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COMPUTER SIMULATIONS OF POSSIBLE FUTURES FOR TWO FLOCKS OF WHOOPING CRANES

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Abstract: We conducted computer simulations using the program VORTEX (version 7) to project population sizes, growth rates, genetic diversity, and probabilities of extinction over the next 100 years for 2 flocks of whooping cranes (*Grus americana*), the Aransas/Wood Buffalo population and the experimental Florida population. Standard runs based on best estimates of demographic, genetic, and environmental parameter values were used as a baseline to which several alternative scenarios were compared. Results generally supported the conclusion of the earlier Population Viability Assessment (Mirande et al. 1991) that the Aransas/Wood Buffalo population will continue to grow steadily with less than a 1% probability of extinction. It was noted, however, that a combination of negative factors such as shrinking habitat and increased probabilities of catastrophes accompanied by increased mortality rates could put this population at risk. Results for the Florida population were less optimistic. The standard run produced a population growth rate (r) of only 0.0026 for the next 100 years, and this shifted down to -0.0001 over a 200-year time frame. Adult mortality in this flock would have to be about 20% lower than the predicted value (10%) in order to raise growth rates to above $r = 0.02$. Amount and duration of supplementation of the Florida flock had minimal impacts on the long-term growth rate of the flock. It is the enduring rates of mortality, breeding, and disease risk that will have major effects on this population. For example, if disease risks turn out to be greater than the best-estimate scenario, this population could face a relatively high risk of extinction (17%). The formula for success in Florida is lower adult mortality, lower age of first breeding, lower disease risk, and higher productivity than the best-guess estimates. Fortunately, there are some potential management interventions (e.g., predator control, vaccines and health monitoring, selective introductions to balance the sex ratio of the flock) that may be able to push the odds in favor of success.

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Key Words: computer, *Grus americana*, population viability analysis, whooping crane.

In 1970 the whooping crane was listed as an endangered species by the United States Fish and Wildlife Service (USFWS). This species is the most endangered of the world's 15 crane species. The USFWS designated critical habitat in 1978 and has developed recovery plans detailing management goals and strategies for whooping crane conservation. To provide protection for the migratory population across international borders, the Canadian Wildlife Service (CWS) and the USFWS jointly implement whooping crane recovery efforts through the Memorandum of Understanding on the Conservation of the Whooping Crane (USFWS, NBS, CWS, and PC 1995).

One captive and 3 wild populations of whooping cranes currently exist, all of which originate from the same (<14) founding birds (Mirande et al. 1991). The captive population consists of more than 100 birds divided among 4 facilities.

The only remaining natural wild population migrates between Wood Buffalo National Park in the Northwest Territories of Canada and Aransas National Wildlife Refuge in Texas (hereafter AWP). In the fall of 1995, 155 birds of the AWP were counted on their wintering grounds in Texas. A second wild population is an experimental flock introduced to the Kissimmee Prairie, Florida, beginning in 1993 (hereafter FP). In December 1995, this flock had a population of 18 birds ranging from 1 to 3 years of age. A group of 3 wild whooping cranes that migrates annually between Gray's Lake National Wildlife Refuge in Idaho and Bosque del Apache National Wildlife Refuge in New Mexico is the remnant of an experiment to establish a migratory population by cross-fostering by sandhill cranes (*Grus canadensis*). The experiment was terminated in 1988 due to lack of breeding and a high mortality rate within the whooping

crane flock. Failure to breed was attributed to sexual imprinting on the foster species (Mahan and Simmers 1992, USFWS 1994).

The goal of the U.S. Whooping Crane Recovery Plan of 1994 is to downlist the species to "threatened" by the year 2020. The maintenance for at least 10 years of 40 breeding pairs in the AWP, 25 breeding pairs in the FP, and 25 breeding pairs in an additional proposed wild flock would allow downlisting.

