacksonville	209 (female)	Important blood line	Sire- 42 Dam- 23
Lowry Park	207 (male)	Bilaterally cryptorchid	Sire- 26 Dam- 36
Lowry Park	208 (female)	Critical blood line	Sire- 12 Dam- 32

Initial breeding recommendations (made with consideration to leave breeding females at current facilities):
202 and 204
210 and 208

Moves to support breeding recommendations:
210 from Jacksonville Zoo to Lowry Park Zoo
207 from Lowry Park Zoo to Tallahassee Zoo

Note: Individuals 202, 204, 209 and 210 share a distant Piper lineage.

Modeling Working Group Report

Participants: Jane Comiskey, Patricia Cramer, Stephen Williams
Facilitator: Robert Lacy

PRIORITY ISSUES

The Modeling Working Group began its discussions by listing issues related to PVA modeling. A paired ranking procedure was then used to identify the issues which were broadly viewed as of the highest priority – either in terms of urgency of action or in terms of overall importance for the conservation of the Florida panther. Below is the list of the issues, in order of priority, with the cumulative priority scores given in parentheses.

ISSUE 1: Inclusion of landscape/habitat features in models to assess probability of panther survival so that land use, changes in landscape which produce changes in carrying capacity, habitat fragmentation, and connectivity issues can be addressed. There are spatial components to many of the factors which influence panther survival. Spatial proximity among individuals in a small population, barriers to movement, ground surface elevation patterns, hydrologic factors, spatial distribution of panther habitat (stalking cover, bedding and denning sites), and spatial variations in prey densities are all critical to panther growth and survival. Averaging over spatial domains and individuals can obscure the contribution of maximum and minimum values to overall survival. (36)

ISSUE 2: Determine whether there a consensus on the Maehr et al. model (the recent reanalysis of Florida panther viability, presented by David Maehr at the workshop). Determine whether there are significant points of disagreement. Compare input parameters for '89, '92, and '99 runs of VORTEX model. Focus on which parameters have changed and why. Are these changes justified based on current data? (32)

ISSUE 3: Inclusion of cultural/social/economic/regulatory/legal aspects in future models. (28)

ISSUE 4: Metapopulation/reintroduction/expanded population models. (27)

ISSUE 5: Facilitate data gathering and sharing for spatial models. Data requirements for detailed spatial models are substantial. Good communication is needed to facilitate data gathering and sharing of results among field biologists, landscape people, modelers, and planners. Agreement on parameter values and data layers across models would facilitate comparisons of model results. (25)

ISSUE 6: Determine implications of results from current PVA models for needed actions. (25)

ISSUE 7: Develop a “world map” of threats and impacts on Florida panther viability. Incorporate regional planning and projected effects of human growth -- factors which are ignored in many wildlife projections/models. This representation or map would reflect the role of the Florida panther in ecosystems and the role of a healthy ecosystem in maintaining the panther's prey base. (24)

ISSUE 8: Inclusion of political analysis in modeling efforts: including funding issues, legislative agendas, and development trends. (11)

ISSUE 9: Cost/benefit of various recovery actions, such as education, construction of underpasses, etc. Quantify parameters, look for spatial differences in values. (8)

ISSUE 10: Compare the panther situation to lessons learned from other species being recovered. (6)

While all the above issues are ones that need further exploration within the Florida panther recovery program, the Modeling Group focused on addressing the first 6 priority issues. For some issues (2, 4, and 6), analyses and some resolution of the issues could be obtained in the further work of the group at the workshop. These analyses are presented in the next section. For the other issues, the working group clarified goals and identified actions needed to better address these issues. These recommended actions are described at the end of the Modeling Group report.

REVIEW AND ASSESSMENT OF THE PVA PRESENTED BY D. MAEHR ET AL.

David Maehr presented a recent population viability analysis for the Florida panther at the workshop. An abstract of this analysis is given within Box 1.

Maehr et al. obtained their values for the reassessment of Florida panther viability by first having each co-author determine independently what values he could extract from published literature, agency reports (especially the recent annual report on Florida Panther Genetic Restoration and Management [Land and Taylor 1998]), field experience, and other information available to each co-author. The co-authors then reviewed the differences in their initial, independent PVA models, and arrived at a consensus model which those five co-authors felt adequately describes the current viability of the Florida panther. Maehr reported that this consensus model indicates that the existing wild population of Florida panthers has adequate reproduction and survival to be stable demographically and even to expand into new habitat if it becomes available. However, the population in south Florida has so few breeding individuals that substantial genetic deterioration is likely over the next century, leading subsequently to the possibility of extinction, even if genetic restoration continues with the release of two more cougars from Texas every 10 years. However, the population was projected by Maehr et al. to expand rapidly into additional habitat (if it could be made available and were accessible to the Florida panthers), potentially increasing to a more demographically and genetically stable population size.

Box 1.

A REASSESSMENT OF FLORIDA PANTHER VIABILITY ANALYSIS AND RECOVERY EFFORTS FROM MULTIPLE PERSPECTIVES

DAVID S. MAEHR, University of Kentucky, Dept. of Forestry, Lexington, KY; ROBERT C. LACY, Chicago Zoological Society, Brookfield, IL; E. DARRELL LAND, Florida Game and Fresh Water Fish Commission, Naples, FL; ORON L. BASS, Everglades National Park, Homestead, FL; and THOMAS S. HOCTOR, University of Florida, Gainesville, FL.

Abstract -- We used Vortex (Lacy et al. 1995) to model Florida panther (*Cougar concolor coryi*) population viability from five perspectives. Independent analyses were based on demographic inputs provided by a federal field biologist, a state field biologist, a university conservation biologist, a university landscape ecologist, and an NGO population biologist. Despite a lack of full consensus regarding the inputs and results of earlier modeling efforts (Seal et al. 1989, Seal and Lacy 1992), management of this endangered subspecies moved forward first with a plan for captive breeding (which has yet to be implemented) and more recently with genetic restoration. Since 1994, 8 female cougars, introduced from Texas, have produced at least 12 hybrid kittens. Eight may nearly equal the breeding female segment of the population where N_e/N may be as low as 0.26. Panther recovery has been controversial, with genetic restoration efforts being questioned by analyses which suggest demographic stability of the population may obviate the need for such a radical approach to small population management (Maehr and Caddick 1995). Our analyses suggest that the Florida panther has a high probability of persisting for 100 years, however genetic problems will become increasingly severe with time - especially beyond 100 years. We recommend an approach that incorporates genetic introgression, rapid population growth in captivity, and an increased emphasis on expanding the current range of the Florida panther. Improvement in habitat trend data will make substantial improvements to future simulations.

The Modeling Working Group reviewed the values used by Maehr et al. to describe the present population. The values used by Maehr et al. are summarized, and compared to values used in earlier PVA efforts for the taxon, in Box 2. In this review, the Modeling Working Group felt that the values used by Maehr et al. were based on reasonable interpretations of the currently available data, but that some parameters were only poorly known and alternative characterizations of the population were possible. In particular, the much lower estimate of (20%) first-year mortality was based on observed losses of kittens, including those cases in which kittens were documented to have disappeared prior to the expected age of dispersal from the den. Yet, if young panthers that were not radio-collared or otherwise re-observed had died after the last observation of kittens at the den, then first-year mortality could have been as much as three-fold higher.

The rationale for the shifts in values from the PVA models assessed in 1989 and 1992 to those used by Maehr et al. in 1999 was presented to the workshop plenary. Some participants at the workshop expressed concern that the first year mortality might be much greater than had been estimated by Maehr et al. This controversy over the mortality of juveniles existed when the analyses were completed in 1992: In that PVA, the dominant view was that mortality was near 50%, but some participants thought that the rate of mortality was nearer 20% and that alternate scenario was also examined in the 1992 modeling.

Given the uncertainty regarding this critical demographic variable, the Modeling Working Group conducted sensitivity tests to explore the effects of higher levels of first-year mortality (while using the other values proposed by Maehr et al.). We also projected the effects of various possible future conservation and management actions: including varying rates of release of additional Texas cougars; provision of additional habitat, either to allow expansion of the existing population or to create a second, largely independent population; and possible losses of existing habitat.

Box 2. Comparison of input parameters used in 1989, 1992, and Maehr et al. (1999) Population Viability Analyses

Primary estimates used are given first; other values tested are given in parentheses.

	1989	**1992**	**Maehr et al.**
Inbreeding depression (lethal equivalents)	3.4 (0,1.0,1.7)	3.0 (0,1.0)	3.14
Female breeding age	3 (2)	2 (3)	2
Male breeding age	3 (2)	2 (3)	4
Maximum age	15	12	12
Females breeding / yr	50	50	50
Mean litter size	3.0 (2.5)	2.0	2.175
% males breeding	100	50	50
1st yr mort	50	50 (20)	20
2nd yr mort (F/M)	30	20	20/30
3rd yr mort	25 (20)	20	17/30
4th + yr mort	25 (20)	20	17/15
Catastrophes	none	none	0.5% probability 5% repro. decline & mort.
N(0)	45	50 (30)	60
K	45 (30,60,80)	50	70
Change in K	0 (-10,-20,-50%) -	25% (0,-50%)	0 (-25%)
Removals	0 (6,12)	none	none (6 f)
Releases	none	none	2 f / 10 y (none)
Mean growth			
deterministic	-0.057	-0.018	0.120
simulation	not reported	-0.069	0.083
Prob. Persistence	0	0	100%
N			66

FURTHER POPULATION VIABILITY ANALYSES

Additional models were analyzed and tabulated during the workshop to address questions raised in plenary discussions. For each question discussed, sets of simulations were run, assuming different possible rates of first year mortality from 20% to 60%, spanning the range of proposed values, and different rates of possible future releases of Texas cougars to continue genetic restoration.

For each simulation, projected results (at 100 years) are presented for:

- mean population growth (r): the rate at which the population is potentially capable of growing until carrying capacity is reached,
- probability of extinction (PE), determined by the proportion of simulated populations out of 100 that went extinct,
- average population size (N) at 100 years, with a carrying capacity ceiling at 70 individuals,
- variation in population size (SD(N)), to give an indication of the stability of the population,
- percent of initial gene diversity retained, or what geneticists generally call "expected heterozygosity", and
- percent of the genes in the final population descended from original Florida panther genes rather than Texas cougar genes. The starting point is assumed to be 20% Texas cougar and 80% Florida panther genes, which is the stated goal of the current genetic introgression project, although this target has not yet been met. With no future releases, this ratio will be maintained. Although deviations from this ratio could result from chance occurrences or differences in fitness, this is the long-term expected average if there are no further releases of Texas cougars.

