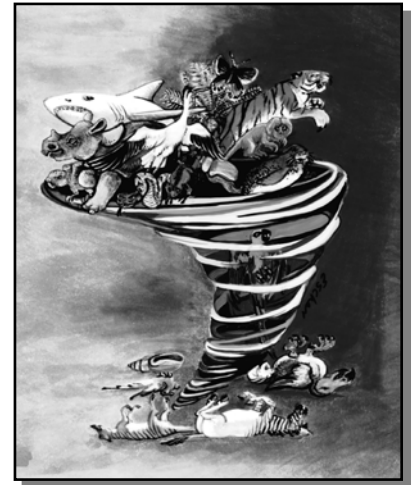


Appendix



An Overview of Population Viability Analysis Using *VORTEX*



Introduction

This Appendix presents an overview of processes threatening the health and persistence of wildlife populations, the methods of population viability analysis, the *VORTEX* simulation program for PVA, and the application of such techniques to wildlife conservation. Much of the following material is adapted from Lacy (1993a) and Lacy (1993/4).

The Dynamics of Small Populations

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat have been reduced to one or more small, isolated populations. The primary causes of the decline of many species are obvious and deterministic: Populations are over-harvested; natural habitat is converted and lost to the species, often involving the replacement of diverse ecological communities with monocultures; environments are polluted, with the dumping of toxins into the air, water, and soil; local and now even global climates are modified by the actions of humans; and numerous exotic competitors, predators, parasites and diseases are introduced into communities that have never evolved defenses to the new invaders. The primary causes of species decline are usually easy to understand, and often easy to study and model, but usually, though not always, difficult to reverse. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990).

Of particular impact on small populations are stochastic, or random or probabilistic, processes. Indeed, the final extinction of most populations often occurs not so much because of a continuation of the pressures that led to the initial decline, but because of bad luck. Chance, or stochastic, processes usually have little impact on long-term population dynamics, as long as the population is abundant and spread over a wide geographic range and a number of habitats. Deterministic processes, such as those listed above, predominate in widespread, still common species, while local chance events impacting subsets of the population will average out across the broader, diverse range. When a population becomes small, isolated, and localized, however, chance events can become important, even dominating the long-term dynamics and fate of a population.

Many stages in the life history of an organism, and the processes that define the history of a biological population, are essentially stochastic sampling phenomena. Births, deaths, dispersal, disease, sex determination, and transmission of genes between generations all are largely probabilistic phenomena. Small samples intrinsically have greater variance around the probabilistic mean or expectation than do large samples, and therefore small populations will experience greater fluctuations in births, deaths, sex ratio, and genetic variation than will larger populations. The fundamental problem facing small populations is that the fluctuations they experience due to the multiple stages of sampling each generation make it increasingly likely that the populations will, unpredictably, decline to zero. Once populations are small, the probability that they will become extinct can become more strongly determined by the amount of fluctuations in population size than in the mean, deterministic population growth rate. Thus, extinction can be viewed as a process in which once common and widespread populations become reduced to small, isolated fragments due to extrinsic factors, the small remnant populations then become subjected to large fluctuations due to intrinsic processes, the local populations occasionally and unpredictably go extinct, and the cumulative result of local extinctions is the eventual extinction of the taxon over much or all of its original range (Gilpin and Soulé 1986; Clark et al. 1990).

The stochastic processes impacting on populations have been usefully categorized into demographic stochasticity, environmental variation, catastrophic events, and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate, and sex ratio of a population even if the probabilities of birth and death remain constant. Assuming that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be most important to population viability perhaps only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means.

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The fluctuations in demographic rates caused by environmental variation is additive to the random fluctuations due to demographic stochasticity. Thus, the difference between the observed variation in a demographic rate over time and the distribution describing demographic variation must be accounted for by environmental variation.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analyzed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease, hurricanes, large-scale fires, and floods are outliers in the distributions of environmental variation. As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993b). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls et al. 1988; Lacy et al. 1992). Even if the immediate loss of fitness of inbred individuals is not large, the loss of

genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations negatively impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerates genetic drift (Crow and Kimura 1970). These synergistic destabilizing effects of stochastic process on small populations of wildlife have been described as “extinction vortices” (Gilpin and Soulé 1986).

What is Population (and Habitat) Viability Analysis?

Analyses which have used the *VORTEX* simulation for guiding conservation decisions refer variously to “Population Viability Analysis (PVA)”, “Population and Habitat Viability Analysis (PHVA),” “Population Vulnerability Analysis”, “Population Viability (or Vulnerability) Assessment”, and other variants on the name. This diversity of terminology has caused some confusion among practitioners of the PVA (or PHVA) approach, and probably even more confusion among wildlife managers who have tried to understand what analysis was being described, and whether it could be a useful tool in their efforts to conserve biodiversity. The diversity of perceptions about the PVA approach is not limited to its name. Different people mean different things by PVA, and the definitions and practice of PVA are constantly evolving. We don’t think it is not the case, as has sometimes been suggested, that some people are doing PVA correctly, and others incorrectly, but rather that people are using different (if related) kinds of analyses and labeling them with the same (or similar) terms. What analysis is correct depends on the need and the application. Below, we attempt to clarify what PVA is, by suggesting a more consistent terminology and by describing the features that characterize the application of the PVA approach to conservation. The perspective offered here is necessarily biased by personal experiences in conservation; we will not attempt an exhaustive historical account of this field.

Population viability analysis originally described methods of quantitative analysis to determine the probability of extinction of a population. Shaffer (1981) first defined a minimum viable population (MVP) as the size at which a population has a 99% probability of persistence for 1000 years, but it might be more meaningful biologically to consider it to be the size below which a population's fate becomes determined largely by the stochastic factors that characterize extinction vortices. One concept of population viability analysis is any methodology used to determine an MVP (Shaffer 1990). More broadly, PVA is the estimation of extinction probabilities and other measures of population performance by analyses that incorporate identifiable threats to population survival into models of the extinction process (Brussard 1985; Gilpin and Soulé 1986; Burgman et al. 1993; Lacy 1993/1994).