Interest in the plight of the whooping crane has provided the rare opportunity to conduct long-term population monitoring and research in genetics, captive-breeding, and reintroduction. Due to the efforts of biologists working with the last remaining natural population (AWP), 57 years of demographic data on whooping cranes are available. These data (Appendix A) allow extensive analyses of population viability to be conducted under a variety of potential scenarios.

This report presents whooping crane population viability assessments (PVA's) for both the AWP and the FP using VORTEX version 7. VORTEX is a "Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wildlife populations" (Lacy et al. 1995:4). A PVA is just one of many tools that can be used to guide management decisions and research priorities for populations of species of concern. It should be understood that this tool is only as credible as the data that are used, and that long-term population studies are a prerequisite to receiving reliable PVA results.

The objectives of this study were to (1) update the 1991 PVA of the AWP by making adjustments to specific demographic and environmental parameters (these adjustments were made based on new population data obtained from 1991 to 1995 and other more recent estimates of environmental variability and human-induced threats to habitat); (2) update the 1991 PVA of the FP by incorporating population data obtained from 1993 to 1995 and information on environmental variability and human-induced threats to habitat; (3) identify how specific variations in demographic, genetic, and environmental parameters affect population size, extinction probability, rate of growth, and genetic diversity in both populations; and (4) determine how potential management strategies may impact the populations and assist in meeting the USFWS downlisting goal by 2020.

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METHODS

VORTEX Input Parameters for the AWP

The set of standard parameters developed for the AWP is shown in Table 1. These values are our best estimates based on the best available data, expert opinion, current literature, and existing conditions and management technology. These values provide a baseline to which other simulations can be compared. Variations from standard values were tested to explore the response of the population to variation in these parameters. Those variations that proved most interesting or sensitive were explored further through combination variations. The AWP viability assessment results table presented later in the report itemizes the parameter(s) varied for each AWP simulation. These parameters are discussed below.

Using the inputs for the standard run, and both an estimated actual age distribution and a stable age distribution, we conducted 2 "check runs" to verify the accuracy of the input parameters. The population growth during the past 20 years was modeled with the actual 1975 population size of 49 individuals as the starting population. The estimated actual age distribution of the 49 individuals was calculated by using actual annual survival rates for the years prior to 1975 (see Appendix B for an example of this type of age distribution estimation).

For the purposes of all AWP simulations, "birth" was defined as the arrival of migrating chicks at Aransas National Wildlife Refuge in the fall because data exist on these arrivals since 1938-39. In a similar manner, "death" was defined as failure to return to Aransas the following year. Because of these conventions, values for reproduction are not fecundity rates for cranes and should not be viewed as such.

For the standard run 1,000 simulations were run for 100 years. For all variations, 100 simulations were run for 100 years, unless otherwise noted.

Inbreeding Depression.—Inbreeding depression is possible because the population experienced a bottleneck in 1941. The heterosis model was chosen since there is not much information about recessive lethal alleles in the population. The value "3 lethal equivalents" was chosen because that value represents an approximate average number for many large vertebrate species, such as mammals, which have been well-studied for inbreeding (Lacy et al. 1995).

Age of First Breeding.—A standard age of first breeding of 4 years was used for both males and females. This value was established from the estimated current age distribution (Appendix B) by determining that a breeding age of 4 was necessary to account for the actual number of nests present in Wood Buffalo National Park (WBNP) in 1995. A variation

Table 1. Input parameters for standard run of VORTEX simulation of Aransas/Wood Buffalo whooping crane population.

