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April 21, 1999

**BLM**

# Current Events Population Viability

Ft. Collins, Colorado



**Wild Horse and Burro Population Viability Forum**



# **WILD HORSE and BURRO POPULATION VIABILITY FORUM**

**APRIL 21, 1999**

**A Bureau of Land Management Sponsored Event**

**FORT COLLINS MARRIOTT, FORT COLLINS, COLORADO**

The intent of this Forum is to provide a unique opportunity for useful discussion and strategy development on important conceptual and practical topics pertaining to population viability. Our approach will include thought-provoking, science-based presentations, followed by in-depth question and answer sessions between scientific researchers, BLM Horse Program specialists and managers, Advisory Board members, and interested members of the public. For additional information, please contact Linda Coates-Markle, Montana/Dakotas State Program Specialist at 406-238-1540.

## **GOALS AND FOCUS FOR THE FORUM**

**Session 1:** Identify and define the equine resource. Are there unique genetic resources, and/or smaller populations, in need of genetic conservation efforts or are we dealing primarily with larger metapopulations where genetic conservation is not a critical issue? Draw inference from wild equids of Africa and Asia. In other words, comparisons to other wild equid populations may help us to define and further understand critical inbreeding and/or density dependent issues.

**Session 2:** Clarify genetic terms and issues such as Effective Genetic Population ( $N_e$ ) size and Minimum Viable Population (MVP) size. What is meant by genetic diversity or heterozygosity and how does it relate to levels of inbreeding within a population? These are all terms used by researchers and interested public requesting information about BLM herds, and it is important that we both understand these concepts and their applicability to populations and management decisions.

**Session 3:** Define Population Viability Analysis (PVA) and identify possible benefits and limitations to modeling efforts. What types of demographic, genetic and/or ecological data are needed for these models? Compare and contrast different methods of population monitoring which are used to provide the necessary data to estimate viability.

**Session 4:** And finally, use PVA to evaluate real-life scenarios involving wild horse populations. What are the consequences of different management alternatives? Compare and contrast the complexities of herd management, using both removals and immunocontraception, for two very different populations. Demonstrate the potential for enhancing the adaptive decision-making process through the use of PVA.



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The intent of this Forum is to provide a unique opportunity for useful discussion and strategy development on important conceptual and practical topics pertaining to population viability. Our approach will include thought-provoking, science-based presentations, followed by in-depth question and answer sessions between scientific researchers, BLM Horse Program specialists and managers, Advisory Board members, and interested members of the public. For additional information, please contact Linda Coates-Markle, Montana/Dakotas State Program Specialist at 406-238-1540.

## **FORUM AGENDA**

**Introductions:** Welcome to Participants and Discuss Forum Goals and Agenda

8:00am-8:10am - Welcome & Opening Remarks - Henri Bisson, BLM, WO  
- Forum Goals and Focus - Linda Coates-Markle, BLM, Mt/Dks

8:10am-8:20am - Introductory Remarks - Dr. Daniel Rubenstein, Princeton University,  
Session Moderator

**Session 1:** Identify and define the equine resource. Are there unique genetic resources, and/or smaller populations, in need of genetic conservation efforts or are we dealing primarily with larger metapopulations where genetic conservation is not a critical issue? Draw inference from wild equids of Africa and Asia. In other words, comparisons to other wild equid populations may help us to define and further understand critical inbreeding and/or density dependent issues.

8:20am-8:45am - Conservation Issues for Wild Zebras, Asses, and Horses in Africa and Asia - Dr. Patricia Moehlman, IUCN/SSC Equid Specialist Group.  
\*8:45am-9:00am - Discussion Period

9:00am-9:30am - Feral Horses as Genetic Resources - Dr. Phil Sponenberg, Virginia-Maryland Regional College of Veterinary Medicine.  
\*9:30am-9:45am - Discussion Period

9:45am-10:10am - Density Dependence in Population Dynamics of Wild Horses - Dr. Stephen Jenkins, University of Nevada, Reno.  
\*10:10am-10:25am - Discussion Period

**BREAK 10:25AM-10:40AM**

**Session 2:** Clarify genetic terms and issues such as Effective Genetic Population ( $N_e$ ) size and Minimum Viable Population (MVP) size. What is meant by genetic diversity or heterozygosity and how does it relate to levels of inbreeding within a population? These are all terms used by researchers and interested public requesting information about BLM herds, and it is important that we both understand these concepts and their applicability to populations and management decisions.

10:40am-11:05am - Genetic Variation in Horse Populations - Dr. Gus Cothran, University of Kentucky.  
\*11:05am-11:20am - Discussion Period

11:20am-11:45am - Genetic Management of Small Populations: The Special Case of Feral Horses - Dr. Oliver Ryder, University of California, San Diego.  
\*11:45am-12:00noon - Discussion Period

**LUNCH BREAK 12:00noon-1:00PM**  
Additional Poster Sessions will be available  
for viewing at back of the meeting room.

**Session 2 continued:** Clarify genetic terms and issues such as Effective Genetic Population size ( $N_e$ ) and Minimum Viable Population size (MVP).

1:00pm-1:30pm - Genetic Effective Population Size in the Pryor Mountain Wild Horse Herd - Dr. Francis Singer, Biological Resources Division, USGS.  
\*1:30pm-1:45pm - Discussion Period

1:45pm-2:00pm - SYNOPSIS OF SESSIONS 1 AND 2 . Identify major points of consideration and recommendations for future efforts - Dr. Daniel Rubenstein, Session Moderator and Linda Coates-Markle, BLM.

**Session 3:** Define Population Viability Analysis (PVA) and identify possible benefits and limitations to modeling efforts. What types of demographic, genetic and/or ecological data are needed for these models? Compare and contrast different methods of population monitoring which are used to provide the necessary

data to estimate viability.

2:00pm-2:30pm - Essential Components of a Defensible PVA - Dr. Barry Noon,  
Colorado State University.

\*2:30pm-2:45pm - Discussion Period

2:45pm-3:15m - Methods to Collect Required Data to Develop Rigorous PVA Models  
- Dr. Gary White, Colorado State University.

\*3:15pm-3:30pm - Discussion Period

### **BREAK 3:30PM-3:45PM**

**Session 4:** And finally, use PVA to evaluate real-life scenarios involving wild horse populations. What are the consequences of different management alternatives? Compare and contrast the complexities of herd management, using both removals and immunocontraception, for two very different populations. Demonstrate the potential for enhancing the adaptive decision-making process through the use of PVA.

3:45pm-4:15pm - Viability of Feral Horse Populations on Atlantic Coastal Barrier  
Islands: Implications for Management - Dr. Brian Underwood, USGS  
Patuxent Wildlife Research Center.

\*4:15pm-4:30pm - Discussion Period

4:30pm-5:00pm - Genetic and Population Consequences of Contraception and  
Removal Programs in the Pryor Mountain Wild Horse Range -  
Dr. John Gross, Natural Resource Ecology Laboratory, CSU.

\*5:00pm-5:15pm - Discussion Period

5:15pm-5:30pm - SYNOPSIS OF SESSIONS 3 AND 4 - Identify major points of  
consideration and recommendations for future efforts - Dr. Daniel  
Rubenstein, Session Moderator and Linda Coates-Markle, BLM.

**Forum Final Synopsis:** Summarize major points of consideration and  
recommendations from all Forum Sessions. Prioritize items for a preliminary action  
plan, identifying areas needing further clarification and/or possible research efforts.

5:30pm-6:00pm - SYNOPSIS OF ALL FORUM SESSIONS - Dr. Daniel Rubenstein,  
Session Moderator and Linda Coates-Markle, BLM

ABSTRACTS



# **WILD HORSE and BURRO POPULATION VIABILITY FORUM**

**APRIL 21, 1999**

**A Bureau of Land Management Sponsored Event**  
Marriott Hotel, Fort Collins, Colorado

## **GOALS, TOPICS, SPEAKERS and ABSTRACTS**

Prepared & Organized by: Linda Coates-Markle, State Wild Horse & Burro Specialist, Montana/Dakotas.

### **FORUM GOALS:**

#### **To develop an enhanced understanding of:**

- 1) reasons and guidelines regarding the number of horses and/or burros needed to maintain self-sustaining herds;
- 2) reasons and guidelines regarding the number of animals needed for supplementary introductions (or level of mixing among subpopulations) in order to maintain genetic diversity within herds of different sizes;
- 3) how to determine and collect types of data needed to assess population viability using different PVA models based on demography, genetics, and/or ecological processes;
- 4) how to evaluate the applicability and incorporation of PVA information in management policy and decisions, with respect to determining appropriate management levels (AMLs) and population control techniques in different herd areas.

### **FORUM FORMAT:**

Two to three qualified individuals will address each topic area, with an emphasis on specifics related to BLM goals for the Forum. It is expected that each speaker will bring a different opinion and concentration on the topic, based on individual background and area of expertise. Format of presentations will include a 25-30 minute slide-visual aid presentation per speaker, followed by 15 minutes of an open question

and answer period with discussion. This will result in an approximate two-hour focus per topic. **A structured agenda is available under separate cover.**

The entire Forum will be moderated, with a well-versed and qualified researcher directing all questions and discussion. In order to optimize the value of this Forum, all participants and attendees are encouraged to preview the enclosed abstracts and develop relevant questions pertaining to individual areas of concern, interest and/or field experience. At the conclusion of the Forum, a minimum of a one-half (1/2) hour period will be used to summarize highlights and emphasize recommendations for future efforts.

**FORUM MODERATOR:** The entire Forum will be moderated by the highly-qualified and well-respected equid researcher, **Dr. Daniel Rubenstein**, from Princeton, N.J., who will direct questions within all discussion periods.

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**FORUM SESSION TOPICS:**

**SESSION I: Define the resource which we are responsible for protecting and establish realistic management goals for conservation.** For example using genetic considerations, one goal might be to ensure (with a 95% probability) that 90% of genetic variation in a population is retained over a 200 year period. Are these conservation issues critical for all herds or only smaller (<100) populations? Should we be identifying the presence of unique herds? What are the possible roles of inbreeding and density dependent regulation in populations with annual growth rates of 18-25%? Compare with conservation issues for wild equids in Asia and Africa.

## Session 1 - Speakers and Abstracts of Presentations:

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### CONSERVATION ISSUES FOR WILD ZEBRAS, ASSES, AND HORSES IN AFRICA AND ASIA

Family Equidae is composed of zebras, asses, and horses. During the Pleistocene they were the most abundant medium-sized grazing animals of the grasslands and steppes of Africa, Asia, and the Americas. Today there remain only seven species. In Africa, the African wild ass (*Equus africanus*) is critically endangered, the Grevy's zebra (*Equus grevyi*) and the Mountain zebra (*Equus zebra*) are endangered, and the Plains zebra (*Equus burchelli*) is dependent on conservation support. In Asia, the Asian wild ass (*Equus hemionus*) is vulnerable with some subspecies in an endangered state. The Kiang (*Equus kiang*) is considered a lower risk, but data are inadequate for the assessment of the status of two of the subspecies. The Przewalski's horse exists in captivity, but is extinct in the wild. Re-introduction projects for the Przewalski's horse are occurring in China and Mongolia. The majority of species in this small family are endangered or vulnerable. Equids are significant for conservation both for their unique genetic heritage and their role as flagship species for the conservation of biodiversity in desert and grassland ecosystems in Africa and Asia.

At present better information is needed on:

- national and local population status and trends
- genetic definition of sub-species
- genetic viability of isolated and re-introduced populations
- behavioral ecology, resource requirements, disease epidemiology , and demography
- risk assessment of geographically distinct populations
- socio-economics and viability of alternative conservation/utilization strategies

National capability needs to be supported by training and a communication network. In addition, the involvement of local communities in the conservation of their natural resources is fundamental to the future of these species. Conservation of wildlife and natural resources often results in economic and cultural deprivation for local resource users. It is important to develop economic and political mechanisms which allow local people to benefit from the conservation of wildlife.

Most of the endangered equids live in desert ecosystems. These habitats are not rich in species, but do contain unique and endemic animals and plants. Zebras, asses, and horses can serve as 'flagship' species for the conservation of desert ecosystems and their biodiversity.

**D. P. "Phil" Sponenberg, DVM, PhD.**  
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#### **FERAL HORSES AS GENETIC RESOURCES**

Feral horses in the USA originate from a wide variety of breeds and types of horses. Most populations are influenced by several breeds, each of which has been common at some point in the USA after European contact. These composite populations vary from one to the other, but generally represent horse types that are well represented in domesticated, managed horse herds. A very few feral populations remain that descend from types and breeds now otherwise rare or extinct, mainly the Colonial Spanish type. These few populations (Cerbat, Sulphur, Pryor, Kiger, perhaps others) represent genetic resources of significance to horse biodiversity and warrant special consideration for conservation and management as unique resources. While breed origin makes some populations unique, all feral horses persist in environments in which natural selection is one of the major selection pressures. This selection environment is unique among equine environments, and its role in shaping the genetic composition of the herds is important as a biological process. While it shapes all populations, its role in shaping those that are unique by virtue of founder type is especially worth consideration since this phenomenon is an ongoing, if unplanned, experiment that cannot be duplicated should these populations become extinct.

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## DENSITY DEPENDENCE IN POPULATION DYNAMICS OF WILD HORSES

Two general methods can be used to test for density dependence in population dynamics of organisms: experimental manipulations of abundance and statistical analysis of sequences of abundance estimates for unmanipulated populations. Statisticians and population ecologists have made substantial progress in recent years in developing appropriate techniques for the second approach, although there is still disagreement about how much can be learned about population regulation without doing experiments. Populations of wild horses in the western U.S. are censused regularly, providing many opportunities to test statistically for evidence of density dependence, at least in the form of reduced growth rates when densities are high. However, relatively few of these data sets meet the assumptions necessary for applying currently accepted methods for conducting these tests. Nevertheless, a meta-analysis of data for 7 populations in Idaho, Montana, Nevada, Oregon, and Utah showed a significant negative correlation between population growth rate and population size. The implications of this density dependence for modeling and management of horse populations are not necessarily straightforward.

**SESSION 2: Discuss effective genetic population size ( $N_e$ ) versus minimum viable population (MVP).** MVP is the minimum number of breeding individuals that must be maintained (in the absence of a catastrophe), for a population to survive a given period of time. A major concern is the loss of genetic variation through genetic drift and/or inbreeding. The effective population size is essentially the number of breeding individuals (both male and female) that contribute to the next generation and is greatly affected by population social structure and sex ratio. Discuss definitions, means of assessment for different populations and broad application of  $N_e$  and MVP in management decisions.

### **Session 2 - Speakers and Abstracts of Presentations:**

**E. Gus Cothran, PhD.**  
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## GENETIC VARIATION IN HORSE POPULATIONS

One of the major focuses of conservation biology and genetic management of small populations is the preservation of genetic variability. In this talk I will discuss what is meant by genetic variability and how it can be measured in feral horse populations. Genetic variation is the amount of inheritable diversity present in a population or an individual. It can be observed as morphological variations in size, conformation or color, but we actually are concerned with variability of genes, whether we can observe an effect of this variation or not. There are several different measures of genetic variation but two of the basic ways it is expressed are heterozygosity, the proportion of genes variable within an individual, and some type of estimate of allelic diversity, such as the total number of genetic types observed within the population. The actual measurement of variability of a sample of a population is based upon a small number of genetic systems that can be typed using biochemical techniques. These are blood group systems, isozyme systems and DNA variation such as seen in microsatellite systems. Blood group testing requires a fresh blood sample while isozyme typing can use frozen blood or other tissues such as a muscle biopsy. Direct testing of DNA can utilize almost any bodily product including hair (if the hair root bulb is present) or even feces. The estimates of genetic variation we can get from these techniques perhaps do not accurately correspond to total genomic variation, although that is not certain. However, with a sufficient comparative data base, these measures can be used to determine the variation within a population as it compares to other horse populations and can be used to make inferences about the genetic health of the population at the time of sampling.

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## GENETIC MANAGEMENT OF SMALL POPULATIONS: THE SPECIAL CASE OF FERAL HORSES

Only the plains zebra, among all the Equidae, can be counted as a wild species that is not endangered. The Przewalski's horse (*Equus przewalskii*), the African wild ass (*Equus africanus somaliensis*), the Asiatic wild asses (*E. kiang*; *E. hemionus onager*; *E. hemionus luteus*; *E. hemionus khur*), Grevy's zebra (*E. grevyi*) and the mountain

zebras (*E. zebra zebra*; *E. zebra hartmannae*) are all endangered species. Donkeys and horses, the domestic equids, thrive in the presence of human culture, contrary to the situation pertaining for populations of wild equids.

Conservation efforts for wild equids include establishment of protected areas for surviving populations, such as Samburu National Park in Kenya and Cape Mountain Zebra National Park in South Africa. Often, habitat alterations are undertaken in order to support these native species, including management action to assure access to water resources. Conservation of equid gene pools *ex situ* involve intensive management of small populations through programs like the Species Survival Plans of the American Zoo and Aquarium Association. The goal of the structured breeding programs of SSPs is to preserve target amounts of genetic variation for defined periods of time (typically 90-95% of average heterozygosity over 100-200 years). Equalizing founder contribution and family size maximizes the genetically effective size of these managed populations. Domestic horses have become feral numerous times and at numerous place in the world, establishing expanding populations that have produced a variety of environmental impacts.

Feral horse populations have tended to be managed first for demographic considerations (carrying capacity, number of individuals removed). Founder effect, natural selection, genetic drift, and gene flow through introduction of new individuals into relatively isolated breeding populations serve as the major features influencing the gene pool of feral horse populations. Selective forces acting on feral horses include the impacts of the natural environment as well as anthropogenic influences, such as removal of individuals from the herd.

Assuming that management of populations of feral horses requires identification of the maximum number of individuals to occupy individual management units (carrying capacity), managers are faced with decisions regarding impacts of intervention on the gene pool. Differing scenarios for removal of individuals in order to maintain populations below carrying capacity produce different impacts on the population's gene pool over time, especially under circumstances in which migration of individuals between populations is rare. Modern methods of genetic analysis applied to horses that have been removed from feral populations can shed insights into population structure and help constrain alternatives for population management.

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**GENETIC EFFECTIVE POPULATION SIZE IN THE PRYOR MOUNTAIN WILD HORSE HERD: Implications for conservation genetics and viability goals in wild horses.**

**FRANCIS J. SINGER and LINDA ZEIGENFUSS**

Genetics are typically presumed to be the least important component of minimum viable population predictions (and the PVA process), and catastrophe is the most important. Catastrophe can be guarded against with large population sizes with longer predicted persistence times, but also with better management of any given population. We introduce the concepts of food-limited ecological carrying capacity (hereafter ECC) and economic carrying capacity. The tarpan and Przewalski's wild horses of Europe and Asia might have been limited by predation by a combination of wolves, brown bears, and 1 or more large cats, but predation (mostly by mountain lions) is significant in only a very small number of wild horse herds in the US West. Most herds grow at phenomenal rates, for ungulates, of 16-22% per year. We observe that most wild horse herds are managed close to economic carrying capacity (which is typically 50-65% of ECC in numbers) and, at this lowered population level, animals are in better body condition, survival is higher (there is less starvation or dehydration), recruitment is higher, there is less conflict with other vertebrates and soil and vegetation resources, population fluctuations are less, and there is less risk of a resource-limited catastrophe. Evidence is presented from the Pryor Mountain wild horse herd to support the hypothesis that long-term management of wild horse numbers below the unmanaged maximum, has resulted in improved wild horse conditions, apparently improved range conditions, and a lower probability of large starvation losses. In the 1990's, foal rates were higher, 0.608, for the youngest breeding mares (3-5 year-olds), the most sensitive group to better conditions, than in the 1970-86 period, 0.392 ( $P=0.048$ ). Population growth rates did not differ statistically between the periods ( $P=0.528$ ), but numerical growth rates were higher ( $\lambda=1.176$ ) in the 1990's than in the 1970-86 period ( $\lambda=1.119$ ) and the coefficient of variation on growth rates was less (3.21 vs. 17.09) in the 1990's.

While genetics is not a consideration in many free-ranging vertebrates, genetic consideration will become a serious consideration over future decades in wild horse management since so many of the herds are now isolated and small. In the Intermountain West region, 61% of all populations numbered less than 100 and 40% of isolated populations managed at <50 animals for a number of decades might be inbred. Genetic effective population size (commonly referred to as  $N_e$ ) is defined as the number of breeding individuals (both male and female) that contribute to the next generation.  $N_e$  is a useful number since it can be used to calculate the loss of



genetic variation through genetic drift and/or inbreeding from one generation to the next with the formula  $1/4N_e$ . But  $N_e$  is a difficult number to calculate for wild horses, since the calculation is complicated by overlapping generations, a harem structure greatly limits male participation in breeding (an uneven ratio of breeding sexes reduces  $N_e$ ), there is high variance in reproductive success of both sexes, populations fluctuate due to removals, and mares do not typically breed until 3 years and stallions until 7 years. No single, universally acceptable formula exists to deal with these complexities. We studied the population and mating dynamics of the Pryor Mountain wild horse herd, 1992-98, in collaboration with a talented volunteer (Rev. Floyd Schwieger) and Linda Coates-Markle of the Bureau of Land Management Billings Field Office. We found the 7 estimators for  $N_e$  averaged 27% of the census population size ( $N$ ) up until 1994. Birth sex ratio and management scenarios that resulted in more males on the range and smaller average harem size since 1994 (which increased male participation in breeding) increased  $N_e$  to 36% of census  $N$ .

No standard goal for  $N_e$  or for loss of genetic resources currently exists for wild horse herds. If a goal of  $N_e=50$  was applied-- the goal for maintenance of domestic livestock production and thus probably an absolute minimum for a population in the wild--census  $N$  would need to be in excess of 139-185 wild horses, the excess to account for 3-5 removals per wild horse generation. Management could greatly alter this relationship by: (a) altering breeding sex ratios to increase  $N_e$  through removals, (b) increasing generation length through removal scenarios (which reduces the rate of loss of genetic resources, or (c) introducing breeding animals periodically from other genetically similar herds to maintain genetic resources. Only one to two breeding animals per generation (=about every 10 years in wild horses) would maintain the genetic resources in small populations of about 100 animals, thus obviating the need for larger populations in all cases. We stress that there is little imminent risk since most wild horse herds sampled have large amounts of genetic heterozygosity and genetic resources are lost slowly over periods of many generations, and wild horses are long-lived with long generation interval. We are currently investigating the complexities of the simple calculations of  $N_e$  through detailed stallion parentage studies using DNA (to test how many foals are sired by harem stallions) and to test if high genetic heterozygosity is maintained through selection (i.e. is positively correlated to high reproductive success). This work is in collaboration with Gus Cothran of the Equine Studies Lab, University of Kentucky, through a contract to USGS.

**SESSION 3: Discuss generating data for PVA demographic, genetic and ecological modeling efforts.** Define benefits and limitations to PVA modeling efforts. Discuss types of demographic (e.g. birth and survival rates, generation time, age to first reproduction), genetic (e.g. observed and expected heterozygosity) and ecological (e.g. predators, disease, loss of habitat) data currently used as input variables and the need to monitor over time to capture variability in

these estimates. Evaluate the current techniques for acquiring population data using aerial surveys combined with Idaho sightability or mark-recapture methods.

### **Session 3 - Speakers and Abstracts of Presentations:**

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#### **ESSENTIAL COMPONENTS OF A DEFENSIBLE PVA.**

All PVAs should have certain elements in common. Where they will differ most is in terms of the details, dictated ultimately by the availability of data. Data-rich PVAs will be more sophisticated, provide more reliable assessments of risks to a species' persistence, and provide clearer guidance to an appropriate management response. In the usual case of sparse data, however, addressing the following issues will still prove useful, even if the final assessment is largely a qualitative one. A fundamental understanding of the species' ecology, including what constitutes suitable habitat and some insights to the species ability to disperse to distant patches of habitat.

- An understanding of what environmental disturbances constitute threats to the species' persistence, and their mechanism of action.
- An understanding of the likely response of the population when exposed to the threat(s). That is, to what extent can the species accommodate the perturbation? What are the limits to the species' resilience? Are the population responses to disturbance linear, or nonlinear with steep threshold regions?
- Some knowledge of the likelihood of a threat occurring, and given its occurrence, the expected magnitude of its impact on the population.
  - + Insights into the deterministic threats to persistence (e.g., timber harvest, water diversions, grazing pressure).
  - + Insights into the stochastic threats to persistence (e.g., precipitation, temperature, fire, droughts, floods, etc.).
- An assessment of the current state of the population in terms of its vulnerability to disturbance. Where is the population at this point in time (in terms of its resilience) and what is its expected response to disturbance of different types and magnitudes?

- An assessment of both the risks to persistence and possible population responses in a probabilistic context. Estimates of the certainty associated with population forecasts (i.e., the statistical reliability of projections).
- Formal connection to the concepts of decision-making in the context of uncertainty. A clear exposition of the tradeoffs between statistical type I and type II errors and how the error likelihoods were allocated in the decision-making process.
- Assuming that habitat degradation, loss, and fragmentation are the major threats to persistence, PVA must address both the dynamics of the habitat as well as the dynamics of the population. Most PVAs have ignored habitat dynamics, variation in habitat quality, and the importance of habitat geometry and distribution.
- The results of a PVA are valuable to the extent that they inform the management decision making process.

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#### **METHODS TO COLLECT REQUIRED DATA TO DEVELOP RIGOROUS PVA MODELS**

Population viability analysis examines the question of whether a biological population of a given size will persist (remain viable) for some specified time period. To develop useful estimates of population viability, stochastic population models must be developed that incorporate demographic, temporal, and individual variation. The lack of individual heterogeneity in previous population viability analyses has resulted in underestimates of persistence, making the conclusions overly pessimistic. Additionally, spatial and genetic variation may be required, depending on the population being modeled and the time frame of the analysis. Estimates of these variance components must be constructed by removing the sampling variation inherent in estimates of population parameters. Most previous population viability analyses have not separated sampling variation from process variation in the parameter estimates, so they underestimate population persistence. Further, the uncertainty (sampling variance) of parameter estimates must be incorporated into estimates and confidence intervals of persistence if valid inferences are to be made back to the population under consideration.

Marked animals have been widely used to estimate population size, survival rate, and recruitment in biological populations. Wild horse populations seem particularly suited to methods of analysis based on marked animals because of the individual heterogeneity in appearance makes many individuals uniquely identifiable, so that capture to apply marks is not required. In addition, DNA techniques provide alternative methods to obtain data on identifiable individuals. Estimation methods based on the Cormack-Jolly-Seber model available in Program MARK seem well-suited to estimation of wild horse survival rates from inferences on identifiable individuals. Procedures to separate sampling variation from process variation are already available in the program.

Recruitment to reproductive age can be estimated from age ratios estimated by population surveys. Population size can be estimated from ratios of uniquely identifiable individuals to unidentifiable animals during the same surveys with estimators provided in Program NOREMARK. Thus the techniques required to obtain the data to develop rigorous PVA models for wild horse populations are available and doable. However, the cost of information is always high, so the real question is whether this information is considered worth the expense by policy makers, and ultimately, the voting public.

**SESSION 4: Discuss using PVA models to simulate and potentially forecast population dynamics and genetic consequences of different management decisions.** Types of models (e.g. individual-based, density independent), limitations of model application within a risk analysis format, and model validation to be discussed and evaluated using real-life scenarios. Models will not predict a "magic" single number for appropriate population size. Management scenarios may include varying population numbers and/or carrying capacity, applying female and/or male contraception, modifying herd age/sex structure through selective removals, modifying herd spatial distribution or subdivision, periodic introductions of outside animals or various combinations of any these methods.

**Session 4 - Speakers and Abstracts of Presentations:**

**H. Brian Underwood, PhD.  
USGS Patuxent Wildlife Research Center,  
Cooperative Park Studies Unit,  
350 Illick Hall, 1 Forestry Drive,  
State University of New York, and  
College of Environmental Science/Forestry,  
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#### **VIABILITY OF FERAL HORSE POPULATIONS ON ATLANTIC COASTAL BARRIER ISLANDS: IMPLICATIONS FOR MANAGEMENT.**

Feral and free-ranging horses have a long and illustrious legacy common to many Atlantic coastal barrier islands. I analyzed the population dynamics of the horses of Assateague Island National Seashore. Using population reconstruction methods and computer simulation of feral horse life-history, I developed a demographic PVA for this population for the expressed purpose of assessing the impacts of fertility control, disease epidemics, and catastrophic storm events on population persistence. Partial pedigrees were constructed to examine lineage-specific effects on population demography and heterozygosity. The reconstructed population varied from a low of 35 horses in 1975 to a high of 171 in 1988. Two-hundred forty-seven observations of survival histories (58 uncensored) of horses demonstrated that reconstructed March population size added significant prognostic value to the prediction of hazards for ASIS horses. There were no statistically detectable differences in survival between the sexes and no dramatic differences in the age at first foaling over time. Analysis of the inter-birth interval revealed a strong population size influence, however, there was a pronounced change in the early-age hazards as population size increased, while adult survival changed very little and remained quite high over a wide range in population sizes. The levels of adult mortality due to storms, diseases and accidents, which are impossible to predict, had the most profound effect on population viability. The simulation also suggested that management directed at specific matriline exerts a disproportionate effect on rate of increase, population viability and heterozygosity.

**John E. Gross, PhD.**  
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**Colorado State University,**  
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#### **GENETIC AND POPULATION CONSEQUENCES OF CONTRACEPTION AND REMOVAL PROGRAMS IN THE PRYOR MOUNTAIN WILD HORSE RANGE**

Management of wild horse populations frequently combines objectives to control a rapidly increasing population while at the same time managing to conserve genetic

resources. These objectives result in conflicting population goals, and there is thus a need to evaluate the relative merits of management strategies that can include contraceptives, periodic removals or a combination of the two. I evaluated these strategies by simulating population dynamics and changes in genetic constitution of the Pryor Mountain Wild Horse population when it was subjected to a variety of management controls.