Varying Juvenile Mortality and Supplemental Texas Cougar Releases

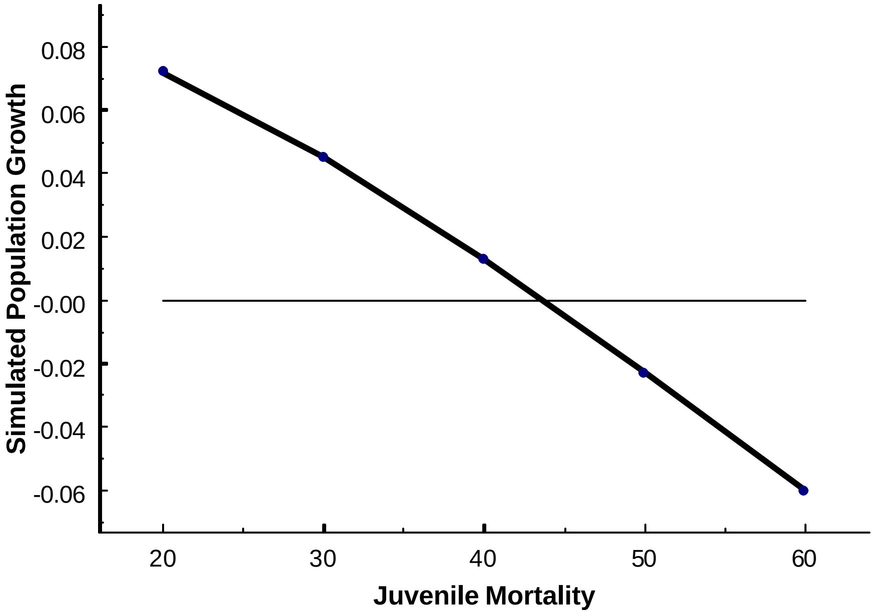
The first set of simulations, summarized in Table 1, varies the number of future releases of Texas cougars (0, 2, 4, or 8 individuals every 10 years) into populations with each hypothesized rate of first year mortality (20, 30, 40, 50, and 60%). Figure 1 graphs the relationship between simulated population growth (y-axis) and juvenile mortality rates (x-axis), for the case of no further releases of Texas cougars.

With no additional releases and first-year mortality 40% or lower, population growth rates are positive in the simulated populations. At mortality rates of 20 or 30%, population size stays close to carrying capacity (set at 70 individuals), with low probability of extinction. The trend shown in Figure 1 can be used both as a means to help evaluate what mortality rates have impacted the population and as a means of projecting future needs for population viability. In the earlier PVAs on the Florida panther, in 1989 and 1992, first-year survival was estimated to be 50%, and the population was projected to be in demographic (as well as genetic) decline. The trend shown in Figure 1 also shows that the population would not be self-sustaining with such a mortality rate. However, estimates of population

Table 1. Effects of varying 1st year mortality and future releases of non-FL animals

Input parameters		Simulation results – at 100 years					
1st yr mortality	Future releases	Mean pop. growth (r)	Prob. of extinction	N	SD(N)	% initial gene diversity	% original FL genes
20	None	0.072	0.00	63	9	65	80
30		0.044	0.01	55	16	65	80
40		0.015	0.09	37	22	64	80
50		-0.026	0.81	4	11	60	80
60		-0.061	1.00	0	0	0	
20	2 / 10 y	0.083	0.00	63	10	74	57
30		0.058	0.00	60	13	72	60
40		0.028	0.02	50	18	75	54
50		-0.009	0.33	17	17	70	41
60		-0.036	0.91	1	3	63	37
20	4 / 10 yr	0.093	0.00	66	8	76	46
30		0.068	0.00	63	9	80	45
40		0.039	0.00	58	12	80	43
50		0.009	0.07	39	19	79	35
60		-0.023	0.55	7	10	78	9
20	8 / 10 yr	0.108	0.00	66	7	82	29
30		0.083	0.00	65	8	84	27
40		0.054	0.00	62	8	85	27
50		0.024	0.00	53	11	86	21
60		-0.004	0.09	28	17	84	10

Figure 1. Relationship between first-year mortality and mean population growth. See last column of Box 2 for other parameter values.



size have not decreased since 1992 (indeed, some estimates are slightly higher), and field data do not otherwise indicate that the population has been in steady decline over the past decade. Therefore, the actual rate of first-year mortality must have been less than 40% during the past decade, unless other aspects of the demography have been better than estimated. The mortality rate could have been as low as 20% (as was estimated by Maehr et al.), but lack of habitat may have prevented any population expansion. It is not known whether estimates of juvenile survival were overly pessimistic in 1989 and 1992 (or overly optimistic now), or whether the lower current estimates are due to the availability of more data, or whether juvenile mortality has declined from the 1980s (on which data the earlier estimates were based) to the 1990s (which constitute the bulk of the data now available). If mortality has declined, it is not known whether the improvement was due to the chance variation that can occur in small populations (either bad luck in the 1980s or good luck in the 1990s), or whether improvements have occurred in the habitat or management practices.

The trend shown in Figure 1 is also prescriptive. Whatever the past juvenile mortality, the population is self-sustaining demographically only if the rate remains below about 40%. Actions that improve juvenile survival – such as vaccinations, medical treatment of sick and injured panthers, and ensuring a good prey base for breeding females – may be important for population persistence and growth. Moreover, more complete monitoring of the fates of kittens is probably necessary for reducing the ongoing uncertainty in survival rates.

The analyses presented by Maehr et al. and those shown in Table 1 suggest that the Florida panther population may be demographically stable and capable of growth. However, even if the population remains near a present carrying capacity of 70 animals, the population would lose a substantial percentage of initial genetic diversity over time. Projected over 100 years, about 35% of current genetic variation would be lost. Adding one animal from Texas every 10 years would slightly improve the situation in terms of extinction risk without significantly affecting final population numbers. Populations that were growing would still grow; those that were shrinking would still be in trouble. More genetic diversity is maintained over time, which is the purpose of those additional releases, but gene diversity within the population still declines about 25% below current levels.

Varying Juvenile Mortality and Carrying Capacity

The set of simulations summarized in Table 2 represents another strategy for slowing the steady decay of genetic diversity: increasing total population size. This approach would require finding additional suitable habitat for panthers. Without addressing where this habitat would be located, these sets of simulations consider habitats with carrying capacity of 10, 20, 30, 40 and 50 animals, evaluated at each hypothesized level of first year mortality (20, 30, 40, 50, and 60%). The potential population growth rates would be similar to those in the earlier simulations, but panthers would move into the additional habitat space and exploit it, resulting in larger final population sizes.

Table 2. Effects of varying 1st year mortality and carrying capacity (K); no further releases

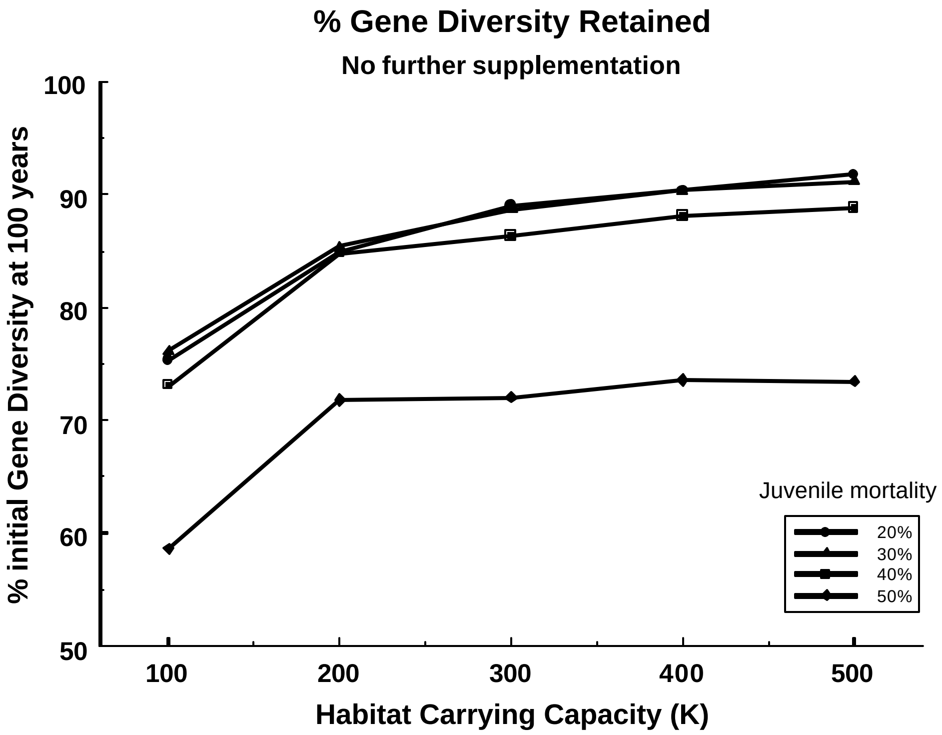
Input parameters		Simulation results – at 100 years					
1st yr mortality	Habitat K	Mean pop. growth (r)	Prob. of extinction	N	SD(N)	% initial gene diversity	% original FL genes
20	100	0.084	0.00	96	7	75	80
30		0.057	0.00	92	11	76	80
40		0.022	0.03	68	29	73	80
50		-0.020	0.51	11	15	59	80
60		-0.064	0.99	0	0	50	80
20	200	0.095	0.00	196	10	85	80
30		0.066	0.00	190	15	85	80
40		0.032	0.02	172	41	85	80
50		-0.017	0.48	35	51	72	80
60		-0.063	1.00	0	0	0	0
20	300	0.098	0.00	296	13	89	80
30		0.069	0.00	292	15	89	80
40		0.034	0.01	266	60	86	80
50		-0.013	0.41	52	71	72	80
60		-0.062	1.00	0	0	0	0
20	400	0.103	0.00	395	15	90	80
30		0.072	0.00	389	18	90	80
40		0.035	0.02	354	79	88	80
50		-0.016	0.46	44	77	74	80
60		-0.058	0.99	1	1	70	80
20	500	0.104	0.00	497	13	92	80
30		0.072	0.00	489	23	91	80
40		0.037	0.02	448	101	89	80
50		-0.017	0.48	57	106	73	80
60		-0.060	1.00	0	0	0	0

If an area with a carrying capacity of 100 animals is successfully colonized, population growth would be in a healthy range, but about 25% of current genetic diversity would still be lost over the next century, a level which would concern most geneticists. The population would still have 80% Florida panther genes, since no new Texas cougar genes would be introduced in this scenario. If projected final population numbers increase to

200, 85% of initial genetic diversity would be maintained, while a population of 300 could maintain about 89% of
initial levels.

For these cases of no additional releases, Figure 2 graphs the relationship between projected percentage of initial genetic diversity retained (y-axis) and carrying capacities (x-axis) for each of the first year survival rates analyzed. If the juvenile mortality rate is 50% or greater, the population fares poorly regardless of carrying capacity, whereas if the juvenile mortality rate is 20%, 30% or 40%, the population is able to expand into new habitat and increase total population numbers, with less loss of initial genetic variation.