Shaffer's (1981) original term “minimum viable population” (MVP) has fallen into disfavor (Soulé 1987), even as the PVA approach has risen in popularity. Shaffer stressed that an MVP was an estimate of the population size below which the *probability* of extinction was unacceptably high, that different populations would have different MVPs, and that the MVP determined for a population would depend on the threatening factors that were considered. However, the term implied to some people that there was a well-defined number below which extinction was certain and above which persistence was assured. Re-emphasizing the probabilistic nature of the extinction process, a number of conservation biologists have focused on methods for estimating the probability of extinction over defined time periods for a designated population exposed to a specific scenario of environmental conditions, threats to persistence, and future management actions and other foreseeable events (Brussard 1985; Starfield and Bleloch 1986; Soulé 1987; Simberloff 1988; Gilpin 1989; Shaffer 1990; Boyce 1992; Burgman et al. 1993). Thus, “Population Viability Analysis” (or the synonymous “Population Viability Assessment” and “Population Vulnerability Analysis”) came to describe any of the array of methods for quantifying the probability of extinction of a

population. Although PVA has been extended by some to encompass a broader approach to conservation (see below), the term “Population Viability Analysis”, or PVA, should perhaps be reserved for its original, yet still rather broad, meaning.

Beginning in about 1989 (Lacy et al. 1989; Seal and Lacy 1989; Seal et al. 1990), it became increasingly recognized that PVA can often be most usefully incorporated into a strategy for the conservation of a taxon if it is part of, and often central to, a conservation workshop that mobilizes collaboration among the array of people with strong interest in or responsibility for a conservation effort (e.g., governmental wildlife agencies, conservation NGOs, and the local people who interact with the species or its habitat) or with particular expert knowledge about the species, its habitats, or the threats it faces (e.g., academic biologists, conservation professionals, other wildlife biologists, experts on human demographics and resource use). Conservation problems are almost always multi-faceted, involving not only complex dynamics of biological populations, but also interactions with human populations, the past, present, and future impacts of humans on habitats, and human political, social, and economic systems (Alvarez 1993; Bormann and Kellert 1991; Clark 1989, 1993). Many people need to contribute knowledge, expertise, and ideas in order to achieve the recovery of threatened species. Population viability analyses can provide a framework for incorporating the many needed kinds of knowledge into species conservation efforts, because PVAs do allow the assessment of many kinds of factors that threaten the persistence of populations (Lacy 1993a; Lindenmayer et al. 1993a).

The Conservation Breeding Specialist Group (CBSG) of the IUCN’s Species Survival Commission especially has advocated and used workshops centered on PVAs to provide guidance to conservation assessment and planning (see references to CBSG workshops in Appendix III). Over the past few years, the PVA workshop as an approach to species conservation has expanded considerably beyond the quantitative analysis of extinction probabilities as advanced by Shaffer (1981, 1990), Soulé (1987), Gilpin (1989), Clark et al. (1991), Boyce (1992), and others. PVA workshops have incorporated consideration of resource use and needs by local human populations (Seal et al. 1991; Bonaccorso et al. 1999), education programs for the local human populations (Odum et al. 1993), trade issues (Foose et al. 1993), and trends in human demographics and land use patterns (Walker and Molur 1994; Herrero and Seal 1999). Recognizing that the conservation assessment workshops increasingly incorporated more than just the population biology modeling (which still formed a core organizing and analysis framework for the workshop), the CBSG has termed their workshops *Population and Habitat Viability Analyses* (PHVA). We would recommend that the term *Population and Habitat Viability Analysis* (PHVA) be used to describe the collaborative workshop approach to species conservation that centers on, but encompasses more than, a Population Viability Analysis (in the narrow sense). The concept of a PHVA continues to expand and evolve, as it should considering the need for more holistic and flexible approaches to conservation (e.g., Ruggiero et al. 1994). Thus, in the usage I recommend, PVA is a quantitative analysis of the probability of population persistence under defined sets of assumptions and circumstances. PHVA is a workshop process that brings to bear the knowledge of many people on species conservation, eliciting and assessing multiple options for conservation action, principally by using the tool of PVA as a way evaluate present threats to population persistence and likely fates under various possible scenarios.

Population Viability Analysis (PVA)

Two defining characteristics of a PVA are an explicit model of the extinction process and the quantification of threats to extinction. These features set PVA apart from many other analyses of the threats facing species, including, for example, the IUCN Red Books of Threatened Species. As a methodology to estimate the probability of extinction of a taxon, PVA necessarily must start with an understanding, or model, of the extinction process (Clark et al. 1990).

Generally, the model of extinction underlying a PVA considers two categories of factors: deterministic and stochastic. Deterministic factors, those that can shift species from long-term average population growth to population decline include the well-known threats of over-harvest, habitat destruction, pollution or other degradation of environmental quality, and the introduction of exotic predators, competitors, and diseases. Singly or combined, these forces have driven many wildlife populations to low numbers and, for some, to extinction. Once a population becomes small, and isolated from conspecific populations that might serve as sources for immigrants that could stabilize demographics and genetics, its dynamics and fate can become dominated by a number of random or stochastic processes (as outlined above and by Shaffer 1981). Thus, even if the original deterministic causes of decline are stopped or reversed, the instability caused by the action of stochastic processes acting on small populations can cause the extinction of a population.

In nature, most threatening processes have both deterministic and stochastic features. For example, a high level of poaching might be seen as a deterministic factor driving a wildlife population toward extinction, but whether an individual animal is killed might be largely a matter of chance. In a PVA, poaching might be modeled as a deterministic process by killing a determined proportion of the animals, or it might be modeled as a stochastic process by giving each animal that probability of being killed but allowing the exact numbers killed to vary over time. If the population is large and the percent of animals killed is high, then these two ways of modelling the effects of poaching will yield the same results: the deterministic component of poaching dominates the population dynamics. If the population is small or the percent of animals killed is very low, then the numbers killed in a stochastic model (and in nature) might vary substantially from year to year: the stochastic nature of poaching further destabilizes the population.