Management alternatives included changes in population objective (AML), contraceptive treatment, and removals. Treatments (contraception and/or removal) focused on treatment/removal of young horses, old horses, or a random selection of individuals. Population responses included average population size, variance in population size, age structure, growth rate, changes in genetic heterozygosity (= diversity), inbreeding coefficient, and loss of alleles.

Model results revealed striking differences in terms of population structure and persistence of genetic diversity. When comparing contraceptives to removal, use of contraceptives can greatly reduce the variation in yearly population size, and average population sizes remained much closer to the objective. However, population growth rate is highly sensitive to the level of infertility, and there are sharp contrasts between the dynamics of populations controlled by harvest or contraception. With contraception, populations can increase rapidly if a high level of infertility is not achieved, but population size declines slowly because natural mortality is low. In contrast, removals permit managers to rapidly reduce population size. For most wild horse populations, about 70% of all reproductively active females will need to be maintained in an infertile state to achieve a stable population size.

To maintain genetic diversity, it is far better to remove or apply contraceptive to young rather than old animals. Allowing mares to breed once and then removing them is a particularly poor policy for managing genetic resources, because loss of genetic diversity is related to both the number of breeding animals and to generation time. Relative to late breeding, early breeding can dramatically reduce generation time, contribute to rapid population growth, and result in a high rate of loss of genetic diversity.

Overall, the most practical strategy for managing horses in the Pryor Mountain Wild Horse Range will likely employ the use of contraceptives and periodic removals. Simulations were used to identify treatments involving both contraceptives and removals so that the population achieved a slow growth rate and removals were employed at approximately 5-year intervals. These simulations identified criteria that could be widely employed to develop management protocols for many wild horse herds.

## **ADDITIONAL POSTER SESSIONS:**

Information to be available in a poster format. Authors will be available to discuss content of poster presentations during the day of the Forum. More presentations, all relevant to session topics and Forum goals, may be prepared and available by the date of the Forum.

**Francis Singer, PhD.**  
**Biological Resources Division, USGS**  
**Midcontinent Ecological Science Center, USGS, and**  
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### **DEVELOPMENT OF TOOLS THAT MANAGERS COULD USE TO MONITOR WILD HORSE POPULATIONS**

**FRANCIS J. SINGER and RONALD OSBORN**

Management will be more effective with modern, defensible, rapid, easy-to-use techniques for the counting, demographic analysis, range assessment, and the assessment of removal scenarios of wild horse populations. The Midcontinent Ecological Science Center is committed to assisting in development of new tools for wild horse and land managers. We review several techniques that have been developed for use in the Pryor Mountain and Book Cliffs wild horse herds by the BLM and the Midcontinent Ecological Science Center, US Geological Survey.

Identification and (nearly) complete enumeration of all individual horses in both herds were conducted using two different techniques. First, a unique marking system was developed, based on visual markings, that is also computer compatible. The system is rapid, inexpensive, easy to use, and requires only a PC computer and a data entry program, such as QPRO, EXCEL, ACCESS, or DBASE. It is most useful only for herds with excellent access and easy to observe animals. Second, a computerized photo-ID system (WHIMS) was developed for greater accuracy in identification of animals. WHIMS is most practical for herds of <200 animals, that are accessible from the ground, and where animals are approachable and easy to photograph. The WHIMS system would be very useful for contraceptive application where individual recognition is critical, and also for total enumeration or census, and the types of demographic analysis used in MARK and described in the talk by Gary White.

Many populations do not meet the criteria for a complete census of the animals, and an aerial technique is required. The technique should meet the criteria of defensible, tested, and accurate, yet be relatively easy to use and not require extensive capture or handling of animals. Four likely candidates are: (1) mark-resight using some individually recognizable animals (but this proved to be biased in the Pryor Mountains), (2) mark-resight of entire herd based on photos, recognition during pre-survey prior to the survey (this was used in another herd and shows good promise), (3) the Idaho sightability model--tested and used extensively on elk in many areas of the US west, and (4) population reconstruction models. Our work in the Pryor Mountain suggests that only about two-thirds of the known<sup>1</sup> population was observed during helicopter surveys, apparently because some harem groups, and especially bachelor groups, were under conifer cover during the survey. Thus, some population estimation technique is probably also needed for other herds that inhabit areas with some conifer cover. The US Geological Survey, Midcontinent Ecological Science Center has worked extensively with several of the aerial population estimators for elk and bighorn sheep, that might have potential for use with wild horses.

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1

The population was "known" 1995 through 1999 with only 1-2% error.

#### **PROPOSED END PRODUCT FOR FORUM:**

This Forum presents an opportunity for BLM Wild Horse and Burro Program Specialists and personnel, other agency individuals, researchers, Advisory Board members, and members of Advocacy groups and/or the general public to hear summaries of important issues and address specific items of concern during discussion periods following each speaker (or topic). The main end products of the Forum will include an annotated summary of important points and an annual review of BLM response to recommendations generated during each discussion period. Both the summary and reviews can be made available for general distribution to interested parties. Several researchers have recommended publication of forum proceedings and BLM is currently checking into the feasibility of this approach.





## **BIOGRAPHICAL SKETCH**

### **MODERATOR:**

**Daniel I. Rubenstein, PhD.**  
**Department of Ecology and Evolutionary Biology,**  
**205 Eno Hall,**  
**Princeton University,**  
**Princeton, New Jersey, 08544.**  
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**phone: 609-258-5698**  
**fax: 609-258-6818**

### **EDUCATION:**

University of Michigan - 1972, B.S.  
Duke University - 1977, Ph.D  
Cambridge University - 1978, M.A.  
King's College, Cambridge, England - 1978-1980, Post-doctoral

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(1991-Present) Professor and Chair of the Dept. of Ecology and Evolutionary Biology  
(1990-1991) Associate Professor, Department of Ecology and Evolutionary Biology  
(1986-1990) Associate Professor, Program in Ecology, Evolution and Behavior  
(1980-1986) Assistant Professor, Department of Biology, Princeton University  
(1977-1980) Research Fellow, King's College, Cambridge University, U.K.

### **RESEARCH FOCUS:**

Dr. Rubenstein is Professor of Biology and Chair of Princeton University's Department of Ecology and Evolutionary Biology. He received his B.S. from the University of Michigan in 1972 and his Ph.D. from Duke University in 1977 before receiving NSF-NATO and King's College Junior Research Fellowships for post-doctoral studies at Cambridge University. Since coming to Princeton he has received NIH and NSF research grants, the prestigious Presidential Young Investigator Award and has been elected Fellow of the Animal Behavior Society. He has co-edited two books, "Current Problems in Sociobiology" and "Ecological Aspects of Social Evolution" and has published over 50 articles.

Dr. Rubenstein studies how environmental variation and individual differences change the adaptive behavior, social structure, and dynamics of populations. He has special interests in all species of wild horses, zebras and asses, and has done field work on these species throughout the world. He has recently extended his field work to prediction of the effects of environmental change on the social behavior and population biology of horses and other species, including the changes wrought by management and by global warming. Studies are currently underway for measuring the impact of wildlife and livestock on an African grassland ecosystem and of wild

horses on a frontline barrier island habitat.

**RECENT PUBLICATIONS:**

Hack, M.A., R. East & D.I. Rubenstein (1998) Plains Zebra (Equus burchelli Gray). In: Zebras, Asses, and Horses: An Action Plan for the Conservation of Wild Equids (P. Moehlman, ed.) Gland, Switzerland: IUCN- The World Conservation Union (in Press).

Hack, M.A., D.I. Rubenstein (1998) Zebra Zones. *Natural History*. 107(2): 26-29.

Rubenstein, D.I. (1998) Behavioral Ecology and Conservation Policy: On Balancing Science, Application, and Advocacy. In: (ed) Behavioral Ecology & Conservation Biology. (T. Caro) Oxford University Press. pp 527-553

Krause J., G.D. Ruxton & D.I. Rubenstein (1998). Is there an influence of group size on predator hunting success? *Journal of Fish Biology*. 52:494-501.

Krause J., G.D. Ruxton & D.I. Rubenstein (1998). Group choice as a function of group size difference and assessment time in fish: the influence of species vulnerability to predation. *Ethology*. 104(1):68-74.

Bumann D., J. Krause & D.I. Rubenstein (1997). Mortality risk of spatial positions in animal groups: the danger of being in the front. *Behaviour*. 134:1063-1076.

Krause, J., Rubenstein, D.I., and Brown, D. (1997). Shoal choice behaviour in fish; the relationship between assessment time and assessment quality. *Behaviour*. 134: 1051-1062.

Gueron, S., Levin, S.A., and Rubenstein, D.I. (1996). The dynamics of mammalian herds: from individuals to aggregations. *Journal of Theoretical Biology* 182:85-98.

Saltz, D., and Rubenstein, D.I. (1995). Population Dynamics of a Reintroduced Asiatic Wild Ass (Equus hemionus) Herd. *Ecological Applications* Volume 5:327-335.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKERS:**

**Patricia D. Moehlman, PhD.**  
**Chair, IUCN/SSC Equid Specialist Group**  
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### **EDUCATION:**

Wellesley College - 1965, B.A. Biology  
University of Texas, Austin - 1968, M.A. Zoology (Ecology), Minor-Botany  
University of Wisconsin, Madison -1974, Ph.D. Zoology (Behavioral Ecology),  
Minor-Botany

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(1997 - Present) Chair, IUCN/SSC Equid Specialist Group  
(1997 - Present) Tanzania site Coordinator and Research Scientist for the USAID/GL-CRSP Project "Integrated Modeling and Assessment for Balancing Food Security, Conservation, and Ecosystem Integrity in East Africa".  
(1974 - Present) Research Associate, Tanzania Wildlife Research Institute, Tanzania.  
(1986-1996) Senior Conservation Scientist, The Wildlife Conservation Society  
(1981-1986) Assistant Professor of Wildlife Ecology, School of Forestry and Environmental Studies, Yale University

### **RESEARCH FOCUS:**

1989 - Present: African Wild Ass Research and Conservation Program. In cooperation with wildlife department personnel in Somalia, Ethiopia, and Eritrea this is a program that does research on the current status, population dynamics, and genetics of the critically endangered African Wild Ass. This program also provides training for local wildlife biologists.

1997 - Present: Tanzania Site Coordinator for a USAID funded Global Livestock Collaborative Research Support Program (GL-CRSP) to conduct research on "Integrated Modeling and Assessment for Balancing Food Security, Conservation, and Ecosystem Integrity in East Africa". The principal investigators are Michael B. Coughenour, Kathy Galvin, and Jim Ellis from Colorado State University and the team is composed of scientists from Colorado State University, the University of Colorado, the University of Dar es Salaam, and Sokoine University.

1974 - present. Research program on the behavioral ecology of jackals and the evolution of cooperative breeding in Canidae. Serengeti National Park and Ngorongoro Conservation Area, Tanzania.

1993 -1996: Biodiversity Assessment and Professional Capacity Building for Tanzanian National Parks. Principal Investigator.

1995: Member of the Ngorongoro Conservation Area Management Planning Team.

1988-1993: Development of ecological monitoring and training programs for Tanzania National Parks and the Ngorongoro Conservation Area.

**RECENT PUBLICATIONS:**

Moehlman, P.D., F. Kebede, and H. Yohannes.(1998). The African Wild Ass (*Equus africanus*): Conservation Status in the Horn of Africa. *Applied Animal Behavior Science*. Vol. 60(2,3):115-124.

Moehlman, P.D., L. Fowler, and J. Roe. (1998). Feral asses (*Equus africanus*) of Volcano Alcedo, Galapagos: behavioral ecology, spatial distribution, and social organization. *Applied Animal Behavior Science*. Vol. 60(2,3):197-210.

Moehlman, P.D. (1998) Behavioral Patterns and Communication in Feral Asses (*Equus africanus*). *Applied Animal Behavior Science*. Vol.60(2,3):125-169.

Moehlman, P.D. (1998) Feral Asses (*Equus africanus*): Intraspecific Variation in Social Organization in Arid and Mesic Habitats. *Applied Animal Behavior Science*. Vol. 60(2,3):171-195.

Moehlman, P.D., V.A. Runyoro, H. Hofer. (1997). Wildlife Population Trends in the Ngorongoro Crater, Tanzania. In: M. Thomson (ed). *Multiple Land-Use: The Experience of the Ngorongoro Conservation Area Tanzania*. IUCN Protected Areas Series Publication.

Moehlman, P.D., and H. Hofer. (1996). Cooperative Breeding, Reproductive Suppression, and Body mass in Canids. in: *Cooperative Breeding in Mammals*. N. Solomon and J. French (eds). Cambridge University Press.pp76-128.

Moehlman, P.D., G.Amato, and V.Runyoro. (1996). Genetic and demographic threats to the black rhinoceros population in the Ngorongoro Crater. *Conserv. Biol.* 10(4) 1107-1114.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

**D. P. "Phil" Sponenberg, DVM, PhD.**

**Technical Coordinator, American Livestock Breeds Conservancy,  
Professor, Pathology and Genetics, Virginia-Maryland Regional College of  
Veterinary, Medicine, Virginia Tech, Blacksburg, VA 24061.**

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### **EDUCATION:**

**Texas A&M University - 1976, DVM**

**Cornell - 1979, PhD in Pathology and Genetics**

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

**(1981 - Present) Virginia Maryland Regional College of Veterinary Medicine, Professor  
of Pathology and Genetics**

**Technical Coordinator of the American Livestock Breeds Conservancy.**

### **RESEARCH FOCUS:**

**Research interest lies in the conservation of genetic resources of domesticated  
animals, especially those that arose in North America from early introductions during  
the colonial period.**

**Other research areas include pigmentation genetics and morphology of mammals,  
including horses, sheep, goats, genetic conservation of rare breeds of domesticated  
animals and reproductive pathology.**

### **RECENT PUBLICATIONS:**

**Dascanio J.J., N. A. Parker, W. B. Ley, L. D. Warnick, D.P. Sponenberg. (1998).  
Magnesium sulfate intrauterine therapy in the mare. Equine Practice 20: 10-13.**

**Scarratt, W.K., M.L. Moon, D.P. Sponenberg, and B. Feldman. (1998). Case Report:  
Inappropriate administration of mineral oil resulting in lipid pneumonia in three  
horses. Equine Veterinary Journal 30: 85-88.**

**Sponenberg, D.P. and M.C. Weise. (1997). Dominant Black in Horses. Genetics,  
Selection, and Evolution 29:405-410.**

**Sponenberg, D.P., and A.T. Bowling. (1996). Champagne, a Dominant Color Dilution  
of Horses. Genetics, Selection, Evolution. 28:457-462.**

Baptiste, K.E., R.S. Pleasant, J.C. Jones, D.P. Sponenberg, A. Sysel, and D.J. McLamb. (1996). Paranasal Sinus Osteoma in an American Miniature Horse: Computed Tomographic Evaluation and Surgical Management. *Equine Practice* 18, 9:14-19.

Wallace, M.A., M.V. Crisman, J.P. Pickett, C.B. Carrig, D.P. Sponenberg. (1996). Central Blindness Associated with a Pituitary Adenoma in a Horse. *Equine Practice*. 18, 6: 8-13.

Chapters:

Sponenberg, D.P. Genetic Resources and Conservation. (1999). In: Bowling, A and A. Ruvinsky, (eds) *The Genetics of the Horse*. CAB International, Wallingford. In press.

Sponenberg, D.P. Genetics of Colour and Hair Texture. (1997). In: Piper L and A Ruvinsky, (eds) *The Genetics of Sheep*. CAB International, Wallingford.

Sponenberg, D.P. (1996). The Proliferation of Horse Breeds. In: Sandra L. Olsen (ed) *Horses Through Time*. Roberts Rinehart Publishers for Carnegie Museum of Natural History. Dublin, Ireland. pp153-174.

Books:

Christman, C.J., D.P. Sponenberg, and D.E. Bixby. (1997). *A Rare Breeds Album of American Livestock*. The American Livestock Breeds Conservancy, Pittsboro, North Carolina, USA. 118 pages.

Sponenberg, D.P. (1996) *Equine Color Genetics*. Iowa State University Press, Ames, Iowa. 156 pages.

Sponenberg, D.P. and C.J. Christman. (1995). *A Conservation Breeding Handbook*. American Livestock Breeds Conservancy. Pittsboro, NC. 136 pages.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

**Stephen H. Jenkins, Ph.D.**  
**Department of Biology/314**  
**University of Nevada, Reno**  
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**fax: 775-784-1302**

### **EDUCATION:**

Dartmouth College, Hanover, NH – 1968, A.B., Biology  
Harvard University, Cambridge, MA – 1975, Ph.D., Biology

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

Currently Professor of Biology at University of Nevada, Reno

### **RESEARCH FOCUS:**

Dr. Jenkins' research focuses on behavioral ecology and population ecology, particularly of mammals, and on plant-animal interactions. He has done extensive work on foraging behavior and ecology of various rodents and some work on population dynamics of feral horses and porcupines in Nevada, and beavers in northern Minnesota. His past work on foraging includes using observational and experimental approaches to test models of central-place foraging by beavers, to examine the role of plant secondary compounds in tree selection, and to study effects of predation risk on beaver foraging. He has also studied the development of food preferences in Belding's ground squirrels and nutritional reasons for differential seed preferences of desert rodents.

One aspect of foraging that Dr. Jenkins finds especially interesting is food-hoarding behavior. He uses laboratory experiments with kangaroo rats and pocket mice to test hypotheses about the adaptive value of various spatial patterns of food storage such as larderhoarding all seeds in a burrow or scatterhoarding seeds throughout an individual's home range. This work has led to the discovery of consistent individual differences in food-hoarding behavior among individuals of the same species, which raises several intriguing questions that can be addressed in field studies of these rodents. Food hoarding also has important implications for impacts of rodents on plant populations and communities, and Dr. Jenkins has been involved in field experiments to examine these implications for Indian ricegrass, a desert plant species which provides forage for large grazers such as horses and cattle.

Dr. Jenkins has developed a computer model which is being used by BLM personnel to evaluate and compare various management strategies for feral horses. This flexible



and user-friendly program is available without charge. Dr. Jenkins has also served on the editorial boards of American Midland Naturalist and Ecology.

**RECENT PUBLICATIONS:**

Jenkins, S. H., and S. W. Breck. (1998). Differences in food hoarding among six species of heteromyid rodents. *Journal of Mammalogy* 79:1221-1233.

Sweitzer, R. A., S. H. Jenkins, and J. Berger. (1997). The near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin desert. *Conservation Biology* 11:1407-1417.

Hayes, J. P., and S. H. Jenkins. (1997). Individual variation in mammals. *Journal of Mammalogy* 78:274-293.

Breck, S. W., and S. H. Jenkins. (1997). Use of an ecotone to test the effects of soil and desert rodents on the distribution of Indian ricegrass. *Ecography* 20:253-263.

Jenkins, S. H. (1996). Wild Horse Population Model, version 3.2 (includes 42-page user's manual).

Basey, J. M., and S. H. Jenkins. (1995). Influence of predation risk and energy maximization on food selection by beavers (*Castor canadensis*). *Canadian Journal of Zoology* 73:2197-2208.

Jenkins, S. H., A. Rothstein, and W. C. H. Green. (1995). Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. *Ecology* 76:2470-2481.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

**E. Gus Cothran, PhD.**

**Veterinary Science, Equine Blood Typing and Research Laboratory,  
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University of Kentucky,  
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### **EDUCATION:**

North Texas State University, Denton, Texas - 1973, B.S. Biology

North Texas State University, Denton, Texas - 1975, M.S. Zoology

University of Oklahoma, Norman, Oklahoma - 1982, Ph.D. Zoology

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(1989 - Present) Director of the Equine Blood Typing Research Laboratory

(1992 - Present) Associate Research Professor - Department of Veterinary Science

(1991-1992) Adjunct Professor, Department of Biological Sciences, University of North Texas, Denton.

(1986-1992) Assistant Research Professor, Department of Veterinary Science, 101 Animal Pathology, University of Kentucky, Lexington.

### **RESEARCH FOCUS:**

Dr. Cothran was born and raised in Texas, primarily living in El Paso. His major area of study was ecological and population genetics of natural populations. He went to Savannah River Ecology laboratory near Alken, South Carolina where he did research on population genetics and genetic management of white-tailed deer. He then went to the Southwest Foundation in San Antonio, Texas where he first began studies of horse genetics. From there he came to the University of Kentucky where he currently is an Associate Research Professor in the Department of Veterinary Science and the Director of the Equine Blood Typing Research Laboratory. His current research includes Biochemical genetic relationships and evolution of the Equidae, population structure and the maintenance of genetic variation in horse breeds, the genetic relationship of domestic horse breeds genetics of wild horse populations, conservation genetics of rare breeds, evolution of the protease inhibitor system in equids, and the relationships among genetic variation and reproductive characteristics in horses; gene mapping in the horse.

### **Current projects include:**

-Heredity basis of equine congenital defects. -Interrelationships of inbreeding, genetic polymorphism, and reproductive performance in horses. -Population genetics of feral

horses. -Comparative aspects of genic variation in horses under human selection and under natural selection. -Genetic aspects of captivity. Management of genetic polymorphism in small populations. -Genetic relationship among domestic horse breeds -Gene mapping of the horse -Gene mapping of the alpaca.

#### **RECENT PUBLICATIONS:**

Cothran, E.G. and E. Van Dyk. (1999) Genetic analysis of three native South African horse breeds. South African J. of Vet. Science, in press.

Horin, P., E.G. Cothran, K. Trtkova, E. Marti, V. Glasnak, M. Vyskocil, S. Lasary, and P. Henney. (1998). Polymorphism of old Kladruber horses, a surviving but endangered baroque breed. Eur. J. Immunogenetics. 25:357-363.

Cothran, E.G., S.A. Santos, M.C.M. Mazza, T.L. Lear, and J.R.B Sereno. (1998). Genetics of the Pantaniero horse of the Pantanal region of Brazil. Genetics and Molecular Biology. 21:343-349.

Behara, A.M.P., D.T. Colling, E.G. Cothran and J.P. Gibson. (1998). Genetic relationships between horse breeds based on microsatellite data: Applications for livestock conservation. 6th World Congress of Genetics as Applied to Livestock Production. 28:119-123.

Tikhonov, V.N., E.G. Cothran and S.P. Knyazev. (1998). Population genetic parameters of aboriginal Yakut horses as related to the phylogeny of modern breeds of the domestic horse (*Equus caballus*) L. Russian J. of Genetics 34:654-666. Translated from Genetica 34:796-809.

Tikhonov, V.N., E.G. Cothran and S.P. Knyazev. (1997). The screening of alleles found in Yakut horses using a broadened spectrum of genetic markers. Proc. Russian Academy of Agricultural Sciences. 636.1:575. 113.2:33-35. (in Russian)

Cothran, E.G. and M. Kovac. (1997). Genetic analysis of the Croatia Trakehner and Posavina horse breeds. Zivocisna Vyroba (Animal Production). 42:207-212.

Cothran, E.G. (1995). Genetic markers and breed identification in genetic conservation. In: Proceedings of the Third Global Conference on Conservation of Domestic Animal Genetic Resources. Crawford, R.D., E.E. Lister, and J.T. Buckley (eds.), Rare Breeds International, pp 291-306.

Bailey, E., K.T. Graves, E.G. Cothran, R. Reid, T.L. Lear, and R.B. Ennis. (1995). Synteny mapping horse microsatellite markers using a hetero-hybridoma panel. Animal Genetics. 26:177-180.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

**Dr. Oliver Ryder, PhD.**  
**Adjunct Professor of Biology,**  
**University of California, San Diego,**  
**Center for Reproduction of Endangered Species,**  
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### **EDUCATION:**

UC San Diego (UCSD), 1975 - Ph.D in Biology.

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(Present) Adjunct Professor of Biology, University of California, San Diego.  
(Present) Center for Reproduction of Endangered Species (CRES) Kleberg Chair in Genetics.  
(1979- 1986) Geneticist, CRES, Zoological Society of San Diego.  
(1975 - 1979) Postdoctoral fellow, Zoological Society of San Diego (ZSSD), and Research Associate, Department of Biology and Reproductive Medicine, UCSD.

### **RESEARCH FOCUS:**

Dr. Ryder is a world leader in the application of genetics to the field of wildlife biology. He is the Head of the Genetics Division, and holder of the Kleberg Chair in Genetics at CRES, of the Zoological Society of San Diego which operates the San Diego Zoo and Wild Animal Park.

Twenty years ago when Dr. Ryder joined CRES, there had been little, if any interface between the fields of molecular biology and conservation. He was among the first geneticists who, dedicated to protecting endangered animals, pioneered the links now bridging zoological parks and those working in the field to conserve natural populations.

In addition to his involvement in preservation efforts involving such well-known species as the California condor, Dr. Ryder has also studied such local threatened animal species as bighorn sheep, endangered toads of Southern California, and pronghorn antelope of the Baja California peninsula. His international efforts include research and collaborations around the globe focusing on such animals as African rhinos, giant pandas, and gorillas.

Dr. Ryder has authored more than 170 scientific and popular articles and lectures frequently to international audiences.

**RECENT PUBLICATIONS:**

Field, D., L. Chemnick, M. Robbins, K. Garner and O. Ryder. (1998). Paternity determination in captive lowland gorillas and orangutans and wild mountain gorillas by microsatellite analysis. *Primates* 39/2:199-209.

Oakenfull, E.A. and O.A. Ryder. (1998). Control region and 12S rRNA variation in all the extant mitochondrial lineages of Przewalski's horse (*Equus przewalskii*). *Animal Genetics*. 29:456-459.

Burrows, W. and O.A. Ryder. (1997). Y-chromosome variation in great apes. *Nature*. 385:125-126.

Garner, K.J., and O.A. Ryder. (1996). Mitochondrial DNA diversity in gorillas. *Molec. Phyl. Evol.* 6:39-48.

Zhang, Y., and O.A. Ryder. (1995). Different rates of mitochondrial DNA sequence evolution in Kirk's dik-dik (*Madoqua kirkii*) populations. *Mol. Phyl. Evol.* Vol. 4(3):291-297.

Ryder, O.A. (1995). Zoological Parks and the Conservation of Biological Diversity: Linking ex situ and in situ Conservation Efforts. *Journal of Environment and Development*. Vol. 4(2):105-120.

Ryder, O.A., and A.T.C. Feistner. (1995). Research in zoos: A growth area in conservation. *Biodiversity and Conservation* 4:671-677.

Ryder, O.A. (1993). Przewalski's Horse: Prospects for reintroduction into the wild. *Conservation Biology*. 7:13-15.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

**Francis Singer, PhD.**

**Biological Resources Division, USGS**

**Midcontinent Ecological Science Center, USGS, and**

**Natural Resource Ecology Lab,**

**Colorado State University,**

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### **EDUCATION:**

Cornell University, Ithaca, NY - 1967-1971, B.S. Ecology and Systematics

University of Idaho, Moscow - 1972-1975, M.S. Wildlife Ecology

Colorado State University - 1992-1995, Ph.D., Rangeland Ecosystems

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(1991 - Present) Biological Resources Division, USGS - Research Ecologist

### **RESEARCH FOCUS:**

Francis Singer is a research ecologist and Project Leader, in Ungulate ecology studies. He supervises a large, interdisciplinary study team that is investigating the elk herbivory and elk-plant interactions in Rocky Mountain National Park. This team includes several Colorado State University researchers, and researchers from Brigham Young University, University of Wyoming and other universities. The ungulate studies program at BRD-Midcontinent Ecological Science Center seeks to meet the technical data collection and management guidance needs for a large number of national park units and BLM lands within the central region of USGS. The research is focused on several major themes including studies of the biological effects of different management scenarios for ungulates, conservation biology and restoration of ungulates in a number of parks and other interior lands. Major research projects have included studies of effects of ungulates on ecosystem processes in national parks, models of bison and elk management scenarios in Jackson Valley, bighorn sheep conservation biology and restoration in 15 national parks, and studies of water relations and the effects of beaver decline on willow-elk relationships. These studies are better detailed in an attached strategic plan.

### **RECENT PUBLICATIONS:**

Smith, B.L., W.P. Burger, and F.J. Singer. (1998). An expandable radio collar for elk calves. Wildlife Society Bulletin 26(1):113-117.

Singer, F.J., Zeigenfuss, R.G. Cates, and D. Barnett. (1998). Elk, multiple factors, and willows in national parks. *Wildlife Society Bulletin* 26(3):419-428.

Singer, F.J., D.M. Swift, M.B. Coughenour, and J. Varley. Thunder on the Yellowstone revisited: an assessment of natural regulation management of native ungulates. *Wildlife Society Bulletin* 26(3):375-390.

Gross, J.E., M.E. Moses, and F.J. Singer. (1997). Simulating desert bighorn sheep populations to support management decisions: effects of patch size, spatial structure, and disease. *Desert Bighorn Council Transactions* 41:26-36.

Singer F.J., and Mack. (1997). Yellowstone's prey: Effects of the fires of 1988 and cascading effects of restoration of a keystone predator. Cornell University Press. Book, "Predators and ecosystems" (invited chapter).

Singer, F.J., A. Harting, K.S. Symonds and M.B. Coughenour. (1997). Elk calf mortality in Yellowstone National Park: the evidence for density dependence and compensation. *J. Wild. Manage.* 61:(in press).

Coughenour, M.B., and F.J. Singer. (1996). Yellowstone elk population responses to fire- a comparison of landscape carrying capacity and spatial dynamic ecosystem modeling approaches. Pages 169-180 in *Ecological Implication of Fire in Greater Yellowstone*. International Association of Wildland Fire, Fairfield, Washington.

Singer, F.J., and M.K. Harter. (1996). Comparative effects of elk herbivory and the fires of 1988 on grasslands in northern Yellowstone National Park. *Ecological Applications* 6:185-199.

Singer, F.J., editor. (1996). *Effects of grazing by wild ungulates in Yellowstone National Park*, U.S. Department of Interior, National Park Service, Technical Report NRTR/9601, Denver Colorado. 375 pp.

Coughenour, M.B., and F.J. Singer. (1996). Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecological Applications* 6:573-593?

Coughenour, M.B., and F.J. Singer. (1995). Elk responses to precipitation, density, and winter weather under natural regulation management in Yellowstone National Park. *Ecol. Applic.* 6:573-593.