Parameter	Input value	Reference/rationale
Number of simulations	1,000	
Number of years	100	
Reporting interval	10	
Number of populations	1	
Inbreeding depression	N	Mirande et al. (1991)
Environmental variance (EV) correlation	Y	Edwards et al. (1994)
Number of catastrophe types	3	Mirande et al. (1991), consensus of expert estimates
Monogamous or polygamous	M	Ehrlich et al. (1988)
Female breeding age	4	Based on current number of breeding pairs and estimated age distribution
Male breeding age	4	Based on current number of breeding pairs and estimated age distribution
Maximum age	40	Based on actual annual survival rates (see Appendix B)
Sex ratio	0.5	Edwards et al. (1994)
Maximum brood size	1	Assumes continuing egg removals
Density dependent breeding	N	Edwards et al. (1994)
Percent brood size	0=52.4% 1=47.6%	Calculations based on breeding data in Edwards et al. (1994) applied to 20-year data set (see Appendix C)
EV-reproduction	10	Calculations based on 20-year data set (see Appendix C) Square root of annual variance in recruitment for the last 20 years minus expected stochastic variance (see Lacy et al. 1995)
Female mortality: age 0	8%	Weighted mean mortality for last 20 yrs (see Appendix C)
EV in mortality	3	Square root of variance in annual mortality for the last 20 years minus expected stochastic variance (see Lacy et al. 1995)
Female mortality: all ages above 0	8%	Weighted mean mortality for last 20 yrs (see Appendix C)
EV in mortality	3	Square root of variance in annual mortality for the last 20 years minus expected stochastic variance (see Lacy et al. 1995)
Male mortality: age 0	8%	Weighted mean mortality for last 20 yrs (see Appendix C)
EV in mortality	3	Square root of variance in annual mortality for the last 20 years minus expected stochastic variance (see Lacy et al. 1995)
Male mortality: all ages above 0	8%	Weighted mean mortality for last 20 yrs (see Appendix C)
EV in Mortality	3	Square root of variance in annual mortality for the last 20 years minus expected stochastic variance (see Lacy et al. 1995)
<i>P</i> of catastrophe 1 (chemical spill)	2%	T. Stehn (pers. commun.)
Severity-reproduction	1.0	Impact reflected in reduced survival
Severity-survival	0.9	T. Stehn (pers. commun.)
<i>P</i> of catastrophe 2 (hurricane)	0.33%	Mirande et al. (1991), T. Stehn (pers. commun.)
Severity-reproduction	1.0	Impact reflected in reduced survival
Severity-survival	0.5	Mirande et al. (1991), consensus of expert estimates
<i>P</i> of catastrophe 3 (disease)	5%	J. Langenberg, C. Brand, and T. Stehn (pers. commun.)
Severity-reproduction	1.0	Impact reflected in reduced survival
Severity-survival	0.9	J. Langenberg, C. Brand, T. Stehn (pers. commun.)
All male breeders?	1	Mirande et al. (1991)
Stable age distribution?	N	Number of known breeders too large for stable age distribution assumption
Initial female ages: age 1 to age 40	Age 1 to age 40 ^a	All of the values are based on estimated actual age distribution derived from actual annual survival rates (see Appendix B)
Initial male ages: age 1 to age 40	Age 1 to age 40 ^b	All of the values are based on estimated actual age distribution derived from actual annual survival rates (see Appendix B)
Carrying capacity (K)	500	T. Stehn (pers. commun.)
EV in K	0	T. Stehn (pers. commun.)
Trend in K	N	T. Stehn (pers. commun.)
Harvest	N	Illegal
Supplement	N	Consensus of U.S. and Canadian Recovery Teams

^a 3,7,6,3,4,6,5,6,5,4,3,1,2,0,1,1,0,1,2,1,1,0,1,0,1,0,1,1,0,0,0,0,0,1,0,0,0,1 years.

^b 4,7,6,3,4,6,5,5,3,3,1,1,0,1,1,1,2,1,0,0,0,0,1,0,1,0,0,0,1,1,0,0,0,0,0,0,0 years.

was also conducted using 5 as the age of first breeding.

Maximum Age.—Maximum age was determined from the age distribution calculated from annual survival rates over the last 50 years (Appendix B). Variations on maximum age were used to determine how reduced longevity, and thus productivity, affected population growth (r) and the final population size.