Which of the various deterministic and stochastic factors are important to consider in a PVA will depend on the species biology, the present population size and distribution, and the threats it faces. For example, orang utans may be threatened by forest destruction and other largely deterministic processes, but inbreeding and randomly skewed sex ratios resulting from highly stochastic processes are unlikely to be problems, at least not on a species-wide basis. On the other hand, even if the remnant Atlantic coastal rainforest of Brazil is secured for the future, the populations of golden lion tamarins (*Leontopithecus rosalia*) which can persist in that remnant forest are not sufficiently large to be stable in the face of stochastic threats (Seal et al. 1990; Rylands 1993/4; Ballou et al. 1997). The identification of the primary threats facing a taxon via a comprehensive PVA is important for conservation planning. For example, tamarin populations might be stabilized by the translocations and reintroductions that are underway and planned, but an orang utan PHVA recognized that releases of confiscated “pet” orang utans are unlikely to have a conservation benefit for those populations which are facing habitat destruction, not stochastic fluctuations and inbreeding. For many species, such as the whooping crane (*Grus americana*), the temporarily extinct-in-the-wild black-footed ferret (*Mustela nigripes*), and the Puerto Rican parrot (*Amazona vitatta*), only a single population persisted in the wild. Although those populations may have been maintained or even increased for a number of years, the principal threat was that a local catastrophe (e.g., disease epidemic, severe storm) could decimate the population (Clark 1989; Lacy et al. 1989; Mirande et al. 1991). The primary recovery actions therefore needed to include the establishment of additional populations. Tragically, some taxa, such the eastern barred bandicoot (*Perameles gunnii*) in Australia, may be critically threatened simultaneously by deterministic factors and stochastic processes (Lacy and Clark 1990).

PVA is formally an assessment of the probability of extinction, but PVA methods often focus on other indicators of population health. Mean and variance in population growth (Lindenmayer and Lacy 1995a, 1995b, 1995c), changes in range, distribution, and habitat occupancy (Hanski and Gilpin 1991), and losses of genetic variability (Soulé et al. 1986; Lande and Barrowclough 1987; Seal 1992; Lacy and Lindenmayer 1995) can be analyzed and monitored. Although not yet common, monitoring of population health could also utilize measures of developmental stability (Clarke 1995), physiological parameters

such as body condition (Altmann et al. 1993) or levels of the hormones related to stress and reproduction (Sapolsky 1982, 1986), or the stability of behavior and the social structure of the population (Samuels and Altmann 1991).

The interactions and synergism among threatening processes will often cause numerical, distributional, physiologic, behavioral, and genetic responses to concordantly reflect species decline and vulnerability. It remains important, however, to understand and target the primary causal factors in species vulnerability. The recent proposal to base IUCN categories of threat on quantified criteria of probability of extinction, or changes in such indicators as species range, numbers, and trends (Mace and Lande 1991; Mace et al. 1992; Mace and Stuart 1994; IUCN Species Survival Commission 1994) reflects the increased understanding of the extinction process that has accompanied the development of PVA, and simultaneously demands that much more progress be made in developing predictive models, gathering relevant data on status and threats, and applying the PVA techniques.

Population and Habitat Viability Analysis (PHVA)

Population and Habitat Viability Analysis is a multi-faceted process or framework for assisting conservation planning, rather than a singular technique or tool. It is often interwoven with other techniques for managing complex systems, such as decision analysis (Maguire 1986; Maguire et al. 1990). Even when viewed as *the* PHVA workshop, all such conservation workshops involved and required substantial pre-workshop and post-workshop activities. Some PHVA workshops have been extended into multiple workshops and less formal, smaller collaborative meetings, often focused on subsets of the larger problems of species conservation.

Although PHVAs are diverse and not well defined, the PHVA process contains a number of critical components. First, it is essential to gather an array of experts who have knowledge of the species or problem. A PHVA is not required to bring together experts, but it often facilitates such sharing of expertise because the collective knowledge of many is essential for a useful PVA (in the narrow sense) to be completed. In addition to a diversity of people, a PHVA workshop also requires and therefore facilitates the involvement of a number of agencies and other concerned organizations. For example, the PVA on the two endemic primates of the Tana River Primate Reserve in Kenya (Seal et al. 1991) was convened by the Kenya Wildlife Service, facilitated by the IUCN SSC Captive Breeding Specialist Group, benefited from the expertise contributed by members of the IUCN SSC Primate Specialist Group, and was sponsored by the World Bank. The involvement of many agencies and interested parties is critical to endangered species recovery.

An early requirement, or prerequisite, of a PHVA workshop is to determine the conservation problem to be addressed, and to state the goals of the management plan. Many endangered species programs have not clearly identified their goals. For example, at a PHVA and Conservation Assessment and Management Plan workshop on the forest birds of the Hawaiian islands (Ellis et al. 1992a, 1992b), it became apparent that the agencies responsible for the conservation of Hawaii's bird fauna had not determined whether their goal was to prevent species extinctions, prevent taxa (species or subspecies) from becoming extirpated on any of the islands they presently inhabit, preserve species in sufficient numbers and distribution to allow them to continue to fill ecological roles in the biological communities, or the restoration of taxa to most or all parts of the original ranges. The management actions required to achieve these various levels of conservation are quite different. In contrast, a PHVA on the Grizzly Bear in the Central Rockies of Canada (Herrero and Seal 1999) clearly identified that provincial policy called for maintenance of stable or growing populations of the species. Thus, the criterion against which alternative management scenarios were judged was whether the PVA projections indicated that the populations would not decline.