Figure 2.



What level of maintenance of genetic diversity is adequate for a population is an unanswered question. Many other recovery programs have a target of maintaining over 90% of initial gene diversity. In domestic livestock breeding, falling below that level results in some drop in productivity, fecundity, growth rates, and survival. Using the 90% level as the long-term target for Florida panthers, with the model assumptions described above, a total population in the range of 400-500 individuals would be required to meet this goal. If the goal is lowered to 80% of initial gene diversity, 100-200 animals might be adequate. This analysis provides a way of scaling the amount of habitat which should be available and occupied by panthers to sustain a genetic population which maintains specific levels of diversity.

The next set of simulations, summarized in Table 3, looks at the same scenarios of habitat expansion, but asks what would happen if the population were supplemented by two Texas cougars every 10 years. This illustrates a combined strategy of building up population numbers somewhere, with augmentation by some Texas cougar releases. Demographically, this rate of release provides too few animals to have a significant impact,

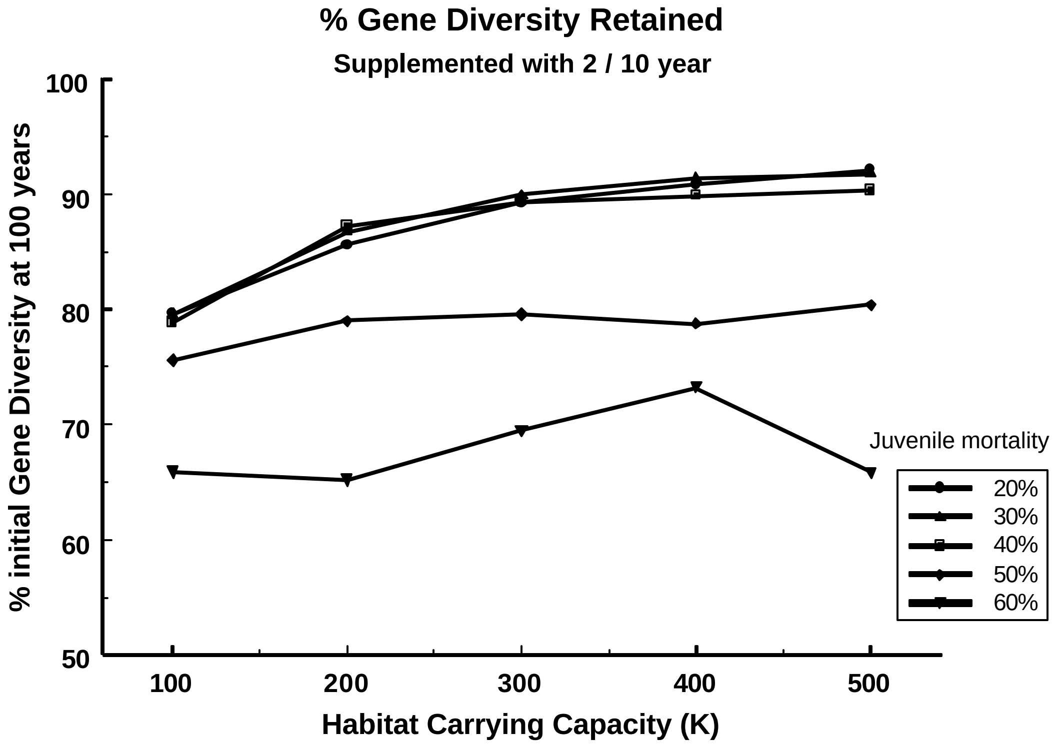
Table 3. Effects of varying 1st year mortality and carrying capacity (K); 2 cougars released / 10 y

Input parameters		Simulation results – at 100 years					
1st yr mortality	Habitat K	Mean pop. growth (r)	Prob. of extinction	N	SD(N)	% initial gene diversity	% original FL genes
20	100	0.091	0.00	95	9	80	64
30		0.063	0.00	94	9	80	64
40		0.031	0.00	79	21	79	61
50		-0.005	0.18	32	28	76	52
60		-0.037	0.85	2	5	66	37
20	200	0.100	0.00	197	9	86	71
30		0.068	0.00	194	12	87	72
40		0.038	0.00	185	21	87	68
50		-0.003	0.10	68	59	79	59
60		-0.038	0.86	2	3	65	34
20	300	0.103	0.00	296	11	89	74
30		0.074	0.00	293	14	90	73
40		0.040	0.00	280	32	89	71
50		-0.002	0.11	89	85	80	56
60		-0.040	0.91	1	4	70	28
20	400	0.104	0.00	396	14	91	74
30		0.073	0.00	395	14	91	73
40		0.041	0.00	373	44	90	72
50		-0.003	0.13	98	111	79	56
60		-0.039	0.90	2	5	73	34
20	500	0.104	0.00	496	13	92	74
30		0.075	0.00	493	20	92	75
40		0.041	0.00	462	75	90	73
50		-0.004	0.15	90	113	80	57
60		-0.041	0.91	1	3	66	28

but in terms of genetic variation somewhat more gene diversity is retained than in the previous simulations. If these additional individuals were released, about 25% to 50% of the genes in the population would eventually be replaced by genes descended from Texas cougars.

For additional Texas cougar releases of two every 20 years, Figure 3 graphs the relationship between projected percentage of initial genetic diversity retained (y-axis) and carrying capacities (x-axis) for each of the hypothesized first year survival rates. Again, fairly large population sizes are required to maintain gene diversity above 90% of the present level.

Figure 3.



Expansion of Panthers into Newly Connected Habitat

We looked at the question of expanding the population to some adjacent habitat. If there was an area of suitable habitat connected in some way to the existing population, either naturally, as when panthers cross the Caloosahatchee River, or by artificial manipulation, how effective would the South Florida population be in colonizing that territory and what effect would establishment of a new subpopulation have on maintaining genetic diversity? Taking the South Florida population as modeled previously, and adding the assumption that there is space for 100 additional animals in some adjacent habitat, we looked at scenarios with three possible juvenile mortality rates (20%, 30% and 40%) and three rates of dispersal into the new habitat (1%, 2%, and 5%).

In these models, it was assumed that both sexes disperse, which may not be realistic in terms of natural dispersal, but obviously colonization would not be biologically effective if only males dispersed. Thus, in each simulation year, each 1, 2, and 3 year old animal is give an x% chance of emigrating, where x is the chosen level of emigration (1%, 2%, or 5%). A 1% level corresponds to one animal moving into the new habitat about every other year, a 2% level corresponds to about one animal moving per year, while a 5% level would mean that several animals move each year.

Results of these simulations, presented in Table 4, show that when the South Florida population has just a few animals dispersing or being translocated to the newly available habitat, there is not a major impact on the demography of the existing population. With 1% emigration per year, the South Florida population is projected to perform about as well as in the models with just the single existing population. Higher levels of dispersal into a new habitat do not depress population size or gene diversity in south Florida, and can improve viability in the case of moderate (30-40%) juvenile mortality, because of dispersal from the newly established population back into the existing population.

Table 4. Expansion of panthers into newly connected habitat. Dispersal is by 1-3 year old panthers; new population has K = 100

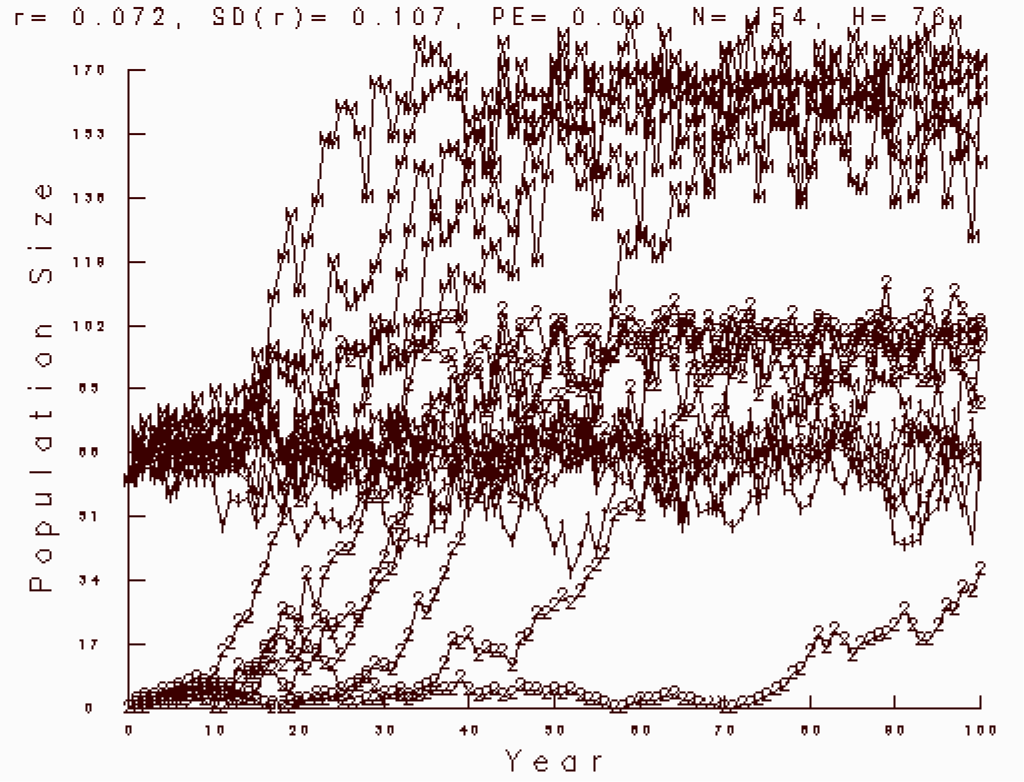
Input parameters		Simulation results – at 100 years						
1st yr mortality	Dispersal rate	South FL Population			New Population			MetaPop
		PE	N	%GD	PE	N	%GD	%GD
20	1%	0.00	65	71	0.04	82	70	74
20	2%	0.00	66	77	0.00	95	76	79
20	5%	0.00	68	79	0.00	96	79	80
30	1%	0.01	59	72	0.06	63	68	74
30	2%	0.01	62	76	0.01	90	78	79
30	5%	0.00	66	80	0.00	91	81	82
40	1%	0.25	28	62	0.50	21	63	64
40	2%	0.18	36	71	0.19	44	72	73
40	5%	0.06	54	78	0.05	67	78	79

In terms of colonization of the new territory, simulation results in Table 4 indicate that recolonization is usually successful at some time during the next century (population extinction, PE, of the New Population is near 0) at low levels of juvenile mortality, even with a 1% chance of movement. Once sufficient colonizers reach the new habitat, the population is projected to grow quickly to exploit that habitat. This scenario would result in comparable predicted percentages of initial gene diversity retained for the two subpopulations. The fact that the gene diversity of metapopulation, or total population, is similar to the gene diversities for the two subpopulations indicates that the subpopulations have essentially the same genetic composition in these models. Thus, the dispersal rates are high enough to prevent the two populations from diverging genetically.