Twinning/Productivity.—Because some natural breeding pairs produce twins, twinning was tested to compare against the standard run that reflects egg removal and a maximum brood size of 1. For years when data were available on the number of known breeding pairs at WBNP (Edwards et al. 1994), the average percentage of the total flock that were potential breeders was calculated to be 49%. This value was then used to determine the total number of breeders and breeding pairs (i.e., one-half the number of breeders) in the 57-year data set (804 pairs) and the 20-year data set (502 pairs).

Since no twins arrived at Aransas during the 20-year data set period, the percentage of successful nests during this period was determined as the total number of chicks arriving during the 20 years divided by the total number of pairs of breeders. This was the value for brood size 1 during the 20-year period (47.6%). Brood size 0 was simply 1.0 minus 0.476, or 52.4%. Similar calculations were obtained for the 57-year data set, no twins assumed (a false assumption for the past, but a possible scenario for the future if egg removals in WBNP were to continue indefinitely).

To obtain brood sizes for scenarios that included twinning, we analyzed data from the 29-year period of Aransas records before egg removals began (i.e., 1938–39 through 1966–67) (T. Stehn, USFWS, pers. commun.). During this period, nesting success (again, as indicated by Aransas arrivals) was as follows: brood size 0 = 41.7%, brood size 1 = 50.8%, and brood size 2 = 7.5%. These values account for the 131 chicks (101 singletons and 15 pairs of twins) that were produced by 199 pairs of breeders ($0.5 \times 49\%$ of the 815 total birds) during the 29-year period. Twinning was also run for 1,000 simulations to more adequately test the impacts of having brood sizes of 2. These latter brood size percentages constitute our best estimates of broods that would be produced under conditions of no removal or manipulation (i.e., nest switching) of eggs.

To test for the effect of twinning with all other variables (e.g., number of breeding birds) held constant, we conducted a simulation in which the brood size 0 of 52.4% from the standard run was used and the other 47.6% that was brood size 1 in the standard run was divided into brood size 1 of 41.5% and brood size 2 of 6.1%. These latter percentages were calculated by using the historic twinning ratio derived from the data from 1938–39 through 1966–67. This simula-

tion was run for 1,000 iterations just like the standard run. Additional sensitivity runs were conducted setting the twinning percentages at 2% and 10% (i.e., in the low twinning run, 0=52.4%, 1=45.6%, and 2=2%; in the high twinning run, 0=52.4%, 1=37.6%, and 2=10%). The environmental variation (EV) value for reproduction was calculated by taking the square root of the variance in the annual number of chicks per female minus the expected stochastic variance (Lacy et al. 1995).

Mortality.—The mortality values used for the AWP simulations were weighted means from AWP data for the last 20 years (Appendix C) or for the last 57 years (Appendix A). The effects of higher and lower annual mortality were explored because, potentially, mortality can be managed to some extent (e.g., mortality due to powerlines can be decreased by management practices). The EV for mortality was calculated by taking the square root of the variance in annual mortality minus the expected stochastic variance (Lacy et al. 1995).

Catastrophes.—The major catastrophes potentially affecting the AWP are disease, hurricanes, and chemical spills. The hurricane season usually occurs when the flock is in Canada (Mirande et al. 1991). Thus, there is a low probability that a hurricane will affect the survival of the population.

Several experts have estimated the upper range of the probability of disease outbreak to be about 5% annually (J. Langenberg, C. Brand, and T. Stehn, pers. commun.). Chemical spills from barges traveling along the Gulf Intra-coastal Waterway (GIWW) may pose the greatest threat to the survival of this population (USFWS 1994). Chemical spills are also the catastrophes over which people have the most potential for control through GIWW traffic restrictions. To explore this catastrophe further, we varied the severity and frequency of chemical spills. Note that in all these variations the severity of reproductive impacts was considered to be reflected in the severity of survival impacts and thus was kept at a value of 1.0 (no impact).