PHVA workshops facilitate the assembly of all available data. Often, important information is found in the field notes of researchers or managers, in the heads of those who have worked with and thought about the problems of the species, and in unpublished agency reports, as well as in the published scientific literature. A pending PHVA can be the impetus that encourages the collection of data in anticipation of presentation, review, and analysis at the workshop. For example, a Sumatran Tiger PHVA helped stimulate the systematic collection of data on sightings and signs of tigers in protected areas throughout the island of Sumatra, and collation and integration with a Geographic Information System (GIS) map of habitats and human pressures on those habitats. The PHVA on the Grizzly Bear in the Central Canadian Rockies Ecosystem provided the opportunity for detailed habitat mapping data to be integrated with population biology data on the bears, resulting in the development of models which would allow projection of the impacts of habitat changes on the bear populations.

It is important to specify the assumptions that underlay a PHVA, and any consequent management recommendation. For example, the Hawaiian bird conservation efforts are constrained by a belief that no birds bred outside of the islands should ever be brought back to the islands for release. While this position derives from a reasonable concern for disease transmission (much of the decline of Hawaii's native birds is thought to be due to introduced avian diseases) as much as from any political or philosophical stand, any justification for the restriction must be questioned in light of the fact that wildlife agencies import and release, without quarantine, 1000s of exotic gamebirds onto the islands annually.

Once experts are assembled, problems stated and goals set, data gathered, and assumptions specified, then the PHVA process can proceed with what I describe as PVA in the narrow sense: estimation of the probability of population persistence. The available data are used to estimate the parameters that are needed for the model of population dynamics to be applied. Often, data are not available from which to estimate certain key parameters. In those cases, subjective and objective, but non-quantified, information might be solicited from the assembled experts, values might be obtained from data on related species, or a factor might simply be omitted from the model. While such a non-precise process might consist simply of intuitive judgements made by experts, it is important to specify how values for the parameters in the model were obtained. The resulting limitations of the analyses should be acknowledged, and a decision made if, how, by whom, and when the missing data would be collected so that more refined analyses could be conducted. With the PVA model, projections of the most likely fate, and distribution of possible fates, of the population under the specified assumptions are made.

Because so much of a PVA – the data, the model, and even the interpretation of output – is uncertain, a PVA that provides an estimate of the probability of extinction under a single scenario is of very limited usefulness. An essential component of the PHVA process, therefore, is sensitivity testing. Ranges of plausible values for uncertain parameters should be tested, to determine what effects those uncertainties might have on the results. In addition, several different PVA models might be examined at a PHVA workshop, or the same general model tested under different structural assumptions. Different participants in the process should assess and interpret the results. Such sensitivity testing reveals which components of the data, model, and interpretation have the largest impact on the population projections. This will indicate which aspects of the biology of the population and its situation contribute most to its vulnerability and, therefore, which aspects might be most effectively targeted for management. In addition, uncertain parameters that have a strong impact on results are those which might be the focus of future research efforts, to better specify the dynamics of the population. Close monitoring of such parameters might also be important for testing the assumptions behind the selected management options and for assessing the success of conservation efforts.

Closely parallel to the testing of uncertainties in the present situation is the testing of options for management. PVA modeling allows one to test the expected results of any given management action, under the assumptions of the model and within the limitations of present knowledge, on the computer

before implementation in the field. This process can guide selection of the management options most likely, given current knowledge, to be effective, and will define target recovery goals that should be obtained if our knowledge is adequate and the recommended actions are followed. A PHVA workshop on the Black Rhinoceros in Kenya's 11 rhino sanctuaries (Foose et al. 1993) suggested that periodic movement of rhinos between fenced sanctuaries to reduce inbreeding and demographic fluctuations would be necessary to stabilize the populations in the smaller parks. Moreover, the modeling provided estimates of the rate at which the larger populations would be able to provide surplus animals for translocation.

It would be an error to assume that any PVA model incorporates everything of interest. A PVA simulation program can only include those processes that are known to the programmer. This will likely be a subset of what might be known to the field biologists, which in turn will definitely be a subset of those processes that impact natural populations. A number of variables affecting population dynamics and viability are not yet commonly examined in PVA models. These include: social and ecological determinants of dispersal; complex social processes, such as the role of non-breeders in group stability and the impacts of other aspects of the social environment on reproductive success and survival; competitive, exploitative, or mutualistic interactions with other species experiencing their own population dynamics; and the effects of changes in the global environment. To date, most PVA models treat organisms as independent actors in spatially homogeneous physical, biotic, and social environments. There is tremendous opportunity and need for elaboration of PVA models, and it is likely that increasingly sophisticated models will also become more specific to the individual taxa and environments under study.

PHVA workshops must incorporate consideration of the assumptions of the PVA model used and the biases or limitations in interpretation that could result. PHVAs consider only those threatening processes of which we have knowledge, for which we can develop algorithms for modeling or other methods for analysis, and for which we have some data. As a result, it is likely that PVAs will underestimate the vulnerability of most populations to extinction, and that PHVA workshops will be less comprehensive than is desirable. We need always to be cognizant of the limits of our understanding of wildlife populations, and to include appropriate margins for error in our conservation strategies.

PVA is, by definition, an assessment of the probability of persistence of a population over a defined time frame. Yet, persistence of a population, while a necessary condition for effective conservation of natural systems, is often not sufficient. Prevention of extinction is the last stand of conservationists, but the goals should be higher: conservation of functional biological communities and ecosystems. PVA usually ignores the functional role of a species in a community, but a PHVA workshop should consider much more than the prevention of the final biological extinction of the taxon. A species, such as the American Bison (*Bison bison*), can be functionally extinct in terms of no longer filling its original role in nature, even as it is praised as a conservation success story and would be considered safe from extinction and viable.

The use of the PHVA process to help guide conservation decisions is not a singular event, in which an analysis can be completed, management actions recommended and implemented, and conservation thereby assured. The many uncertainties in the process mandate that PVA be used as a tool in an adaptive management framework, and a PHVA workshop is just one stage of an effective conservation strategy. In adaptive management, the lack of knowledge adequate to predict with certainty the best course of action is recognized, management actions are designed in such a way that monitoring will allow testing of the adequacy of our model and understanding, and corrective adjustments to management plans are made whenever the accumulating data suggest that the present course is inadequate to achieve the goals and that a better strategy exists (Holling 1978). The urgency of the biodiversity crisis will not permit us ethically to refrain from aggressive conservation action until we have scientifically sound understanding of all the

factors that drive population, community, and ecosystem dynamics. PHVA provides a forum for making use of the information we do have, in a well-documented process that is open to challenge and improvement. PHVA workshops can, therefore, assist wildlife managers in the very difficult and important job of using science to safeguard the future of wildlife populations.

