Minimum Viable Population

Extinction in small populations has led to the theory of minimum viable population size, defined as the smallest number of individuals necessary to give a population a high probability of surviving over a specified time (Primack 1993). Small populations are subject to rapid decline due to 3 main causes: (1) genetic fluctuations (e.g., genetic drift, inbreeding); (2) demographic fluctuations (e.g., variations in birth and death rates); (3) environmental fluctuations in predation, disease, competition, food supply, and natural catastrophes. As the population increases, the threat of extinction due to stochastic events diminishes, and loss of genetic diversity slows, thereby increasing species security.

Shaffer (1981) provided a specific technique for determining the minimum viable population (MVP):

"A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1,000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes,"

(e.g., the smallest population size that can be predicted to have a very high chance of persisting for the next 1,000 years). In this case, the probability for remaining extant could be set at 95% or 99%, and the time frame could be adjusted to 100 or 500 years. The theory of MVP is simply a guide to aid in the preservation of a species.

Opinions vary widely as to the population sizes necessary to achieve a minimum viable population. One rule of thumb is to protect 1,000 individuals of a vertebrate species, because this number seems adequate to preserve genetic diversity (Shaffer 1981, Salwasser et al. 1984). Others suggest that an effective population size of 5,000 individuals is needed to retain evolutionary potential (Lande 1995). More recently, Reed et al. (2003) used population viability analysis to estimate MVP for a variety of vertebrate species. Their definition of MVP is a population that has a 99% probability of persistence for 40 generations. Their results indicate that the lack of long-term studies for endangered species may lead to an underestimation in the extinction rates for the species. They recommend that recovery/conservation programs should be designed to support a population of up to 7,000 adults to ensure long-term survival.

Downlisting Based on MVP Criteria

Population sizes sufficient to be referred to as a minimum viable population depend highly on the effective population size ($N_e$). The effective population size is the size of a population that maintains heterozygosity at the same rate of the entire species’ population and is a function of mating behavior, mutation rate, gene flow, demographics, and population size, among other factors. As not all breeding adults pass on their genetic material equally and randomly, there is a difference between the number of breeders and effective population size. When defining the population size sufficient for downlisting, criteria must account for the difference between the total population and the breeding population size (i.e., the $N_e/N$ ratio). For the wild whooping crane population, breeders comprise approximately 50% of the population. However, as the effective population will always be less than the number of breeders, proper estimates for $N_e$ will need to be obtained before the minimum viable population for whooping cranes can be determined.
Given the data to date, this plan recognizes growth of the AWBP to 1,000 individuals and 250 productive pairs as criteria for downlisting. The Memorandum of Understanding on Conservation of Whooping Cranes, approved by Canadian and U.S. federal officials, recognizes a goal of 1,000 individuals in the AWBP population. If two additional self-sustaining populations can be established in the wild, each with 25 nesting pairs, and with the AWBP projected to reach 125 nesting pairs by the year 2020, a figure approaching a population of 1,000 whooping cranes may be obtained from these three populations. However due to the uncertainty surrounding the exact figure required, with suggested values ranging between 1,000 and 7,000, this Plan does not set a delisting goal for the whooping crane. If additional research into the exact calculation of a $\frac{N_e}{N}$ ratio for the wild whooping crane population and additional research with other conservation programs can provide more assurances of the $N_e$ required, a delisting goal will be set prior to the anticipated downlisting in 2035.

**Population Growth and Retention of Genetic Material**

A Conservation Viability Assessment (CVA) workshop held in 1991 for the whooping crane was funded by the USFWS as a cooperative endeavor with CWS, U.S. Whooping Crane Recovery Team, Canadian Whooping Crane Recovery Team, ICF, The Captive Breeding Specialist Group, and Species Survival Commission of the International Union for Conservation of Nature. The final report includes priorities for research and management of the wild and captive populations as a meta-population to maximize retention of genetic heterozygosity and minimize the risk of extinction (Mirande et al. 1993). The CVA developed stochastic simulation models to estimate rates of genetic loss for the wild and captive whooping crane populations. As a consequence of the 1941 population bottleneck, the current population is derived from an estimated 6 or 8 founders (Mirande et al. 1993, Glenn et al. 1999), with an estimated genetic loss of 66% (Glenn et al. 1999). Mirande et al. (1993) showed that a loss of 6% to 8% of gene diversity would have resulted in the first generation following the bottleneck, where generation time is 12 years. It was estimated that about 87% of the gene diversity that survived the bottleneck has persisted from 1938 to 1990. In contrast, the captive-hatched descendants have retained about 96% of the gene diversity present in the post-bottleneck wild flock. As continued loss of genetic material could lead to inbreeding and declining productivity, the AWBP must increase to the level where creation of new alleles will offset the loss of genetic diversity.