Stable Age Distribution.—A simulation with a stable age distribution was performed to compare to the results obtained from use of the estimated actual age distribution.

Carrying Capacity.—The standard value for carrying capacity (K) was based on expert opinion (T. Stehn, pers. commun.). Carrying capacity was varied due to uncertainty regarding what constitutes acceptable habitat and how existing habitat may be altered in the future. The reduction of freshwater flow into the habitat surrounding Aransas is projected to cause a decline in the blue crab (*Callinectes sapidus*) population, a major food source for the cranes (see Trends in K , below) (T. Stehn, pers. commun.). Higher carrying capacities were included as variations to explore the effect of increased habitat on population growth.

Trends in Carrying Capacity.—Trends in carrying capacity were modeled to reflect the impact of reduced freshwater inflow into the Aransas area caused by upstream diversions by humans. Discussions with experts indicated that reduced freshwater inflow is expected to reduce the blue crab population by about 8% over the next 50 years. This reduction could increase crane mortality rates, particularly for juveniles. Experts estimate that mortality could increase to the maximum that has ever occurred over the past 20 years (T. Stehn, pers. commun.). A possible relationship between crab population numbers and whooping crane nesting the following spring has been observed. For example, the crab population was low in the winter of 1993–94 (Chavez-Ramirez 1996), and the following spring only 61% of pairs nested. In 1994–95, a year of high blue crab population, 96% of available pairs nested. In addition to impacting mortality and reproduction, reduced inflows could lower overall carrying capacity of the habitat.

Supplementation.—Supplementation was modeled to determine any potential positive impacts on population growth rate and size.

Combination Variations.—Combinations of reduced carrying capacity and increased catastrophe probability and severity were modeled to reflect possible worst case scenarios for the AWP.

Simulation Based on the 57-year Data Set.—Data from 1938–39 to 1994–1995 (i.e., all 57 years as opposed to the last 20 years) were investigated due to their higher variability. A set of parameters based on the 57-year data set was derived in a similar fashion as that for the standard run (refer to Table 1 and above discussions). Simulations using the 57-year data were run both with catastrophes and without catastrophes. It can be argued that the 57-year mortality data set extends over a sufficiently long period of time to include natural catastrophes. For example, the existence of 7 outliers in the mortality data could be viewed as caused by catastrophes (Mirande et al. 1991). Following this argument, adding catastrophes to the simulation might in fact double their projected impact. On the other hand, if catastrophe risks are increasing over time (e.g., chemical spills), it can be argued that the 57-year data set underestimates the probable impacts of catastrophes during the next 100 years. To allow for the possible validity of both arguments, we conducted simulations both with and without catastrophes included. In addition, variations in mortality were made to the 57-year-based parameter set following the same reasoning used to vary the standard run (described above).

VORTEX Input Parameters for the FP

The parameters for the FP standard run are presented in

Table 2. These parameter values reflect the professional knowledge and data available at the time the simulations were run. Parameters are based upon the 57 years of study of the AWP, as well as expert knowledge and observations by crane biologists at Kissimmee Prairie, Florida (hereafter Kissimmee). The FP viability assessment results table presented later in the report itemizes the parameter(s) varied for each FP simulation. These parameters are discussed below.

Inbreeding Depression.—As discussed for the AWP, a simulation with inbreeding depression (we used a heterosis model with 3.0 lethal equivalents) was performed.

Age of First Breeding.—An age of first breeding of 5 years was selected as the standard value for the FP (in comparison to 4 for the AWP) because observations of captive behavior indicate that introduced birds are generally expected to begin reproduction later than wild birds. Age of first breeding was increased to 7 under the assumption that the effect of captive rearing was even more pronounced. However, it was also decreased to 4, based on the uncertainty regarding future crane behavior at Kissimmee (e.g., a pair of introduced 3-year-old birds built a nest in 1995).