In summary, Population Viability Analysis (PVA) and Population and Habitat Viability Analysis (PHVA) refer to an array of interrelated and evolving techniques for assessing the survival probability of a population and possible conservation actions. It might be useful to restrict the term PVA to its original meaning -- the use of quantitative techniques to estimate the probability of population persistence under a chosen model of population dynamics, a specified set of biological and environmental parameters, and enumerated assumptions about human activities and impacts on the system. PHVA refers to a workshop approach to conservation planning, which elicits and encourages contributions from an array of experts and stakeholders, uses PVA and other quantitative and non-quantitative techniques to assess possible conservation actions, and strives to achieve consensus on the best course of action from competing interests and perspectives, incomplete knowledge, and an uncertain future.

Many of the components of PVAs and PHVAs, even when used in isolation, can be effective educational and research tools. To be a useful framework for advancing the conservation of biodiversity, however, PHVA must incorporate all of: (1) collection of data on the biology of the taxon, status of its habitat, and threats to its persistence, (2) quantitative analysis of available data, (3) input of population status and identifiable threats to persistence into analytical or simulation models of the extinction process, (4) assessment of the probability of survival over specified periods of time, given the assumptions and limitations of the data and model used, (5) sensitivity testing of estimates of extinction probability across the range of plausible values of uncertain parameters, (6) specification of conservation goals for the population, (7) identification of options for management, (8) projection of the probability of population survival under alternative scenarios for future conservation action, (9) implementation of optimal actions for assuring accomplishment of conservation goals, (10) continued monitoring of the population, (11) reassessment of assumptions, data, models, and options, and (12) adjustment of conservation strategies to respond to the best information available at all times. There are many uncertain aspects of population dynamics, especially of endangered taxa, including few data on species biology and habitats, uncertain political and social climate for implementing conservation actions, and the unpredictability inherent in small populations due to the many stochastic forces that drive population dynamics.

The rapid development of PVA as a research and management tool, and the concurrent but not always parallel expansion of the scope of what conservation threats, options, and actions are considered in PHVA workshops, has led to confusion. Different people can describe rather distinct kinds of analyses with the same terminology, while others use different terms to describe nearly identical approaches. The ever-changing concepts of PVA and PHVA are confusing, but the flexibility of the processes is also their strength. Current tools are inadequate to address fully the challenges of stemming the losses of biodiversity. The PVA/PHVA framework allows and encourages rapid application of new tools, data, and interpretations into increasingly effective conservation programs.

Methods for Analyzing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction-recolonization dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991).

Shaffer (1981) suggested several ways to conduct PVAs. Perhaps the most rigorous method, and the one that would produce the most defensible estimates, would be an empirical observation of the stability and long term fates of a number of populations of various sizes. Berger (1990) presented a good example of this approach, in which he observed that populations of bighorn sheep in the mountains of the western USA persisted only when the populations consisted of more than 100 animals. A few other studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g., Belovsky 1987; Thomas 1990), but presently only order of magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). More empirical studies are needed, but the time and numbers of populations required for such studies are precluded in the cases of most species threatened with extinction -- exactly those for which estimates of population vulnerability are most urgently needed.

A more elegant and general approach to PVA is to develop analytical models of the extinction process that will allow calculation of the probability of extinction from a small number of measurable parameters. Goodman's (1987) model of demographic fluctuations, and applications to conservation of the classic population genetic models of loss of genetic diversity by genetic drift (Franklin 1980; Soulé et al. 1986; Lande and Barrowclough 1987) are valuable efforts in this direction. Unfortunately, our understanding of population biology is not yet sufficient to provide fully adequate analytical models of the extinction process. For example, none of the existing analytical models incorporate all three of demographic, environmental, and genetic fluctuations, and thus they do not begin to model the array of extinction vortices described by Gilpin and Soulé (1986). Moreover, the analytical models make extremely simplifying assumptions about a number of the intricacies of population structure. For example, social groupings or preferences are often assumed to be invariant or lacking, resulting in random mating; and dispersal is usually assumed to be random between all sites (the "island model") or only to occur between adjacent sites (the "stepping stone model"). Much more work is needed either to develop more complex and flexible models or to demonstrate that the simple models are sufficient to provide guidance for conservation.

A third method of conducting a PVA is the use of computer simulation modeling to project the probability distribution of possible fates of a population. Simulation models can incorporate a very large number of threatening processes and their interactions, if the processes can be described in terms of quantitative algorithms and parameterized. Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The focus is on detailed and explicit modeling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations.

Modeling and Population Viability Analysis

A model is any simplified representation of a real system. We use models in all aspects of our lives, in order to: (1) extract the important trends from complex processes, (2) permit comparison among systems, (3) facilitate analysis of causes of processes acting on the system, and (4) make predictions about the future. A complete description of a natural system, if it were possible, would often decrease our understanding relative to that provided by a good model, because there is "noise" in the system that is extraneous to the processes we wish to understand. For example, the typical representation of the growth of a wildlife population by an annual percent growth rate is a simplified mathematical model of the much more complex changes in population size. Representing population growth as an annual percent change assumes constant exponential growth, ignoring the irregular fluctuations as individuals are born or immigrate, and die or emigrate. For many purposes, such a simplified model of population growth is very useful, because it captures the essential information we might need regarding the average change in

population size, and it allows us to make predictions about the future size of the population. A detailed description of the exact changes in numbers of individuals, while a true description of the population, would often be of much less value because the essential pattern would be obscured, and it would be difficult or impossible to make predictions about the future population size.