With the highest juvenile mortality rate (40%), so that fewer animals survive to move into new habitat, the situation changes in terms of probability of successful colonization of an adjacent habitat. With a 1% rate of emigration, the new territory remains uncolonized in 50% of the simulations, and the existing population goes extinct in 25% or the simulations.

Figure 4 was extracted from one of the simulation analyses to illustrate the dynamics of how colonizations might proceed in terms of time scale of colonization with a 1% rate of dispersal from the current population when adjacent territory is available for 100 additional animals. Eight of the simulated populations from Table 4 are graphed over 100 years.

Figure 4.



The cluster of lines marked by 1's represents the South Florida population holding its own, maintaining numbers close to the capacity of the habitat. The cluster of lines starting along the x axis and rising to population size of 100 (marked by 2's), represents the population size in the new habitat being colonized. The upper cluster of lines represents total population size (marked by M's), the combined numbers of the South Florida population and the new population in adjacent habitat. With a slow rate of dispersal, animals may find and colonize the new habitat in as few as 10 years, but it often takes much longer, sometimes 50 to 70 years, for a subpopulation to become established. When 100 simulations are performed, some do not show successful colonization within 100 years. Once a new subpopulation does become established, it quickly reaches the carrying capacity of the new territory, 100 animals.

With a slow rate of dispersal a new area would be colonized eventually in most cases, but with a higher rate of emigration successful colonization is projected to occur much sooner. When the dispersal rate is 5%, the new populations usually become successfully colonized within the first decade.

Effects of Habitat Loss

Although we modeled the benefits of possible increases in available habitat (see above), the current situation is that panthers are losing rather than gaining habitat. Habitat is being lost from conversion of privately owned land to other uses. The rate of loss of habitat is not yet well known. Previous PVAs on the Florida panther estimated that up to 50% of the habitat (approximately the portion that is on private lands) could be lost unless actions are taken to protect those areas of habitat. To examine the possible effects of loss of habitat we analyzed simulations with 3 possible percentages of cumulative habitat loss (none, 25%, and 50%) over 25 years, for each of four rates of juvenile mortality (20%, 30%, 40%, and 60%). Table 5 summarizes the results of these analyses.

Not surprisingly, final population numbers are depressed when habitat is lost. More importantly, perhaps, a reduction in habitat can cause extinctions, as the population is compressed to levels that are unstable demographically and genetically. Given either a high rate of habitat decline, or a moderate rate with the addition of high juvenile mortality, simulations project a significant probability of population extinction. The probability of extinction is low only if the present habitat is conserved and there is low juvenile mortality (robust demographics). Loss of a considerable amount of habitat can be disastrous, even if reproductive and survival rates are initially good. Habitat loss also leads to more rapid loss of genetic diversity as the population size is depressed.

Table 5. Effects of habitat loss and varying 1st year mortality

Input parameters		Simulation results – at 100 years				
1st yr mortality	% decline in K over 25 years	Mean pop. growth (r)	Prob. of extinction	N	SD(N)	% initial gene diversity
20	None	0.072	0.00	63	9	65
30		0.044	0.01	55	16	65
40		0.015	0.09	37	22	64
50		-0.026	0.81	4	11	60
20	25%	0.064	0.02	42	12	59
30		0.034	0.10	30	17	56
40		0.002	0.53	11	15	60
50		-0.029	0.88	1	3	39
20	50%	0.044	0.33	14	12	45
30		0.021	0.52	9	12	42
40		-0.003	0.86	2	5	35
50		-0.030	0.98	0	1	35

Importance of more spatially explicit models

The models make the simplistic assumptions that breeding and mortality rates would be similar in all areas for the simulations described above. Any new habitat is assumed to be comparable in quality to habitat of the current population in South Florida, and it is assumed that no additional mortality is incurred in movement into the new habitat. If habitat is lost, it is assumed that the remaining habitat is of equal quality to what was lost. For all simulations, it is also assumed that all habitat within a population area is comparable and equally accessible, and that genetic composition does not affect fitness of individuals to survive and breed in their environment. In actuality, habitat areas may vary widely in productivity and suitability, and geographic barriers may isolate some sub-areas from others; some components of fitness may be enhanced by genetic introgression, while others may be compromised.

Genetic assumptions and uncertainty

In the above analyses, genetic changes in the Florida panthers were quantified in terms of losses of gene diversity and percent of the gene pool which descended from the original Florida panthers. In interpreting the results presented above, it is important to remember that the models make simplistic assumptions about the effects on the panthers of these genetic changes. With respect to inbreeding, the models assume that the panthers present in 1999 (the starting point of the simulations) are not inbred and are all unrelated. In the model, there is higher mortality for any kittens in future generations which are inbred relative to these starting conditions. In actuality, many of the present Florida panthers are closely related, and inbreeding (and its deleterious effects) would accumulate more rapidly than is assumed in the simulation model. Thus, although the models project that genetic losses and inbreeding would cause demographic decline beginning after about 100 years (or sooner, if demographic rates are not as high as estimated), these effects would likely be seen several decades sooner.

The models also assume that, except for the higher mortality of inbred kittens, fitness of individual panthers is not affected by which genes they carry. Inbreeding also causes reduction in the percent of animals that are fertile and in mean litter size in many species of mammals. No such reductions in breeding success of the population as a whole have yet been demonstrated, although the severe effect on fertility of cryptorchid males has been a concern. On the positive side, more severe effects of inbreeding could also lead to better retention of gene diversity than has been projected in the models, especially with respect to diversity at genetic loci which have major effects on fitness.

Similarly, the simulations assume that the Texas cougars and their intercross descendants have the same rates of reproduction and survival as do the panthers descended only from original Florida stock (with the exception that intercross descendants would be less likely to be inbred and therefore to have higher juvenile mortality). Yet one reason for the releases of Texas cougars was that it was believed that the intercrossed descendants, with restored genetic diversity, would have higher fitness than would the Florida panthers, which have reduced genetic variation. Relative to the results presented here, such an improvement in demographics due to the genetic restoration would increase numbers of the species in Florida (if there is suitable habitat for them to occupy), reduce probabilities of extinction, and reduce the rate of loss of gene diversity from the population. Beneficial effects of the genetic restoration on fitness would also accelerate the rate at which alleles descended from Texas cougars replace Florida-source alleles in the population.

Some alleles from the Texas animals may have deleterious effects in the Florida population, either because the alleles are maladapted to the Florida environment or because they function poorly when in combination with Florida alleles at the same locus (heterozygotes having reduced fitness) or at other loci (disruption of co-adapted epistatic gene combinations). If such outbreeding depression occurs, the effects would be opposite those described above for the effects of expected benefits of genetic restoration. Such detrimental effects of intercrossing would be reduced through the generations, as selection removes alleles that are not adapted to the local conditions.

Any or all of the above genetic processes – inbreeding depression of other components of fitness, outbreeding enhancement of demographic rates, or outbreeding depression – could be modeled relatively easily, using existing software. However, at this time data do not exist that would allow specification of the fitness effects of genetic changes occurring in the population. Further modeling of the effects of inbreeding and genetic restoration might be instructive, but alternative assumptions would remain entirely speculative until there are more data on consequences for the panthers. Intensive and detailed monitoring of the fates and pedigrees of panthers and especially the intercross descendants is a prerequisite for determining the consequences of genetic changes to demographic performance, genetic diversity, and the probability of persistence of the population.

GOALS AND PROPOSED ACTIONS

The modeling group considered the need to include aspects of landscape / habitat factors and projections of future change in the panther modeling efforts as the highest priority. Our second highest priority was assessing whether the most recent PVA model simulation (Maehr et al. 1999) is an accurate representation of reality, or if some parameters need to be modified. Our third highest priority issue was including other impacts -- social, cultural, economic, and political -- in our thinking and modeling. The fourth priority was considering expanded models of metapopulations, where panthers have dispersed or been reintroduced into new areas. A few of our other priorities were facilitating data flow between models and looking at implications of model results and analyses for management actions. The following goals and proposed actions were formulated to address some of these issues.

GOAL 1: Quantify potential/likely loss and change of Florida panther habitat in South Florida. In terms of modeling, this would provide better estimates of habitat loss to feed into panther viability simulations.

RECOMMENDED ACTIONS:

1. Complete a retrospective analysis of landscape changes over the past two decades. Dave Maehr and colleagues are working on such as project.

2. Forecast/project future landscape changes. The trajectory from the past can provide a rate and direction of change, but should be supplemented with projections into the future. This might take the form of a spatially explicit current habitat map with an application or overlay of information from various sources: planning agencies, water management agencies, and other entities mapping out projected land use changes for various purposes. We need to project what the landscape might look like 10, 20, and 50 years from now.

3. Increased communication and coordination among various modeling approaches and efforts to coordinate spatial and temporal scales, formats, units, and methodologies. For example, land use models should be able to feed information about projected landscape changes into spatial panther models which might predict how panthers will

respond to these changes, and both should feed into the population model, perhaps modifying parameters such as carrying capacity and percent of habitat loss.

GOAL 2: Better quantify demographic characteristics of the panther population which serve as input parameters for simulation models, specifically kitten/juvenile mortality rates, percentage of females breeding each year, and initial population size.

Considerable attention was focused on this issue in workshop discussions. Model results are sensitive to variations in estimates of these parameters; therefore, estimates should be based on the best available data. Model projections suggest that if first-year mortality rates were 50% or higher the population would have a negative growth rate and would be in decline, while if the rate were 40% or lower, the population could be demographically stable. Breeding and survival rates impact how quickly population pressures are felt within limited habitat ranges, how many panthers are available to disperse into new areas, how much flexibility exists for various management options, and how much medical intervention is necessary to maintain a stable population.

RECOMMENDED ACTIONS:

1. More support for the radio-telemetry efforts that provide needed data. Better estimation of parameters which drive VORTEX and other models depends on a high percentage of kittens being radio-collared before dispersal. The extended 1999 capture season covered about 120 days, but captures only occurred on half those days due to unavailability of veterinary support and inadequate water levels and temperatures. While the modeling group did not propose specifically how best to increase the intensity of radio-collaring, suggestions included:
    a. A longer capture season. Currently, the intensive capture season begins in early January and terminates when turkey season begins on March 6. Conditions are often cool and dry enough to begin captures in October or November.

    b. More consistently available veterinary support for panther captures, including weekend captures. When the assigned veterinarian is unable to attend captures, a field-ready substitute should be available.

    c. Formation of additional capture team(s) as necessary. Due to population growth and/or increased intensity of monitoring, additional personnel may be necessary to meet monitoring and intervention goals.

    d. Development of a quick-response capture capability would make it possible to collar and handle cats that are encountered in the course of activities other than scheduled hunts. Over the past three years, 11 uncollared cats were caught opportunistically (e.g., while dogs were being exercised) but could not be handled or collared due to unavailability of field support.