Maximum Age.—The standard maximum age of 40 years was based on the findings for the AWP. This parameter was decreased to 30 years and to 20 years to gauge its effect on population viability.

Brood Size/Productivity.—The calculations of the standard run values for percentages for each brood size were based on the historical productivity data from the AWP prior to egg removals. These calculations were described above in the AWP section of the paper. To explore the effects of varied productivity on population viability, we varied productivity by $\pm 10\%$. The 10% increase in productivity scenario had brood-size values as follows: 0 = 35.7%, 1 = 56.0%, and 2 = 8.3%. The 10% decrease in productivity scenario had the following brood-size values: 0 = 47.7%, 1 = 45.6%, and 2 = 6.7%. The reproduction EV value (10%) was the value calculated for the AWP standard run.

Mortality.—The chick mortality value (26.7%) and associated EV value (18.4%) were based on AWP data from 1976 through 1989 (Mirande et al. 1991). Comparable chick mortality rates for non-migratory Florida sandhill cranes (*G. c. pratensis*) range from 12.8% (Mirande et al. 1991) to 41% (Nesbitt 1992, Seal et al. 1992). The selected standard mortality value (10%) and EV (7%) for older birds were based on the 57-year data set from the AWP (see Appendix A) and on data from non-migratory Florida sandhill cranes (Mirande et al. 1991). To explore the effects of mortality, we varied adult mortality values (increased to 12% and decreased to 8%). In addition, a simulation was conducted with both chick mortality and adult mortality set at 10%, and a simulation was conducted with chick mortality at 10% and

Table 2. Input parameters for standard run of VORTEX simulation of Florida whooping crane population.

Parameter	Input value	Reference/rationale
Number of simulations	1,000	
Number of years	100	
Reporting interval	5	
Number of populations	1	
Inbreeding depression	N	Consensus of captive breeders
Environmental variance (EV) correlation	Y	Edwards et al. (1994)
Number of catastrophe types	2	Consensus of expert estimates
Monogamous or polygamous	M	Ehrlich et al. (1988)
Female breeding age	5	Consensus of captive breeders
Male breeding age	5	Consensus of captive breeders
Maximum age	40	Based on actual annual survival rates for Aransas/Wood Buffalo population (AWP) (see Appendix B)
Sex ratio	0.5	Edwards et al. (1994)
Maximum brood size	2	Assumes twinning at rates of AWP prior to egg removals
Density dependent breeding	N	Edwards et al. (1994)
Percent brood size	0=41.7% 1=50.8% 2=7.5%	Calculations based on AWP data prior to egg removals
EV-reproduction	10	Value calculated for AWP standard run
Female mortality: age 0	26.7%	Mirande et al. (1991)
EV in mortality	18.4	Mirande et al. (1991)
Female mortality: all ages above 0	10%	Based on approximate rate for AWP adults using 57-year data and non-migratory Florida sandhill crane data (Mirande et al. 1991)
EV in mortality	7	Calculated from AWP data for last 57 years (see Lacy et al. 1995)
Male mortality: age 0	26.7%	Mirande et al. (1991)
EV in mortality	18.4	Mirande et al. (1991)
Male mortality: all ages above 0	10%	Based on approximate rate for AWP adults using 57-year data and non-migratory Florida sandhill crane data (Mirande et al. 1991)
EV in mortality	7	Calculated from AWP data for last 57 years (see Lacy et al. 1995)
P of catastrophe 1 (disease)	10%	Average of expert estimates
Severity-reproduction	1.0	Impact reflected in reduced survival
Severity-survival	0.75	Average of expert estimates
P of catastrophe 2 (hurricane)	0.33%	S. Nesbitt (pers. commun.)
Severity-reproduction	1.0	Impact reflected in reduced survival
Severity-survival	0.9	S. Nesbitt (pers. commun.)
All male breeders?	Y	Mirande et al. (1991)
Stable age distribution?	N	Current population does not constitute a stable age distribution
Initial female ages: ages 1, 2, 3	5, 5, 1	Values are based on known ages of live birds at Kissimmee as of 20 Sep 1995
Initial male ages: ages 1, 2, 3	9, 1, 3	Values are based on known ages of live birds at Kissimmee as of 20 Sep 1995
Carrying capacity (K)	300	S. Nesbitt (pers. commun.)
EV in K	0	S. Nesbitt (pers. commun.)
Trend in K	N	S. Nesbitt (pers. commun.)
Harvest	N	Illegal
Supplement	Y	U.S. Fish and Wildlife Service (1994)
First year of supplementation	1	All of the values are based on a conservative estimate of birds available for supplementation (see text)
Last year of supplementation	20	
Supplementation interval	1	
Females age 1	15	
Females above age 1	0	
Males age 1	15	
Males above age 1	0	