In considerations of the vulnerability of a population to extinction, as is so often required for conservation planning and management, the simple model of population growth as a constant annual rate of change is inadequate for our needs. The fluctuations in population size that are omitted from the standard ecological models of population change can cause population extinction, and therefore are often the primary focus of concern. In order to understand and predict the vulnerability of a wildlife population to extinction, we need to use a model which incorporates the processes which cause fluctuations in the population, as well as those which control the long-term trends in population size. Many processes can cause fluctuations in population size: variation in the environment (such as weather, food supplies, and predation), genetic changes in the population (such as genetic drift, inbreeding, and response to natural selection), catastrophic effects (such as disease epidemics, floods, and droughts), decimation of the population or its habitats by humans, the chance results of the probabilistic events in the lives of individuals (sex determination, location of mates, breeding success, survival), and interactions among these factors (Gilpin and Soulé 1986).

Models of population dynamics which incorporate causes of fluctuations in population size in order to predict probabilities of extinction, and to help identify the processes which contribute to a population's vulnerability, are used in Population Viability Analysis (PVA). For the purpose of predicting vulnerability to extinction, any and all population processes that impact population dynamics can be important. Much analysis of conservation issues is conducted by largely intuitive assessments by biologists with experience with the system. Assessments by experts can be quite valuable, and are often contrasted with "models" used to evaluate population vulnerability to extinction. Such a contrast is not valid, however, as *any* synthesis of facts and understanding of processes constitutes a model, even if it is a mental model within the mind of the expert and perhaps only vaguely specified to others (or even to the expert himself or herself).

A number of properties of the problem of assessing vulnerability of a population to extinction make it difficult to rely on mental or intuitive models. Numerous processes impact population dynamics, and many of the factors interact in complex ways. For example, increased fragmentation of habitat can make it more difficult to locate mates, can lead to greater mortality as individuals disperse greater distances across unsuitable habitat, and can lead to increased inbreeding which in turn can further reduce ability to attract mates and to survive. In addition, many of the processes impacting population dynamics are intrinsically probabilistic, with a random component. Sex determination, disease, predation, mate acquisition -- indeed, almost all events in the life of an individual -- are stochastic events, occurring with certain probabilities rather than with absolute certainty at any given time. The consequences of factors influencing population dynamics are often delayed for years or even generations. With a long-lived species, a population might persist for 20 to 40 years beyond the emergence of factors that ultimately cause extinction. Humans can synthesize mentally only a few factors at a time, most people have difficulty assessing probabilities intuitively, and it is difficult to consider delayed effects. Moreover, the data needed for models of population dynamics are often very uncertain. Optimal decision-making when data are uncertain is difficult, as it involves correct assessment of probabilities that the true values fall within certain ranges, adding yet another probabilistic or chance component to the evaluation of the situation.

The difficulty of incorporating multiple, interacting, probabilistic processes into a model that can utilize uncertain data has prevented (to date) development of analytical models (mathematical equations developed from theory) which encompass more than a small subset of the processes known to affect

wildlife population dynamics. It is possible that the mental models of some biologists are sufficiently complex to predict accurately population vulnerabilities to extinction under a range of conditions, but it is not possible to assess objectively the precision of such intuitive assessments, and it is difficult to transfer that knowledge to others who need also to evaluate the situation. Computer simulation models have increasingly been used to assist in PVA. Although rarely as elegant as models framed in analytical equations, computer simulation models can be well suited for the complex task of evaluating risks of extinction. Simulation models can include as many factors that influence population dynamics as the modeler and the user of the model want to assess. Interactions between processes can be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes. In theory, simulation programs can be used to build models of population dynamics that include all the knowledge of the system which is available to experts. In practice, the models will be simpler, because some factors are judged unlikely to be important, and because the persons who developed the model did not have access to the full array of expert knowledge.

Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon, facilitate testing of the effects of unknown or uncertain data, and expedite the comparison of the likely results of various possible management options.

PVA models also have weaknesses and limitations. A model of the population dynamics does not define the goals for conservation planning. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used. Because the models incorporate many factors, the number of possibilities to test can seem endless, and it can be difficult to determine which of the factors that were analyzed are most important to the population dynamics. PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models probably underestimate the threats facing the population. Finally, the models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed.

Dealing with uncertainty

It is important to recognize that uncertainty regarding the biological parameters of a population and its consequent fate occurs at several levels and for independent reasons. Uncertainty can occur because the parameters have never been measured on the population. Uncertainty can occur because limited field data have yielded estimates with potentially large sampling error. Uncertainty can occur because independent studies have generated discordant estimates. Uncertainty can occur because environmental conditions or population status have been changing over time, and field surveys were conducted during periods which may not be representative of long-term averages. Uncertainty can occur because the environment will change in the future, so that measurements made in the past may not accurately predict future conditions.

Sensitivity testing is necessary to determine the extent to which uncertainty in input parameters results in uncertainty regarding the future fate of the population. If alternative plausible parameter values result in divergent predictions for the population, then it is important to try to resolve the uncertainty with better data. Sensitivity of population dynamics to certain parameters also indicates that those parameters describe factors that could be critical determinants of population viability. Such factors are therefore good candidates for efficient management actions designed to ensure the persistence of the population.

The above kinds of uncertainty should be distinguished from several more sources of uncertainty about the future of the population. Even if long-term average demographic rates are known with precision, variation over time caused by fluctuating environmental conditions will cause uncertainty in the fate of the population at any given time in the future. Such environmental variation should be incorporated into the model used to assess population dynamics, and will generate a range of possible outcomes (perhaps represented as a mean and standard deviation) from the model. In addition, most biological processes are inherently stochastic, having a random component. The stochastic or probabilistic nature of survival, sex determination, transmission of genes, acquisition of mates, reproduction, and other processes preclude exact determination of the future state of a population. Such demographic stochasticity should also be incorporated into a population model, because such variability both increases our uncertainty about the future and can also change the expected or mean outcome relative to that which would result if there were no such variation. Finally, there is “uncertainty” which represents the alternative actions or interventions that might be pursued as a management strategy. The likely effectiveness of such management options can be explored by testing alternative scenarios in the model of population dynamics, in much the same way that sensitivity testing is used to explore the effects of uncertain biological parameters.