Several other population viability analysis packages have been tested using whooping crane data (Mirande et al. 1997a, Brook et al. 1999). Modeling of the AWBP showed the population large enough to sustain a fairly steady annual growth rate of 0.046 (SD=0.081) over the last 50 years (Mirande et al. 1997a). The standard deviation is about double the mean growth rate so in many years the population will decline temporarily even though long-term growth may be good. If this rate continues, the population will reach 500 birds in 17 years (about 2020) and 1,000 in 33 years (2035). The population is projected to have a very low probability of extinction over the next 100 years (less than 1%).

Given the current genetic analyses based on captive pedigrees, an estimated 153 whooping cranes (21 productive pairs) are needed in captivity to retain 90% of genetic material for 100 years (Jones and Lacy 2003). This Plan recommends having 50 captive breeder pairs of whooping cranes by 2010, including 15 pairs at PWRC, 12 at ICF, 10 at CZ, 10 at SSC, and 3 at the SAZ. Production from these five facilities will be the principal source of birds for release to the wild. However, sources of release birds should be based on the optimal genetic mix to ensure long-term population viability.

**Loss of Genetic Diversity and Estimates of Relatedness**

For most of the 1940’s, the AWBP teetered on the brink of extinction. Mitochondrial DNA from museum specimens collected before and after 1941, when the AWBP declined to 15 birds, showed a 66%
reduction in haplotypes post-bottleneck, with the rarest haplotype before 1940 now the most common (Glenn et al. 1999). Although we lack pre-bottleneck diversity estimates for nuclear DNA, we realize that similar declines for this genome must have also occurred (Jones et al. 2002). This is evident from AWBP’s lack of genetic diversity as compared to other cranes. Compared with a subset of other cranes, an electrophoretic study of blood proteins showed that whooping crane diversity was less than that known from out-bred populations of Sandhill Cranes, and greater than that of the Mississippi Sandhill which was known to have undergone a similar genetic bottleneck (Dessauer et al. 1992). When diversity was compared across other markers, the whooping cranes were shown to be below average in band sharing of DNA fingerprints (Longmire et al. 1992), average in polymorphism of the major histocompatibility complex (Jarvi et al. 1992), and less than average in microsatellite DNA diversity (Jones et al. 2002, Jones 2003). From these studies, it is evident that the extant whooping cranes show an overall reduction in genetic diversity compared to their pre-bottleneck ancestors and to that of out-bred cranes. This known diversity reduction, along with the fact that generations of captivity increase inbreeding and decrease genetic diversity (Woodworth et al. 2002), indicates that genetic changes within the population threaten to reduce vitality before the population is large enough for mutation to offset losses in diversity from genetic drift (Frankel and Soule 1981, Ballou et al. 1995).

In addition to the knowledge of genetic diversity, understanding relatedness among individuals within the captive whooping crane populations is important to adequately manage the captive population and to establish viable wild populations (Jones et al. 2002). In addition to pedigree management, there have been various molecular genetic techniques used in relatedness estimation. These studies have resolved unknown paternities (Longmire et al. 1992; Jones and Nicolich 2001), developed a species-specific probe for the whooping crane (Love and Deininger 1992), and identified inter-relatednesses within the captive founder lines (Jones et al. 2002). A recently developed technique that could provide additional insights into the whooping crane population is Amplified Fragment Length Polymorphisms (AFLP). Because of the relative paucity of information in birds in general, and cranes in particular, the usefulness of this technique in cranes is currently unknown. An AFLP study currently underway at PWRC will include samples from other crane populations with robust populations and those of reduced diversity. This comparison across crane species should provide additional understanding of crane diversity in general and the relative state of genetic diversity of the whooping crane.