2. More intensive ongoing monitoring of kittens before dispersal from the natal area, with the goal of obtaining more complete records and recording them in the SPARKS

database provided for that purpose, so that more reliable determinations may be made as to whether kittens have survived or perished.

3. Apply mark-recapture methodologies developed over the past decade to existing capture data, field notes, and photo-records from trail and underpass cameras to derive unbiased estimates of survival rates. (We noted that David Shindle, wildlife biologist with the Panther Capture Team, is currently conducting a project to gather additional photo-records using trail cameras within panther ranges.)

4. Compile and review all data (from various sources) on kitten/juvenile survival, female breeding percentages and population size.

GOAL 3: Gain a better understanding of potential Florida panther habitat in terms of what is currently available and what is projected to be available in the future for dispersal or reintroduction.

RECOMMENDED ACTIONS:

1. Assess habitat characteristics of the current range of panthers in South Florida. Such characteristics would include minimum size of patches of suitable panther habitat based on current range sizes, availability of resting and denning areas and stalking cover, support for prey productivity, and human land use.

2. Apply measures of habitat suitability derived from this analysis to potential new areas of panther habitat. An example of this kind of analysis was presented to the working group by Patricia Cramer. An abstract of that work is given in Box 3, below.

3. Rank the suitability of potential sites identified for population expansion or reintroduction.

4. Use the population viability model to evaluate potential effects on overall metapopulation stability in terms of genetic diversity, population growth, and effectiveness of modes of repopulating those sites.

Progress reports on efforts to meet each of these goals should be presented in conjunction with the proposed workshop proposed by other working groups for early next year.

Box 3.

A SPATIALLY EXPLICIT MODEL TO PREDICT MOVEMENTS OF POTENTIAL REINTRODUCED FLORIDA PANTHERS IN NORTH FLORIDA

Cramer, Patricia C.
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Florida panther reintroductions are considered crucial to this endangered subspecies' survival. Movements of potential reintroduced Florida panthers are modeled for the Upper Suwannee River Basin of north Florida, a prime reintroduction site. Objectives of the PANTHER model were to identify specific regional landscape features and conservation strategies most critical to panthers, other species, and the ecosystems they depend on. The model is based in part on data from the Florida Game and Fresh Water Fish Commission's Florida Panther Reintroduction Feasibility Study. The spatially explicit model mimics panther behavior, and implements wide ranging cat movement over Geographic Information Systems (GIS) maps representing natural communities, roads, deer densities, human densities, and future human development conditions. The model identifies locations within 7,000 square kilometers of the reintroduction study area that have a high probability of being used by Florida panthers, and variables that play important roles in panther survival and dispersal capabilities. Model results identify areas along the Suwannee River and other areas where both humans and panthers would prefer to reside. Results indicate specific sites along Interstates I-75 and I-10 and other roads that have a high probability of panther crossings. Outputs from PANTHER simulations also predict the effects of roads and human densities on panther movement and survival. Results support the need for conservation-oriented regional land use planning, and environmental education programs and agency initiatives designed specifically for private landowners of land identified as most critical to a potential population of Florida panthers.

Florida Panther
Population and Habitat Viability Assessment
and Genetics Workshop

8-11 June 1999
Gainesville, Florida

Final Report

Section 3
Appendix

APPENDIX I

List of Participants, Florida Panther PHVA Workshop
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June 8 - 11, 1999

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APPENDIX II

APPENDIX III

APPENDIX IV

Florida Panther
Population and Habitat Viability Assessment
and Genetics Workshop

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Gainesville, Florida

Final Report

Section 4
VORTEX Reference

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VORTEX: A Computer Simulation Model for Population Viability Analysis

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Abstract

Population Viability Analysis (PVA) is the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process. Extrinsic forces, such as habitat loss, over-harvesting, and competition or predation by introduced species, often lead to population decline. Although the traditional methods of wildlife ecology can reveal such deterministic trends, random fluctuations that increase as populations become smaller can lead to extinction even of populations that have, on average, positive population growth when below carrying capacity. Computer simulation modelling provides a tool for exploring the viability of populations subjected to many complex, interacting deterministic and random processes. One such simulation model, VORTEX, has been used extensively by the Captive Breeding Specialist Group (Species Survival Commission, IUCN), by wildlife agencies, and by university classes. The algorithms, structure, assumptions and applications of VORTEX are described in this paper.

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, to determine the number of progeny produced by each female each year, and to determine which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Fecundity is assumed to be independent of age after an animal reaches reproductive age. Mortality rates are specified for each pre-reproductive age–sex class and for reproductive-age animals. Inbreeding depression is modelled as a decrease in viability in inbred animals.

The user has the option of modelling density dependence in reproductive rates. As a simple model of density dependence in survival, a carrying capacity is imposed by a probabilistic truncation of each age class if the population size exceeds the specified carrying capacity. VORTEX can model linear trends in the carrying capacity. VORTEX models environmental variation by sampling birth rates, death rates, and the carrying capacity from binomial or normal distributions. Catastrophes are modelled as sporadic random events that reduce survival and reproduction for one year. VORTEX also allows the user to supplement or harvest the population, and multiple subpopulations can be tracked, with user-specified migration among the units.

VORTEX outputs summary statistics on population growth rates, the probability of population extinction, the time to extinction, and the mean size and genetic variation in extant populations.

VORTEX necessarily makes many assumptions. The model it incorporates is most applicable to species with low fecundity and long lifespans, such as mammals, birds and reptiles. It integrates the interacting effects of many of the deterministic and stochastic processes that have an impact on the viability of small populations, providing opportunity for more complete analysis than is possible by other techniques. PVA by simulation modelling is an important tool for identifying populations at risk of extinction, determining the urgency of action, and evaluating options for management.

Introduction

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat, have been reduced to one or more small, isolated populations. The causes of the original decline are often obvious, deterministic forces, such as over-harvesting,

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habitat destruction, and competition or predation from invasive introduced species. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990). Of particular impact on small populations are stochastic processes. With the exception of aging, virtually all events in the life of an organism are stochastic. Mating, reproduction, gene transmission between generations, migration, disease and predation can be described by probability distributions, with individual occurrences being sampled from these distributions. Small samples display high variance around the mean, so the fates of small wildlife populations are often determined more by random chance than by the mean birth and death rates that reflect adaptations to their environment.

Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The use of simulation modelling, often in conjunction with other techniques, to explore the dynamics of small populations has been termed Population Viability Analysis (PVA). PVA has been increasingly used to help guide management of threatened species. The Resource Assessment Commission of Australia (1991) recently recommended that 'estimates of the size of viable populations and the risks of extinction under multiple-use forestry practices be an essential part of conservation planning'. Lindenmayer *et al.* (1993) describe the use of computer modelling for PVA, and discuss the strengths and weaknesses of the approach as a tool for wildlife management.

In this paper, I present the PVA program VORTEX and describe its structure, assumptions and capabilities. VORTEX is perhaps the most widely used PVA simulation program, and there are numerous examples of its application in Australia, the United States of America and elsewhere.

The Dynamics of Small Populations

The stochastic processes that have an impact on populations have been usefully categorised into demographic stochasticity, environmental variation, catastrophic events and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate and sex ratio of a population even if the probabilities of birth and death remain constant. On the assumption that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be important to population viability only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means. The distribution of annual adult survival rates observed in the remnant population of whooping cranes (*Grus americana*) (Mirande *et al.* 1993) is shown in Fig. 1. The innermost curve approximates the binomial distribution that describes the demographic stochasticity expected when the probability of survival is 92·7% (mean of 45 non-outlier years).

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The second narrowest curve on Fig. 1 shows a normal distribution that statistically fits the observed frequency histogram of crane survival in non-outlier years. The difference between this curve and the narrower distribution describing demographic variation must be accounted for by environmental variation in the probability of adult survival.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analysed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease,

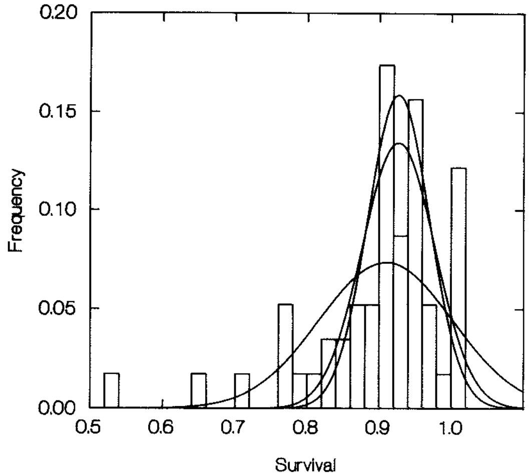

Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938–90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution that most closely fits the histogram, excluding the five leftmost bars (7 outlier 'catastrophe' years). The narrowest and tallest curve is the normal approximation to the binomial distribution expected from demographic stochasticity. The difference between the tallest and second tallest curves is the variation in annual survival due to environmental variation.

hurricanes, large-scale fires, and floods are outliers in the distribution of environmental variation (e.g. five leftmost bars on Fig. 1). As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls *et al.* 1988; Lacy *et al.* 1993). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations have a negative impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerate genetic drift (Crow and Kimura 1970). These synergistic destabilising effects of stochastic process on small populations of wildlife have been described as an 'extinction vortex' (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered a 'minimum viable population' (MVP) (Seal and Lacy 1989), although Shaffer (1981) first defined a MVP more stringently as a population that has a 99% probability of persistence for 1000 years. The estimation of MVPs or, more generally, the investigation of the probability of extinction constitutes PVA (Gilpin and Soulé 1986; Gilpin 1989; Shaffer 1990).

Methods for Analysing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction–recolonisation dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991). Because demographic and genetic processes in small populations are inherently unpredictable, the expected fates of wildlife populations can be described in terms of probability distributions of population size, time to extinction, and genetic variation. These distributions can be obtained in any of three ways: from analytical models, from empirical observation of the fates of populations of varying size, or from simulation models.

As the processes determining the dynamics of populations are multiple and complex, there are few analytical formulae for describing the probability distributions (e.g. Goodman 1987; Lande 1988; Burgmann and Gerard 1990). These models have incorporated only few of the threatening processes. No analytical model exists, for example, to describe the combined effect of demographic stochasticity and loss of genetic variation on the probability of population persistence.

A few studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g. Belovsky 1987; Berger 1990; Thomas 1990), but presently only order-of-magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). Threatened species are, by their rarity, unavailable and inappropriate for the experimental manipulation of population sizes and long-term monitoring of undisturbed fates that would be necessary for precise empirical measurement of MVPs. Retrospective analyses will be possible in some cases, but the function relating extinction probability to population size will differ among species, localities and times (Lindenmayer *et al.* 1993).