Often, the uncertainty regarding a number of aspects of the population biology, current status, and threats to persistence is too large to allow scientifically accurate and reliable projections of population dynamics. Therefore, the predictions made from PVA models should be considered to be projections about what would most likely happen to the population *if* various hypotheses about the status of the populations and the threats are true. Conservation and management decisions must be made based on the most plausible hypotheses about the population status, before sufficient data could be collected to test those hypotheses scientifically. An important advantage of PVA models is that they forced systematic consideration and specification of the assumptions and hypotheses that must be made in the absence of adequate data. This facilitates careful reassessment and improvement in the analyses, as better data become available.

Questions that can be explored with PVA models

Below are some of the conservation and management questions that can be explored by Population Viability Analysis modeling. References describing uses of *VORTEX* give many examples of these and other applications of PVA techniques to guide conservation.

Using the best current information on the biology of the taxon and its habitat, are the populations projected to persist if conditions remain as they are now? Beyond just the persistence of the population, what is the most likely average population size, range of population sizes across years, and rate of loss of genetic variation? If the population is at risk of extinction, is the extinction expected to result primarily from negative average population growth (mean deaths exceeding mean births), from large fluctuations in numbers, from effects of accumulated inbreeding, or from a combination of these factors?

Given that there is considerable uncertainty about several aspects of the species biology and its habitat, is the population likely to persist across the plausible ranges of parameters that might characterize the population? In particular, how sensitive are the population dynamics to varying estimates of reproductive success, juvenile survival, adult survival, effects of natural catastrophes, initial population size, carrying capacity of the habitat, and dispersal among populations? Are there critical values for any of these parameters which demarcate a transition from a population that would be considered viable to one that is not?

Which factors have the greatest influence on the projected population performance? If important factors are identified, management actions might be designed to improve these factors or ameliorate the negative effects. How much change would be required in aspects of the population in order to ensure population survival?

What would be the effect of removing some individuals from the population? Would there be a significant benefit from supplementing the population with individuals translocated from other populations or released from captive breeding stocks? Can the population sustain controlled harvest? Can it sustain poaching?

Would a corridor connecting fragmented habitats improve long-term viability? Could the same effect be achieved by translocating a few individuals? What will happen to population viability if mortality increases for individuals dispersing between habitat patches?

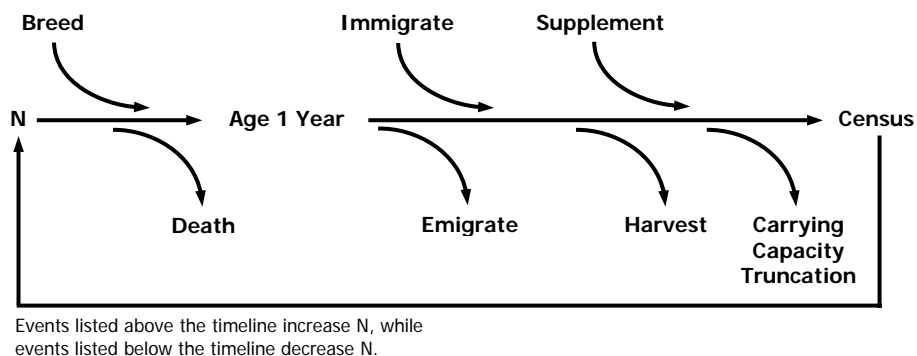
What will happen to the wildlife population if trends in human populations and human impacts on the environment continue unabated?

The *VORTEX* Population Viability Analysis Model

The *VORTEX* computer program is a simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochastic events on wildlife populations. It is an attempt to model many of the extinction vortices that can threaten persistence of small populations (hence, its name). *VORTEX* models population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions. *VORTEX* simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. Although *VORTEX* simulates life events on an annual cycle, a user could model "years" that are other than 12 months duration. The simulation of the population is iterated many times to generate the distribution of fates that the population might experience.

VORTEX is an individual-based model. That is, it creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *VORTEX* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. (See figure below.)

VORTEX Simulation Model Timeline



VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the

catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because *VORTEX* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

In the program explanation that follows, demographic rates are described as constants specified by the user. Although this is the way the program is most commonly and easily used, *VORTEX* does provide the capability to specify most demographic rates as functions of time, density, and other parameters (see Appendix I).

Demographic stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination, and death with a pseudo-random number generator. For each life event, if the random value sampled from a specified distribution falls above the user-specified probability, the event is deemed to have occurred, thereby simulating a binomial process. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

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

$$N = \frac{p(1-p)}{s^2}$$

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

Environmental variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modeled as binomial distributions. Environmental variation in carrying capacity is modeled as a normal distribution. Environmental variation in demographic rates can be correlated among populations.

Catastrophes

Catastrophes are modeled in *VORTEX* as random events that occur with specified probabilities. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors 50% for the year. Such a catastrophe would be modeled as a random event with 0.02 probability of occurrence each year, and severity factors of 0.75 for survival and 0.50 for reproduction. Catastrophes can be local (impacting populations independently), or regional (affecting sets of populations simultaneously).

Genetic processes

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical neutral (non-selected) genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. Each offspring created during the simulation is randomly assigned one of the alleles from each parent. *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or “expected heterozygosity”) relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

Inbreeding depression is modeled as a loss of viability of inbred animals during their first year. The severity of inbreeding depression is commonly measured by the number of “lethal equivalents” in a population (Morton et al. 1956). The number of lethal equivalents per diploid genome estimates the average number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due entirely to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual, it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles which equate in effect with one lethal allele per individual.