Singer, F.J., and R.A. Renkin. (1995). Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. *Great Basin Nat.* 55:210-212.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

**Barry R. Noon, PhD.**  
**Department of Fishery & Wildlife Biology,**  
**240 J.V.K. Wager,**  
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### **EDUCATION:**

Princeton University, Princeton, NJ - 1971, B.A. Biology  
State University of New York, Albany, NY - 1977, Ph.D. Biology

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(Present) Associate Professor, Department of Fishery and Wildlife Biology, and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO.  
Chief Scientist, National Biological Service, U.S. Department of the Interior, Washington, DC  
Project Leader, Pacific Southwest Research Station, Redwood Sciences Laboratory, U.S. Forest Service, Arcata, CA.  
Associate Professor, Department of Wildlife Management, Humboldt State University, Arcata, CA

### **RESEARCH FOCUS:**

Conservation planning for threatened and endangered species; science-based management of public lands to conserve biological diversity; population dynamics and viability analyses (spatially explicit modeling); vertebrate demography and life history; methods to study natural populations of vertebrate wildlife; ecological monitoring; biometrics.

### **Current Research Support:**

1. \$1.4 million (over 8 years), "Demography and habitat relationships of spotted owls in the Southern Cascade Mountains, California." Sponsor: USDA, Forest Service; 1989-present.
2. \$140,000, "Effects of forest fragmentation on the biological diversity of small mammals, primates, and herpetofauna in the Western Ghats Mountains, South India." Sponsor: US State Department/USFWS; 1995-2000. Jointly with Drs. Ravi Chellam and Ajith Kumar.



3. \$696,000, "Predicting the effects of ecosystem fragmentation and restoration: Management models for animal populations. Sponsor: Strategic Environmental Research and Development Program. 1998-2002. Jointly with Dr. Thomas Sisk.
4. \$25,000, "The effects of fragmentation on grassland birds." Sponsor: U.S. Forest Service. 1998-1999.
5. \$132,000, "Development of a population viability analysis for the southwest willow flycatcher." 1998-1999. Sponsor: Bureau of Reclamation. Jointly with Dr. Rolland Lamberson.

**RECENT PUBLICATIONS:**

Noon, B.R., T. Spies, and M. Raphael. (1999) Conceptual basis for designing an effectiveness monitoring program. In: *The Strategy and Design of the Effectiveness Monitoring Program for the Northwest Forest Plan*. Mulder, B., B. Noon, T. Spies, and M. Raphael (eds.). General technical Report PNW-XXX. Portland, OR: U.S. Department of Agriculture, Forest Service. In Press

Bingham, B.B., and B.R. Noon. (1998). The use of core areas in comprehensive mitigation strategies. *Conservation Biology* 12:241-243.

Bingham, B.B., and B.R. Noon. (1997). Mitigation of habitat "take": application to habitat conservation planning. *Conservation Biology* 11:127-139.

Rosenberg, D., B.R. Noon, and E.C. Meslow. (1997). Biological corridors: Form, function, and efficacy. *Bioscience* 47:677-687.

Noon, B.R., and K.S. McKelvey. (1996). Management of the spotted owl: A case history in conservation biology. *Annual Reviews Ecology and Systematics* 27:135-162.

Conroy, M.J., and B.R. Noon. (1996). Mapping of species richness for conservation of biological diversity: Conceptual and methodological issues. *Ecological Applications* 6:763-773.

Noon, B.R., and K.S. McKelvey. (1996). A common framework for conservation planning: linking individual and metapopulation models. *In Metapopulations and Wildlife Conservation*. D.R. McCullough, (ed.) Island Press. pp. 139-166.

Noon, B.R., K.S. McKelvey, and D.D. Murphy. (1996). Developing an analytical context for multispecies conservation planning. *In The Ecological Basis of Conservation*. S.T.A. Pickett, R.S. Ostfeld, M. Shachak, and G.E. Likens, (eds.) Chapman and Hall. pp. 43-59.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

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### **EDUCATION:**

Iowa State University - 1970, B.S. Fisheries & Wildlife Biology  
University of Maine at Orono - 1972, M.S. Wildlife Biology  
Ohio State University - 1976, Ph.D Zoology  
Utah State University - 1976-1977, Post-Ph.D. Wildlife Science

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(1991 - Present) Professor, Dept of Fishery and Wildlife, CSU.  
(1984 - 1991) Associate Professor, Dept of Fishery and Wildlife, CSU.

### **RESEARCH FOCUS:**

Quantitative ecology, estimation of population parameters, compensatory mortality in mule deer populations. Statistical analysis of demographic data from northern spotted owls, Corvallis, Oregon, 1998. Program MARK workshop in Dunedin, New Zealand, and St. Andrews, Scotland, 1998. Guest of the South African Statistical Society, 1997. Presented lectures on population viability analysis, statistical modeling and parameter estimation, Program MARK, and mule deer density dependence. Program MARK workshop to Striped Bass Working Group, Reston, Virginia, 1997. Mexican Spotted Owl Recovery Team, 1993-1998. Responsibilities involved developing delisting criteria and developing a population monitoring plan to meet the delisting criteria. Workshop in Erice, Sicily, Italy, 1996 on Research Techniques in Ethology and Animal Ecology: Uses and Misuses. Presented a lecture on population viability analysis. Associate Editor, journal of Wildlife Management, 1993-1995.

### **RECENT PUBLICATIONS:**

White, G.C. (1999). Modeling Population Dynamics. in S. Demarais and P. Krausman, (eds.) Big Game Management. In Press.

White, G.C. (1999). Population viability analysis: data requirements and essential analyses. In: L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York USA. In press.

White, G.C., and K.P. Burnham. (1999). Program MARK: survival estimation from populations of marded animals. *Bird Study*. In Press

Unsworth, J.W., D.F. Pac, G.C. White, and R.M Bartmann. (1999). Mule deer survival in Colorado, Idaho, and Montana. *Journal of Wildlife Management* 63:315-326.

Thompson, W.L., G.C. White, and C. Gowan. (1998). *Monitoring Vertebrate Populations*. Academic Press, New York, NY. 365 pp.

Shenk, T.M., G.C. White, and K.P. Burnham. (1998). Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological Monographs* 86:445-463.

Anderson, D.R., K.P. Burnham, and G.C. White. (1998). Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. *Journal of Applied Statistics* 25(2):263-282.

White, G.C., and R.M. Bartmann. (1998). Effect of density reduction on overwinter survival of free-ranging mule deer fawns. *Journal of Wildlife Management* 62:214-225.

White, G.C., and R.M. Bartmann. (1998). Mule deer management what should be monitored? In: *Journal C. Vos, Jr., editor. Proceedings of the 1997 deer-elk workshop, Rio Rico, Arizona*. Arizona Game and Fish Department, Phoenix, Arizona, USA. pp 102-116

White, G.C. and R.M. Bartmann. (1997). Density dependence in deer populations. In: *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood, and J.H. Rappole, eds. Smithsonian Institution Press, Washington, D.C. pp 120-135.

Miller, S.G., G.C. White, et al. (1997). Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. *Wildlife Monographs* 133:1-55.

Lubow, B., G.C. White, and D.R. Anderson. (1996). Evaluation of a linked-sex harvest strategy for cervid populations. *Journal of Wildlife Management* 60:787-796.

White, G.C., and R.E. Bennetts. (1996). Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549-2557.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

**H. Brian Underwood, PhD.  
USGS Patuxent Wildlife Research Center,  
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### **EDUCATION:**

State University of New York College of Environmental Science and Forestry,  
Syracuse, NY - 1990, Ph.D. Wildlife Ecology

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

Research Wildlife Ecologist, USGS Patuxent Wildlife Research Center,  
Cooperative Park Studies Unit, College of Environmental Science/Forestry,  
Syracuse, NY

### **RESEARCH FOCUS:**

Current Research Emphasis applied population biology and demography, natural resource conservation and management, systems modeling and simulation, spatial analysis and GIS.

### **RECENT PUBLICATIONS:**

Porter, W. F. and H. B. Underwood. (1999). Of elephants and blind men: deer management in the Eastern United States. *Ecological Applications* 9(1):3-9.

Underwood, H. B., F. D. Verret, and J. P. Fischer. (1998). Density and herd composition of white-tailed deer populations on Fire Island National Seashore. Final Report to the National Park Service. 42pp.

Underwood, H. B. (1997). Feasibility of a fertility control program for white-tailed deer at Morristown National Historical Park: Phase I. Final report to the National Park Service. 20pp.

Underwood, H. B. (1997). Implications of fertility control for feral horse management on Assateague Island National Seashore. Final report to the National Park Service. 135pp.

Underwood, H. B. and W. F. Porter. (1997). Reconsidering paradigms of overpopulation in ungulates. Pages 185-198 in W. J. McShea, H. B. Underwood and J. H. Rappole (eds.). The science of overabundance: deer ecology and population management. The Smithsonian Institution Press. 402pp.

McShea, W. J, H. B. Underwood and J. H. Rappole. (1997). Deer management and the concept of overabundance. Pages 1-7 in W. J. McShea, H. B. Underwood and J. H. Rappole (eds.). The science of overabundance: deer ecology and population management. The Smithsonian Institution Press. 402pp.

Nielson, C. K., W. F. Porter and H. B. Underwood. (1997). An adaptive management approach to controlling suburban deer. Wildlife Society Bulletin. 25(2):470-477.

Risenhoover, K. L. and H. B. Underwood. (1997). Mitigating the biotic effects of overabundant deer populations on National Parks: Modeling spatial aspects of resource use at the individual level. Final report to the National Park Service. 32pp.

Risenhoover, K. L., H. B. Underwood, W. Yan and J. L. Cooke. (1997). A spatially explicit modeling environment for evaluating deer management strategies. pp 366-379 In: W. J. McShea, H. B. Underwood and J. H. Rappole (eds.). The science of overabundance: deer ecology and population management. The Smithsonian Institution Press. 402pp.

Underwood, H. B. (1996). A review of Wildlife 2001: Populations. Book Review. Ecology 77:983-984.

Garner, D. L., H. B. Underwood, and W. F. Porter. (1995). Use of modern infrared thermography for wildlife population surveys. J. Environ. Manage. 19(2):233-238.

## **BIOGRAPHICAL SKETCH**

### **SESSION SPEAKER:**

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### **EDUCATION:**

University of Colorado, Boulder - 1980, B.S. Environmental, Population, and Organismal Biology  
Colorado State University - 1984, M.S. Zoology  
University of California, Davis - 1990, Ph.D. Ecology

### **ACADEMIC AND RESEARCH APPOINTMENTS:**

(1994- Present) Research Associate, Senior Scientific Staff. Natural Resource Ecology Laboratory, Colorado State University.  
(1990-1994) Postdoctoral Fellow. Natural Resource Ecology Laboratory, Colorado State University.  
(1984-1989) Research Assistant. Department of Agronomy and Range Science, University of California, Davis.

### **RESEARCH FOCUS:**

(1994- Present) Research Associate, Senior Scientific Staff. Natural Resource Ecology Laboratory, Colorado State University. My research program focuses on wildlife ecology, including habitat-population interactions, disease ecology, and the application of ecological theory to solving environmental problems. Research grants totaling over a million dollars have been generated during this tenure.

Recent Teaching experience at Colorado State University: EY500, Organism and Population Ecology (required course for graduate core curriculum in Ecology), 1996, 1997. EY501, Community and Landscape Ecology discussion leader, 1998. Guest lecturer: Methods in Ecological Research (modeling. population viability analysis).

(1990-1994) Postdoctoral Fellow. Natural Resource Ecology Laboratory, Colorado State University. Examined factors regulating intake rate of mammalian herbivores ranging in body size from 0.05 to 500 kg. in collaboration with Drs. N.T. Hobbs, B.A. Wunder, and D.E. Spalinger. Research grants totaling almost two hundred thousand dollars were generated during this tenure.

(1984-1989) Research Assistant. Department of Agronomy and Range Science, University of California, Davis. Conducted research on the nutritional ecology of Nubian ibex, including controlled experiments on captive animals (digestion and passage rates, intake, rumination experiments), as well as extensive field work with a wild population. Supervisor: Dr. M.W. Demment. Research grants totaling almost one hundred fifty thousand dollars were generated during this tenure.

**RECENT PUBLICATIONS:**

Gross, J.E., F.J. Singer, and M.E. Moses. (1999). Assessing restoration decisions to enhance the persistence of translocated populations of bighorn sheep: implications of disease. *Restoration Ecology* in review.

Gross, J.E. (1998). Sexual segregation in ungulates: a comment. *Journal of Mammalogy* 49(4): 1401-1409.

Gross, J.E., M.E. Moses, and F.J. Singer. (1997). Simulating desert bighorn sheep populations to support management decisions: effects of patch size, spatial structure, and disease. *Desert Bighorn Council Transactions* 41: 26-36.

Gross, J.E., P.U. Alkon, and M.W. Demment. (1996). Nutritional ecology of dimorphic herbivores: digestion and passage rates in Nubian ibex. *Oecologia* 107: 170-178.

Bailey, D.W., J.E. Gross, E.A. Laca, L.R. Rittenhouse, M.B. Coughenour, D.M. Swift, and P.L. Sims. (1996). Invited synthesis paper: Mechanisms that result in large herbivore distribution patterns. *Journal of Range Management* 49: 386-400.

Shipley, L.A., D.E. Spalinger, J.E. Gross, and N.T. Hobbs, and B.A. Wunder. (1996). The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores. *Functional Ecology* 10: 234-244.

Gross, J.E., P.U. Alkon, and M.W. Demment. (1995a). Grouping patterns and spatial segregation by Nubian ibex. *Journal of Arid Environments* 30: 423-440.

Gross, J.E., M.W. Demment, P.U. Alkon, and M. Kotzman. (1995b). Mastication and feeding behaviors of male and female Nubian ibex: compensation for differences in body size. *Functional Ecology* 9: 385-393.

Gross, J.E., C. Zank, N.T. Hobbs, and D.E. Spalinger. (1995c). Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. *Landscape Ecology* 10: 209-217.





# Population Viability Analysis: Data Requirements and Essential Analyses

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## ABSTRACT

Population viability analysis examines the question of whether a biological population of a given size will persist (remain viable) for some specified time period. To develop useful estimates of population viability, stochastic population models must be developed that incorporate demographic, temporal, and individual variation. The lack of individual heterogeneity in previous population viability analyses has resulted in underestimates of persistence, making the conclusions overly pessimistic. Additionally, spatial and genetic variation may be required, depending on the population being modeled and the time frame of the analysis. Estimates of these variance components must be constructed by removing the sampling variation inherent in estimates of population parameters. Most previous population viability analyses have not removed sampling variation from parameter estimates, so they underestimate population persistence. Further, the uncertainty (sampling variance) of parameter estimates must be incorporated into estimates and confidence intervals of persistence. Because data are lacking for most populations requiring a viability analysis, surrogate species such as game species should be considered for estimates of temporal and spatial variation, and possibly individual variation. Continued use of unreliable estimates of population persistence will discredit the field of conservation biology.

## INTRODUCTION

The biological diversity of the earth is threatened by the burgeoning human population. To prevent extinctions of species, conservationists must manage many populations in isolated habitat parcels that are smaller than desirable. An example is maintaining large-bodied predator populations in isolated, limited area nature reserves (Clark et al. 1996).

A population is defined as "a group of individuals of the same species occupying a defined area at the same time" (Hunter 1996). The viability of a population is the probability that the population will persist for some specified time. Two procedures are commonly used for evaluating the viability of a population. Population viability analysis (PVA) is the methodology of estimating the probability that a population of a specified size will persist for a specified length of time. The minimum viable population (MVP) is the smallest population size that will persist some specified length of time with a specified probability. In the first case, the probability of extinction is estimated, whereas in the second, the number of animals that is needed in the population to meet a specified probability of persistence is estimated. For a population that is expected to go extinct, the time to extinction is the expected time the population will persist. Both PVA and MVP require a time horizon, i.e., a specified, but arbitrary, time to which the probability of extinction pertains.

Definitions and criteria for viability, persistence, and extinction are arbitrary, e.g., a 95% probability of a population persisting for at least 100 years (Boyce 1992). Mace and Lande (1991) discuss criteria for extinction. Ginzburg et al. (1982) suggest the phrase "quasiextinction risk" as the probability of a population dropping below some critical threshold, a concept also promoted by Ludwig (1996a) and Dennis et al. (1991). Schneider and Yodzis (1994) use the term quasiextinction to mean the population dropped to only 20 females remaining.

The usual approach for estimating persistence is to develop a probability distribution for the number of years before the model "goes extinct", or falls below a specified threshold. The percentage of the area under this distribution where the population persists beyond a specified time period is taken as an estimate of the probability of persistence. To obtain MVP, probabilities of extinction are needed for various initial population sizes. The expected time to extinction is a misleading indicator of population viability (Ludwig 1996b) because for small

populations, the probability of extinction in the immediate future is high, even though the expected time until extinction may be quite large. The skewness of the distribution of time until extinction thus makes the probability of extinction for a specified time interval a more realistic measure of population viability.

Simple stochastic models have yielded qualitative insights into population viability questions (Dennis et al. 1991). But because population growth is generally considered to be nonlinear, with nonlinear dynamics making most stochastic models intractable for analysis (Ludwig 1996b), and because catastrophes and their distribution pose even more difficult statistical problems (Ludwig 1996b), analytical methods are generally inadequate to compute these probabilities. Hence, computer simulation is commonly used to produce numerical estimates for persistence or MVP. Analytical models lead to greater insights given the simplifying assumptions used to develop the model. However, the simplicity of analytical models precludes their use in real analyses because of the omission of important processes governing population change such as age structure and periodic breeding. Lack of data suggests the use of simple models, but lack of data really means lack of information. Lack of information suggests that no valid estimates of population persistence are possible, since there is no reason to believe that unstudied populations are inherently simpler (and thus justify simple analytical models) than well-studied populations where the inadequacy of simple analytical models is obvious. The focus of this paper is on computer simulation models to estimate population viability via numerical techniques, where the population model includes the essential features of population change relevant to the species of interest.

The most thorough, recent review of the PVA literature is provided by Boyce (1992). Shaffer (1981, 1987), Soulé (1987), Nunney and Campbell (1993) and Remmert (1994) provide an historical perspective of how the field developed. In this paper, I will discuss procedures to develop useful viability analyses. Specifically, statistical methods to estimate the variance components needed to develop a PVA, the need to incorporate individual heterogeneity into a PVA, and the need to incorporate the sampling variance of parameter estimates used in a PVA will be discussed.

#### QUALITATIVE OBSERVATIONS ABOUT POPULATION PERSISTENCE

Qualitatively, population biologists know a considerable amount about what allows populations to persist. Some generalities about population persistence (Ruggiero et al. 1994) are:

1. connected habitats are better than disjointed habitats;
2. suitable habitats in close proximity to one another are better than widely separated habitats;
3. late stages of forest development are often better than younger stages;
4. larger habitat areas are better than smaller areas;
5. populations with higher reproductive rates are more secure than those with lower reproductive rates; and
6. environmental conditions that reduce carrying capacity or increase variance in the growth rates of populations decrease persistence probabilities.

This list should be taken as a general set of principles, but you should recognize that exceptions will occur often. In the following section, I will discuss these generalities in more detail, and in particular, suggest contradictions that occur.

Typically, recovery plans for an endangered species try to 1) create multiple populations of the species, so that a single catastrophe will not wipe out the entire species, and 2) increase the size of each population so that genetic, demographic, and normal environmental uncertainties are less threatening (Meffe and Carroll 1994:191-192). However, Hess (1993) argues that connected populations can have lower viability over a narrow range in the presence of a fatal disease transmitted by contact. He demonstrates the possibilities with a model, but doesn't have data to support his case. However, the point he makes seems biologically sound, and the issue can only be resolved by optimizing persistence between these two opposing forces.

Spatial variation, i.e., variation in habitat quality across the landscape, affects population persistence. Typically, extinction and metapopulation theories emphasize that stochastic fluctuations in local populations cause extinction and that local extinctions generate empty habitat patches that are then available for recolonization. Metapopulation persistence depends on the balance of extinction and colonization in a static environment (Hanski 1996, Hanski et al. 1996). For many rare and declining species, Thomas (1994) argues (1) that extinction is usually the deterministic consequence of the local environment becoming unsuitable (through habitat loss or modification, introduction of a predator, etc.); (2) that the local environment usually remains unsuitable following local extinction, so extinctions only rarely generate empty patches of suitable habitat; and (3) that colonization usually follows improvement of the local environment for a particular species (or long-distance transfer by humans). Thus, persistence depends predominantly on whether organisms are able to track the shifting spatial mosaic of suitable environmental conditions or on maintenance of good conditions locally.

Foley (1994) uses a model to agree with 5 above, that populations with higher reproductive rates are more persistent. However, mammals with larger body size can persist at lower densities (Silva and Downing 1994), and typically have lower annual and per capita reproductive rates. Predicted minimal density decreases as the  $-0.68$  power of body mass, likely because of less variance in reproduction relative to life span in larger-bodied species.

The last item on the list above suggests that increased variation over time leads to lower persistence (Shaffer 1987, Lande 1988, 1993). One reason that increased temporal variation causes lowered persistence is that catastrophes, such as hurricanes, fires, or floods are more likely to occur in systems with high temporal variation. Populations in the wet tropics can apparently sustain themselves at densities much lower than those in temperate climates, likely because of less environmental variation. Basically the distinction between a catastrophe and a large temporal variance component is arbitrary, and on a continuum (Caughley 1994). Further, even predictable effects can have an impact. Beissinger (1995) models the effects of periodic environmental fluctuations on population viability of the snail kite (*Rostrhamus sociabilis*), and suggests that this source of variation is important in persistence.

Few empirical data are available to support the generalities above, but exceptions exist. Berger (1990) addressed the issue of MVP by asking how long different-sized populations persist. He presents demographic and weather data spanning up to 70 years for 122 bighorn sheep (*Ovis canadensis*) populations in south-western North America. His analyses reveal that: (1) 100 percent of the populations with fewer than 50 individuals went extinct within 50 years; (2) populations with greater than 100 individuals persisted for up to 70 years; and (3) the rapid loss of populations was not likely to be caused by food shortages, severe weather, predation, or interspecific competition. Thus, 50 individuals, even in the short term of 50 years, are not a minimum viable population size for bighorn sheep. However, Krausman et al. (1993) questioned this result, because they know of populations of 50 or less in Arizona that have persisted for more than 50 years.

Pimm et al. (1988) and Diamond and Pimm (1993) examined the risks of extinction of breeding land birds on 16 British islands in terms of population size and species attributes. Tracy and George (1992) extended the analysis to include attributes of the environment, as well as species characteristics, as potential determinants of the risk of extinction. Tracy and George (1992) conclude that the ability of current models to predict the risk of extinction of particular species on particular island is very limited. They suggest models should include more specific information about the species and environment to develop useful predictions of extinction probabilities. Haila and Hanski (1993) criticized the data of Pimm et al. (1988) as not directly relating to extinctions because the small groups of birds breeding in any given year on single islands were not populations in a meaningful sense. Although this criticism may be valid, most of the "populations" that conservation biologists will study will be questionable "populations". Thus, results of the analysis by Tracy and George (1992) do contribute useful information, because the populations they studied are representative of populations to which PVA techniques are applied. Specifically, small populations of small-bodied birds on oceanic islands (more isolated) are more likely to go extinct than are large populations of large-bodied birds on less isolated (channel) islands. However, interaction of body size with type of island (channel vs. oceanic) indicated that body size influences time to extinction

differently depending on the type of island. The results of Tracy and George (1992, 1993) support the general statements presented above. As with all ecological generalities, exceptions quickly appear.

### SOURCES OF VARIATION AFFECTING POPULATION PERSISTENCE

The persistence of a population depends on stochasticity, or variation (Dennis et al. 1991). Sources of variation, and their magnitude, determine the probability of extinction, given the population growth mechanisms specific to the species. The total variance of a series of population measurements is a function of process variation (stochasticity in the population growth process) and sampling variation (stochasticity in measuring the size of the population). Process variation is a result of demographic, temporal and spatial (environmental variation), and individual phenotypic and genotypic) variation. In this section, I will define these sources of variation more precisely, and I will develop a simple mathematical model to illustrate these various sources of stochasticity, thus demonstrating how stochasticity affects persistence.

Consider a population with no variation, one that qualifies for the simple, density-independent growth model  $N_{t+1} = N_t(1 + R)$ , where  $N_t$  is the population size at time  $t$  and  $R$  is the finite rate of change in the population. This model is deterministic, and hence, so is the population.  $R \geq 0$  guarantees that the population will persist, in contrast to  $R < 0$ , which guarantees that the population will go extinct (albeit in an infinite amount of time, because a fraction of an animal is allowed in this model).  $R$  can be considered to be a function of birth and death rates, so that  $R = b - d$  defines the rate of change in the population as a function of birth rate ( $b$ ) and death rate ( $d$ ). When the birth rate exceeds or equals the death rate, the population will persist with probability 1 in this deterministic model. These examples are illustrated in Fig. 1.

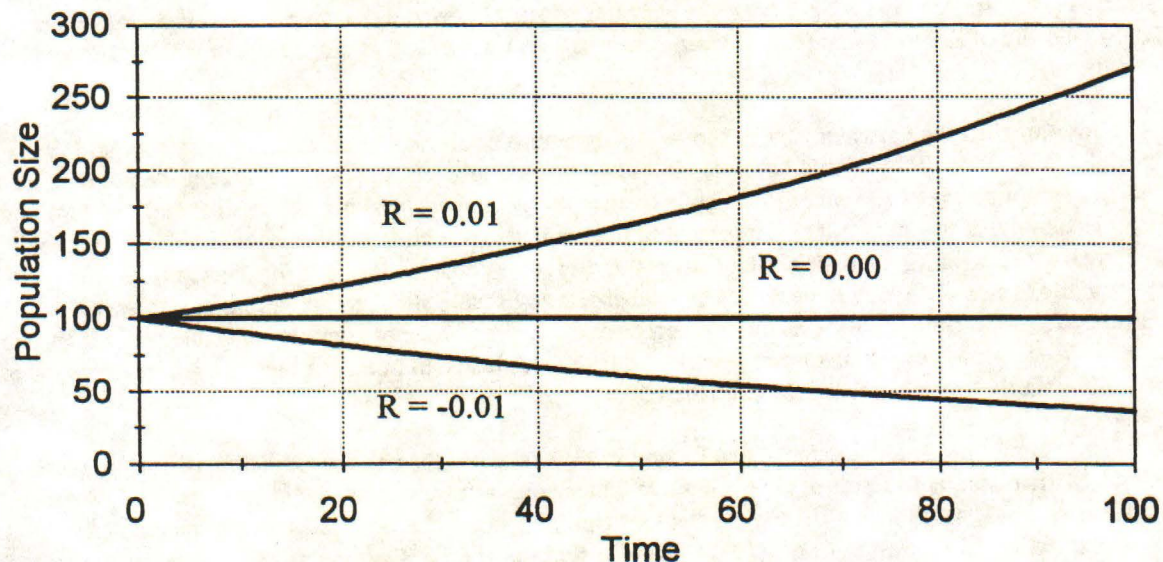


Figure 1. Deterministic model of population growth. For values of  $R \geq 0$ , the population persists indefinitely. For values of  $R < 0$ , the population will eventually go extinct in that the number of animals will approach zero.

Let us extend this naive model by making it stochastic. I will change the parameter  $R$  to be a function of 2 random variables. At each time  $t$ , I determine stochastically the number of animals to be added to the population by births, and then the number to be removed by deaths. Suppose the birth rate equals the death rate, say

$b = d = 0.5$ . That is, on average 50% of the  $N_t$  animals would give birth to a single individual and provide additions to the population, and 50% of the  $N_t$  animals would die and be removed from the population. Thus, the population is expected to stay constant, because the number of births equals the number of deaths. A reasonable stochastic model for this process would be a binomial distribution. For the binomial model, you can think of flipping a coin twice for each animal. The first flip determines if the animal gives birth to 1 new addition to the population in  $N_{t+1}$ , and the second flip determines if the animal currently a member of  $N_t$  remains in the population for another time interval to be a member of  $N_{t+1}$ , or dies. If we start with  $N_0 = 100$ , what is the probability that the population will persist until  $t = 100$ ? Three examples are shown in Fig. 2.