Modelling the Dynamics of Small Populations

Because of the lack of adequate empirical data or theoretical and analytical models to allow prediction of the dynamics of populations of threatened species, various biologists have turned to Monte Carlo computer simulation techniques for PVA. By randomly sampling from defined probability distributions, computer programs can simulate the multiple, interacting events that occur during the lives of organisms and that cumulatively determine the fates of populations. The focus is on detailed and explicit modelling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations. Computer programs available to PVA include SPGPC (Grier 1980*a*, 1980*b*), GAPPS (Harris *et al.* 1986), RAMAS (Ferson and Akçakaya 1989; Akçakaya and Ferson 1990; Ferson 1990), FORPOP (Possingham *et al.* 1991), ALEX (Possingham *et al.* 1992), and SIMPOP (Lacy *et al.* 1989; Lacy and Clark 1990) and its descendant VORTEX.

SIMPOP was developed in 1989 by converting the algorithms of the program SPGPC (written by James W. Grier of North Dakota State University) from BASIC to the C programming language. SIMPOP was used first in a PVA workshop organised by the Species Survival Commission's Captive Breeding Specialist Group (IUCN), the United States Fish and Wildlife Service, and the Puerto Rico Department of Natural Resources to assist in planning and assessing recovery efforts for the Puerto Rican crested toad (*Peltophryne lemur*). SIMPOP was subsequently used in PVA modelling of other species threatened with extinction, undergoing modification with each application to allow incorporation of additional threatening processes. The simulation program was renamed VORTEX (in reference to the extinction vortex) when the capability of modelling genetic processes was implemented in 1989. In 1990, a version allowing modelling of multiple populations was briefly named VORTICES. The only version still supported, with all capabilities of each previous version, is VORTEX Version 5.1.

VORTEX has been used in PVA to help guide conservation and management of many species, including the Puerto Rican parrot (*Amazona vittata*) (Lacy *et al.* 1989), the Javan rhinoceros (*Rhinoceros sondaicus*) (Seal and Foose 1989), the Florida panther (*Felis concolor coryi*) (Seal and Lacy 1989), the eastern barred bandicoot (*Perameles gunnii*) (Lacy and Clark 1990; Maguire *et al.* 1990), the lion tamarins (*Leontopithecus rosalia* ssp.) (Seal *et al.* 1990), the brush-tailed rock-wallaby (*Petrogale penicillata penicillata*) (Hill 1991), the mountain pygmy-possum (*Burramys parvus*), Leadbeater's possum (*Gymnobelideus leadbeateri*), the long-footed potoroo (*Potorous longipes*), the orange-bellied parrot (*Neophema chrysogaster*) and the helmeted honeyeater (*Lichenostomus melanops cassidix*) (Clark *et al.* 1991), the whooping crane (*Grus americana*) (Mirande *et al.* 1993), the Tana River crested mangabey (*Cercocebus galeritus galeritus*) and the Tana River red colobus (*Colobus badius rufomitratus*) (Seal *et al.* 1991), and the black rhinoceros (*Diceros bicornis*) (Foose *et al.* 1992). In some of these PVAs, modelling with VORTEX has made clear the insufficiency of past management plans to secure the future of the species, and alternative strategies were proposed, assessed and implemented. For example, the multiple threats to the Florida panther in its existing habitat were recognised as probably insurmountable, and a captive breeding effort has been initiated for the purpose of securing the gene pool and providing animals for release in areas of former habitat. PVA modelling with VORTEX has often identified a single threat to which a species is particularly vulnerable. The small but growing population of Puerto Rican parrots was assessed to be secure, except for the risk of population decimation by hurricane. Recommendations were made to make available secure shelter for captive parrots and to move some of the birds to a site distant from the wild flock, in order to minimise the damage that could occur in a catastrophic storm. These recommended actions were only partly implemented when, in late 1989, a hurricane killed many of the wild parrots. The remaining population of about 350 Tana River red colobus were determined by PVA to be so fragmented that demographic and genetic processes within the 10 subpopulations destabilised population dynamics. Creation of habitat corridors may be necessary to prevent extinction of the taxon. In some cases, PVA modelling has been reassuring to managers: analysis of black rhinos in Kenya indicated that many of the populations within sanctuaries were recovering steadily. Some could soon be used to provide animals for re-establishment or supplementation of populations previously eliminated by poaching. For some species, available data were insufficient to allow definitive PVA with VORTEX. In such cases, the attempt at PVA modelling has made apparent the need for more data on population trends and processes, thereby helping to justify and guide research efforts.

Description of VORTEX

Overview

The VORTEX computer simulation model is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events, on wildlife populations. VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables, following user-specified distributions. The input parameters used by VORTEX are summarised in the first part of the sample output given in the Appendix.

VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. The program was designed to model long-lived species with low fecundity, such as mammals, birds and reptiles. Although it could and has been used in modelling highly fecund vertebrates and invertebrates, it is awkward to use in such cases as it requires complete specification of the percentage of females producing each possible clutch size. Moreover, computer memory limitations often hamper such analyses. Although VORTEX iterates life events on an annual cycle, a user could model 'years' that are other than 12 months' duration. The simulation of the population is itself iterated to reveal the distribution of fates that the population might experience.

Demographic Stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination and death with a pseudo-random number generator. The probabilities of mortality and reproduction are sex-specific and pre-determined for each age class up to the age of breeding. It is assumed that reproduction and survival probabilities remain constant from the age of first breeding until a specified upper limit to age is reached. Sex ratio at birth is modelled with a user-specified constant probability of an offspring being male. For each life event, if the random value sampled from the uniform 0–1 distribution falls below the probability for that year, the event is deemed to have occurred, thereby simulating a binomial process.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), according to the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value, according to

$$N = p(1-p)/s^2 .$$

N binomial trials are then simulated by sampling from the uniform 0–1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

The 'carrying capacity', or the upper limit for population size within a habitat, must be specified by the user. VORTEX imposes the carrying capacity via a probabilistic truncation whenever the population exceeds the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation.

Environmental Variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions. Environmental variation in carrying capacity is modelled as a normal distribution. The variance across years in the frequencies of births and deaths resulting from the simulation model (and in real populations) will have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and additional fluctuations due to environmental variation and catastrophes (see Fig. 1 and section on The Dynamics of Small Populations, above).

Data on annual variations in birth and death rates are important in determining the probability of extinction, as they influence population stability (Goodman 1987). Unfortunately, such field information is rarely available (but see Fig. 1). Sensitivity testing, the examination of a range of values when the precise value of a parameter is unknown, can help to identify whether the unknown parameter is important in the dynamics of a population.

Catastrophes

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. Any number of types of catastrophes can be modelled. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors by 50% for the year. Such a catastrophe would be modelled as a random event with 0·02 probability of occurrence each year, and severity factors of 0·75 for survival and 0·50 for reproduction.

Genetic Processes

Genetic drift is modelled in VORTEX by simulation of the transmission of alleles at a hypothetical locus. At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring is randomly assigned one of the alleles from each parent. Inbreeding depression is modelled as a loss of viability during the first year of inbred animals. The impacts of inbreeding are determined by using one of two models available within VORTEX: a Recessive Lethals model or a Heterosis model.

In the Recessive Lethals model, each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive lethal allele in its genome. The fact that the simulation program assumes that all the lethal alleles are at the same locus has a very minor impact on the probability that an individual will die because of homozygosity for one of the lethal alleles. In the model, homozygosity for different lethal alleles are mutually exclusive events, whereas in a multilocus model an individual could be homozygous for several lethal alleles simultaneously. By virtue of the death of individuals that are homozygous for lethal alleles, such alleles would be removed slowly by natural selection during the generations of a simulation. This reduces the genetic variation present in the population relative to the case with no inbreeding depression, but also diminishes the subsequent probability that inbred individuals will be homozygous for a lethal allele. This model gives an optimistic reflection of the impacts of inbreeding on many species, as the median number of lethal equivalents per diploid genome observed for mammalian populations is about three (Ralls *et al.* 1988).

The expression of fully recessive deleterious alleles in inbred organisms is not the only genetic mechanism that has been proposed as a cause of inbreeding depression. Some or most of the effects of inbreeding may be a consequence of superior fitness of heterozygotes (heterozygote advantage or 'heterosis'). In the Heterosis model, all homozygotes have reduced fitness compared with heterozygotes. Juvenile survival is modelled according to the logarithmic model developed by Morton *et al.* (1956):

$$\ln S = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is a measure of the rate at which survival decreases with inbreeding. B is termed the number of 'lethal equivalents' per haploid genome. The number of lethal equivalents per diploid genome, $2B$, estimates the number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual (as in the Recessive Lethals model, above), it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles that equate in effect with one lethal allele per individual. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at heterotic loci because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under the Heterosis model, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.

Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects varies considerably among species (Falconer 1981; Ralls *et al.* 1988; Lacy *et al.* 1993). Moreover, whether a Recessive Lethals model or a Heterosis model better describes the underlying mechanism of inbreeding depression and therefore the response to repeated generations of inbreeding is not well-known (Brewer *et al.* 1990), and could be determined empirically only from breeding studies that span many generations. Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterosis), applications of PVA must make assumptions about the effects of inbreeding on the population being studied. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3·14 lethal equivalents per diploid) reported in the survey by Ralls *et al.* (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0·90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5·62 lethal equivalents).

Deterministic Processes

VORTEX can incorporate several deterministic processes. Reproduction can be specified to be density-dependent. The function relating the proportion of adult females breeding each year to the total population size is modelled as a fourth-order polynomial, which can provide a close fit to most plausible density-dependence curves. Thus, either positive population responses to low-density or negative responses (e.g. Allee effects), or more complex relationships, can be modelled.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodelled) population. The numbers of additions and removals are specified according to the age and sex of animals. Trends in the carrying capacity can also be modelled in VORTEX, specified as an annual percentage change. These changes are modelled as linear, rather than geometric, increases or decreases.

Migration among Populations

VORTEX can model up to 20 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. This probability is independent of the age and sex. Because of between-population migration and managed supplementation, populations can be recolonised. VORTEX tracks the dynamics of local extinctions and recolonisations through the simulation.

Output

VORTEX outputs (1) probability of extinction at specified intervals (e.g., every 10 years during a 100-year simulation), (2) median time to extinction if the population went extinct in at least 50% of the simulations, (3) mean time to extinction of those simulated populations that became extinct, and (4) mean size of, and genetic variation within, extant populations (see Appendix and Lindenmayer *et al.* 1993).

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction (*SE*) is reported by VORTEX as

$$SE(p) = \sqrt{[p \times (1-p)/n]}\,,$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Availability of the VORTEX Simulation Program

VORTEX Version 5.1 is written in the C programming language and compiled with the Lattice 80286C Development System (Lattice Inc.) for use on microcomputers using the MS-DOS (Microsoft Corp.) operating system. Copies of the compiled program and a manual for its use are available for nominal distribution costs from the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124, U.S.A. The program has been tested by many workers, but cannot be guaranteed to be error-free. Each user retains responsibility for ensuring that the program does what is intended for each analysis.