VORTEX partitions the total effect of inbreeding (the total lethal equivalents) into an effect due to recessive lethal alleles and an effect due to loci at which there is heterozygote advantage (superior fitness of heterozygotes relative to all homozygote genotypes). To model the effects of lethal alleles, each founder starts with a unique recessive lethal allele (and a dominant non-lethal allele) at up to five modeled loci. By virtue of the deaths of individuals that are homozygous for lethal alleles, such alleles can be removed slowly by natural selection during the generations of a simulation. This diminishes the probability that inbred individuals in subsequent generations will be homozygous for a lethal allele.

Heterozygote advantage is modeled by specifying that juvenile survival is related to inbreeding according to the logarithmic model:

$$\ln(S) = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is the portion of the lethal equivalents per haploid genome that is due to heterozygote advantage rather than to recessive lethal alleles. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at loci in which the heterozygote has higher fitness than both homozygotes, because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under heterozygote advantage, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.

Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects apparently varies considerably among species (Falconer 1981; Ralls et al. 1988; Lacy et al. 1992) and even among populations of the same species (Lacy et al. 1996). Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterozygote advantage), PVAs must make assumptions about the effects of inbreeding on the population being studied. If genetic effects are ignored, the PVA will overestimate the viability of small populations. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3.14 lethal equivalents per diploid) reported in the survey by Ralls et al. (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0.90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5.62 lethal equivalents). In the few species in which inbreeding depression has been studied carefully, about half of the effects of inbreeding are due recessive lethal alleles and about half of the effects are due to heterozygote advantage or other genetic mechanisms that are not diminished by natural selection during generations of inbreeding, although the proportion of the total inbreeding effect can vary substantially among populations (Lacy and Ballou 1998).

A full explanation of the genetic mechanisms of inbreeding depression is beyond the scope of this manual, and interested readers are encouraged to refer to the references cited above.

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

Deterministic processes

VORTEX can incorporate several deterministic processes, in addition to mean age-specific birth and death rates. Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional mortality is imposed across all age classes to bring the population back down to the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation. The carrying capacity can be specified to change over time, to model losses or gains in the amount or quality of habitat.

Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size. The default functional relationship between breeding and density allows entry of Allee effects (reduction in breeding at low density) and/or reduced breeding at high densities.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodeled) population. The numbers of additions and removals are specified according to the age and sex of animals.

Migration among populations

VORTEX can model up to 50 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. Migration among populations can be restricted to one sex and/or a limited age cohort. Emigration from a population can be restricted to occur only when the number of animals in the population exceeds a

specified proportion of the carrying capacity. Dispersal mortality can be specified as a probability of death for any migrating animal, which is in addition to age-sex specific mortality. Because of between-population migration and managed supplementation, populations can be recolonized. *VORTEX* tracks the dynamics of local extinctions and recolonizations through the simulation.

Output

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

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

$$SE(p) = \sqrt{\frac{p(1-p)}{n}}$$

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

Sequence of program flow

- (1) The seed for the random number generator is initialized with the number of seconds elapsed since the beginning of the 20th century.
- (2) The user is prompted for an output file name, duration of the simulation, number of iterations, the size below which a population is considered extinct, and a large number of population parameters.
- (3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

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

in which K is the maximum carrying capacity (carrying capacity can be specified to change during a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size.

- (4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{\max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{\max} . Because N_{\max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it has been adjusted downward because of limiting memory often will not hamper the analyses.
- (5) The deterministic growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also calculated. Life-table calculations assume constant birth and death rates, no limitation by carrying capacity, no limitation of mates, no loss of fitness due

to inbreeding depression, and that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

- (6) Iterative simulation of the population proceeds via steps 7 through 26 below.
- (7) The starting population is assigned an age and sex structure. The user can specify the exact age-sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.
- (8) Two unique alleles at a hypothetical neutral genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. *VORTEX* therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant neutral alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by

$$H_e = 1 - \sum (p_i^2)$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity through random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by *VORTEX* is the mean inbreeding coefficient of the population.

- (9) For each of the 10 alleles at five non-neutral loci that are used to model inbreeding depression, each founder is assigned a unique lethal allele with probability equal to 0.1 x the mean number of lethal alleles per individual.
- (10) Years are iterated via steps 11 through 25 below.
- (11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).
- (12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number

is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

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

- (13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.
- (14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of adult males specified to be breeding. Breeding males are selected independently each year; there is no long-term tenure of breeding males and no long-term pair bonds.
- (15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. If the user specifies that the breeding system is monogamous, then each male can only be paired with a single female each year. Males are paired only with those females which have already been selected for breeding that year. Thus, males will not be the limiting sex unless there are insufficient males to pair with the successfully breeding females.

If the breeding system is polygynous, then a male may be selected as the mate for several females. The degree of polygyny is determined by the proportion of males in the pool of potential breeders each year.

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

- (16) The genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal A , and another existing animal, B , is

$$f_{AB} = 0.5(f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j , M is the mother of A , and P is the father of A . The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_A = 0.5(1 + F)$. (See Ballou 1983 for a detailed description of this method for calculating inbreeding coefficients.)

- (17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If a newborn individual is homozygous for a lethal allele, it is killed. Otherwise, the survival probability for individuals in their first year is multiplied by

$$e^{-b(1 - \Pr[\text{Lethals}]F)}$$

in which b is the number of lethal equivalents per haploid genome, and $\text{Pr}[Lethals]$ is the proportion of this inbreeding effect due to lethal alleles.

- (18) The age of each animal is incremented by 1.
- (19) If more than one population is being modeled, migration among populations occurs stochastically with specified probabilities.
- (20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, *VORTEX* continues but reports that harvest was incomplete.
- (21) Dead animals are removed from the computer memory to make space for future generations.
- (22) If population supplementation is to occur in a particular year, new individuals of the specified age-class are created. Each immigrant is assumed to be genetically unrelated to all other individuals in the population, and it carries the number of lethal alleles that was specified for the starting population.
- (23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.
- (24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N - K)/N$, so that the expected population size after the additional mortality is K .
- (25) Summary statistics on population size and genetic variation are tallied and reported.
- (26) Final population size and genetic variation are determined for the simulation.
- (27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate are calculated across iterations and output.