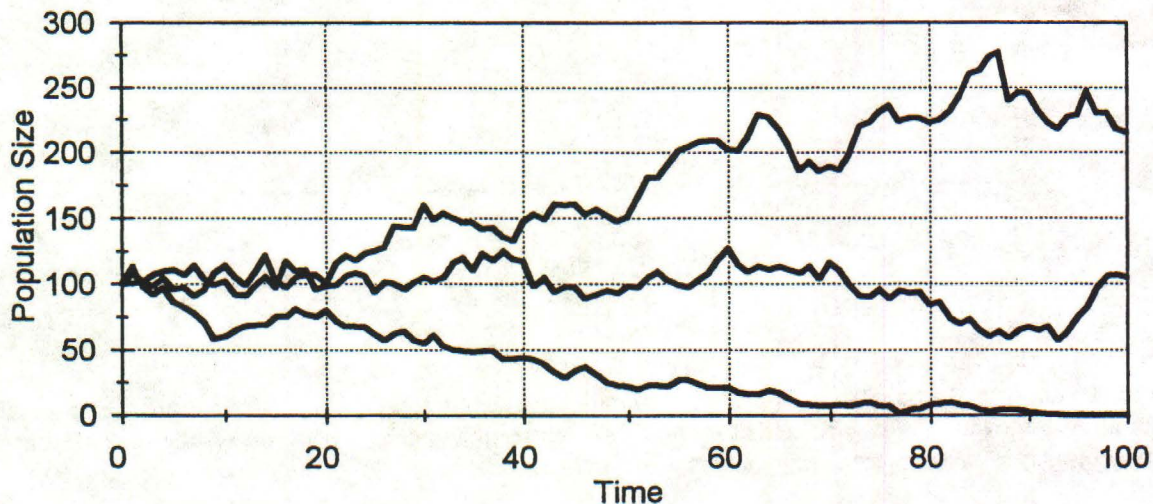
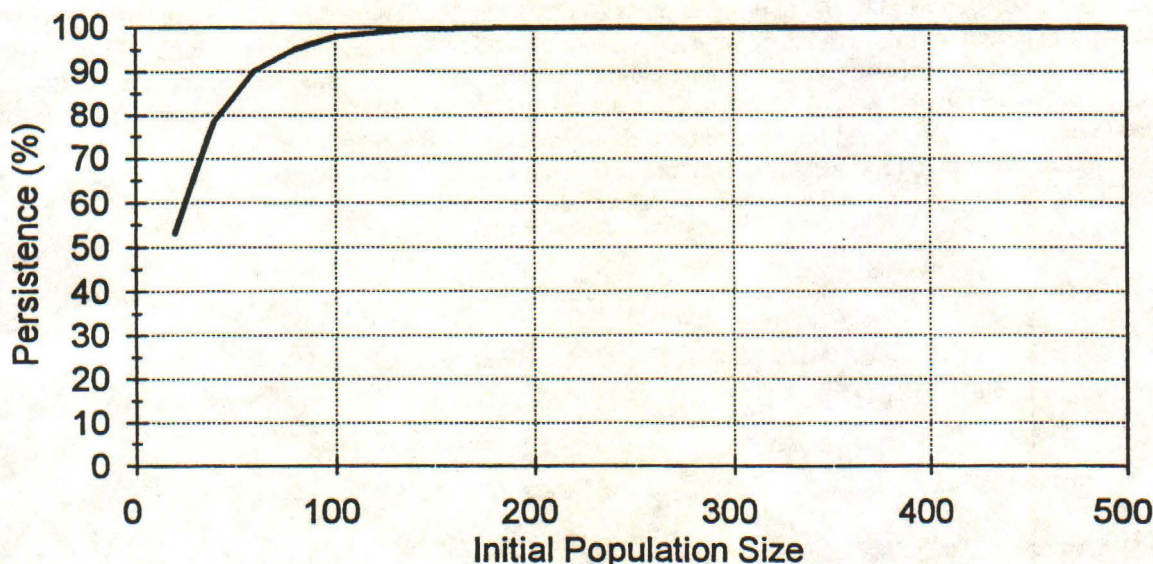


Figure 2. Three examples of the outcome of the population model with only demographic variation. The lower population goes extinct at time 93. Birth and death probabilities are both 0.5, making the expected value of  $R = 0$ .

You might be tempted to say the probability is 1 that the population will persist until  $t = 100$  because the expected value of  $R$  is 0 given that the birth rate equals the death rate, i.e.,  $E(R) = 0$ , so that  $E(N_{t+1}) = E(N_t)$ . You would be wrong! Implementation of this model on a computer shows that the probability of persistence is 98.0%, i.e., 2.0% of the time the population does not persist for 100 years without  $N_t$  becoming 0 for some  $t$ . These estimates were determined by running the population model 10,000 times, and recording the number of times the simulated population went extinct before 100 years had elapsed. Lowering the initial population to  $N_0 = 20$  results in persistence of only 53.2% of the populations, again based on 10,000 runs of the model. Setting  $N_0 = 500$  improves the persistence rate to nearly 100%. Note that the persistence is not linear in terms of  $N_0$  (Fig. 3). Initial population size has a major influence on persistence.



**Figure 3.** Persistence of a population as a function of initial population size ( $N_0$ ), when only demographic variation is incorporated into the model. Birth and death probabilities are both 0.5, making the expected value of  $R = 0$ . The model was run 10,000 times to estimate the percent of runs where the population persisted until  $t = 100$ .

Other considerations affect persistence. The value of  $R$  (equals the birth rate minus the death rate) is critical.  $R$  can be negative (death rate exceeds birth rate), and the population can still persist for 100 years, which may seem counterintuitive. Furthermore,  $R$  can be positive (birth rate exceeds death rate), and the population can still go extinct. For example, suppose  $R$  is increased to 0.02 by making the birth rate 0.51 and the death rate 0.49. The persistence for  $N_0 = 20$  increases to 84.3% from 53.2% for  $R = 0$ . Thus, even though the population is expected to increase, stochasticity can still cause the population to go extinct.

The type of stochasticity illustrated by this model is known as **demographic variation**. I like to call this source of variation “penny flipping variation” because the variation about the expected number of survivors parallels the variation about the observed number of heads from flipping coins. To illustrate demographic variation, suppose the probability of survival of each individual in a population is 0.8. Then on average, 80% of the population will survive. However, random variation precludes exactly 80% surviving each time this survival rate is applied. From purely bad luck on the part of the population, a much lower proportion of the population may survive for a series of years, resulting in extinction. Because such bad luck is most likely to happen in small populations, this source of variation is particularly important for small populations, and hence the name demographic variation. The impact is small for large populations. As the population size becomes large, the relative variation decreases to zero. That is, the variance of  $N_{t+1}/N_t$  goes to zero as  $N_t$  goes to infinity. Thus, demographic variation is generally not an issue for persistence of larger populations.

To illustrate further how demographic variation operates, consider a small population with  $N = 100$  and a second population with  $N = 10,000$ . Assume both populations have identical survival rates of 0.8. With a binomial model of the process, the probability that only 75% or less of the small population survives is 0.1314 for

the small population, but  $3.194E-34$  for the larger population. Thus, the likelihood that up to 25% of the small population is lost in one year is much higher than for the large population.

A feature of all population persistence models is evident in Fig. 2. That is, the variation of predicted population size increases with time. Some realizations of the stochastic process climb to very large population values after long time periods, whereas other realizations drop to zero and extinction. This result should be intuitive, because as the model is projected further into the future, certainty about the projections decreases.

However, in contrast to population size, our certainty about the extinction probability increases as time increases to infinity. The probability of eventual extinction is always unity if extinction is possible. This result is because the only absorbing state of the stochastic process is extinction, i.e., the only population size where there is no chance of change is zero.

Another way to decrease persistence is to increase the stochasticity in the model. One way would be to introduce temporal variation by making  $b$  and  $d$  random variables. Such variation would be exemplified by weather in real populations. Some years, winters are mild and survival and reproduction are high. Other years, winters are harsh and survival and reproduction are poor. To incorporate this phenomena into our simple model, suppose that the mean birth and death rates are again 0.5, but the values of the birth rate and the death rate at a particular time  $t$  are each selected from a statistical distribution, say a beta distribution. That is, each year, new values of  $b$  and  $d$  are selected from a beta distribution.

A beta distribution is bounded by the interval 0-1, and can take on a variety of shapes. For a mean of 0.5, the distribution is symmetrical about the mean, but the amount of variation can be changed by how "peaked" the distribution is (Fig. 4).

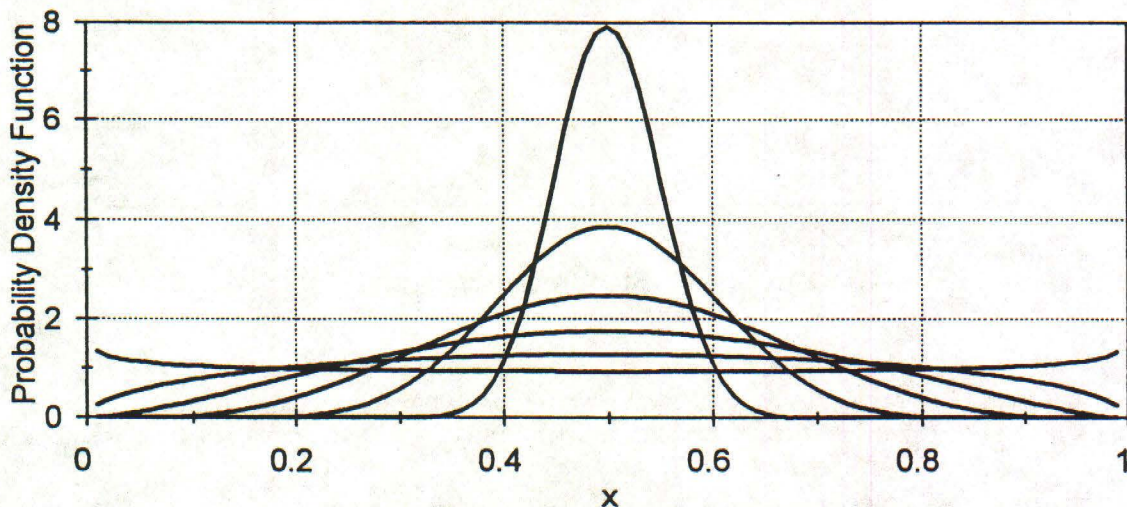


Figure 4. Examples of the beta distribution, all with mean 0.5. The standard deviations proceeding from the tallest curve to the lowest curve at  $x = 0.5$  are 0.05 to 0.3 in increments of 0.05.

The beta distribution is described by 2 parameters,  $\alpha > 0$  and  $\beta > 0$ . The mean of the distribution is given by  $\alpha/(\alpha + \beta)$  and the variance as  $\alpha\beta/[(\alpha + \beta)^2(\alpha + \beta + 1)]$ , with the mode  $(\alpha - 1)/(\alpha + \beta - 2)$  (mode only for  $\alpha \geq 1$ ). Most random number generation techniques for the beta distribution require you to specify values for  $\alpha$  and  $\beta$ . For a given mean ( $\mu$ ) and variance ( $\sigma^2$ ) or standard deviation ( $\sigma$ ),

$$\alpha = \frac{\mu^2(1 - \mu)}{\sigma^2} - \mu, \text{ and}$$

$$\beta = \frac{(\sigma^2 + \mu(\mu - 1))(\mu - 1)}{\sigma^2}.$$

However, the amount of variation possible is limited because the distribution is bounded on the [0,1] interval. Thus, for a mean of 0.5, the maximum variance approaches 0.25 as  $\alpha$  and  $\beta$  approach zero.

The standard deviation of the birth and death rates over time affect persistence because these values determine the standard deviation of  $R$ . The smaller the standard deviations, the more the model approaches the demographic variation case, and thus, as  $N_t$  approaches infinity, the deterministic case. As the standard deviation increases, the more the variation in  $N_t$ , regardless of population size, and the less likely the population is to persist. Thus, a standard deviation of 0.2 for both the birth and death rates results in only 28.5% persistence for  $N_0 = 100$ . Compare this to the 77.4% persistence achieved for a standard deviation of 0.1 (Fig. 5), or to the 98.0% persistence when no variation in birth and death rates occurred but demographic variation is still present.

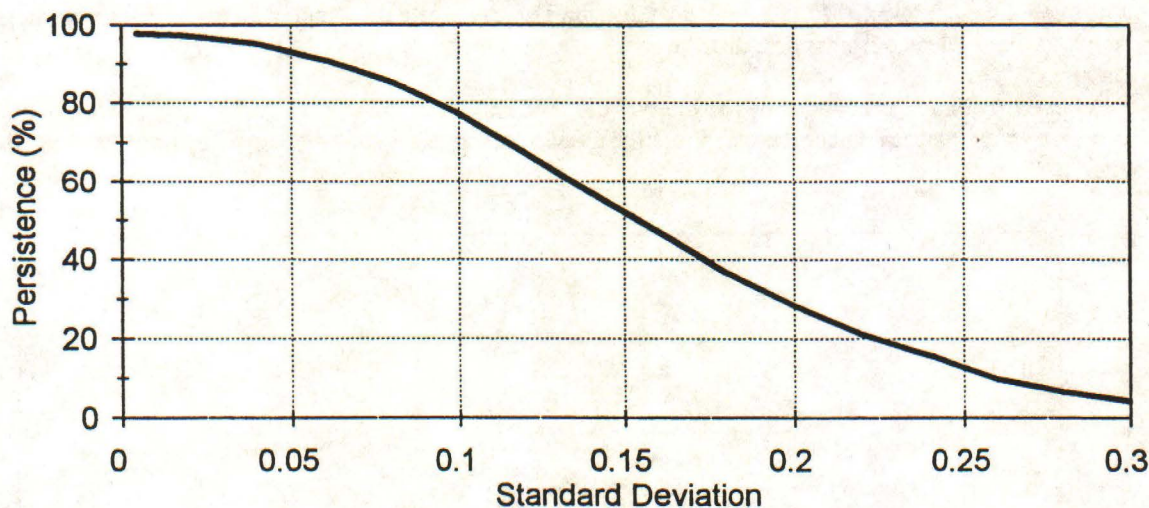


Figure 5. Persistence of a population of 100 animals at  $t = 0$  to  $t = 100$  years as a function of the standard deviation of birth ( $\bar{x} = 0.5$ ) and death ( $\bar{x} = 0.5$ ) rates (temporal variation). Demographic variation is still included in the model.

This second source of variation in our simple model is **temporal variation**, i.e., variation in the parameters of the model across time. As the example shows, increasing temporal variation decreases persistence. The simple model illustrated assumed that no correlation existed between the birth rate and the death rate, i.e., that the 2 rates were independent. However, in real populations, there is likely a high correlation between birth rates and death rates across years. Good years with lots of high quality resources available to the animals probably result in increased reproduction and survival, whereas bad years result in poor reproduction and high mortality. Including a negative covariance of birth and death rates (or a positive covariance between birth and survival rates) in the model results in an even bigger impact of temporal variation on persistence. That is, the bad years are really bad because of both poor reproduction and high mortality, and the good years are really good. The net effect of this negative covariance of birth and death rates is to decrease persistence.



**Spatial variation** is the variation across the landscape that is normally associated with populations. Factors causing geographic variation include geologic differences that affect soil type, and thus habitat, and weather patterns, e.g., differences in rainfall across the landscape. If the immigration and emigration rates are high across the landscape, so that subpopulations that are depleted because of local conditions, high spatial variation can lead to higher persistence. This is because the probability of all the subpopulations of a population being affected simultaneously by some catastrophe is low when high spatial variation exists and spatial autocorrelation is low. High positive spatial autocorrelation causes low levels of spatial variation, whereas high negative spatial autocorrelation causes high levels of spatial variation, as generally do low levels of spatial autocorrelation. In contrast, with low spatial variation (and hence high positive spatial autocorrelation), the likelihood of a bad year affecting the entire population is high. Thus, in contrast to temporal variation, where increased variation leads to lowered persistence, increased spatial variation and low spatial autocorrelation leads to increased persistence given that immigration and emigration are effectively mixing the subpopulations. If immigration and emigration are negligible, then spatial variation divides the population into smaller subpopulations, which are more likely to suffer extinction from the effect of demographic variation on small populations.

The combination of temporal and spatial variation is termed **environmental variation**. Both dictate the animal's environment, one in time, one in space.

All the models examined so far assume that each animal in the population has exactly the same chance of survival and reproducing, even though these rates are changing with time. What happens if each animal in the population has a different rate of survival and reproduction? Differences between the individuals in the population are termed **individual heterogeneity**, and creates **individual variation**. Many studies have demonstrated individual heterogeneity of individual survival and reproductions, e.g., Clutton-Brock (1982) demonstrated lifetime reproductive success of female red deer (*Cervus elaphus*) varied from 0 to 13 calves reared per female. Differences in the frequency of calf mortality between mothers accounted for a larger proportion of variance in success than differences in fecundity. Bartmann et al. (1992) demonstrated that overwinter survival of mule deer fawns was a function of the fawn's weight at the start of the winter, with larger fawns showing better survival.

Individual variation is caused by **genetic variation**, i.e., differences between individuals because of their genome. Individual heterogeneity is the basis of natural selection, i.e., differences between animals is what allows natural selection to operate. However, **phenotypic variation** is also possible, where individual heterogeneity is not a result of genetic variation. Animals that endure poor nutrition during their early development may never be as healthy and robust as animals that are on a higher nutritional plane, even though both are genetically identical. Animals with access to more and better resources have higher reproductive rates, e.g., red deer (*Cervus elaphus*) (Clutton-Brock et al. 1982). Thus, individual heterogeneity may result from both genetic and phenotypic variation. Lomnicki (1988) develops models of resource partitioning that result in phenotypic variation of individuals.

Another example of individual heterogeneity in reproduction is provided by Burnham et al. (1996) in northern spotted owls (*Strix occidentalis caurina*). In the case of northern spotted owls, repeated observations of reproduction across numerous individuals were used to estimate individual variation with analysis of variance procedures. The age of the female produced individual heterogeneity. This study also demonstrated temporal and spatial variation in owl fecundity rates.

Undoubtedly, natural selection plays a role in the genetic variation left in a declining population. Most populations where we are concerned about extinction probabilities have suffered a serious decline in numbers. The genotypes remaining after a severe decline are unlikely to be a random sample of the original population (e.g. Keller et al. 1994). I would expect that the genotypes persisting through a decline are the "survivors", and would have a much better chance of persisting than would a random sample from the population prior to the decline. Of course, this argument assumes that the processes causing the decline remain in effect, so that the same natural selection forces continue to operate.

To illustrate individual variation, start with the basic demographic variation model developed above. Instead of each animal having exactly a birth rate of 0.5 and a death rate of 0.5, let's select these values from beta distributions with a mean of 0.5. The birth and death rates assigned to an animal remain for its life time. As new animals are added to the population, they likewise are assigned life-time birth and death rates. How does persistence of this new model compare with the results from the demographic model? The answer is in Fig. 6.



Figure 6. Effect of individual variation on population persistence. The 3 lines from top to bottom have standard deviations of 0.1, 0.05, and 0.01 for the birth and death rates. Compare these results with Fig. 3, where the standard deviation of individual variation is zero.

The reason that increased individual heterogeneity increases population persistence is that increased variation results in more chance a few animals have exceptionally high reproductive potential and high survival. Therefore, these animals are unlikely to suffer mortality and be removed from the population, and also can be relied upon to contribute new births each year. As a result, the population may remain small, but will not go extinct as often. Individual heterogeneity has seldom, if ever, been included in a population viability analysis, except as genetic variation. Yet, as the simple example shows, individual heterogeneity not a function of genetic variation is a very important element in maintaining viability.

The combined effects of demographic, temporal, spatial, and individual variation is termed **process variation**. That is, each of these sources of variation affect population processes. Process variation is used as a general term for the inherent stochasticity of changes in the population level. Process variation is in contrast to **sampling variation**, which is the variation contributed when biologists attempt to measure population processes. That is, researchers are unable to measure the exact survival rate of a population. Rather, they observe realizations of the process, but not the exact value. Even if the fate of every animal in the population is observed, the resulting estimate of survival is only an estimate of the true, but unknown, population survival rate. The concept of sampling variation will be further explained below, where methods of separating sampling variation from process variation will be developed.

Several lessons should be learned from this simple exercise. Persistence is a stochastic phenomena. Even though the expected outcome for a particular model is to persist, random variation prevents this outcome from always occurring. Small populations are much more likely to go extinct than larger populations because of demographic variation. Increased temporal variation results in decreased persistence. Increased individual variation results in increased persistence.

### COMPONENTS OF A PVA

As demonstrated above, many factors affect the persistence of a population. What components are needed to provide estimates of the probability that a population will go extinct, and what are the trade-offs if not all these components are available?

1. A basic population model is needed. A recognized mechanism of population regulation, density dependence, should be incorporated, because no population can grow indefinitely. "Of course, exponential growth models are strictly unrealistic on time scales necessary to explore extinction probabilities." (Boyce 1992:489). The population cannot be allowed to grow indefinitely, or persistence will be over estimated. Further, as discussed below, the shape of the relationship between density and survival and reproduction can affect persistence, and density dependence cannot be neglected for moderate or large populations (Ludwig 1996b). Density dependence can provide a stabilizing influence that increases persistence in small populations.
2. Demographic variation must be incorporated in this basic model. Otherwise, estimates of persistence will be too high because the effect of demographic variation for small populations is not included in the model.
3. Temporal variation must be included for the parameters of the model, including some probability of a natural catastrophe. Examples of catastrophes (for some species!) are fires (e.g., Yellowstone National Park, USA, during 1988), hurricanes, typhoons, earth quakes, extreme drought or rainfall resulting in flooding, etc. Catastrophes must be rare, or else the variation would be considered as part of the normal temporal variation. However, the covariance of the parameters is also important. Good years for survival are likely also good years for reproduction. Vice versa, bad years for reproduction may also lead to increased mortality. The impact of this correlation of reproduction and survival can drastically affect results. For example, the model of Stacey and Taper (1992) of acorn woodpecker population dynamics performs very differently depending on whether adult survival, juvenile survival, and reproduction are bootstrapped as a triplet, or as individual rates across the 10 year period. By allowing the positive correlation of the survival rates and reproduction, persistence is improved.
4. Spatial variation in the parameters of the model must be incorporated if the population is spatially segregated. If spatial attributes are to be modeled, then immigration and emigration parameters must be estimated, as well as dispersal distances. The difficulty of estimating spatial variation is that the covariance of the parameters must be estimated as a function of distance, i.e., what is the covariance of adult survival of 2 subpopulations as a function of distance?
5. Individual heterogeneity must be included in the model or the estimates of persistence will be too low. Individual heterogeneity requires that the basic model be extended to an individual-based model (DeAngelis and Gross 1992). As the variance of individual parameters increases in the basic model, the persistence time increases. Thus, instead of just knowing estimates of the parameters of our basic model, we also need to know the statistical distributions of these parameters across individuals. This source of variation is not mentioned in discussions of population viability analysis, e.g., Boyce (1992), Remmert (1994), Hunter (1996), Meffe and Carroll (1994), or Shaffer (1981, 1987).

6. For short-term projects, the above sources of variation may be adequate. However, if time periods of more than a few generations are projected, then genetic variation should be considered. I would expect the population to change as selection takes place. Even if no selection is operating, then genetic drift is expected for small population sizes. However, the importance of genetic effects is still an issue in question, e.g., Joopouborg and Van Groenendael (1996). Lande (1988, 1995) has suggested either demographic variation and/or genetic effects can be lethal to a small population.
7. For long-term persistence, we must be willing to make the assumption that the system will not change, i.e., the levels of stochasticity will not change through time, the species will not evolve through selection, and the supporting capacity of the environment (the species habitat) remains static. That is, natural processes such as long-term succession and climatic change do not affect persistence, and that humans cease and desist, given that humans have been responsible for most recent extinctions! To believe the results, we have to assume that the model and all its parameters stays the same across inordinately long time periods.

After examining this list, I am sure you agree with Boyce (1992:482): "Collecting sufficient data to derive reliable estimates for all the parameters necessary to determine MVP is simply not practical in most cases." Of course, limitations of the data seldom slow down modelers of population dynamics. Further, managers are forced to make decisions, so modelers attempt to make reasonable "guesses". In the next 3 sections, I will explore statistical methods to obtain the necessary data to develop a reasonable PVA model and suggest modeling techniques to incorporate empirical data into the persistence model.

#### DIRECT ESTIMATION OF VARIANCE COMPONENTS

The implication of the list of requirements in the previous section is that population parameters or their distributions are known without error, i.e., exact parameter values are observed, not estimated. In reality, we may be fortunate and have a series of survival or reproduction estimates across time that provides information about the temporal variation of the process. However, the variance of this series is not the proper estimate of the temporal variation of the process. This is because each of our estimates includes sampling variation, i.e., we only have an estimate of the true parameter, not its exact value. To properly estimate the temporal variation of the series, the sampling variance of the estimates must be removed. In this section, I demonstrate a procedure to remove the sampling variance from a series of estimates to obtain an estimate of the underlying process variation (which might be temporal or spatial variation). The procedure is explained in Burnham et al. (1987:260-278).

Consider the example situation of estimating over-winter survival rates each year for 10 years from a deer population. Each year, the survival rate is different from the overall mean, because of snow depth, cold weather, etc. Let the true, but unknown, overall mean be  $S$ . Then the survival rate for each year can be considered to be  $S$  plus some deviation attributable to temporal variation, with the expected value of the  $e_i$  equal zero:

| Environmental Variation |          |                                   |                        |
|-------------------------|----------|-----------------------------------|------------------------|
| <i>I</i>                | Mean     | Year <i>I</i>                     | Year <i>I</i>          |
| 1                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>1</sub>  | <i>S</i> <sub>1</sub>  |
| 2                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>2</sub>  | <i>S</i> <sub>2</sub>  |
| 3                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>3</sub>  | <i>S</i> <sub>3</sub>  |
| 4                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>4</sub>  | <i>S</i> <sub>4</sub>  |
| 5                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>5</sub>  | <i>S</i> <sub>5</sub>  |
| 6                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>6</sub>  | <i>S</i> <sub>6</sub>  |
| 7                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>7</sub>  | <i>S</i> <sub>7</sub>  |
| 8                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>8</sub>  | <i>S</i> <sub>8</sub>  |
| 9                       | <i>S</i> | <i>S</i> + <i>e</i> <sub>9</sub>  | <i>S</i> <sub>9</sub>  |
| 10                      | <i>S</i> | <i>S</i> + <i>e</i> <sub>10</sub> | <i>S</i> <sub>10</sub> |
| Mean                    | <i>S</i> | $\bar{S}$                         | $\bar{S}$              |

The true population mean *S* is computed as  $\bar{S}$ :

$$\bar{S} = \frac{\sum_{i=1}^{10} S_i}{10},$$

with the variance of the *S*<sub>*i*</sub> is computed as:

$$\sigma^2 = \frac{\sum_{i=1}^{10} (S_i - \bar{S})^2}{10},$$

where the random variables *e*<sub>*i*</sub> are selected from a distribution with mean 0 and variance  $\sigma^2$ . In reality, we are never able to observe the annual rates because of sampling variation or demographic variation. For example, even if we observed all the members of a population, we would still not be able to say the observed survival rate was *S*<sub>*i*</sub> because of demographic variation. Consider flipping 10 coins. We know that the true probability of a head is 0.5, but we will not always observe that value exactly. Imagine if you had 11 coins -- the true value is not even in the set of possible estimates. The same process operates in a population as demographic variation. Even though the true probability of survival is 0.5, we would not necessarily see exactly 1/2 of the population survive on any given year.

Hence, what we actually observe are the quantities:

Environmental Variation  
+  
Sampling Variation

| <i>I</i> | Mean     | Truth<br>Year <i>I</i> | Observed<br>Year <i>I</i> |
|----------|----------|------------------------|---------------------------|
| 1        | <i>S</i> | $S + e_1 + f_1$        | $\hat{S}_1$               |
| 2        | <i>S</i> | $S + e_2 + f_2$        | $\hat{S}_2$               |
| 3        | <i>S</i> | $S + e_3 + f_3$        | $\hat{S}_3$               |
| 4        | <i>S</i> | $S + e_4 + f_4$        | $\hat{S}_4$               |
| 5        | <i>S</i> | $S + e_5 + f_5$        | $\hat{S}_5$               |
| 6        | <i>S</i> | $S + e_6 + f_6$        | $\hat{S}_6$               |
| 7        | <i>S</i> | $S + e_7 + f_7$        | $\hat{S}_7$               |
| 8        | <i>S</i> | $S + e_8 + f_8$        | $\hat{S}_8$               |
| 9        | <i>S</i> | $S + e_9 + f_9$        | $\hat{S}_9$               |
| 10       | <i>S</i> | $S + e_{10} + f_{10}$  | $\hat{S}_{10}$            |
| Mean     | <i>S</i> | $\bar{S}$              | $\bar{\hat{S}}$           |

where the  $e_i$  are as before, but we also have additional variation from sampling variation, or demographic variation, or both, in the  $f_i$ .

The usual approach to estimating sampling variance separately from temporal variance is to take replicate observations within each year, so that within-cell replicates can be used to estimate the sampling variance, whereas the between cell variance is used to estimate the environmental variation. Years are assumed to be a random effect, and mixed model analysis of variance procedures are used (e.g., Bennington and Thayne 1994). This approach assumes that each cell has the same sampling variance. An example of the application of a random effects model is Koenig et al. (1994). They considered year effects, species effects, and individual tree effects.

Classical analysis of variance methodology assumes that the variance within cells is constant across a variety of treatment effects. This assumption is often not true, i.e., the sampling variance of a binomial distribution is a function of the binomial probability. Thus, as the probability changes across cells, so does the variance. Another common violation of this assumption is caused by the variable of interest being distributed lognormally, so that the coefficient of variation is constant across cells, and the cell variance is a function of the cell mean. Further, the empirical estimation of the variance from replicate measurements may not be the most efficient procedure. Therefore, the remainder of this section describes methods that can be viewed as extensions of the usual variance component analysis based on replicate measurements within cells. We will be examining estimators for the situation where the within cell variance is estimated by an estimator other than the moment estimator based on replicate observations.

Assume that we can estimate the sampling variance for each year, given a value of  $\hat{S}_i$  for the year. For example, an estimate of the sampling variation for a binomial is

$$\text{var}(\hat{S}_i|S_i) = \frac{\hat{S}_i(1 - \hat{S}_i)}{n_i} ,$$

where  $n_i$  is the number of animals monitored to see if they survived. Then, can we estimate the variance term due to environmental variation, given that we have estimates of the sampling variance for each year?