Sequence of Program Flow

(1) The seed for the random number generator is initialised with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for input and output devices, population parameters, duration of simulation, and number of interations.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as

$$N_{max} = (K + 3s) \times (1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change linearly for a number of years in a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size. It is theoretically possible, but very unlikely, that a simulated population will exceed the calculated N_{max}. If this occurs then the program will give an error message and abort.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning it has been adjusted downward because of limiting memory often will not hamper the analyses. Except for limitations imposed by the size of the computer memory (VORTEX can use extended memory, if available), the only limit to the size of the analysis is that no more than 20 populations exchanging migrants can be simulated.

(5) The expected mean growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also estimated. Life-table estimations assume no limitation by carrying capacity, no limitation of mates, and no loss of fitness due to inbreeding depression, and the estimated intrinsic growth rate assumes that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life-table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7–26 below. For exploratory modelling, 100 iterations are usually sufficient to reveal gross trends among sets of simulations with different input parameters. For more precise examination of population behaviour under various scenarios, 1000 or more simulations should be used to minimise standard errors around mean results.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age–sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. VORTEX therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy–Weinberg equilibrium, is given by

$$H_e = 1 - \Sigma(p_i^2),$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1·0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity by means of random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (assuming that the initial value was not zero) (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by VORTEX is the mean inbreeding coefficient of the population.

(9) The user specifies one of three options for modelling the effect of inbreeding: (a) no effect of inbreeding on fitness, that is, all alleles are selectively neutral, (b) each founder individual has one unique lethal and one unique non-lethal allele (Recessive Lethals option), or (c) first-year survival of each individual is exponentially related to its inbreeding coefficient (Heterosis option). The first case is clearly an optimistic one, as almost all diploid

populations studied intensively have shown deleterious effects of inbreeding on a variety of fitness components (Wright 1977; Falconer 1981). Each of the two models of inbreeding depression may also be optimistic, in that inbreeding is assumed to have an impact only on first-year survival. The Heterosis option allows, however, for the user to specify the severity of inbreeding depression on juvenile survival.

(10) Years are iterated via steps 11–25 below.

(11) The probabilities of females producing each possible litter size are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percentage of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates for their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) of the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for linear changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of breeding-age males specified to be breeding.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified sex ratio at birth. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) If the Heterosis option is chosen for modelling inbreeding depression, the genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between a new animal, A, and another existing animal, B is

$$f_{AB} = 0{\cdot}5 \times (f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_{AA} = 0{\cdot}5 \times (1 + F)$. [See Ballou (1983) for a detailed description of this method for calculating inbreeding coefficients.]

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If the Heterosis model of inbreeding depression is used and an individual is inbred, the survival probability is multiplied by e^{-bF} in which b is the number of lethal equivalents per haploid genome.

If the Recessive Lethals model is used, all offspring that are homozygous for a lethal allele are killed.

(18) The age of each animal is incremented by 1, and any animal exceeding the maximum age is killed.

(19) If more than one population is being modelled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age–sex class, VORTEX continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age class are created. Each immigrant is assigned two unique alleles, one of which will be a recessive lethal in the Recessive Lethals model of inbreeding depression. Each immigrant is assumed to be genetically unrelated to all other individuals in the population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N-K)/N$, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported. A simulated population is determined to be extinct if one of the sexes has no representatives.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate, are calculated across iterations and printed out.

Assumptions Underpinning VORTEX

It is impossible to simulate the complete range of complex processes that can have an impact on wild populations. As a result there are necessarily a range of mathematical and biological assumptions that underpin any PVA program. Some of the more important assumptions in VORTEX include the following.

(1) Survival probabilities are density independent when population size is less than carrying capacity. Additional mortality imposed when the population exceeds K affects all age and sex classes equally.

(2) The relationship between changes in population size and genetic variability are examined for only one locus. Thus, potentially complex interactions between genes located on the same chromosome (linkage disequilibrium) are ignored. Such interactions are typically associated with genetic drift in very small populations, but it is unknown if, or how, they would affect population viability.

(3) All animals of reproductive age have an equal probability of breeding. This ignores the likelihood that some animals within a population may have a greater probability of breeding successfully, and breeding more often, than other individuals. If breeding is not at random among those in the breeding pool, then decay of genetic variation and inbreeding will occur more rapidly than in the model.

(4) The life-history attributes of a population (birth, death, migration, harvesting, supplementation) are modelled as a sequence of discrete and therefore seasonal events. However, such events are often continuous through time and the model ignores the possibility that they may be aseasonal or only partly seasonal.

(5) The genetic effects of inbreeding on a population are determined in VORTEX by using one of two possible models: the Recessive Lethals model and the Heterosis model. Both models have attributes likely to be typical of some populations, but these may vary within and between species (Brewer *et al.* 1990). Given this, it is probable that the impacts of inbreeding will fall between the effects of these two models. Inbreeding is assumed to depress only one component of fitness: first-year survival. Effects on reproduction could be incorporated into this component, but longer-term impacts such as increased disease susceptibility or decreased ability to adapt to environmental change are not modelled.

(6) The probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum longevity. This assumes that animals continue to breed until they die.

(7) A simulated catastrophe will have an effect on a population only in the year that the event occurs.

(8) Migration rates among populations are independent of age and sex.

(9) Complex, interspecies interactions are not modelled, except in that such community dynamics might contribute to random environmental variation in demographic parameters. For example, cyclical fluctuations caused by predator–prey interactions cannot be modelled by VORTEX.

Discussion

Uses and Abuses of Simulation Modelling for PVA

Computer simulation modelling is a tool that can allow crude estimation of the probability of population extinction, and the mean population size and amount of genetic diversity, from data on diverse interacting processes. These processes are too complex to be integrated intuitively and no analytic solutions presently, or are likely to soon, exist. PVA modelling focuses on the specifics of a population, considering the particular habitat, threats, trends, and time frame of interest, and can only be as good as the data and the assumptions input to the model (Lindenmayer *et al.* 1993). Some aspects of population dynamics are not modelled by VORTEX nor by any other program now available. In particular, models of single-species dynamics, such as VORTEX, are inappropriate for use on species whose fates are strongly determined by interactions with other species that are in turn undergoing complex (and perhaps synergistic) population dynamics. Moreover, VORTEX does not model many conceivable and perhaps important interactions among variables. For example, loss of habitat might cause secondary changes in reproduction, mortality, and migration rates, but ongoing trends in these parameters cannot be simulated with VORTEX. It is important to stress that PVA does not predict in general what will happen to a population; PVA forecasts the likely effects only of those factors incorporated into the model.

Yet, the use of even simplified computer models for PVA can provide more accurate predictions about population dynamics than the even more crude techniques available previously, such as calculation of expected population growth rates from life tables. For the purpose of estimating extinction probabilities, methods that assess only deterministic factors are almost certain to be inappropriate, because populations near extinction will commonly be so small that random processes dominate deterministic ones. The suggestion by Mace and Lande (1991) that population viability be assessed by the application of simple rules (e.g., a taxon be considered Endangered if the total effective population size is below 50 or the total census size below 250) should be followed only if knowledge is insufficient to allow more accurate quantitative analysis. Moreover, such preliminary judgments, while often important in stimulating appropriate corrective measures, should signal, not obviate, the need for more extensive investigation and analysis of population processes, trends and threats.

Several good population simulation models are available for PVA. They differ in capabilities, assumptions and ease of application. The ease of application is related to the number of simplifying assumptions and inversely related to the flexibility and power of the model. It is unlikely that a single or even a few simulation models will be appropriate for all PVAs. The VORTEX program has some capabilities not found in many other population simulation programs, but is not as flexible as are some others (e.g., GAPPS; Harris *et al.* 1986). VORTEX is user-friendly and can be used by those with relatively little understanding of population biology and extinction processes, which is both an advantage and a disadvantage.

Testing Simulation Models

Because many population processes are stochastic, a PVA can never specify what will happen to a population. Rather, PVA can provide estimates of probability distributions describing possible fates of a population. The fate of a given population may happen to fall at the extreme tail of such a distribution even if the processes and probabilities are assessed precisely. Therefore, it will often be impossible to test empirically the accuracy of PVA results by monitoring of one or a few threatened populations of interest. Presumably, if a population followed a course that was well outside of the range of possibilities predicted by a model, that model could be rejected as inadequate. Often, however, the range of plausible fates generated by PVA is quite broad.

Simulation programs can be checked for internal consistency. For example, in the absence of inbreeding depression and other confounding effects, does the simulation model predict an average long-term growth rate similar to that determined from a life-table calculation? Beyond this, some confidence in the accuracy of a simulation model can be obtained by comparing observed fluctuations in population numbers to those generated by the model, thereby comparing a data set consisting of tens to hundreds of data points to the results of the model. For example, from 1938 to 1991, the wild population of whooping cranes had grown at a mean exponential rate, r, of 0·040, with annual fluctuations in the growth rate, SD (r), of 0·141 (Mirande *et al.* 1993). Life-table analysis predicted an r of 0·052. Simulations using VORTEX predicted an r of 0·046 into the future, with a SD (r) of 0·081. The lower growth rate projected by the stochastic model reflects the effects of inbreeding and perhaps imbalanced sex ratios among breeders in the simulation, factors that are not considered in deterministic life-table calculations. Moreover, life-table analyses use mean birth and death rates to calculate a single estimate of the population growth rate. When birth and death rates are fluctuating, it is more appropriate to average the population growth rates calculated separately from birth and death rates for each year. This mean growth rate would be lower than the growth rate estimated from mean life-table values.

When the simulation model was started with the 18 cranes present in 1938, it projected a population size in 1991 ($N \pm \mathrm{SD} = 151 \pm 123$) almost exactly the same as that observed ($N = 146$). The large variation in population size across simulations, however, indicates that very different fates (including extinction) were almost equally likely. The model slightly underestimated the annual fluctuations in population growth [model SD (r) = 0·112 *v.* actual SD (r) = 0·141]. This may reflect a lack of full incorporation of all aspects of stochasticity into the model, or it may simply reflect the sampling error inherent in stochastic phenomena. Because the data input to the model necessarily derive from analysis of past trends, such retrospective analysis should be viewed as a check of consistency, not as proof that the model correctly describes current population dynamics. Providing another confirmation of consistency, both deterministic calculations and the simulation model project an over-wintering population of whooping cranes consisting of 12% juveniles (less than 1 year of age), while the observed frequency of juveniles at the wintering grounds in Texas has averaged 13%.