If we assume all the sampling variances are equal, the estimate of the overall mean is still just the mean of the 10 estimates:

$$\bar{S} = \frac{\sum_{i=1}^{10} \hat{S}_i}{10} ,$$

with the theoretical variance being

$$\text{var}(\bar{S}) = \frac{\sigma^2 + E[\text{var}(\hat{S}|S)]}{10} ,$$

i.e., the total variance is the sum of the environmental variance plus the expected sampling variance. This total variance can be estimated as

$$\text{var}(\bar{S}) = \frac{\sum_{i=1}^{10} (\hat{S}_i - \bar{S})^2}{10(10 - 1)} .$$

We can estimate the expected sampling variance as the mean of the sampling variances

$$\hat{E}[\text{var}(\hat{S}|S)] = \frac{\sum_{i=1}^{10} \text{var}(\hat{S}_i|S_i)}{10} ,$$

so that the estimate of the environmental variance obtained by solving for  $\sigma^2$

$$\hat{\sigma}^2 = \frac{\sum_{i=1}^{10} (\hat{S}_i - \bar{S})^2}{(10 - 1)} - \frac{\sum_{i=1}^{10} \text{var}(\hat{S}_i|S_i)}{10} .$$

However, sampling variances are usually not all equal, so that we have to weight them to obtain an unbiased estimate of  $\sigma^2$ . The general theory says to use a weight,  $w_i$

$$w_i = \frac{1}{\sigma^2 + \text{var}(\hat{S}_i|S_i)} ,$$

so that by replacing  $\text{var}(\hat{S}_i|S_i)$  with its estimator  $\text{vâr}(\hat{S}_i|S_i)$ , the estimator of the weighted mean is

$$\bar{S} = \frac{\sum_{i=1}^{10} w_i \hat{S}_i}{\sum_{i=1}^{10} w_i},$$

with theoretical variance (i.e., sum of the theoretical variances for each of the estimates)

$$\text{var}(\bar{S}) = \frac{1}{\sum_{i=1}^{10} w_i},$$

and empirical variance estimator

$$\text{vâr}(\bar{S}) = \frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{\left[ \sum_{i=1}^{10} w_i \right] (10 - 1)}.$$

When the  $w_i$  are the true (but unknown) weights, we have

$$\frac{1}{\sum_{i=1}^{10} w_i} = \frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{\left[ \sum_{i=1}^{10} w_i \right] (10 - 1)},$$

giving the following

$$1 = \frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{(10 - 1)}.$$

Hence, all we have to do is manipulate this equation with a value of  $\sigma^2$  to obtain an estimator of  $\sigma^2$ .

To obtain a confidence interval on the estimator of  $\sigma^2$ , we can substitute the appropriate chi-square values in the above relationship. To find the upper confidence interval value,  $\hat{\sigma}_U^2$ , solve the equation

$$\frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{(10 - 1)} = \frac{\chi^2_{10 - 1, \alpha_U}}{10 - 1},$$

and for the lower confidence interval value,  $\hat{\sigma}_L^2$ , solve the equation



$$\frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{(10 - 1)} = \frac{\chi^2_{10 - 1, \alpha_U}}{10 - 1}$$

As an example, consider the following fawn survival data from over-winter survival of mule deer fawns at the Little Hills Wildlife Area, west of Meeker, Colorado, USA.

| Year | Collared | Lived | Estimated Survival | Estimated Variance |
|------|----------|-------|--------------------|--------------------|
| 1981 | 46       | 15    | 0.3260870          | 0.0047773          |
| 1982 | 114      | 38    | 0.3333333          | 0.0019493          |
| 1983 | 118      | 5     | 0.0423729          | 0.0003439          |
| 1984 | 106      | 19    | 0.1792453          | 0.0013879          |
| 1985 | 155      | 59    | 0.3806452          | 0.0015210          |
| 1986 | 161      | 61    | 0.3788820          | 0.0014617          |
| 1987 | 116      | 15    | 0.1293103          | 0.0009706          |

The survival rates are the number of collared animals that lived divided by the total number of collared animals. For example,  $\hat{S}_{1981} = 15/46 = 0.326087$  for 1981. The sampling variance associated with this estimate is computed as

$$\text{var}(\hat{S}_{1981}) = \frac{\hat{S}_{1981}(1 - \hat{S}_{1981})}{46}$$

which equals 0.0047773. A spreadsheet program (VARCOMP.WB1) computes the estimate of temporal process variation for 1981-87,  $\hat{\sigma}^2$ , as 0.0170632 ( $\hat{\sigma} = 0.1306262$ ), with a 95% confidence interval of (0.0064669, 0.0869938) for  $\sigma^2$ , and (0.0804167, 0.2949472) for  $\sigma$ . These confidence intervals represent the uncertainty of the estimate of temporal variation, i.e., the sampling variation of the estimate of temporal variation.

The procedure demonstrated here is applicable to estimation of other sources of variation (e.g., spatial variation), and to variables other than survival rates, e.g., per capita reproduction. The method is more general than the usual analysis of variance procedures because each observation is not assumed to have the same variance in contrast to analysis of variance where each cell is assumed to have the same within cell variance.

#### INDIRECT ESTIMATION OF VARIANCE COMPONENTS

Individual heterogeneity occurs in both reproduction and survival. Estimation of individual variation in reproduction is an easier problem than estimation of individual variation in survival because some animals reproduce more than once, whereas they only die once. Bartmann et al. (1992) demonstrated that over-winter survival of mule deer fawns is related to their mass at the start of the winter. Thus, one approach to modeling individual heterogeneity is to find a correlate of survival that can be measured, and develop statistical models of the distribution of this correlate. Then, the distribution of the correlate can be sampled to obtain an estimate of

survival for the individual. Lomnicki (1988) also suggests mass as an easily measured variable that relates to an animal's fitness.

To demonstrate this methodology, I will use a simplification of the logistic regression model of Bartmann et al. (1992):

$$\log\left(\frac{S}{1-S}\right) = \beta_0 + \beta_1 \text{mass} ,$$

where survival ( $S$ ) is predicted as a function of weight. Weight of fawns at the start of winter was approximately normally distributed with mean 32 kg and standard deviation 4.2. To simulate individual heterogeneity in over-winter fawn survival, values can be drawn from this normal distribution to generate survival estimates.

This model can be expanded to incorporate temporal variation (year effects), sex effects, and area effects, as described for mule deer fawns by Bartmann et al. (1992). An example of modeling temporal variation in greater flamingos (*Phoenicopterus ruber roseus*) as a function of winter severity is provided by Cézilly et al. (1996). The approach suggested here of modeling winter severity as a random variable and estimating survival as a function of this random variable is an alternative to the variance estimation procedures of the previous section. Both provide a mechanism for injecting variation into a population viability model. The main advantage of using weather data to drive the temporal variation of the model is that considerably more weather data is available than is biological data on survival or reproductive rates.

The major drawback of the indirect estimation approach proposed in this section is that sampling variation of the functional relationship is ignored in the simulation procedure. That is, the logistic regression model includes sampling variation because its parameters are estimated from observed data. The parameter estimates of the logistic regression model include some unknown estimation error. Their direct use results in potentially biased estimates of persistence, depending on how much sampling error is present. Thus, a "good" model relating the covariate to the biological process is needed.

### BOOTSTRAP APPROACH

Stacy and Taper (1992) used a bootstrap procedure to incorporate temporal variation into a model of acorn woodpecker (*Melanerpes formicivorus*) population viability. They used estimates of adult and juvenile survival and reproductive rates resulting from a 10-year field study to estimate population persistence. To incorporate the temporal variation from the 10 years of estimates, they randomly selected with replacement 1 estimate from the observed values to provide an estimate in the model for a year.

This procedure is known in the statistical literature as a bootstrap sampling procedure. The technique is appealing because of its simplicity. However, for estimating population viability, a considerable problem is inherent in the procedure. That is, the estimates used for bootstrapping contain sampling variation and demographic variation, as well as the environmental variation which the modeler is attempting to incorporate. To illustrate how demographic variation is included in the estimates, consider an example population of 10 animals with a constant survival rate of 0.55. Thus, the actual temporal variation is zero, yet a sequence of estimates of survival from this population would suggest considerable variation. That is, the estimates of survival would have a variance of  $0.55(1 - 0.55)/10 = 0.02475$  if all 10 animals had a survival probability of 0.55. Further, the only observed values of survival would be 0, 0.1, ..., 1.0. However, if the size of the population is increased to 100, you find that the variance of the sequence of estimates is now 0.002475, a considerable decrease from above. Thus, randomly sampling the estimates from a population of size 10 results in considerably more variation than from a population of 100. As a result, the demographic variation from the sampled population will be incorporated into the persistence model if the bootstrap approach is used.

A similar example can be used to demonstrate that sampling variation is also inherent in bootstrapping from a sample of observed estimates. Suppose a sample of 10 radiocollared animals is used to estimate survival for a population of 100,000 animals, i.e., the finite sample correction term can be ignored. The sampling variation of the estimates would be  $S(1 - S)/10$ , where  $S$  is the true survival rate for the population assuming all animals had the same survival rate. Now if a sample of 100 radiocollared animals is taken, the sampling variation reduces to  $S(1 - S)/100$ . Thus, randomly sampling estimates with a bootstrap procedure incorporates the sampling variation of the estimates into the persistence model. As a result of the increased variation, persistence values will be underestimated.

Therefore, I suggest not using the bootstrap approach demonstrated by Stacey and Taper (1992) if unbiased estimates of persistence are required. Persistence estimates developed with this procedure will generally be too low, i.e., you will conclude the population is more likely to go extinct than it really will. However, methodologies such as shrinkage estimation of variances (K. P. Burnham, Pers. Commun.) may prove useful in removing sampling variance from the estimates, and make the bootstrap procedure more applicable to estimating population persistence.

#### BASIC POPULATION MODEL AND DENSITY DEPENDENCE

Leslie matrix models (Leslie 1945, 1948; Usher 1966; Lefkovich 1965; Caswell 1989; Manly 1990) are commonly used as the modeling framework for population viability models. Density dependence must be incorporated into the model, i.e., basic parameters must be a function of population size. Thus, the resulting model is not a true Leslie matrix. Each iteration of the calculation also requires a temporal variance component, and making the parameters of the Leslie matrix into random variables (Burgman et al. 1993) is the standard approach, but eradicates the analytical results that normally are benefits of Leslie's creative work. If multiple patches are modeled, each patch requires a spatial variance component. Demographic variation can be built into the model. However, the resulting model doesn't resemble the elegant matrix model that Leslie originally developed.

However, use of the Leslie matrix framework ignores individual heterogeneity, and thus is likely to underestimate persistence. Incorporation of individual heterogeneity requires an individual-based model (e.g., DeAngelis and Gross 1992), and thus, is conceptually different from the basic Leslie matrix approach. Individual-based models can be spatially explicit (e.g., Conroy et al. 1995, Dunning et al. 1995, Holt et al. 1995, Turner et al. 1995), providing another approach to incorporating spatial stochasticity into the model.

As suggested by Boyce (1992), Stacey and Taper (1992), and Burgman et al. (1993), density dependence is an important part of estimating a population's persistence. Lande (1993) demonstrates that the importance of environmental stochasticity and random catastrophes depends on the density-dependence mechanism operating in the population based on the value of  $K$  carrying capacity. However, how density dependence is incorporated into the model greatly affects the estimates of persistence (Pascual et al. 1997). In persistence models, as a population declines, compensation for small population size takes the form of increased birth rates and decreased death rates (density dependence), and so is a significant factor in increasing population persistence.

Consider the model

$$N_{t+1} = N_t[1 + R(t)]$$

Stacey and Taper (1992) tested 2 forms of density dependence with their data: logistic

$$R(t) = R_0 \left( 1 - \frac{N(t)}{K} \right)$$

and  $\theta$ -logistic

$$R(t) = R_0 \left[ 1 - \left( \frac{N(t)}{K} \right)^\theta \right]$$

Expressed as a difference equation, the  $\theta$ -logistic model would be

$$N_{t+1} = N_t \left\{ 1 + R_0 \left[ 1 - \left( \frac{N_t}{K} \right)^\theta \right] \right\}$$

For  $\theta = 1$ , the 2 models are identical. Although Stacey and Taper's data precluded a significant test between these models, their data did show significant correlations between adult survival and population size, suggesting that density dependence was operating in the population.

The distinction between the 2 models can be very important. In the first, the rate of change of the birth and death rates with population size is linear, i.e., the classic logistic population growth model. In the second, the change can be very nonlinear. As a result, the  $\theta$ -logistic model can cause populations to be very persistent, or very extinction prone, depending on the shape of the function. In Fig. 7, the curve for per capita recruitment with  $\theta = 10$  will result in a population with much greater persistence than the curve with  $\theta = 0.1$  because as the population size becomes small, the  $\theta = 10$  population will be at peak reproduction for populations  $< 60$ , whereas peak reproduction is only reached at a population size of zero for the  $\theta = 0.1$  population.

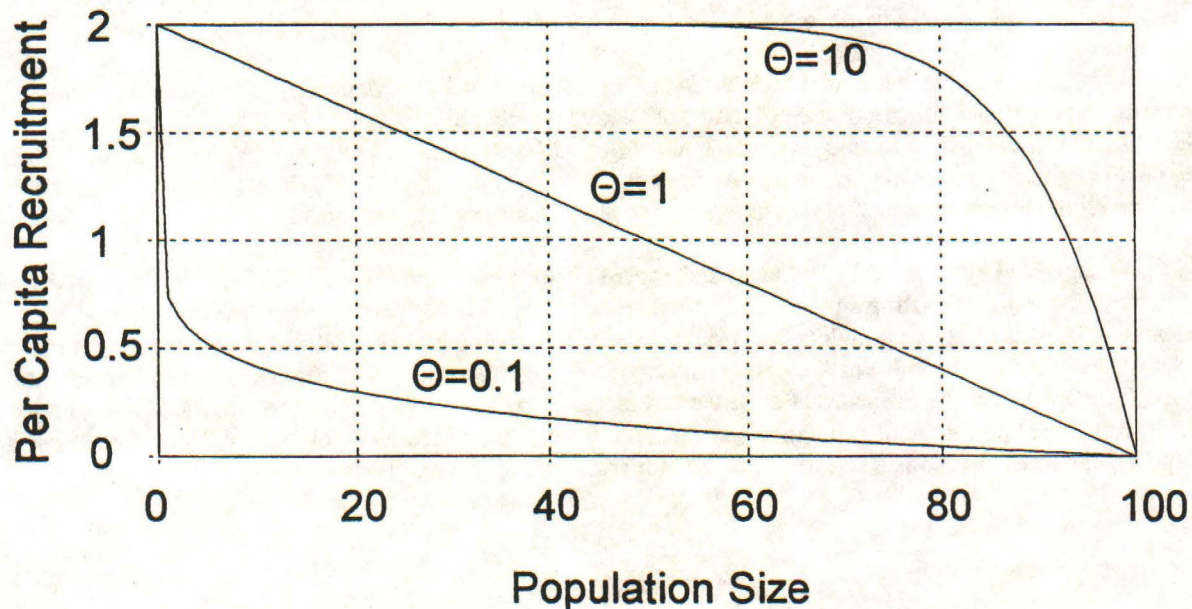


Figure 7. Three examples of possible relationships of recruitment per individual  $[(N_{t+1} - N_t)/N_t]$  to population size ( $N_t$ ). Typical sigmoid population growth demonstrated by the logistic curve results for  $\theta = 1$ . A steeper curve initially results for  $\theta = 10$ , whereas a flatter curve initially results for  $\theta = 0.1$ .

Burgman et al. (1993) and May and Oster (1976) summarize other functional relationships to incorporate density dependence. Possibilities, expressed as a difference equations, include those by Hassell (1975), Hassell et al. (1976) and May (1976)

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^b} ,$$

Moran (1950) and Ricker (1954, 1975:282)

$$N_{t+1} = N_t \exp \left[ r \left( 1 - \frac{N_t}{k} \right) \right] ,$$

Pennycuik et al. (1968), Usher (1972), and Beddington (1974) taken from May et al. (1976)

$$N_{t+1} = \frac{\lambda N_t}{1 + \exp[-A(1 - N_t/B)]}$$

Beverton and Holt (1957) and Ricker (1975:291)

$$N_{t+1} = \frac{1}{\rho + (k/N_t)} ,$$

and Maynard-Smith and Slatkin (1973)

$$N_{t+1} = \frac{R_0 N_t}{1 + (R_0 - 1) \left( \frac{N_t}{k} \right)^c} .$$

Each of these models results in a different relationship between per capita recruitment and population size. Further, these simple models can be applied to various segments of the life cycle, e.g., fecundity rates, neonatal survival, and adult survival, to achieve more realistic biological models. But the use of different models means density dependence is implemented differently at a particular population level, and population viability is affected. For example, Mills et al. (1996) reported widely differing estimates of population viability of grizzly bear (*Ursus arctos horribilis*) depending on which of 4 computer programs were used to compute the estimate. Probably part of the discrepancy is in how density dependence was implemented in each of the programs, but likely different functions were used, and these relationships were likely applied to differing segments of the life cycle. Unfortunately, distinguishing between these various models of density dependence with data is not practical because of the stochasticity (noise) in observed population levels, as (Pascual et al. (1997) demonstrated by fitting a collection of models to Serengeti wildebeest (*Connochaetes taurinus*) data.

Fowler (1981, 1994) argues that both theory and empirical information support the conclusion that most density-dependent change occurs at high population levels (close to the carrying capacity) for species with life history strategies typical of large mammals, such as deer ( $\theta > 1$ ). The reverse is true for species with life history strategies typical of insects and some fishes, with  $\theta < 1$ .

Note that explicit estimates of carrying capacity ( $K$ ) and its variance are not needed to incorporate density dependence into a population model, although such an approach is possible. If the functional relationships between birth and death rates and population density are available, the carrying capacity is determined by these relationships. Further, if these relationships incorporate temporal and spatial variation, then the resulting model will have temporal and spatial variation in its carrying capacity, and thus stochastic density dependence.

Another example of how density dependence can operate in small populations is provided by the Allee effect (Allee 1931), i.e., the per capita birth rate declines at low densities (Fig. 8) because, for example, of the increased difficulty of finding a mate (Yodzis 1989:12-13). This is known as *Allee-type behavior* (of the per capita birth rate), and its effect on the per capita population growth rate,  $R(t)$ , is called an Allee effect. In theory, a low density equilibrium would be sustained in a deterministic equilibrium, where the birth rate equals the death rate. However, given stochasticity, the population could be driven below the low density equilibrium, and thus slide into extinction.

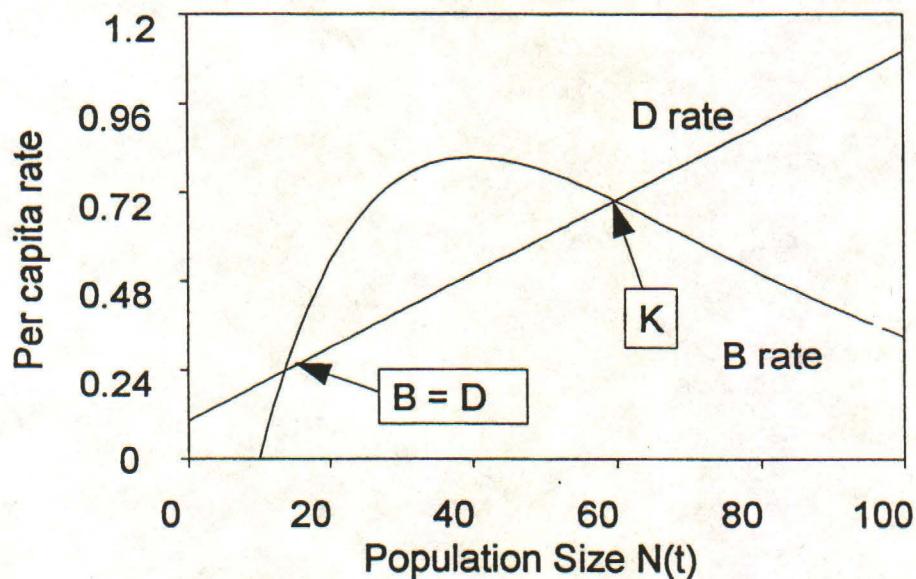


Figure 8. Example of how an Allee Effect is created by a declining birth rate at low densities. Two equilibrium points exist, where the birth rate equals the death rate. The lower equilibrium may be stable in a deterministic system, but could easily lead to extinction in a stochastic system.

A second example of incorporating density dependence into a population viability analysis is provided by Armbruster and Lande (1993). They used estimates of life history parameters of elephant (*Loxodonta africana*) populations in a fluctuating environment from studies at Tsavo National Park, Kenya, to develop an age-structured, density-dependent model. Density regulation was implemented by changes in the age of first reproduction and calving interval. They modeled environmental stochasticity with drought events affecting sex- and age-specific survival.

#### INCORPORATION OF PARAMETER UNCERTAINTY INTO PERSISTENCE ESTIMATES

In a previous section, I demonstrated how to remove the sampling variation from estimates of process variation. Unbiased estimates of process variances such as temporal and spatial variation can be achieved. In this

section, I will examine how to incorporate uncertainty of the parameter estimates into the estimates of persistence, and in the process, provide an unbiased estimate of persistence given the population model.

Any model developed to estimate population persistence will have several to many parameters that must be estimated from available data. Each of these estimates will have an associated estimate of its precision in the form of a variance, assuming that statistically rigorous methods were used to estimate the parameter from data. In addition, because some of the parameters may have been estimated from the same set(s) of data, some parameters in the model may have a non-zero covariance. Thus, the vector of parameter estimates ( $\hat{\theta}$ ) used in the model to estimate persistence has the variance-covariance matrix [ $\text{V}\hat{\text{a}}\text{r}(\hat{\theta})$ ] to measure uncertainty.

Typically, statisticians use the delta method (e.g. Seber 1982:7-9) to estimate the variance of a function of parameters from a set of parameter estimates and their variance-covariance matrix. In the context of persistence, the sampling variance of the estimate of persistence ( $\hat{p}$ ) would be estimated from the sampling variances of the parameters in the model as

$$\text{V}\hat{\text{a}}\text{r}(\hat{p}) = \frac{\partial f(\hat{\theta})}{\partial \theta}^T \text{V}\hat{\text{a}}\text{r}(\hat{\theta}) \frac{\partial f(\hat{\theta})}{\partial \theta}$$

where  $\hat{p} = f(\hat{\theta})$ . That is, the function  $f$  represents the model used to estimate persistence. However, for realistically complex persistence models, the analytical calculation of partial derivatives needed in this formula is likely not feasible.

The lack of explicit analytical partial derivatives suggests that numerical methods be used. The most feasible, albeit numerically intensive, appears to be the parametric bootstrap approach (Effron and Tibshirani 1993, Urban Hjorth 1994). With a parametric bootstrap, a realization of the parameter estimates is generated based on their point estimates and sampling variance-covariance matrix using Monte Carlo methods. Likely a multivariate normal distribution will be used as the parametric distribution describing the set of parameter estimates, although other distributions or combinations of distributions may be more realistic biologically. Using this set of simulated values in the persistence model, persistence is estimated. This step will require a large number of simulations to properly estimate persistence with little uncertainty, typically 10000 simulations are conducted. Then, a new set of parameter values are generated and persistence again estimated. This process is repeated for many sets of parameter estimates (at least 100, but more likely 1000) to obtain a set of estimates of persistence. The variation of the resulting estimates of persistence is then a measure of uncertainty attributable to the variation of the parameter estimates as measured by their variance-covariance matrix. The process is diagrammed as:

PARAMETRIC BOOTSTRAP LOOP (1000 iterations):

Select realization of parameter estimates

MONTE CARLO LOOP (10000 iterations):

Tabulate percentage of model runs resulting in persistence

END MONTE CARLO LOOP

END PARAMETRIC BOOTSTRAP LOOP

However, even more critical to our viability analysis is the fact that the mean of this set of 1000 estimates of persistence is likely less than the estimate we obtained using our original point estimates of model parameters. More formally, the expected value of estimated persistence [ $E(\hat{p})$ ] is less than the value of persistence predicted by

our model using the point estimates of its parameters, i.e.,  $E(\hat{p}) < f[E(\hat{\theta})]$ , an example of Jensen's inequality. This difference is due to large probabilities of early extinction for certain parameter sets that are likely given their sampling variation (Ludwig 1996a). Thus, to estimate persistence, the mean of the bootstrap estimates of persistence should be used, and not the estimate of persistence obtained by plugging our parameter estimates directly into our population model.

Confidence intervals on persistence could be constructed using the usual  $\pm 2SE$  procedure based on the set of 1000 estimates. This confidence interval represents the variation attributable to the uncertainty of the parameter estimates used in the model. Uncertainty about the model is not included in this confidence interval, because the model is assumed to be known. However, a better confidence interval will probably be achieved by sorting the 1000 values into ascending order and using the 25<sup>th</sup> and 975<sup>th</sup> values as a 95% confidence interval. This procedure accounts for the likely asymmetric distribution of the estimates of persistence.

## DISCUSSION

The real problem with PVA is not the model, but obtaining the data to drive the model (Ruggiero et al. 1994). Much of the published work on PVA ignores this essential point (Thomas 1990). For example, Mangel and Tier (1994) simplify the process to the point that they miss major issues concerning data reliability and quality of the product (estimates of persistence). Their 4 "facts" are:

1. "A population can grow, on average, exponentially and without bound and still not persist." This is because of catastrophes that will bring even a thriving population to zero.
2. "There is a simple and direct method for the computation of persistence times that virtually all biologists can use." They suggest a simple model with one age class and a population ceiling that the population cannot exceed, but the ceiling does not cause density dependence effects of growth parameters. As a result, their approach to estimating persistence is likely to underestimate persistence if the ceiling is set too low because the population can never grow away from the absorbing state of extinction.
3. "The shoulder of the MacArthur-Wilson model occurs with other models as well, but disappears when catastrophes are included." They suggest a slow, steady rise in persistence times as the population ceiling is increased.
4. "Extinction times are approximately exponentially distributed and this means that extinctions are likely." Thus, they conclude the most likely value of a population is zero, i.e., the mode of an exponential distribution. I believe this result is because of the simplistic assumptions they have used to obtain it. Realistic models that incorporate the sources of variation described above will not result in such simplistic results.

Another misguided example is Tomiuk and Loeschcke (1994). Their mathematics cover up the real problem of obtaining realistic estimates of the parameter values to use in the models. Their model emphasizes demographic variation, and ignores the bigger issues of temporal variation and individual heterogeneity.

A common problem with PVA is that the sampling variation of the parameter estimates is ignored [e.g., Stacey and Taper (1993) and Dennis et al. (1991)]. In both cases, estimates of persistence are too pessimistic because the sampling variation of the population parameters is included in the population model as if it were temporal variation. Further, individual heterogeneity was left out of the model, further biasing the estimates of persistence too low.

"Most PVAs have ignored fundamentals of ecology such as habitat, focusing instead on genetics or stochastic demography." (Boyce 1992:491). For small populations (<50) of endangered species, such a strategy



may be justified, particularly for short term predictions. But incorporating only demographic variation results in over estimates of persistence, because temporal variation has been ignored. On the other hand, the remaining survivors of an endangered species may be the individuals with high survival and reproductive rates, and so the lack of individual heterogeneity may under estimate persistence.

The above studies should not lead the reader to believe that useful attempts to estimate persistence do not exist. Schneider and Yodzis (1994) developed a model of marten (*Martes americana*) population dynamics that incorporated the behavior and physiology of individual martens, spatial dynamics, and demographic and environmental stochasticity. Undoubtedly some readers would quibble with some of the assumptions and data used to build the model, but I would contend that a realistic model with some of the inputs "guessed" (and clearly stated to be such) is a much more reasonable approach than a simplistic model that ignores important processes affecting persistence. Further, such realistic models identify data needs that can be addressed with time, even though the actual estimate of persistence is of questionable value. The alternative of using simplistic and naive models assures invalid estimates and little progress in improving the situation, with a rapid loss of credibility by the field of conservation biology.

Murphy et al. (1990) have proposed two different types of PVA. For organisms with low population densities that are restricted to small geographic ranges (typical vertebrate endangered species), genetic and demographic factors should be stressed. For smaller organisms such as most endangered invertebrates, environmental uncertainty and catastrophic factors should be stressed because these organisms are generally restricted to a few small habitat patches, but are capable of reaching large population sizes within these patches. Nunney and Campbell (1993) note that demographic models and genetic models both have resulted in similar estimates of minimum viable population size, but that the ideal spatial arrangement of reserves remains an issue.

Lande (1995) suggests that genetic mutations may affect fitness, and thus ignoring genetic effects results in underestimates of viability. Mutation can affect the persistence of small populations by causing inbreeding depression, by maintaining potentially adaptive genetic variation in quantitative characters, and through the erosion of fitness by accumulation of mildly detrimental mutations. Populations of 5000 or more are required to maintain evolutionary viability. Theoretical results suggest that the risk of extinction due to the fixation of mildly detrimental mutations may be comparable in importance to environmental stochasticity and could substantially decrease the long-term viability of populations with effective sizes as large as a few thousand (Lande 1995). If these results are correct, determining minimum viable population numbers for most endangered species is an exercise in futility, because almost all of these populations are already below 5000.

Conservation biologists would like to have "rules of thumb" to evaluate persistence (Boyce 1992), for example the magical Franklin-Soulé number of 500 (Franklin 1980, Soulé 1980) that is the effective population size ( $N_e$ ) to maintain genetic variability in quantitative characters. Unfortunately, these rules lack the realism to be useful. The Franklin-Soulé number was derived from simple genetic models, and hence lacks the essential features of a PVA model discussed here. Attempts with simplistic models such as Mangel and Tier (1994) and Tomiuk and Loeschke (1994) also do not provide defensible results because of the lack of attention to the biology of the species and the stochastic environment in which the population exists. Until conservation biologists do good experimental studies to evaluate population persistence empirically, I question the usefulness of "rules of thumb" and simplistic models suggested various places in the literature.

PVA can be viewed as a heuristic tool to explore the dynamics of an endangered population, and not as a predictive tool. PVA could be used to identify variables that the population may be more or less sensitive to, and to investigate the relative benefits of alternative kinds of management. Some readers will argue that in this context, the absolute reliability of the model estimates of extinction probability, or time to extinction, matter much less than the extent to which risk is affected by different demographic and environmental variables. I disagree with this notion because conclusions from PVA so strongly depend on which sources of variation included in the model and their relative magnitudes. As an example, the importance of demographic variation is stressed in PVA because it happens to be the simplest source of variation to model, generally only requiring the assumption of binomial

variation. Temporal variation has received less emphasis because it is a more difficult to obtain estimates of the temporal variance of population parameters. Individual heterogeneity has receive no attention because this source of variation is by far the most difficult source to quantify, particularly for survival rates. The only way that valid inferences can be drawn about the importance of various sources of stochasticity affecting a population is to have reasonably good estimates of these parameters. Simplistic PVA models based on little or no data lead to simplistic and unreliable answers. Without data, why would you expect anything else?