Convincing evidence of the accuracy, precision and usefulness of PVA simulation models would require comparison of model predictions to the distribution of fates of many replicate populations. Such a test probably cannot be conducted on any endangered species, but could and should be examined in experimental non-endangered populations. Once simulation models are determined to be sufficiently descriptive of population processes, they can guide management of threatened and endangered species (see above and Lindenmayer *et al.* 1993). The use of PVA modelling as a tool in an adaptive management framework (Clark *et al.* 1990) can lead to increasingly effective species recovery efforts as better data and better models allow more thorough analyses.

Directions for Future Development of PVA Models

The PVA simulation programs presently available model life histories as a series of discrete (seasonal) events, yet many species breed and die throughout much of the year. Continuous-time models would be more realistic and could be developed by simulating the time between life-history events as a random variable. Whether continuous-time models would significantly improve the precision of population viability estimates is unknown. Even more realistic models might treat some life-history events (e.g., gestation, lactation) as stages of specified duration, rather than as instantaneous events.

Most PVA simulation programs were designed to model long-lived, low fecundity (K-selected) species such as mammals, birds and reptiles. Relatively little work has been devoted to developing models for short-lived, high-fecundity (r-selected) species such as many amphibians and insects. Yet, the viability of populations of r-selected species may be highly affected by stochastic phenomena, and r-selected species may have much greater minimum viable populations than do most K-selected species. Assuring viability of K-selected species in a community may also afford adequate protection for r-selected species, however, because of the often greater habitat-area requirements of large vertebrates. Populations of r-selected species are probably less affected by intrinsic demographic stochasticity because large numbers of progeny will minimise random fluctuations, but they are more affected by environmental variations across space and time. PVA models designed for r-selected species would probably model fecundity as a continuous distribution, rather than as a completely specified discrete distribution of litter or clutch sizes; they might be based on life-history stages rather than time-increment ages; and they would require more detailed and accurate description of environmental fluctuations than might be required for modelling K-selected species.

The range of PVA computer simulation models becoming available is important because the different assumptions of the models provide capabilities for modelling diverse life histories. Because PVA models always simplify the life history of a species, and because the assumptions of no model are likely to match exactly our best understanding of the dynamics of a population of interest, it will often be valuable to conduct PVA modelling with several simulation programs and to compare the results. Moreover, no computer program can be guaranteed to be free of errors. There is a need for researchers to compare results from different PVA models when applied to the same analysis, to determine how the different assumptions affect conclusions and to cross-validate algorithms and computer code.

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Appendix. Sample Output from VORTEX

Explanatory comments are added in italics

```
VORTEX—simulation of genetic and demographic stochasticity
TEST
```

Simulation label and output file name

```
Fri Dec 20 09:21:18 1991
  2 population(s) simulated for 100 years, 100 runs
```

VORTEX first lists the input parameters used in the simulation:

```
  HETEROSIS model of inbreeding depression
    with 3·14 lethal equivalents per diploid genome

  Migration matrix:
        1       2
  1  0·9900  0·0100
  2  0·0100  0·9900
```

i.e. 1% probability of migration from Population 1 to 2, and from Population 2 to 1

```
  First age of reproduction for females: 2   for males: 2
  Age of senescence (death): 10
  Sex ratio at birth (proportion males): 0·5000

Population 1:

  Polygynous mating; 50·00 per cent of adult males in the breeding pool.
  Reproduction is assumed to be density independent.
    50·00 (EV=12·50 SD) per cent of adult females produce litters of size 0
    25·00 per cent of adult females produce litters of size 1
    25·00 per cent of adult females produce litters of size 2
```

EV is environmental variation

```
    50·00 (EV=20·41 SD) per cent mortality of females between ages 0 and 1
    10·00 (EV=3·00 SD) per cent mortality of females between ages 1 and 2
    10·00 (EV=3·00 SD) per cent annual mortality of adult females (2<=age<=10)
    50·00 (EV=20·41 SD) per cent mortality of males between ages 0 and 1
    10·00 (EV=3·00 SD) per cent mortality of males between ages 1 and 2
    10·00 (EV=3·00 SD) per cent annual mortality of adult males (2<=age<=10)
```

```
EVs have been adjusted to closest values possible for binomial distribution.
   EV in reproduction and mortality will be correlated.
   Frequency of type 1 catastrophes: 1·000 per cent
     with 0·500 multiplicative effect on reproduction
      and 0·750 multiplicative effect on survival
   Frequency of type 2 catastrophes: 1·000 per cent
     with 0·500 multiplicative effect on reproduction
      and 0·750 multiplicative effect on survival

   Initial size of Population 1: (set to reflect stable age distribution)
 Age   1    2    3    4    5    6    7    8    9    10     Total
       1    0    1    1    0    1    0    0    1    0       5  Males
       1    0    1    1    0    1    0    0    1    0       5  Females
    Carrying capacity = 50 (EV = 0·00 SD)
     with a 10·000 per cent decrease for 5 years.

   Animals harvested from population 1, year 1 to year 10 at 2 year intervals:
     1 females 1 years old
     1 female adults (2<=age<=10)
     1 males 1 years old
     1 male adults (2<=age<=10)
   Animals added to population 1, year 10 through year 50 at 4 year intervals:
     1 females 1 years old
     1 females 2 years old
     1 males 1 years old
     1 males 2 years old
```

Input values are summarised above, results follow.

VORTEX now reports life-table calculations of expected population growth rate.

```
Deterministic population growth rate (based on females, with assumptions of no limitation of mates
  and no inbreeding depression):
     r = −0·001     lambda = 0·999     RO = 0·997
   Generation time for:  females = 5·28   males = 5·28
```

Note that the deterministic life-table calculations project approximately zero population growth for this population.

```
Stable age distribution:   Age class     females     males
                               0          0·119      0·119
                               1          0·059      0·059
                               2          0·053      0·053
                               3          0·048      0·048
                               4          0·043      0·043
                               5          0·038      0·038
                               6          0·034      0·034
                               7          0·031      0·031
                               8          0·028      0·028
                               9          0·025      0·025
                              10          0·022      0·022
Ratio of adult (>=2) males to adult (>=2) females: 1·000
```

Population 2:

Input parameters for Population 2 were identical to those for Population 1.
Output would repeat this information from above.

Simulation results follow.

Population1

```
Year 10
    N[Extinct] =       0, P[E] = 0·000
    N[Surviving] =  100, P[S] = 1·000
    Population size =           4·36  (0·10 SE,   1·01 SD)
    Expected heterozygosity =  0·880 (0·001 SE, 0·012 SD)
    Observed heterozygosity =  1·000 (0·000 SE, 0·000 SD)
    Number of extant alleles = 8·57  (0·15 SE,   1·50 SD)
```

Population summaries given, as requested by user, at 10-year intervals.

```
Year 100
    N[Extinct] =     86, P[E] = 0·860
    N[Surviving] =  14, P[S] = 0·140
    Population size =           8·14  (1·27 SE,   4·74 SD)
    Expected heterozygosity =  0·577 (0·035 SE, 0·130 SD)
    Observed heterozygosity =  0·753 (0·071 SE, 0·266 SD)
    Number of extant alleles = 3·14  (0·35 SE,   1·29 SD)

In 100 simulations of 100 years of Population1:
  86 went extinct and 14 survived.
This gives a probability of extinction of 0·8600 (0·0347 SE),
  or a probability of success of            0·1400 (0·0347 SE).
99 simulations went extinct at least once.
Median time to first extinction was 5 years.
Of those going extinct,
  mean time to first extinction was 7·84 years (1·36 SE, 13·52 SD).
123 recolonisations occurred.
Mean time to recolonisation was 4·22 years (0·23 SE, 2·55 SD).
110 re-extinctions occurred.
Mean time to re-extinction was 54·05 years (2·81 SE, 29·52 SD).

Mean final population for successful cases was 8·14 (1·27 SE, 4·74 SD)
  Age 1     Adults     Total
  0·14       3·86       4·00   Males
  0·36       3·79       4·14   Females

During years of harvest and/or supplementation
  mean growth rate (r) was 0·0889 (0·0121 SE, 0·4352 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was  −0·0267 (0·0026 SE, 0·2130 SD)
```

Population growth in the simulation (r = −0·0267) was depressed relative to the projected growth rate calculated from the life table (r = −0·001) because of inbreeding depression and occasional lack of available mates.

```
Note:   497 of 1000 harvests of males and 530 of 1000 harvests of females could not be completed
        because of insufficient animals.

Final expected heterozygosity was    0·5768 (0·0349 SE, 0·1305 SD)
Final observed heterozygosity was    0·7529 (0·0712 SE, 0·2664 SD)
Final number of alleles was          3·14   (0·35 SE,    1·29 SD)

Population2
```

Similar results for Population 2, omitted from this Appendix, would follow.

```
  ********  Metapopulation Summary  ********
Year 10
    N[Extinct] =       0, P[E] = 0·000
    N[Surviving] =  100, P[S] = 1·000
    Population size =            8·65  (0·16 SE,   1·59 SD)
    Expected heterozygosity =   0·939 (0·000 SE, 0·004 SD)
    Observed heterozygosity =   1·000 (0·000 SE, 0·000 SD)
    Number of extant alleles = 16·92  (0·20 SE,   1·96 SD)
```

Metapopulation summaries are given at 10-year intervals.

```
Year 100
   N[Extinct] =    79, P[E] = 0·790
   N[Surviving] = 21, P[S] = 0·210
   Population size =              10·38  (1·37 SE,  6·28 SD)
   Expected heterozygosity =   0·600 (0·025 SE, 0·115 SD)
   Observed heterozygosity =   0·701 (0·050 SE, 0·229 SD)
   Number of extant alleles =  3·57  (0·30 SE,  1·36 SD)

In 100 simulations of 100 years of Metapopulation:
  79 went extinct and 21 survived.
This gives a probability of extinction of  0·7900 (0·0407 SE),
  or a probability of success of           0·2100 (0·0407 SE).
97 simulations went extinct at least once.
Median time to first extinction was 7 years.
Of those going extinct,
  mean time to first extinction was 11·40 years (2·05 SE, 20·23 SD).
91 recolonisations occurred.
Mean time to recolonisation was 3·75 years (0·15 SE, 1·45 SD).
73 re-extinctions occurred.
Mean time to re-extinction was 76·15 years (1·06 SE, 9·05 SD).

Mean final population for successful cases was 10·38 (1·37 SE, 6·28 SD)
  Age 1     Adults    Total
  0·48      4·71      5·19  Males
  0·48      4·71      5·19  Females

During years of harvest and/or supplementation
  mean growth rate (r) was 0·0545 (0·0128 SE, 0·4711 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was  −0·0314 (0·0021 SE, 0·1743 SD)

Final expected heterozygosity was  0·5997 (0·0251 SE, 0·1151 SD)
Final observed heterozygosity was  0·7009 (0·0499 SE, 0·2288 SD)
Final number of alleles was        3·57   (0·30 SE,   1·36 SD)
```

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