Until rigorous experimental work can be conducted, conservation biologists should borrow information from game species, where long-term studies have been done that will provide estimates of temporal and spatial variation and individual heterogeneity. Rules of thumb that predict temporal variation in survival as a function of weather, or individual variation in survival as a function of body characteristics, provide alternative sources of data. For at least some game species, data exist to develop such rules. Further, these kinds of data will probably never be available for many endangered species: the opportunity to collect such data was lost with the decline of the population to current (threatened) levels. Thus, I suggest the use of surrogate species to help meet the data needs of realistic models of persistence. Taxonomically related species may provide information, although species in the same ecological guild may also provide information on temporal and spatial variation. Note the distinction in using estimates of the temporal and spatial variation and individual heterogeneity from a related species, versus using estimates of survival and recruitment from a surrogate species. Estimates of survival and recruitment from a stable or increasing population would obviously be inappropriate for a species with a declining population.

## CONCLUSION

In summary, most estimates of population viability are nearly useless because one or more of the following mistakes or omissions are made in developing a model to estimate persistence. By listing omissions, this list suggests the essential ingredients to develop a useful PVA.

1. Little or no data are available to estimate basic parameters in the population model, with almost all the parameter estimates just guesses. The resulting estimate of persistence is therefore strictly a guess.

Lesson: to do a valid PVA, you must have data to build a realistic population model.

2. The model ignores spatial variation which will increase population viability. As suggested by Stacey and Taper (1992) immigration can occasionally rescue a population from extinction.

Lesson: if the population is widely distributed geographically, incorporate spatial variation.

3. The model uses estimates of temporal variation that are at best, poor guesses. This statement assumes that the modeler understood the difference between process variation and sampling variation. Often, sampling variation is assumed to substitute for process variation, and, as a result, the estimates of persistence are too pessimistic. Sampling variation has nothing to do with population persistence. Estimates of population parameters must not be treated as if they are the true parameter value.

Lesson: obtain reliable estimates of temporal variation, and don't confuse sampling variation and temporal variation.

4. The model uses demographic variation as a substitute for temporal variation in the process, and ignores true temporal variation.

Lesson: incorporate both demographic and temporal variation into the PVA.

5. The model ignores life-long individual heterogeneity that increases population viability, and assumes that all individuals endure the same identical survival and reproduction parameters. Such a naive assumption results in population viability being underestimated.

Lesson: Individual heterogeneity must be incorporated into a PVA model if you don't want to underestimate viability

6. The model assumes that current conditions are not changing, i.e., the stochastic processes included in the model are assumed constant for the indefinite future. Loss of habitat and other environmental changes that affect these stochastic processes are ignored. Thus, as discussed by Caswell (1989), the model is likely not useful in forecasting (i.e., predicting what will happen), but is useful in projecting (i.e., predicting what would happen if conditions do not change).

Lesson: Recognize that your model does not predict the future — it only projects what might happen if the system doesn't change (an unlikely assumption!).

Before you use the estimates of persistence from any population viability analysis, compare your approach to obtain the estimate against the necessary components discussed here. If you discover omissions and errors in the approach used to obtain the estimate, recognize the worth or lack thereof of the estimate of persistence. Although the estimates of persistence obtained from a PVA may have little value, the process of formulating a model and identifying missing information, i.e., parameters that are poorly estimated, may still have value in developing measures to conserve the species in question.

#### Literature Cited

- Allee, W. C. 1931. *Animal aggregations*. Univ. Chicago Press, Chicago, Illinois. 431 pp.
- Armbruster, P. and R. Lande. 1993. A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? *Conservation Biology* 7:602-610.
- Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monograph* 121:1-39.
- Beddington, J. R. 1974. Age distribution and the stability of simple discrete time populations models. *Journal Theoretical Biology* 47:65-74.
- Beissinger, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. *Ecological Applications* 5:618-631.
- Bennington, C. C. and W. V. Thyne. 1994. Use and misuse of mixed model analysis of variance in ecological studies. *Ecology* 75:717-722.
- Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91-98.
- Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. Great Britain Ministry of Agriculture, Fisheries and Food, *Fishery Investigations (Series 2)* 19:5-533.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review Ecology Systematics* 23:481-506.
- Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London, Great Britain. 314 pp.

- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and Analysis Experiments for Fish Survival Experiments Based on Capture-Recapture. American Fisheries Society Monograph No. 5, Pages 260-278.
- Burnham, K. P., D. R. Anderson, and G. C. White. 1996. Meta-analysis of vital rates of the northern spotted owl. *Studies in Avian Biology* 17:92-101.
- Caswell, H. 1989. Matrix population models. Sinauer Associates, Sunderland, Mass. 328 pp.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- Cézilly, F., A. Viallefont, V. Boy and A. R. Johnson. 1996. Annual variation in survival and breeding probability in greater flamingos. *Ecology* 77:1143-1150.
- Clark, T. W., P. C. Paquet, and A. P. Curlee. 1996. Special section: large carnivore conservation in the Rocky Mountains of the United States and Canada. *Conservation Biology* 10:936-936.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer behavior and ecology of two sexes. Univ. Chicago Press, Chicago, Illinois. 378 pp.
- Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications* 5:17-19.
- DeAngelis, D. L. and L. J. Gross, eds. 1992. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Chapman & Hall, New York, N. Y. 525 pp.
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 6:115-143.
- Diamond, J., and S. Pimm. 1993. Survival times of bird populations: a reply. *American Naturalist* 142:1030-1035.
- Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5:3-11.
- Efron, B. and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall, New York, N. Y. 436 pp.
- Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8:124-136.
- Fowler, C. W. 1981. Density dependence as related to life history strategy. *Ecology* 62:602-610.
- Fowler, C. W. 1994. Further consideration of nonlinearity in density dependence among large mammals. Report International Whaling Commission 44:385-391.
- Franklin, I. R. 1980. Evolutionary changes in small populations. Pages 135-149 *In* M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Mass.

- Ginzburg, L. R., L. B. Slobodkin, K. Johnson, A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis* 2:171-181.
- Haila, Y., and I. K. Hanski. 1993. Birds breeding on small British islands and extinction risks. *American Naturalist* 142:1025-1029.
- Hanski, I. 1996. Metapopulation ecology. Pages 13-43 in *Population Dynamics in Ecological Space and Time*, O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, eds. Univ. Chicago Press, Chicago, Illinois.
- Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. *American Naturalist* 147:527-541.
- Hassel, M. P. 1975. Density-dependence in single-species populations. *Journal Animal Ecology* 44:283-295.
- Hassell, M. P., J. H. Lawton, and R. M. May. 1976. Patterns of dynamical behaviour in single-species populations. *Journal Animal Ecology* 45:471-486.
- Hess, G. R. 1993. Conservation corridors and contagious disease: a cautionary note. *Conservation Biology* 8:256-262.
- Holt, R. D., S. W. Pacala, T. W. Smith, and J. Liu. 1995. Linking contemporary vegetation models with spatially explicit animal population models. *Ecological Applications* 5:20-27.
- Hunter, M. L., Jr. 1996. *Fundamentals of conservation biology*. Blackwell Science, Cambridge, Mass. 482 pp.
- Joopouborg, N., and J. M. Van Groenendael. 1996. Demography, genetics, or statistics: comments on a paper by Heschel and Paige. *Conservation Biology* 10:1290-1291.
- Keller, L. F., P. Arcese, J. N. M. Smith, W. M. Hochachka, and S. C. Stearns. 1994. Selection against inbred song sparrows during a natural population bottleneck. *Nature* 372:356-357.
- Koenig, W. D., R. L. Mumme, W. J. Carmen, and M. T. Stanback. 1994. Acorn production by oaks in central California: variation within and among years. *Ecology* 75:99-109.
- Krausman, P. R., R. C. Etchberger, and R. M. Lee. 1993. Persistence of mountain sheep. *Conservation Biology* 7:219.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911-927.
- Lande, R. 1995. Mutation and conservation. *Conservation Biology* 9:782-791.
- Lefkovich, L. P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21:1-18.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183-212.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213-245.
- Lomnicki, A. 1988. *Population ecology of individuals*. Princeton Univ. Press, Princeton, New Jersey. 223 pp.

- Ludwig, D. 1996a. Uncertainty and the assessment of extinction probabilities. *Ecological Applications* 6:1067-1076.
- Ludwig, D. 1996b. The distribution of population survival times. *American Naturalist* 147:506-526.
- Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5:148-157.
- Mangel, M. and C. Tier. 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75:607-614.
- Manly, B. F. J. 1990. Stage-structured population Sampling, analysis and simulation. Chapman and Hall, London, Great Britain. 187 pp.
- May, R. M. 1976. Models for single populations. Pages 4-25 *In* Theoretical Ecology: Principles and Applications. R. M. May, ed. Blackwell, Oxford, Great Britain.
- May, R. M., and G. F. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. *American Naturalist* 110:573-599.
- Maynard-Smith, J. and M. Slatkin. 1973. The stability of predator-prey systems. *Ecology* 54:384-91.
- Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sinauer Associates, Sunderland, Mass. 600 pp.
- Mills, L. S., S. G. Hayes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* 10:863-873.
- Moran, P. A. P. 1950. Some remarks on animal population dynamics. *Biometrics* 6:250-258.
- Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. *Conservation Biology* 4:41-51.
- Nunney, L. and K. A. Campbell. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* 8:234-239.
- Pascual, M. A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* 11:966-976.
- Pennycuik, C. J., R. M. Compton, and L. Beckingham. 1968. A computer model for simulating the growth of a population, or of two interacting populations. *Journal Theoretical Biology* 18:316-329.
- Pimm, S. L., H. L. Jones, and J. M. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757-785.
- Remmert, H. (ed.). 1994. Minimum animal populations. Springer-Verlag, New York, N. Y. 156 pp.
- Ricker, W. E. 1954. Stock and recruitment. *Journal Fisheries Research Board Canada* 11:559-623.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada, Bull.* 191. Ottawa, Canada.

- Ruggiero, L. F., G. D. Hayward, and J. R. Squires. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. *Conservation Biology* 8:364-372.
- Schneider, R. R., and P. Yodzis. 1994. Extinction dynamics in the American marten (*Martes americana*). *Conservation Biology* 4:1058-1068.
- Seber, G. A. F. 1982. Estimation of animal abundance and related parameters. 2<sup>nd</sup> ed. Macmillan, New York. 654pp.
- Shaffer, M. L. 1981. Minimum population size for species conservation. *BioScience* 31:131-134.
- Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 69-86 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge Univ. Press, Cambridge, England.
- Silva, M. and J. A. Downing. 1994. Allometric scaling of minimal mammal densities. *Conservation Biology* 8:732-743.
- Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151-170 In M. E. Soulé and B. A. Wilcox, eds. *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Mass.
- Soulé, M. E. 1987. *Viable Populations for Conservation*. Cambridge Univ. Press, New York. 189 pp.
- Stacey, P. B. and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:18-29.
- Thomas, C. D. 1990. What do real population dynamics tell us about minimum viable population sizes? *Conservation Biology* 4:324-327.
- Thomas, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conservation Biology* 8:373-378.
- Tomiuk, J. and V. Loeschcke. 1994. On the application of birth-death models in conservation biology. *Conservation Biology* 8:574-576.
- Tracy, C. R., and T. L. George. 1992. On the determinants of extinction. *American Naturalist* 139:102-122.
- Tracy, C. R., and T. L. George. 1993. Extinction probabilities for British island birds: a reply. *American Naturalist* 142:1036-1037.
- Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. Usefulness of spatially explicit population models in land management. *Ecological Applications* 5:12-16.
- Urban Hjorth, J. S. 1993. *Computer intensive statistical methods*. Chapman & Hall, London, Great Britain. 263 pp.
- Usher, M. B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. *Journal Applied Ecology* 3:355-67.
- Usher, M. B. 1972. Developments in the Leslie matrix model. Pages 29-60 In J. N. R. Jeffers, ed. *Mathematical models in ecology*. Blackwell, Oxford, Great Britain.

**Yodzis, P. 1989. Introduction to theoretical ecology. Harper and Row, New York, N.Y. 383 pp.**





# POPULATION VIABILITY ANALYSIS

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## INTRODUCTION

Population viability analysis (PVA) is a process. It entails evaluation of data and models for a population to anticipate the likelihood that a population will persist for some arbitrarily chosen time into the future (125, 128). A closely related concept is minimum viable population (MVP) analysis. An MVP is an estimate of the minimum number of organisms of a particular species that constitutes a viable population. Reference is also made to population vulnerability analysis which is a negative appellation for PVA. PVA embraces MVP, but without seeking to estimate the absolute minimum population necessary to keep a species viable (136).

In the United States, the US Forest Service has a mandate to preserve viable populations on its lands under the National Forest Management Act (158). Likewise, the US Fish and Wildlife Service and the National Marine Fisheries Service have been evaluating PVAs for many species or populations proposed for listing under the Endangered Species Act (152). Establishing criteria for what constitutes a viable population is no longer strictly an academic pursuit.

PVAs have been attempted for at least 35 species; perhaps the most celebrated are those for the grizzly bear (*Ursus arctos horribilis*) (126, 129, 144), and the northern spotted owl (*Strix occidentalis caurina*) (18, 79, 95, 98a). Most PVAs are simulation studies that remain unpublished, or when published, they may only include outlines of model structure (95, 126, 131). Others invoke analytical methods or "rules of thumb," always burdened with severe assumptions (31, 152). PVAs vary according to the ecology of the species, the expertise of the modelers, and the extent of available data.

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There are no guidelines on what constitutes a valid PVA, and because each case is unique, I am loathe to devise any. Any attempt is qualified that involves a population simulation or analysis with the intent of projecting future populations or estimating some extinction or persistence parameter, e.g. time to extinction, probability of extinction, probability of persisting for 100 years, etc. Definitions and criteria for viability, persistence, and extinction are arbitrary, e.g. ensuring a 95% probability of surviving for at least 100 years. Discussion of such criteria can be found in Mace & Lande (92) and Thompson (152).

Collecting sufficient data to derive reliable estimates for all the parameters necessary to determine MVP is simply not practical in most cases. It is further questionable how well ecologists can predict the future (34), particularly over time horizons necessary to project extinctions. On the other hand, Soulé (136) suggests that managers have the right to expect population biologists to project the number of animals necessary to ensure the long-term viability of a population. But to do so has proven to be dangerous ground (83) which risks damaging the credibility of conservation biologists.

My purpose in this review is an attempt to place PVA and MVP on more comfortable ground by identifying a realistic domain. I maintain that PVA ought to be an integral part of any species management plan, but rather than being so presumptuous as to claim that we can actually use modeling to define a MVP, or to estimate the probability of extinction, I use it as a forum to champion the adaptive management approach of Holling (67) and Walters (162). For those all-too-frequent cases that cannot wait for a full-blown PVA, I review empirical evidence suggesting that use of rules-of-thumb for MVPs may not be unrealistic.

## MODELING EXTINCTION

Fundamental to MVP is the fact that small populations are more likely to go extinct than larger ones due to inbreeding depression and genetic drift, or simply the threat of chance birth or death events (demographic stochasticity). Under high environmental variance or catastrophes, however, maintaining MVP may not be as effective a conservation target as would be managing for spatial configuration and location of habitats (38, 85, 106, 128). Irrespective of the target, the objective of PVA is to provide insight into how resource management can change parameters influencing the probability of extinction. This change may entail lengthening the expected time to extinction,  $E(T)$ , or reducing the probability of extinction within some time frame.

The most appropriate model structure for a PVA depends on the availability of data and the essential features of the ecology of the organism. In this section

I review structural features of PVA and extinction modeling. I begin with a discussion of stochastic variation, a necessary element in any consideration of extinction processes, and then review approaches focusing on genetics, demography, and ecology. I conclude with the argument that all of these elements ought to occur together in the same model. Because of the complexity of such a model, most PVAs will enter the realm of computer simulation modeling.

### *Stochasticity*

Random events can be extremely important in extinction, especially for small populations, the target of most PVA (121). In a sense, the distinction between deterministic and stochastic processes in ecology is artificial because all ecological processes are stochastic. Maynard Smith (97) points out that "the use of deterministic rather than stochastic models can only be justified by mathematical convenience." For heuristic purposes, use of deterministic models is appropriate. For example, our understanding of a simple model of competition or predation would only be obfuscated by the complex mathematics of a stochastic version. Because they are more tractable, deterministic models may yield robust results; stochastic models are often too complex to be solved analytically and thus require use of simulation methods.

Usually, conclusions from stochastic models in ecology are strikingly different from deterministic ones (26). This is generally true because of (i) large variances, (ii) nonlinear functions, and (iii) highly skewed or otherwise non-normally distributed variables. The significance of high variance is easy to understand in the context of extinction (85). Less transparent is the fact that virtually all ecological processes are nonlinear (17, 122). When the system contains nonlinearities, its behavior may differ markedly due to Jensen's inequality which states that for any concave function,  $\phi$ , of a random variable  $\chi$ ,  $E[\phi(\chi)] \leq \phi[E(\chi)]$ ; the reverse inequality applies for a convex function (72). The greater the magnitude of nonlinearity, say as measured by the second derivative, the greater will be the effect of randomness.

Sampling from a skewed distribution can yield peculiar behaviors in stochastic models. This is illustrated by exponential population growth in a random environment, i.e. random growth rate (88). Under such a model, population sizes at some future time are lognormally distributed (31, 154). This distribution arises because a series of good years will lead to extraordinarily large population sizes due simply to the geometric nature of population growth. Sequential sampling from such skewed distributions of  $N(t)$  results in the most likely population sizes (mode) being less than the mean. As a consequence we obtain the seemingly paradoxical observation that the growth rate for a typical sample path "will in general be less than the growth rate of

average population" (154). Because population dynamics generally involve intrinsically multiplicative processes (83), we may expect complications due to distributional properties to be common.

Environmental stochasticity or "noise" is handled poorly in most PVA models. Environmental stochasticity in nature is not the unstructured "white" noise of a random number generator or "epsilon" term. Rather environmental stochasticity carries structure, such as autocorrelation and distributional properties, stemming from the manner in which errors are propagated through the system (101, 102, 108, 140). It really makes a big difference which variables in the system are fluctuating due to the environment, because this can affect the structure and dynamics of the system. Error propagation (including sampling error) can be examined by simulation methods (104), yet there has been little study of this problem in ecology.

This all calls for detailed understanding of the variance structure of populations (55). To understand the role of stochasticity in population extinction, we must understand how environmental variability affects the organism. Thus it will be a fundamental challenge in any PVA to decide how to model environmental stochasticity. Because data are limited, sampling variance may often overwhelm attempts to decompose variance into individual and environmental components. If sampling variance is included in a simulation model, projected variability will be much larger than in the true population.

### *Genetics*

The ultimate objective behind PVA is to develop prescriptions for species survival for the purpose of preserving genetic diversity (136); thus it seems appropriate that models of genetic variation ought to contribute to the formulation of a PVA. We know that small population size can result in inbreeding depression in some populations, which may increase the risk of extinction for the population (81, 111, 112). We also know that small population size can reduce genetic variation through drift, thereby reducing the raw material for evolutionary change, and genetic variation can be essential to ensure preadaptation to disease, competition, or predation (45). But what we do not know is how much and what type of genetic variation is most important to preserve.

Templeton (149) makes a convincing argument for placing priority in conservation on unique evolutionary lineages such as species or subspecies. But even within a taxonomic group there are many forms of genetic variation, which may respond differentially to particular conservation strategies. Genetic variation is revealed by restriction site analysis of mitochondrial DNA, karyotypy, electrophoresis of allozymes, heritability of quantitative traits (40),

and morphological variation (but see 69). And it is possible for many of these measures to vary almost independently of one another (80, 165). Genetic variation within populations often is measured by mean heterozygosity or the proportion of alleles that are heterozygous. Yet, if preadaptation to future insults from other species (disease, parasites, competitors, predators) is the reason to preserve genetic variation, it may be important to focus on preserving rare alleles (45). Perhaps the number of alleles per locus is a more important measure of genetic variation (2a).

Because quantitative traits are most frequently the target of natural selection, Lande & Barrowclough (81) argue that heritability should be monitored as a measure of genetic variation for conservation. Yet, from a pragmatic perspective, we know that estimates of heritability are often difficult to interpret because the response to selection can be greatly complicated by maternal effects (3). Relatively low levels of genetic variation may confer substantial heritability to some quantitative traits (90). There is also the difficulty of deciding which quantitative traits should be measured. Following Lande & Barrowclough's (81) rationale, the most important traits ought to be those that are most frequently the target of natural selection. Yet, these are exactly the traits expected to bear the lowest heritability as a consequence of selection (16, 40).

How genetic variation is structured within populations can also bear on conservation strategies (12). Many population geneticists believe that spatial heterogeneity is one of the most important mechanisms maintaining genetic variation in natural populations (63). Whether or not this pertains to the importance of inbreeding in natural populations has become the source of a fascinating debate (112, 130), but irrespective of this, there is no question that spatial variation in genetic composition of populations can be substantial. We are just beginning to understand the role of population subdivision on genetic structure and heritability (161). How significant is local adaptation? How important is coadaptation of gene complexes (149)? Although spatial structuring of genetic variation is complex and interesting, it is not clear that our understanding is sufficient to use it as a basis for manipulating populations for conservation. Attempts to manage the species by transplanting individuals between subpopulations is an effective tool to maintain or increase genetic variation within populations (57) but may destroy variance among populations.

The solution to this dilemma may ultimately entail foreseeing the sorts of threats a species is likely to encounter. If local subpopulations are likely to be threatened by habitat destruction or political unrest, it may be extremely important to maintain geographic variants to ensure that the species can continue to survive in other localities (see 142, 149). However, if future

threats due to diseases and parasites are expected, there may be a premium on ensuring the maximum allelic diversity throughout the population (not necessarily all in one place—96).

Is there an optimum amount of mixing among subpopulations that maximizes total genetic variance in the population? Because different genes or gene complexes are found in within-vs-among subpopulation components of genetic variation, a general answer to this question probably does not exist. Furthermore, the genetic variance within populations is a convex function of dispersal (migration) with maximum variance at the highest possible dispersal. Likewise, variance among populations is a convex function of dispersal but with maximum variance at zero dispersal (25). The sum of these two functions is similarly convex, and no intermediate maxima exist. Thus, we need to minimize dispersal among sites to preserve geographic variation while ensuring large enough numbers in subpopulations to avoid inbreeding loss of genetic variance.

An approach commonly used in trying to determine a genetic basis for MVP is to examine effective population size,  $N_e$  (113).  $N_e$  gives insight into the potential consequences of genetic drift to loss of genetic diversity, but as is the case for measures of genetic variation, we have numerous measures of effective population size, depending upon the mechanisms affecting drift. For example, Ewens (37) reviews the calculation of  $N_{ei}$  relative to inbreeding,  $N_{ev}$  for the variance in gene frequencies among subpopulations,  $N_{ee}$  targeting the rate of loss of genetic variation, and  $N_{em}$  for mutation effective population size. Still more measures may be derived. For example,  $N_e^{(meta)}$  defines the effective population size in a metapopulation experiencing repeated extinction-recolonization events (49). Each of these basic measures of  $N_e$  is then subject to adjustment for unequal sex ratio, age structure (65, 66), and variable population size (59). There is no sound basis for selecting one of these basic measures of  $N_e$  over another, yet as Ewens (37) shows, they can lead to much different conclusions about MVP.

I conclude by agreeing with Shaffer (128) and Lande (80) that modeling genetics is not likely to be as important as modeling demographic and ecological processes in the formulation of a PVA. This does not imply that genetic considerations are not important; rather, in many cases we do not yet understand the genetics well enough to use it as the basis for management. There is an urgent need for research on the link between genetics and demography (80, 94; cf 111). This conclusion also does not imply that models of genetic variability should not form the basis for PVAs. Indeed, I think this would be a novel approach for species in which erosion of genetic variability is likely to be an important consideration in the future management of a species, such as the African wild dog (*Lycaon pictus*) which has a highly subdivided population (51). But as Lande has emphasized (80), demography

and associated ecology are likely to be of more practical significance than genetics in most PVAs.

### *Birth-Death and Demography*

**BIRTH AND DEATH PROCESSES** Possibly the simplest approach to modeling extinction is a stochastic birth-death process (53, 91, 116), assuming independent, Poisson-distributed births and deaths. Demographic "accidents" are most likely in small populations due to sampling effects, i.e. simply because individuals do not survive for the same length of time, and individuals vary in the number of offspring they bear. This approach has been used to solve for  $E(T)$  as a function of population size,  $N$ , given density-dependent per capita birth,  $b_N$ , and death rates,  $d_N$ :

$$E(T) = \sum_{i=1}^N \sum_{j=i}^{N_m} (1/jd_j) \prod_{n=i}^{j-1} (b_n/d_n) \quad 1.$$

up to a maximum possible population size,  $N_m$ .

As one might expect, such sampling effects are extremely sensitive to population size (53, 91), and these effects usually can be ignored if the population is larger than about 30 individuals (depending on age structure). The exception is where a population is divided into a large number of subpopulations, each so small that it faces a risk of chance demographic extinction. If recolonization is slow, there can be a significant risk of losing the entire population by demographic stochasticity alone (103).

Environmental stochasticity is much more significant than sampling or demographic stochasticity, except for very small populations (54, 55, 74, 85, 129). Recalling the assumption of Poisson distribution for births ( $b_N$ ) and deaths ( $d_N$ ), the variance in per capita growth rate at population size  $N$  ( $r_N = b_N - d_N$ ) is simply

$$\text{Var}(r_N) = (b_N + d_N)/N \quad 2.$$

Recognizing this, Leigh (85) and Goodman (54, 55) rewrote the birth-death process model (Eq. 1) to make  $E(T)$  a function of the variance in  $r_N$ ,  $\text{Var}(r_N)$ :

$$E(T) = \sum_{i=1}^N \sum_{j=i}^{N_m} \{ [2/j(j\text{Var}[r_j] - E[r_j]) \prod_{n=i}^{j-1} [n\text{Var}(r_n) + E(r_n)] / [n\text{Var}(r_n) - E(r_n)] \} \quad 3.$$

Here,  $\text{Var}(r_N)$  somehow becomes environmental variance (152), albeit still a function of the magnitude of  $b_N$  and  $d_N$ . The important outcome of the modified birth-death process model is that  $E(T)$  increases with population size more slowly when environmental variance is high (55). Goodman (55) validated predictions of the modified birth-death process model by simulating a more complex population that included density dependence and age structure, and he generally found good concordance between simulation results and



analytical predictions from the birth-death model. However, ecological applications of birth-death process models have been criticized for several reasons.

Early interpretations that populations of more than 20–30 individuals were unlikely to risk extinction (91, 116, 132) were a concern given their basis solely in stochastic demography (129, 164). The use of a reflecting boundary,  $N_m$ , for maximum population size is unrealistic (30, 94), although this is resolved by Goel & Richter-Dyn (53). Additionally, the fact that the models are in continuous time renders it “highly questionable” (83) because of the importance of seasonal structure in the population. The assumption at Eq. 2 which is the basis for Eq. 3 (152) also merits consideration. For constant  $E(r_N)$ , increasing variance in  $r_N$  is accomplished by increasing birth and death rates. This is reasonable enough given explicit assumptions in the birth-death model but bears rather heavily on Belovsky’s (6) attempt at empirical verification for Eq. 3 which draws on comparative analyses of the maximum demographic potential for  $r$  and  $b$  in mammals.

Another matter of concern in all models that predict the time to extinction, in general, is that  $E(T)$  can be a misleading characterization of the likelihood of extinction (31, 41, 55). The distribution of time to extinction is positively skewed in each of these models, as well as in the age-structured model (82). The  $E(T)$  is substantially greater than the median or mode of the distribution, because a few populations take extraordinarily long times to become extinct. The time to extinction most likely to occur (mode) or the middle of the distribution (median) may be more meaningful measures than the mean.

Despite these difficulties and restrictive assumptions, Leigh (85) and Goodman (54, 55) made an important point by clarifying that “demographic uncertainty” is most likely to be a concern only at low population sizes, whereas environmental uncertainty can pose significant risks for considerably larger populations (cf 101, 102 for similar results based on branching processes). Understanding the variation in population parameters attributable to environmental fluctuations is clearly fundamental to any PVA (55).

**DEMOGRAPHIC PROJECTIONS** Although “demographic uncertainty” is usually approached using birth-death process models, these models, in fact, do not contain age structure. This may be a serious shortcoming because age structure per se can have a significant effect on population trajectories and thereby on the probability of extinction (82, 154, 156).

Many PVAs employ projection matrices, such as the Leslie matrix, as age-structured models of population growth (95, 126). The Leslie matrix and similar stage-structured models have mathematical properties that give great insight into processes of population growth (24).

For example, sensitivity of population growth rate,  $r$ , to perturbations in

vital rates ( $P_x, F_x$ ) for a Leslie/Lefkovitch matrix can be solved analytically (i.e.  $dR/dP_x$  or  $dR/dF_x$ ) (24, 79, 99). Understanding the response of growth rate to perturbations at various points in the life table may yield insight into how one should target management (79). For long-lived species, such as the spotted owl, adult survival is a very sensitive demographic parameter, whereas in species with shorter generation times, fecundity can be much more important (83, 99).

In nature, the elements of a projection matrix are random variables (14, 153) or functions of the environment (134, 160). Forecasted trajectories of population size depend not only on the schedule of vital rates, but also on the variance in these rates (156). It is important to note that variation in vital rates creates disequilibrium in age structure that further complicates the dynamics. The variance in population growth rate is thus attributable to both the variation in vital rates and the variance in population structure. For demography of humans in the United States in 1960, approximately two thirds of the variance in growth rate can be attributed to variance in vital rates, whereas about one third is due to fluctuations in age structure (154).

Projection matrices in their simplest form are models of exponential population growth. As such, there are essentially two possible outcomes of these models: they increase exponentially to infinity, or decrease to extinction. If the dominant eigenvalue for the average projection matrix is less than one, extinction is assured. But even when the average projection matrix might predict an increasing population, extinction may also occur when vital rates vary (14, 74, 156). Of course, exponential growth models are strictly unrealistic on time scales necessary to explore extinction probabilities.

**FORECASTING METHODS** Development of theory and applications of forecasting mostly have occurred in economics, but the opportunity exists to apply many of these procedures to population projections. Projecting a stochastic process into the future poses problems. First, one must assume that the mechanisms generating the historical data remain intact and unchanged in the future. Second, one must select the correct structural model that drives the population process or risk serious errors in prediction. Third, errors in predictions are magnified progressively into the future such that usually only a few time intervals can be predicted with any confidence or reliability (31a).

A time series model commonly used for forecasting is the ARIMA (auto-regressive integrated moving average) model (10, 15, 19, 31a, 154). Least-squares regression is used to calculate the dependence of  $N(t)$  on lags of the entire time series,  $N(t-1)$ ,  $N(t-2)$ , . . .  $N(t-p)$ . Differencing is employed to remove trends, and moving averages can be calculated to smooth out high-frequency noise. The resulting equation is then extrapolated into the future beginning from the last observed data point. The population's trajectory

determines the forecast. Thus, if the trajectory does not show a population decrease, the forecast may continue to increase without bound. Confidence intervals around the forecasted value will, nevertheless, include 0 at some future time, but this will include sampling error and will be much shorter than  $E(T)$ . Many statistical software packages include programs that perform ARIMA forecasting.

A simplistic approach to forecasting can be derived from a diffusion model without age structure (31, 64). Itô calculus is used to solve a stochastic differential equation model of exponential population growth. The probability distribution function of extinction is the inverse Gaussian distribution (similar to the lognormal), and  $E(T) = (x_0 - x_E) / |a|$ , where  $x_0$  is the  $\log_e$  of the initial population size,  $x_E$  is the positive population size defined to constitute extinction (e.g. 1 in sexually reproducing species), and  $a$  is the average growth rate for the population. A maximum likelihood estimator (MLE) for  $\hat{a} = \ln(n_q/n_0)/(t_q - t_0)$ , which only requires knowledge of the initial,  $n_0$ , and final censuses,  $n_q$ , at times  $t_0$  and  $t_q$  respectively. Or alternatively one may use a linear regression approach (31). MLEs for  $\sigma^2$  are also easily calculated (31, 64).

Although easy to use, one must imagine that the population trajectory observed thus far will also apply into the future. Also, any structural features of the population process, e.g. density dependence, which are reflected in the time series are overlooked in the estimator of  $a$  (154).

Building on the results of Tuljapurkar & Orzack (156) and Heyde & Cohen (64), Lande & Orzack (82) also modelled stochasticity as a diffusion process for exponential age-structured populations. Simulation trials were used to validate their estimators for  $\hat{a}$  and  $\sigma^2$ . Although Lande & Orzack (82) emphasize that only three parameters are needed to use their model, one of these parameters is initial total reproductive value which requires complete life history and age-structure data!

A third approach to forecasting is to characterize the time series of vital rates with ARIMA, and then to insert these models into a projection matrix (84, 154). Such a "time-series matrix" retains more of the dynamic consequences of age structure, and therefore population fluctuations ought to be more realistic. I am unaware of any applications of this method in conservation biology.

For each of these forecasting models we assume a density-independent population. If density dependence acts in an age-specific manner (which it usually does: 43, 44), the complications to the age structure make it difficult to derive analytical results for the distribution of extinction times. Given that density dependence exists in natural populations (133), even in "density vague" populations (143), I am skeptical about using density-independent formulations except in two cases: (i) very small populations where density

dependence may be inconsequential relative to demographic stochasticity (55), or (ii) for short-term forecasting. Further research is needed to develop forecasting models with ecologically realistic structures, e.g. with density dependence. But in the meantime, Monte Carlo simulation procedures (60, 118) can be used to generate estimates and distributions for extinction parameters for models with density dependence.

Sensitivity to initial conditions ensures that long-term forecasting will be unsuccessful for chaotic populations (122), but nonlinear forecasting methods may improve short-term forecasts for populations embedded in complex ecosystems (145). Populations experiencing fluctuations due to time-lagged processes may be particularly suited to one of several nonlinear methods reviewed by Casdagli (23). Software for generating forecasts and calculating confidence intervals is described by Schaffer & Tidd (123). Unfortunately, these methods work best for time series longer than are available for most endangered species.

### *Ecology*

Although much of the literature on PVA has focussed on issues of genetics and stochastic demography, it is clear that ultimate causes and threats of extinction are primarily ecological. Loss or degradation of habitat is the most significant factor threatening species extinctions in the future (107, 164). For avian taxa currently endangered by extinction, 82% are associated with habitat loss, 44% with excessive take, 35% by introductions, and another 12% are threatened by chemical pollution or the consequences of natural events (148).

Most PVAs have ignored fundamentals of ecology such as habitat, focusing instead on genetics or stochastic demography. Although ecological factors influence demographic variables, seldom is our understanding sufficient to isolate these effects. A more appropriate approach for many species may be to model the habitat for the species and various strategies for managing this habitat. For example, Foin & Brenchley-Jackson (42) modelled the salinity, transpiration, and soil moisture of *Spartina* salt marshes in southern California, which is essential habitat for the endangered light-footed clapper rail. Reliable demographic details for the rail were unavailable, and the only connection between the bird and the habitat was a linear relationship between the biomass of Pacific cordgrass, *Spartina foliosa*, and the number of rails.

Most demographic PVAs performed thus far do not model ecological consequences of other species, e.g. predators, competitors, parasites, disease. In particular, exotic species can be a major threat in some systems (159). For example, invasions of exotics may be less likely in communities that possess a diversity of native taxa (114). In some species, dynamics of disease may be the most significant consideration in a PVA (35, 96). Understanding such relationships is necessary to predict population viability.

Regrettably PVAs often do not explicitly include management (136). Consider, for example, application of a forecasting method to a population trajectory for a species whose decline can be attributed to habitat loss. It makes no sense to extend such a trajectory if all remaining habitat for the species is now protected. Yet, this is precisely the inference that one would draw in applying a forecasting model (cf 31, 82). Leaving management out of a PVA is unfortunate because one of the greatest values of PVA modeling is the opportunity to evaluate the efficacy of various management options (67).

Indeed, it is the absence of ecology and management from most attempts at PVAs that is their biggest weakness. These processes ought to be the nuts and bolts of such modeling exercises! The power of ecological modeling rests in our ability essentially to play with nature to anticipate the consequences of various management scenarios (56, 139, 147). Some aspects of ecology such as density dependence, spatial heterogeneity, and the Allee effect are of particular significance to PVA because they have major consequences to the probability of extinction.

**DENSITY DEPENDENCE** The simplest possible model of population growth is an exponential population growth model. It has no ecology. The simplest possible ecological model is a density-dependent model such as the logistic. The existence of negative feedbacks in compensatory density dependence dampens population fluctuations and can greatly reduce the probability of extinction (52). In model selection, the principle of Occam's Razor is commonly invoked, whereby one requires statistical evidence for the existence of density dependence before adopting the more complex density-dependent model. I submit that, instead of requiring statistical demonstration of density dependence, one should test for deviations from a null model of logistic density dependence.

This is not to say that estimating parameters for a density dependent model is not without its difficulties (98, 141), in particular, lack of independence in a time series of census data (20, 110). One can avoid some of these problems by examining density dependence in survival or fecundity, while controlling for key environmental parameters (83). Elements of a projection matrix can be made functions of density, yielding dynamics qualitatively similar to the logistic (134, 160). Because sufficient data are seldom available to do justice to characterizing a density dependent function, one may need to resort to using a form consistent with that observed for similar taxa (43, 44). Because of the difficulties with parameterization of density dependence, it has been argued that it may be most conservative to use density-independent models because they were thought to bear higher probabilities of extinction (41, 52). But this is not necessarily true; for example, extinction under density

dependence is imminent if all habitat for a species has disappeared. Furthermore, I do not accept this rationale on the grounds that reasonable behavior of the model should be a high priority in model validation (56).

**THRESHOLDS** At low densities, an Allee effect creates a positive relationship between per capita population growth rate and population size. This can be caused by difficulties in finding mates (30), difficulty in fending off predators or competitors (11, 28), social or physiological facilitation (80), or reduced predation efficiency (8). Similarly, low density consequent to habitat fragmentation may result in high juvenile mortality during dispersal (78, 79).

The consequences of Allee effects for PVA are exceedingly important because these mechanisms create threshold or critical population sizes below which extinction is much more probable or inevitable. As an example, Lande (78) presents a model where limitations to juvenile dispersal can create an extinction threshold in territorial species, which has been used in PVAs for the spotted owl (79, 151).

However, the mechanisms creating an Allee effect are not well understood except in a few species (11, 75). As a result we do not know the generality of the phenomenon. It has, however, been postulated to occur in a broad diversity of taxa (30, 78–80). Paucity of empirical evidence is in part due to the difficulty of studying populations at low densities. Experimental work such as that by Crowell (29) should help to identify the characteristics of species most likely to experience Allee effects and afford a more objective basis for incorporating relevant statistical functions into PVAs (cf 30).

Inbreeding depression can be modeled demographically as an Allee effect because its effect becomes more severe as population density becomes less. However, inbreeding is more complex because inbreeding depression is expected to erode with time as deleterious alleles are eliminated by a combination of drift and selection (80, 81). Dennis (30) reviews models that can be used to describe the Allee effect, and their statistical properties.

**SPATIAL STRUCTURE** "Habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis," Wilcox & Murphy observe (164). It would seem, therefore, that spatial structure should be incorporated into most PVAs. Yet, because partitioning a population into spatial subunits can be complex to model and parameterize, it is often ignored.

Spatial heterogeneity and dispersal can stabilize population fluctuations (46, 68) but can also have complex consequences depending on nonlinearities in the system (27). Asynchrony can average out fluctuations caused by demographic or environmental stochasticity, and if spatially removed, asynchrony may ensure species survival in the face of catastrophes (47). Of course,

correlated fluctuations among subpopulations can drastically reduce  $E(T)$  (48).

Incorporation of spatial structure into ecological models has involved a diversity of approaches including reaction-diffusion equations (86), discrete interacting subpopulations envisioned on a grid (157), and Markov transition matrices (1). Diffusion usually has a stabilizing effect on the dynamics of single-species models, tending to average population fluctuations in space. But when spatial structure is combined with ecological interactions, e.g. competition or predation, then instability and spatial patterns can emerge. Spatial models in discrete time also show the potential for very complex dynamics, using integrodifference equations (76), or predator-prey difference equations with dispersal simulated on a grid (61).

Spatial structure adds so much complexity to ecological models that generalities can be difficult to obtain (27, 39). For example, depending upon the species in question, corridors among habitat units may be either beneficial or detrimental. Corridors can reduce consequences of inbreeding or demographic stochasticity by facilitating dispersal among sites; but they can also serve as transmission routes for disease, exotic species, or predators (127, 132a).

Recently, considerable work has focussed on metapopulation models, where the occupancy of discrete habitat patches or islands is a consequence of a balance between dispersal and extinction processes (1, 49, 87). Fahrig & Paloheimo (39) show how inter-patch dynamics is fundamental in determining population size in spatially structured models. As the distance between habitat patches increases, say as a consequence of habitat fragmentation, inter-patch dispersal is expected to decrease. The ability of dispersers to detect new habitat patches can be an exceedingly important factor determining population size, patch occupancy, and probability of extinction (39, 78). This has been the guiding principle behind PVAs for the spotted owl by Lande (79) and Thomas et al (151).

The geometry of habitat can be critical (157) and virtually impossible to model with analytical techniques. In a simulation model for the spotted owl, the landscape of suitable habitat has been mapped on a geographic information system (GIS) and imported into a dispersal simulation model (98a). This technology has great potential for coping with the complex problem of identifying an appropriate spatial structure for population modeling.

**MULTI-SPECIES SYSTEMS** To construct a PVA, it is fundamental to develop an understanding of the mechanisms regulating population size (133). Single species models of populations are probably unrealistic characterizations of most populations, because population regulation actually entails dynamic interactions among species, e.g. plant-herbivore, predator-prey, parasite-host

interactions. Herein lies a serious dilemma for PVA. We do not understand multispecies processes well enough for most species to incorporate such complexity into a PVA.

Modeling ecological processes ideally should include the interface with demography. For example, the dynamics of disease in a population can ultimately be determined by demographic processes. Demographic disequilibria sustained by stochastic perturbations in vital rates can result in sustained epidemiological fluctuations (155). Indeed, such interactions between time delays created by age structure and by ecological interactions may be a key to understanding dynamic behavior in general (62). But, of course, to model such processes requires detailed information on the age specificity of the ecological process.

Ecological processes are inherently nonlinear. This fact, along with the destabilizing effects of environmental seasonality and trophic-level interactions, means that complex dynamics, including chaos, are to be expected in many biological populations. It has been argued that chaos seldom occurs in ecological systems because species would be expected to go extinct when chaotic fluctuations reduce populations to low levels (9, 119). This is not necessarily true because a variety of mechanisms can ensure persistence. In particular, refugia and spatial heterogeneity (2, 71) can buffer local populations against extinction. And even if chaotic fluctuations were to cause local extinction, areas may be repopulated in the sense of a metapopulation (61, 119).

If anything, however, recent advances in nonlinear dynamics have made it clear that even simple ecological systems can possess remarkably complex dynamics. The implication is that such complex dynamics may frustrate our ability to predict long-term trajectories necessary to estimate extinction times. If we are to consider PVAs for chaotically fluctuating populations, the only hope may be to focus attention on the mechanisms that bound a systems dynamics, e.g. refugia, spatial heterogeneity, switching to alternative prey.

These remarks only give a glimpse into the true complexity of ecological systems. In performing PVAs we do not yet know how much complexity is necessary to capture the essence of the system. Deciding how much complexity is necessary should be based on advice from field biologists and managers, who have the best sense, and invariably on the availability of data.

### *Interactions Among Mechanisms*

Because several mechanisms can contribute to extinction, and because each is complex in its own right, the usual approach has been to consider the mechanisms only piecewise, one or two at a time. In this approach, one might learn which mechanism appears to be most sensitive and which requires the largest MVP.



Unfortunately this approach is flawed because the interaction among components may yield critical insight into the probability of extinction. Indeed, if Gilpin & Soule's (50) idea of extinction vortices has any validity, the synergism among processes—such as habitat reduction, inbreeding depression, demographic stochasticity, and loss of genetic variability—is exactly what will be overlooked by viewing only the pieces.

It is feasible and straightforward to build a simulation model containing both demographic and environmental stochasticity, postulated consequences of inbreeding depression, Allee effects, habitat trajectories, and consequent ramifications to carrying capacity, etc, all in the same model. Then one can conduct a sensitivity analysis to learn which parameters have the most significant consequences, and one can simulate management alternatives to view their expected consequences. Furthermore, simulation offers the power to explore propagation of variances and the effects of various types of randomness for complex systems which cannot be understood except in the full-blown model (104, 118). All these things are possible, but in practice our ability to predict the behavior of complex ecological systems has been less than exemplary (34).

#### WHAT MAKES A GOOD PVA AND WHO DECIDES?

PVA may be a more ominous proposition than population biologists are accustomed to, given that PVAs have been challenged in court (5, 151). Some of the lessons learned from previous court challenges of population models may be instructive. For example, the statistical reliability of population projections is likely to be scrutinized, and it is therefore important that parameter estimation, robustness of models, and confidence limits for projections be carefully considered. How defensible is time to extinction, for example, if it carries confidence intervals spanning two orders of magnitude?

Presentation of results can be a delicate matter. Even though the model may be complex, it is essential that explanation be clear and understandable to nonscientists. Substantial testimony in one of the spotted owl hearings was ignored by the judge in her ruling because she did not understand the modeling. Yet, to oversimplify may risk misrepresentation.

There exists a delicate trade-off between building a model that realistically captures the essential ecology of the organisms and keeping the model simple enough that the number of parameters for estimation is reasonable (33). One of the beauties of some of the forecasting methods is that straightforward methods exist for extrapolating the confidence intervals and distributional properties of forecasts (31, 31a, 64). But use of such simple models requires bold assumptions about exponential population growth and perpetuation of population trajectories. For models that are more ecologically realistic,

however, such variance estimators do not exist, requiring use of simulation methods, e.g. bootstrapping and jackknifing (100). There are no rules, but a strategic modeler will use the simplest possible model that still retains the essential features of the system's ecology.

To anticipate extinction probabilities, it is essential to understand the structure of variance, particularly environmental variance (cf 55, 99, 101, 102). Yet, obtaining good estimates of variances for environmental and demographic parameters requires vast amounts of data. Most PVAs conducted thus far have been unable to do justice to variance estimation. Shaffer (126) was unable to distinguish between sampling and environmental variance for demographic parameters of grizzly bears. Lande (79) estimated only the binomial component of sampling variance surrounding demographic parameters for the spotted owl.

For time series of population size, variances often increase as the sample size increases (108). At the very least, it would appear from data presented by Pimm & Redfearn (108) that 8 years of data are needed to stabilize the variance in insect census data, and 30–40 years for birds and mammals (150). To characterize the autocorrelation structure in a time series will require even more data, yet autocorrelation is known to be important in predicting extinction probabilities (101, 102).

A large literature exists on the philosophy and methods for simulation modeling in ecology (56, 58, 104, 118, 139, 147). Likewise, there are several book-length treatises on estimation of population and ecological parameters (77, 115, 117, 124, 138, 163). Some parameters such as survival or coefficients for multispecies interactions can present serious estimation problems. And in many cases there is little hope because data are unavailable or insufficient. In these instances, one may use data from similar species or areas, use a simpler model encumbered by unrealistic assumptions on the structure of the system, or explore the behavior of the system over a range of reasonable parameter values.

Deriving statistically reliable estimates for MVP is clearly a difficult if not impossible task. But it can be an even tougher task to extrapolate from the MVP into estimating the area of habitat necessary to support such a population, which requires a detailed understanding of a species' habitat requirements (13). Patches of habitat must not only be larger than some critical size (80), they must also be in a suitable geometric configuration to ensure dispersal among habitat units. Management for spotted owls (151) provides a complex case study.

Grant (56) suggests four important components for validating any PVA model. First, does the model address the problem? Because the "problem" is usually a management issue, it may be useful to interface the PVA with risk analysis (93). Second, does the model possess reasonable structure and

behavior? The third step is to attempt a quantitative assessment of the accuracy and precision of the model's outputs and behavior. And fourth is to conduct a sensitivity analysis of the model by changing selected parameters in the model by an arbitrary amount and then studying system response and behavior.

Given careful consideration of the audience (i.e. who decides?), these validation approaches offer useful baseline criteria for evaluating a PVA model. But still, finding the appropriate balance between complexity and statistical reliability will be arbitrary and difficult to evaluate. Following these validation criteria, some approaches are fundamentally insufficient as PVAs, for example, simple calculations of  $N_e > 50/500$ , or projections of Leslie matrices until extinction. Examples of PVAs that have been particularly successful at stimulating enlightened management include those for grizzly bears (126,144) and spotted owls (98a, 151).

## GETTING EMPIRICAL

We cannot expect that simulation PVAs will be conducted for most endangered species. Data are often insufficient, time is critical, PVAs can be costly, and there are simply too many species needing attention (136). For these reasons, there continues to be great interest in the formulation of "rules of thumb" for MVP, and the  $N_e > 50/500$  guidelines for short-term versus long-term MVPs are commonly cited (136, 152).

The original formulation of these rules of thumb was genetically based, but not based upon defensible criteria (37, 81). Nevertheless, there is empirical evidence that such rules of thumb may be of appropriate magnitude. Studies of extinction of bighorn sheep (*Ovis canadensis*) (7), and birds on oceanic or habitat islands (70, 109, 137) consistently show that  $N < 50$  is clearly insufficient and the probability of extinction was higher or even certain for such small populations. Populations of  $50 < N < 200$  were marginally secure, and when  $N > 200$ , populations were apparently secure over the limited time frames of these studies (see 150). Clearly applications of such limited observations are restricted to particular taxa, and we would expect much larger population sizes to be necessary for insect populations, for example. And there are obvious advantages to maintaining three or more replicate populations (136).

There is opportunity to expand the empirical basis for PVA and rules of thumb (150). This should include extinction studies based upon empirical observations from islands, and experimental work with replicated small populations (29). We need to understand which factors contribute to extinction probabilities for various taxa. For example, social behavior has been shown to be an important contributor in primates (32). And it is of great interest to know whether herbivores undergo greater population fluctuations

than do predators (6). Will simple single-species models suffice for herbivores whereas models incorporating trophic-level dynamics are essential for predators (94)?

Which demographic components are most critical in determining extinction probabilities? Karr (73) found that forest undergrowth bird species that have gone extinct on Barro Colorado Island (BCI) have, on average, lower survival rates, and that species with lower survival rates disappeared earlier. There was little evidence that  $N$  contributed significantly to these extinctions on BCI. Other life history traits may also be important, e.g. do smaller species undergo more violent population fluctuations, thereby predisposing them to a higher probability of extinction (108, 150)?

If conservation biology is truly going to be a scientific discipline (105), it must become more actively involved in experimental research. Experimental manipulation of habitats to determine the consequences to species richness, extinction, population turnover, and dispersal are on target (e.g. 89, 120). Likewise, much could be gained by performing PVAs for species in no danger of extinction, where populations could be manipulated experimentally to rigorously test the predictions of the model.

#### CONCLUSIONS: VIABILITY OF PVA?

Constructing models to include many of the complexities of the ecology of organisms presents no particular difficulties, but we simply do not have sufficient data to validate such models for most endangered species. It is seldom, if ever, that replications exist (34); thus conclusions cannot be robust (83). A great danger exists that resource managers may lend too much credence to a model, when they may not fully understand its limitations.

Nevertheless, there is too much to be gained by developing a stronger understanding of the system by modeling, to shirk modeling for fear of its being misinterpreted. PVA as a process is an indispensable tool in conservation, and it involves much more than feeble attempts to estimate MVP or probabilities of extinction. PVA entails the process of synthesizing information about a species or population, and developing the best possible model for the species given the information available. When done properly this involves working closely with natural resource managers to develop a long-term iterative process of modeling and research that can reveal a great deal about how best to manage a species. Done properly PVA can be a variation on Holling (67) and Walter's (162) notion of adaptive management, which has proven to be a powerful tool in many areas of resource management.

Adaptive management proposes application of different management tactics in time and space to develop a better understanding of the behavior of the system (162). For application to endangered species problems, when possible,

implementation of various management strategies should be attempted in spatially separated subpopulations. By so doing, one can evaluate the efficacy of various conservation strategies. Active manipulation must be part of such a program, i.e. habitat manipulation, predator or disease control, manipulation of potential competitors, provisioning, transplanting individuals from other subpopulations to sustain genetic variation, supplementation of population with releases of captive stock, etc. Monitoring of the genetic and population consequences of such manipulations then provides data to validate and/or refine the PVA model.

PVA raises a large number of exciting research questions in population ecology and genetics. One promising theoretical area appears to be expanding theory and applications of extinction processes in age-structured populations, e.g. developing applications from the general theory outlined by Aythya & Karlin (4)(cf 83, 101, 102, 154). Existence of true threshold populations, i.e. a definitive MVP, depends upon the existence of a density-dependent mechanism such as the Allee effect or inbreeding depression (111). We have distressingly little empirical data on these processes in natural populations to provide a basis for parameterization of models (30, 78). This must be one of the most urgent research needs for PVA.

Most important, I am confident that PVA will prove to be a valuable tool as we face the extinction crisis (114). Time is not available to perform PVAs for all of the species for which it is warranted (128, 136). Indeed, single-species approaches to conservation are too limited in scope for most applications in tropical conservation (22; contra 21, 132). We must choose species for PVAs wisely, because protecting diverse communities and keystone species may afford disproportionate benefits (137a).

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#### Literature Cited

1. Akcakaya, H. R., Ginzburg, L. R. 1991. Ecological risk analysis for single and multiple populations. In *Species Conservation: A Population-Biological Approach*, ed. A. Seitz, V. Loeschke, pp. 73-87. Basel: Birkhauser Verlag
2. Allen, L. J. S. 1983. Persistence and extinction in Lotka-Volterra reaction-diffusion equations. *Math. Biosci.* 65: 1-12
- 2a. Allendorf, F. W. 1986. Genetic Drift and the loss of alleles versus heterozygosity. *Zoo Biol.* 5:181-90
3. Atchley, W. R., Newman, S. 1989. A

- quantitative genetic perspective on mammalian development. *Am. Nat.* 134:486-512
4. Athreya, K. B., Karlin, S. 1971. On branching processes with random environments. I. Extinction probabilities. *Ann. Math. Statist.* 42:1499-1520
  5. Barthouse, L. W., Boreman, J., Christensen, S. W., Goodyear, C. P., VanWinkle, W., Vaughan, D. S. 1984. Population biology in the courtroom: The Hudson River controversy. *Bio-Science* 34:14-19
  6. Belovsky, G. E. 1987. Extinction models and mammalian persistence. See Ref. 136, pp. 35-57
  7. Berger, J. 1990. Persistence of different-sized populations: An empirical assessment of rapid extinctions in bighorn sheep. *Conserv. Biol.* 4:91-96
  8. Berryman, A. A., Dennis, B., Raffa, K. F., Stenseth, N. C. 1985. Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology* 66:898-903
  9. Berryman, A. A., Millstein, J. A. 1989. Are ecological systems chaotic—and if not, why not? *Trends Ecol. Evol.* 4:26-28
  10. Binkley, C. S., Miller, R. S. 1988. Recovery of the whooping crane *Grus americana*. *Biol. Conserv.* 45:11-20
  11. Birkhead, T. R. 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *J. Anim. Ecol.* 46:751-64
  12. Boecklen, W. J. 1986. Optimal design of nature reserves: Consequences of genetic drift. *Biol. Conserv.* 38:323-28
  13. Boecklen, W. J., Simberloff, D. 1986. Area-based extinction models in conservation. In *Dynamics of Extinction*, ed. D. K. Elliot, pp. 247-76. New York: Wiley. 294 pp.
  14. Boyce, M. S. 1977. Population growth with stochastic fluctuations in the life table. *Theor. Popul. Biol.* 12:366-73
  15. Boyce, M. S. 1987. Time-series analysis and forecasting of the Aransas/Wood Buffalo Whooping Crane population. *Proc. Int. Crane Workshop* 4:1-9
  16. Boyce, M. S. 1988. Evolution of life histories: theory and patterns from mammals. In *Evolution of Life Histories of Mammals*, ed. M. S. Boyce, pp. 3-30. New Haven, Conn: Yale Univ. Press. 373 pp.
  17. Boyce, M. S., Daley, D. J. 1980. Population tracking of fluctuating environments and natural selection for tracking ability. *Am. Nat.* 115:480-91
  18. Boyce, M. S., Irwin, L. L. 1990. Viable populations of Spotted Owls for management of old growth forests in the Pacific Northwest. In *Ecosystem Management: Rare Species and Significant Habitats*, ed. R. S. Mitchell, C. J. Sheviak, D. J. Leopold, 471:133-35. Albany, NY: NY State Mus.
  19. Boyce, M. S., Miller, R. S. 1985. Ten-year periodicity in Whooping Crane census. *Auk* 102:658-60
  20. Bulmer, M. G. 1975. The statistical analysis of density-dependence. *Biometrics* 31:901-11
  21. Burgman, M. A., Akcakaya, H. R., Loew, S. S. 1988. The use of extinction models for species conservation. *Biol. Conserv.* 43:9-25
  22. Burks, K. A., Brown, J. H. 1992. Using montane mammals to model extinctions due to global change. *Conserv. Biol.* (In press)
  23. Casdagli, M. 1989. Nonlinear prediction of chaotic time series. *Physica D* 35:335-66
  24. Caswell, H. 1989. *Matrix Population Models: Construction, Analysis and Interpretation*. Sunderland, Mass: Sinauer
  25. Chesser, R. K. 1991. Influences of gene flow and breeding tactics on gene diversity within populations. *Genetics* 129:573-83
  26. Chesson, P. L. 1978. Predator-prey theory and variability. *Annu. Rev. Ecol. Syst.* 9:323-47
  27. Chesson, P. L. 1981. Models for spatially distributed populations: The effect of within-patch variability. *Theor. Popul. Biol.* 19:288-325
  28. Clark, C. W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. *J. Conserv. Int. Explor. Mer.* 36:7-14
  29. Crowell, K. L. 1973. Experimental zoogeography: Introductions of mice to small islands. *Am. Nat.* 107:535-58
  30. Dennis, B. 1989. Allee effects: Population growth, critical density, and the chance of extinction. *Nat. Res. Model.* 3:481-538
  31. Dennis, B., Munholland, P. L., Scott, J. M. 1991. Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.* 61:115-43
  - 31a. Diggle, P. J. 1990. *Time Series: A Biostatistical Introduction*. Oxford: Clarendon. 257 pp.
  32. Dobson, A. P., Lyles, A. M. 1990. The population dynamics and conservation of primate populations. *Conserv. Biol.* 3:362-80
  33. Eberhardt, L. L. 1987. Population pro-

- jections from simple models. *J. Appl. Ecol.* 24:103-18
34. Eberhardt, L. L., Thomas, J. M. 1991. Designing environmental field studies. *Ecol. Monogr.* 61:53-73
  35. Edwards, M. A., McDonnell, U. 1982. *Animal Disease in Relation to Animal Conservation*. London: Academic. 336 pp.
  36. Deleted in proof
  37. Ewens, W. J. 1990. The minimum viable population size as a genetic and a demographic concept. In *Convergent Issues in Genetics and Demography*, ed. J. Adams, D. A. Lam, A. I. Hermalin, P. E. Smouse, pp. 307-16. Oxford: Oxford Univ. Press
  38. Ewens, W. J., Brockwell, P. J., Gani, J. M., Resnick, S. I. 1987. Minimum viable population size in the presence of catastrophes. See Ref. 136, pp. 59-68
  39. Fahrig, L., Paloheimo, J. 1988. Determinants of local population size in patchy habitats. *Theor. Popul. Biol.* 34:194-213
  40. Falconer, D. S. 1981. *Quantitative Genetics*. London: Longman
  41. Ferson, S., Ginzburg, L., Silvers, A. 1989. Extreme event risk analysis for age-structured populations. *Ecol. Model.* 47:175-87
  42. Foin, T. C., Brechley-Jackson, J. L. 1991. Simulation model evaluation of potential recovery of endangered light-footed clapper rail populations. *Biol. Conserv.* 58:123-48
  43. Fowler, C. W. 1981. Density dependence as related to life history strategy. *Ecology* 62:602-10
  44. Fowler, C. W. 1987. A review of density dependence in populations of large mammals. *Curr. Mammal.* 1:401-41
  45. Futuyma, D. 1983. Interspecific interactions and the maintenance of genetic diversity. In *Genetics and Conservation*, ed. C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, W. L. Thomas, pp. 364-73. Menlo Park, Calif: Benjamin/Cummings. 722 pp.
  46. Gadgil, M. 1971. Dispersal: Population consequences and evolution. *Ecology* 52:253-61
  47. Gilpin, M. E. 1987. Spatial structure and population viability. See Ref. 136, pp. 125-39
  48. Gilpin, M. E. 1990. Extinction of finite metapopulations in correlated environments. In *Living in a Patchy Environment*, ed. B. Shorrocks, I. R. Swingland, pp. 177-86. Oxford: Oxford Univ. Press. 246 pp.
  49. Gilpin, M. E., Hanski, I. 1991. *Metapopulation Dynamics*. London: Academic. 336 pp.
  50. Gilpin, M. E., Soulé, M. E. 1986. Minimum viable populations: Processes of species extinction. See Ref. 135, pp. 19-34
  51. Ginsberg, J. R., Macdonald, D. W. 1990. *Foxes, Wolves, Jackals, and Dogs: An Action Plan for the Conservation of Canids*. Morges, Switzerland: IUCN/SSC Canid Specialist Group
  52. Ginzburg, L. R., Ferson, S., Akçakaya, H. R. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conserv. Biol.* 4:63-70
  53. Goel, N. S., Richter-Dyn, N. 1974. *Stochastic Models in Biology*. New York: Academic. 269 pp.
  54. Goodman, D. 1987. Considerations of stochastic demography in the design and management of biological reserves. *Nat. Res. Model.* 1:205-34
  55. Goodman, D. 1987. The demography of chance extinction. See Ref. 136, pp. 11-34
  56. Grant, W. E. 1986. *Systems Analysis and Simulation in Wildlife and Fisheries Science*. New York: Wiley. 338 pp.
  57. Griffith, B., Scott, J. M., Carpenter, J. W., Reed, C. 1989. Translocation as a species conservation tool: Status and strategy. *Science* 245:477-80
  58. Hall, C. A. S. 1988. What constitutes a good model and by whose criteria. *Ecol. Model.* 43:125-27
  59. Harris, R. B., Allendorf, F. W. 1989. Genetically effective population size of large mammals: An assessment of estimators. *Conserv. Biol.* 3:181-91
  60. Harris, R. B., Maguire, L. A., Shaffer, M. L. 1987. Sample sizes for minimum viable population estimation. *Conserv. Biol.* 1:72-76
  61. Hassell, M., Comins, H. N., May, R. M. 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353:255-58
  62. Hastings, A. 1986. Interacting age structured populations. In *Mathematical Ecology*, ed. T. G. Hallam, S. A. Levin, pp. 287-94. New York: Springer-Verlag. 457 pp.
  63. Hedrick, P. W. 1987. Genetic polymorphism in heterogeneous environments: A decade later. *Annu. Rev. Ecol. Syst.* 17:535-66
  64. Heyde, C. C., Cohen, J. E. 1985. Confidence intervals for demographic projections based on products of random

- matrices. *Theor. Popul. Biol.* 27:120-53
65. Hill, W. G. 1972. Effective size of population with overlapping generations. *Theor. Popul. Biol.* 3:278-89
  66. Hill, W. G. 1979. A note on effective population size with overlapping generations. *Genetics* 92:317-22
  67. Holling, C. S. 1978. *Adaptive Environmental Assessment and Management*. New York: Wiley
  68. Huffaker, C. B. 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations. *Hilgardia* 27:343-83
  69. James, F. C. 1983. Environmental component of morphological differentiation in birds. *Science* 221:184-86
  70. Jones, H. L., Diamond, J. M. 1976. Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78:526-49
  71. Joshi, N. V., Gadgil, M. 1991. On the role of refugia in promoting prudent use of biological resources. *Theor. Popul. Biol.* 40:211-29
  72. Karlin, S., Taylor, H. M. 1975. *A First Course in Stochastic Processes*. New York: Academic
  73. Karr, J. R. 1990. Avian survival rates and the extinction process on Barrow Colorado Island, Panama. *Conserv. Biol.* 4:391-97
  74. Keiding, N. 1975. Extinction and exponential growth in random environments. *Theor. Popul. Biol.* 8:49-63
  75. King, C. E., Dawson, P. S. 1972. Population biology and the Tribolium model. *Evol. Biol.* 5:133-227
  76. Kot, M., Schaffer, W. M. 1986. Discrete-time growth-dispersal models. *Math. Biosci.* 80:109-36
  77. Krebs, C. J. 1989. *Ecological Methodology*. New York: Harper & Row. 654 pp.
  78. Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *Am. Nat.* 130:624-35
  79. Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75:601-7
  80. Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-60
  81. Lande, R., Barrowclough, G. F. 1987. Effective population size, genetic variation, and their use in population management. See Ref. 136, pp. 87-123
  82. Lande, R., Orzack, S. H. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proc. Natl. Acad. Sci. USA* 85:7418-21
  83. Lebreton, J.-D., Clobert, J. 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. In *Bird Population Studies: Relevance to Conservation and Management*, ed. C. M. Perrins, J.-D. Lebreton, G. J. M. Hiron, pp. 105-25. Oxford/New York: Oxford Univ. Press
  84. Lee, R. D. 1974. Forecasting births in post-transition populations. *J. Am. Statist. Assoc.* 69:607-14
  85. Leigh, E. G. Jr. 1981. The average lifetime of a population in a varying environment. *J. Theor. Biol.* 90:213-39
  86. Levin, S. A. 1976. Population dynamic models in heterogeneous environments. *Annu. Rev. Ecol. Syst.* 7:287-310
  87. Levins, R. 1970. Extinction. In *Some Mathematical Questions in Biology*, ed. M. Gerstenhaber, pp. 75-107. Providence, RI: Am. Math. Soc.
  88. Lewontin, R. C., Cohen, D. 1969. On population growth in a randomly varying environment. *Proc. Natl. Acad. Sci. USA* 62:1056-60
  89. Lovejoy, T. E., Bierregaard, R. O. Jr., Rylands, A. B., Malcolm, J. R., Quintela, C. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. See Ref. 135, pp. 287-85
  90. Lynch, M. 1985. Spontaneous mutations for life-history characters in an obligate parthenogen. *Evolution* 39:804-18
  91. MacArthur, R. H., Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton Univ. Press
  92. Mace, G. M., Lande, R. 1991. Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. *Conserv. Biol.* 5:148-57
  93. Maguire, L. A. 1991. Risk analysis for conservation biologists. *Conserv. Biol.* 5:123-25
  94. Mangel, M. 1990. Book review: *Viable Populations for Conservation*. *Nat. Res. Model.* 4:255-71
  95. Marcot, B. G., Holthausen, R. 1987. Analyzing population viability of the spotted owl in the Pacific Northwest. *Trans. N. Am. Wildl. Nat. Res. Conf.* 52:333-47
  96. May, R. M. 1986. The cautionary tale of the black-footed ferret. *Nature* 320:13-14
  97. Maynard Smith, J. 1974. *Models in Ecology*. Cambridge, England: Cambridge Univ. Press
  98. McCullough, D. A. 1990. Detecting



- density dependence: Filtering the baby from the bathwater. *Trans. N. Am. Wildl. Nat. Res. Conf.* 55:534-43
- 98a. McKelvey, K., Noon, B. R., Lamberson, R. 1992. Conservation planning for species occupying fragmented landscapes: The case of the northern spotted owl. In *Biotic Interactions and Global Change*, ed. J. Kingsolver, P. Karicva, R. Huey. Sunderland, Mass: Sinauer
99. Meyer, J. S., Boyce, M. S. 1992. Life historical consequences of pesticides and other insults to vital rates. In *The Population Ecology and Wildlife Toxicology of Agricultural Pesticide Use: A Modeling Initiative for Avian Species*. In press
100. Meyer, J. S., Ingersoll, C. G., McDonald, L. L., Boyce, M. S. 1986. Estimating uncertainty in population growth rates: Jackknife vs. bootstrap techniques. *Ecology* 67:1156-66
101. Mode, C. J., Jacobson, M. E. 1987. A study of the impact of environmental stochasticity on extinction probabilities by Monte Carlo integration. *Math. Biosci.* 83:105-25
102. Mode, C. J., Jacobson, M. E. 1987. On estimating critical population size for an endangered species in the presence of environmental stochasticity. *Math. Biosci.* 85:185-209
103. Mode, C. J., Pickens, G. T. 1985. Demographic stochasticity and uncertainty in population projections—A study by computer simulation. *Math. Biosci.* 79:55-72
104. Morgan, B. J. T. 1984. *Elements of Simulation*. London: Chapman & Hall
105. Murphy, D. E. 1990. Conservation biology and scientific method. *Conserv. Biol.* 4:203-4
106. Murphy, D. E., Freas, K. E., Weiss, S. B. 1990. An "environment-metapopulation" approach to population viability analysis for a threatened invertebrate. *Conserv. Biol.* 4:41-51
107. Pimm, S. L., Gilpin, M. E. 1989. Theoretical issues in conservation biology. In *Perspectives in Ecological Theory*, ed. J. Roughgarden, R. M. May, S. A. Levin, pp. 287-305. Princeton, NJ: Princeton Univ. Press
108. Pimm, S. L., Redfearn, A. 1988. The variability of population densities. *Nature* 334:613-14
109. Pimm, S. L., Jones, H. L., Diamond, J. 1988. On the risk of extinction. *Am. Nat.* 132:757-85
110. Pollard, E., Lakhani, K. H., Rothery, P. 1987. The detection of density-dependence from a series of annual censuses. *Ecology* 68:2046-55
111. Ralls, K., Ballou, J. D., Templeton, A. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conserv. Biol.* 2:185-93
112. Ralls, K., Harvey, P. H., Lyles, A. M. 1986. Inbreeding in natural populations of birds and mammals. See Ref. 135, pp. 35-56
113. Reed, J. M., Doerr, P. D., Walters, J. R. 1988. Minimum viable population size of the red-cockaded woodpecker. *J. Wildl. Manage.* 52:385-91
114. Reid, W. V., Miller, K. R. 1989. *Keeping Options Alive: The Scientific Basis for Conserving Biodiversity*. Washington, DC: World Resour. Inst. 128 pp.
115. Richter, O., Söndgerath, D. 1990. *Parameter Estimation in Ecology: The Link Between Data and Models*. Weinheim, Germany: VCH Verlagsgesellschaft mbH
116. Richter-Dyn, N., Goel, N. S. 1972. On the extinction of a colonizing species. *Theor. Popul. Biol.* 3:406-33
117. Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can. Bull.* 19f.
118. Ripley, B. D. 1987. *Stochastic Simulation*. New York: Wiley
119. Ritchie, M. E. 1992. Chaotic dynamics in food-limited populations: Implications for wildlife management. In *Wildlife 2001*, ed. D. A. McCullough. London: Elsevier. In press
120. Robinson, G. R., Quinn, J. F. 1988. Extinction, turnover and species diversity in an experimentally fragmented California annual grassland. *Oecologia* 76:71-82
121. Samson, F. B., Perez-Trejo, R., Salwasser, H., Ruggiero, L. F., Shaffer, M. L. 1985. On determining and managing minimum population size. *Wildl. Soc. Bull.* 13:425-33
122. Schaffer, W. M. 1988. Perceiving order in the chaos of nature. See Ref. 16, pp. 313-50
123. Schaffer, W. M., Tidd, C. W. 1990. *NLF: Nonlinear Forecasting for Dynamical Systems*. Tucson, Ariz: Dynamical Systems. 154 pp.
124. Seber, G. A. F. 1982. *The Estimation of Animal Abundance*. London: Griffen. 2nd ed.
125. Shaffer, M. L. 1981. Minimum population size for species conservation. *BioScience* 31:131-34
126. Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. *Int. Conf. Bear Res. Manage.* 5:133-39
127. Shaffer, M. L. 1985. The metapopula-

- tion and species conservation: The special case of the Northern Spotted Owl. In *Ecology and Management of the Spotted Owl in the Pacific Northwest*, ed. R. J. Gutierrez, A. B. Carey, pp. 86-99. *US For. Serv. Tech. Rep. PNW-185*
- 128. Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. See Ref. 136, pp. 69-86
- 129. Shaffer, M. L., Samson, F. B. 1985. Population size and extinction: A note on determining critical population size. *Am. Nat.* 125:144-52
130. Shields, W. M. 1982. *Philopatry, Inbreeding, and the Evolution of Sex*. Albany, NY: State Univ. New York Press
131. Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annu. Rev. Ecol. Syst.* 19:473-511
132. Simberloff, D., Abele, L. G. 1982. Refuge design and island biogeographic theory: Effects of fragmentation. *Am. Nat.* 120:41-50
- 132a. Simberloff, D., Cox, J. 1987. Consequences and costs of conservation corridors. *Conserv. Biol.* 1:62-71
- 133. Sinclair, A. R. E. 1989. The regulation of animal populations. In *Ecological Concepts*, ed. J. M. Cherrett, pp. 197-241. Oxford: Blackwell
134. Smouse, P. E., Weiss, K. M. 1975. Discrete demographic models with density-dependent vital rates. *Oecologia* 21:205-18
135. Soulé, M. E. 1986. *Conservation Biology*. Sunderland, Mass: Sinauer
136. Soulé, M. E. 1987. *Viable Populations for Conservation*. Cambridge/New York: Cambridge Univ. Press. 189 pp.
137. Soulé, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M., Hill, S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2:75-92
- 137a. Soulé, M. E., Simberloff, D. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biol. Conserv.* 35:19-40
138. Southwood, T. R. E. 1978. *Ecological Methods*. London: Methuen. 2nd ed.
139. Starfield, A. M., Bleloch, A. L. 1986. *Building Models for Conservation and Wildlife Management*. New York: Macmillan
140. Steele, J. H. 1985. A comparison of terrestrial and marine ecological systems. *Nature* 313:355-58
141. Stiling, P., Throckmorton, A., Silvanima, J., Strong, D. R. 1991. Does spatial scale affect the incidence of density dependence? A field test with insect parasites. *Ecology* 72:2143-54
142. Stromberg, M. R., Boyce, M. S. 1986. Systematics and conservation of the swift fox, *Vulpes velox*, in North America. *Biol. Conserv.* 35:97-110
143. Strong, D. R. 1986. Density-vague population change. *Trends Ecol. Evol.* 2:39-42
144. Suchy, W., McDonald, L. L., Strickland, M. D., Anderson, S. H. 1985. New estimates of minimum viable population size for grizzly bears of the Yellowstone ecosystem. *Wildl. Soc. Bull.* 13:223-28
145. Sugihara, G., May, R. M. 1990. Non-linear forecasting: An operational way to distinguish chaos from measurement error. *Nature* 344:734-41
146. Deleted in proof
147. Swartzman, G. L., Kuluzny, S. T. 1987. *Ecological Simulation Primer*. New York: Macmillan. 370 pp.
148. Temple, S. A. 1986. The problem of avian extinctions. *Curr. Ornithol.* 3: 453-85
149. Templeton, A. R. 1986. Coadaptation and outbreeding depression. See Ref. 135, pp. 105-16
- 150. Thomas, C. D. 1990. What do real population dynamics tell us about minimum viable population sizes? *Conserv. Biol.* 4:324-27
151. Thomas, J. W., Forsman, E. D., Lint, J. B., Meslow, E. C., Noon, B. R., Verner, J. 1990. *Conservation Strategy for the Northern Spotted Owl*. Portland, Ore: US Govt. Print. Off.
- 152. Thompson, G. G. 1991. *Determining Minimum Viable Populations under the Endangered Species Act*. US Dep. Commerce, NOAA Tech. Memo NMFS FINWC-198. 78 pp.
153. Tuljapurkar, S. D. 1989. An uncertain life: Demography in random environments. *Theor. Popul. Biol.* 35:227-94
154. Tuljapurkar, S. D. 1990. Population dynamics in variable environments. *Lecture Notes in Biomathematics No. 85*. New York: Springer-Verlag. 154 pp.
155. Tuljapurkar, S. D., John, A. M. 1991. Disease in changing populations: growth and disequilibrium. *Theor. Popul. Biol.* 40:322-53
156. Tuljapurkar, S. D., Orzack, S. H. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor. Popul. Biol.* 18:314-42
157. Turner, M. G. 1989. Landscape ecology: The effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20:171-77

158. USDA Forest Service. 1986. *Draft Supplement to the Environmental Impact Statement for an Amendment to the Pacific Northwest Regional Guide*, Vols. 1, 2. Portland, Ore: USDA For. Serv.
159. Usher, M. B. 1988. Biological invasions of nature reserves: A search for generalizations. *Biol. Conserv.* 44:119-35
160. Van Winkle, W., DeAngelis, D. L., Blum, S. R. 1978. A density-dependent function for fishing mortality rate and a method for determining elements of a Leslie matrix with density-dependent parameters. *Trans. Am. Fish. Soc.* 107:395-401
161. Wade, M. J. 1991. Genetic variance for rate of population increase in natural populations of flour beetles, *Tribolium* spp. *Evolution* 45:1574-84
162. Walters, C. J. 1986. *Adaptive Management of Renewable Resources*. New York: Macmillan
163. White, G. C., Anderson, D. R., Burnham, K. P., Otis, D. L. 1982. *Capture-Recapture and Removal Methods for Sampling Closed Populations*. Los Alamos, New Mex: Los Alamos Natl. Lab. LA-8787-NERP
164. Wilcox, B. A., Murphy, D. D. 1985. Conservation strategy: The effects of fragmentation on extinction. *Am. Nat.* 125:879-87
165. Zink, R. M. 1991. The geography of mitochondrial DNA variation in two sympatric sparrows. *Evolution* 45:329-39

**GARY WHITE**  
**Population Estimates**  
**Mark-resighting Surveys**



# NOREMARK: Population estimation from mark-resighting surveys

Gary C. White

Estimation of population size of a geographically and demographically closed but free-ranging population is a common problem encountered by wildlife biologists. The earliest approaches to this problem were developed by Petersen in 1896 and later by Lincoln in 1930, where capture-recapture techniques were applied. Extensions to the simple 2 occasion Lincoln-Petersen estimator were developed for multiple occasions (Schnabel 1938, Darroch 1958), for removal experiments (Zippin 1956, 1958), and for heterogeneity of individual animals (Burnham and Overton 1978, 1979, Chao 1988). For the capture-recapture technique, Otis et al. (1978) and White et al. (1982) summarized available methods, and others (White et al. 1978, Rexstad and Burnham 1991) described the program CAPTURE for computing these estimators of population size.

More technologically advanced approaches to abundance estimation have incorporated animals marked with radio transmitters. The initial sample of animals is captured and marked with radios, but recaptures of these animals are obtained by observation, not actually recapturing them. The limitation of this procedure is that unmarked animals are not marked on subsequent occasions. The advantage of this procedure is that resightings are generally much cheaper to acquire than physically capturing and handling the animals. The mark-resight procedure has been tested with known populations of mule deer (*Odocoileus hemionus*; Bartmann et al. 1987) and used with white-tailed deer (*O. virginianus*; Rice and Harder 1977), mountain sheep (*Ovis canadensis*; Furlow et al. 1981, Neal et al. 1993), black bear (*Ursus americanus*) and grizzly bear (*U. arctos*; Miller et al. 1987), and coyote (*Canis latrans*; Hein 1992). Arnason et al. (1991) described a method in which the number of marked animals is not known, whereas

the mark-resight estimators described here assume the number of marked animals is known.

Program NOREMARK computes 4 mark-resight estimators of population abundance, modeling variation of sighting probabilities across time, individual heterogeneity of sighting probabilities, or immigration and emigration from a fixed study area (Eberhardt 1990). For all 4 estimators, the marked animals are assumed to have been drawn randomly from the population (i.e., marked animals are a representative sample from the population).

## Joint hypergeometric maximum likelihood estimator

The first estimator in NOREMARK is the joint hypergeometric maximum likelihood estimator (JHE; Bartmann et al. 1987, White and Garrott 1990, Neal 1990, Neal et al. 1993). This estimator assumes that each animal in the population has the same sighting probability on an occasion as every other animal (no individual heterogeneity), but sighting probabilities can vary across occasions. JHE is the value of  $N$  which maximizes the joint hypergeometric likelihood for  $k$  occasions. The estimate  $\hat{N}$  can be found by iterative numerical methods, and confidence intervals are determined with the profile likelihood method (Hudson 1971, Venzon and Moolgavkar 1988). This estimator assumes that all marked animals are on the area examined during each survey (i.e., that the population is geographically closed). Hence, the number of marked animals ( $M$ ) is constant for each survey, although the sighting probability is not assumed to be constant for each survey. Sighting probability is assumed to be the same for all animals on any particular survey, and animals are as-

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sumed to be sampled without replacement (i.e., each animal is observed  $\leq 1$  time on a survey). An extension in NOREMARK allows additional animals to be marked between sighting occasions.

### Immigration–emigration JHE

The JHE estimator has been extended to accommodate immigration and emigration (Neal et al. 1993) through a binomial process. This modified estimator, IEJHE, does not assume a geographically closed population; rather, it assumes that the total population with any chance of being observed on the study area is  $\bar{N}$  and that at the time of the  $i$ th sighting survey,  $N_i$  animals occur on the study area. I want to estimate the mean number of animals on the study area, and possibly  $N^*$ . At the time of the  $i$ th sighting occasion, a known number of the marked animals ( $M_i$ ) are on the study area of the possible  $T_i$  animals with transmitters. The probability that an individual is on the study area on the  $i$ th occasion can be estimated as  $M_i/T_i$ , or in terms of the parameters of interest as  $N_i/N^*$ . The likelihood function for this model that includes temporary immigration and emigration from the study area is a product of the binomial distribution for the probability that the animal is on the study area times the joint hypergeometric likelihood. The parameters  $N^*$  and  $N_i$  for  $i = 1$  to  $k$  can be estimated by numerical iteration to maximize this likelihood, with the constraints that  $N_i > M_i + u_i$ , where  $u_i$  is the number of unmarked animals observed on occasion  $i$ , and  $N^* > N_i$  for  $i = 1$  to  $k$ . Profile confidence intervals can be obtained for the  $k + 1$  parameters. I was not interested in the  $k$  population estimates for each sighting occasion, but rather wanted the mean of the  $N_i$  estimates. Therefore, I reparameterized the likelihood to estimate the total population and mean population size on the study area directly and their profile likelihood confidence intervals. The assumptions of this estimator are the same as the JHE (i.e., sighting homogeneity and sampling without replacement).

### Minta and Mangel estimator

Minta and Mangel (1989) suggested a bootstrap estimator (MM) of population size based on the sighting frequencies of the marked animals,  $f_i$ . The estimator does not assume that sighting probabilities are the same for each animal on a particular occasion, but does assume a closed population. This model assumes a sample drawn with replacement, so that marked animals might be seen more than once on a survey. For unmarked animals, sighting frequencies

are drawn at random from the observed sighting frequencies of the marked animals until the total number of sightings equals the number of unmarked animal sightings. The number of animals sampled estimates the number of unmarked animals in the population, so  $M$  plus the number sampled estimates  $N$ . Only bootstrap samples where the number of sightings was exactly equal to the number of unmarked animal sightings were used (i.e., cases where cumulative sightings were  $> u$  were excluded). Minta and Mangel (1989) accepted the first value where the cumulative sightings equaled or exceeded the number of unmarked animal sightings. The stopping rule I used results in less bias than the rule used by Minta and Mangel (1989). Minta and Mangel (1989) suggested the mode of the bootstrap replicates as the population estimate. Confidence intervals were computed as probability intervals with the 2.5th and 97.5th percentiles from the bootstrapped sample of estimates. White (1993) demonstrated that the MM estimator is basically unbiased, but that the confidence interval coverage was not the expected 95% for  $\alpha = 0.05$ . A modified procedure was suggested, but coverage still was not satisfactory.

### Bowden's estimator

Bowden (1993) suggested an estimator for the Minta-Mangel model where the confidence intervals on the estimate were computed based on the variance of resighting frequencies of marked animals. He approached the problem from a sampling framework, where each animal in the population has sighting frequency  $f_i$ . Values of  $f_i$  are known for the marked animals, and the sum of the  $f_i$ 's are known for the unmarked animals. Bowden (1993) presented an unbiased estimator and its variance and suggested that confidence intervals should be computed using a log transformation. Animals are not assumed to have the same sighting probability on any particular occasion, and the sample can be drawn with or without replacement.

### Design options

NOREMARK contains a design option to assist the user with determining the number of resighting occasions, proportion of the population to mark, and proportion of the population to resight on each occasion to achieve a specified level of precision. This design routine uses simulated results from the JHE estimator.

The 4 estimators also can be simulated with NOREMARK. Output from the simulations includes expected bias, confidence interval length, and coverage.

Program NOREMARK is written to be used interactively, but with options to store data and to save results to a file or printer. The program provides context-sensitive help at any time and the ability to back up and re-enter or verify previous entries.

### Program availability and system requirements

Copies of the program and related documentation are available on the Bird Monitor Bulletin Board at (301) 498-0402 or via WWW at <http://www.cnr.colostate.edu/~gwhite/software.html>. NOREMARK is written in CA-Clipper (user interface; Computer Associates International, Inc., Ispania, N.Y.) and Microsoft FORTRAN (numerical optimization procedures; Microsoft Corporation, Redmond, Wash.) and runs on the MSDOS operating system for personal computers (PC). The program (executable files and source code) is accompanied by an electronically stored manual and by auxiliary files, including data files containing the mountain sheep observations described by Neal et al. (1993).

The system requirements are minimal: a PC with 640k of base memory and approximately 1M of disk space will suffice. Simulation of estimators can be very time consuming, particularly for the immigration-emigration estimator, so I recommend a math coprocessor on a high-speed 80486 or Pentium machine.

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### Literature cited

- ARNASON, A. N., C. J. SCHWARZ, AND J. M. GERRARD. 1991. Estimating closed population size and number of marked animals from sighting data. *J. Wildl. Manage.* 55:716-730.
- BARTMANN, R. M., G. C. WHITE, L. H. CARPENTER, AND R. A. GARROTT. 1987. Aerial mark-recapture estimates of confined mule deer in pinyon-juniper woodland. *J. Wildl. Manage.* 51:41-46.
- BOWDEN, D. C. 1993. A simple technique for estimating population size. *Dep. of Stat., Colorado State Univ., Fort Collins.* 17pp.
- BURNHAM, K. P., AND W. S. OVERTON. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65:625-633.
- BURNHAM, K. P., AND W. S. OVERTON. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60:927-936.
- CHAO, A. 1988. Estimating animal abundance with capture frequency data. *J. Wildl. Manage.* 52:295-300.
- DARROCH, J. N. 1958. The multiple recapture census: I. Estimation of a closed population. *Biometrika* 45:343-359.
- EBERHARDT, L. L. 1990. Using radio-telemetry for mark-recapture studies with edge effects. *J. Appl. Ecol.* 27:259-271.
- FURLOW, R. C., M. HADERLIE, AND R. VAN DEN BERGE. 1981. Estimating a bighorn sheep population by mark-recapture. *Desert Bighorn Council Trans.* 1981:31-33.
- HEIN, E. W. 1992. Evaluations of coyote attractants and a density estimate on the Rocky Mountain Arsenal. M.S. Thesis, Colorado State Univ., Fort Collins. 58pp.
- HUDSON, D. J. 1971. Interval estimation from the likelihood function. *J. Royal Stat. Soc. Series B* 33:256-262.
- MILLER, S. D., E. F. BECKER, AND W. H. BALLARD. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. *Int. Conf. on Bear Res. and Manage.* 7:23-35.
- MINTA, S., AND M. MANGEL. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. *Ecology* 70:1738-1751.
- NEAL, A. K. 1990. Evaluation of mark-resight population estimates using simulations and field data from mountain sheep. M.S. Thesis, Colorado State Univ., Fort Collins. 198pp.
- NEAL, A. K., G. C. WHITE, R. B. GILL, D. F. REED, AND J. H. OLTERMAN. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. *J. Wildl. Manage.* 57:436-450.
- OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* 62. 135pp.
- SCHNABEL, Z. E. 1938. Estimation of the size of animal populations by marking experiments. *U.S. Fish and Wildl. Serv. Fish. Bull.* 69:191-203.
- REXSTAD, E., AND K. BURNHAM. 1991. Users' guide for interactive program CAPTURE. *Colo. Coop. Fish and Wildl. Res. Unit, Colo. State Univ., Fort Collins.* 29pp.
- RICE, W. R., AND J. D. HARDER. 1977. Application of multiple aerial sampling to a mark-recapture census of white-tailed deer. *J. Wildl. Manage.* 41:197-206.
- VENZON, D. J., AND S. H. MOOLGAVKAR. 1988. A method for computing profile-likelihood based confidence intervals. *Appl. Stat.* 37:87-94.
- WHITE, G. C. 1993. Evaluation of radio tagging marking and sighting estimators of population size using Monte Carlo simulations. Pages 91-103 in J.-D. Lebreton and P. M. North, eds. *Marked individuals in the study of bird population*, Birkhäuser Verlag, Basel, Switzerland.
- WHITE, G. C., K. P. BURNHAM, D. L. OTIS, AND D. R. ANDERSON. 1978. User's manual for program CAPTURE. *Utah State Univ. Press, Logan.* 40pp.
- WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. *Los Alamos National Lab. LA-8787-NERP.* Los Alamos, N.M. 235pp.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, New York, N.Y. 383pp.
- ZIPPIN, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* 12:163-169.
- ZIPPIN, C. 1958. The removal method of population estimation. *J. Wildl. Manage.* 22:82-90.

Software Editor: Rexstad.