adult mortality at 8%. For all FP simulations (including the standard), the non-chick mortality EV value used was 7%, calculated from the 57-year data on the AWP. The 57-year data set was utilized because these data include the maximum variation found in the initially small AWP.

Catastrophes.—Disease outbreaks are expected to have a significant impact on mortality of the FP. Experts are particularly concerned about eastern equine encephalitis (EEE). Introduced birds are currently inoculated against this disease, but it is unknown whether the inoculations will be effective over the long run, or to what extent the disease may affect the progeny of the introduced birds. Expert opinion varies greatly about the extent to which disease outbreaks may occur. Because of this uncertainty, the probability of disease outbreak was varied from 10% in the standard run to 20% (increasing probability assumed) and to 5% (an optimistic value). Severity of a disease catastrophe was varied from the standard of 25% mortality to a lower value of 10% mortality.

Because Kissimmee is approximately 100 km inland, the probability of hurricanes of force 4 or 5 at this location is estimated at only 0.33% (S. Nesbitt, pers. commun.). It was not considered realistic to run a variation which decreased the chances of a hurricane hitting, because weather patterns appear to be increasing in severity (Suplee 1995). Therefore, a simulation in which hurricane probability was doubled (to 0.66%) was conducted. For comparison purposes, a simulation was also run without any catastrophes included.

Age Distribution.—The standard values for age distribution were based upon the current actual distribution of introduced birds at Kissimmee. A simulation incorporating the stable age distribution was also conducted.

Carrying Capacity.—The standard carrying capacity ($K = 300$) was estimated based upon expert opinion and studies at Aransas and Kissimmee. It is unknown whether the birds will move into habitat currently believed to be unsuitable. Likewise, it is unknown how human pressures will affect K . Four additional simulations were performed, increasing K to 500, 800, and 1,000, and decreasing K to 150.

Supplementation.—The standard scenario assumes that 40 birds (20 males and 20 females) will be available for introduction into Kissimmee every year for the next 20 years. An immediate (within 30 days) 25% mortality rate was assumed for these 40 birds (so the values entered into VORTEX were actually 15 birds of each sex). Two simulations were performed in which the length of supplementation was shortened (to 10 years and 5 years) and 1 simulation was performed in which more birds were successfully introduced (20 birds of each sex entered into VORTEX rather than 15). Finally, a simulation was conducted in which 20 birds per year were introduced for 10 years. These variations were selected in

order to explore the effects and possible management options regarding supplementation.

Combination Scenarios.—The effects of mortality variations were examined in combination with variations in age of first breeding, productivity, catastrophic disease probability, and supplementation length and numbers. The values were selected to create scenarios that reflected the “best” mortality level in combination with “best values” of the other parameters, the “best” mortality level with the “worst values” of the other parameters, and 2 levels of higher mortality (12% and 15%) combined with the “best values” of the other parameters, based on the descriptions of these parameters given earlier.

General Model Parameters

Because “it is impossible to simulate the complete range of complex processes and dynamics typical of a wild population” (Lacy 1993:56), some general assumptions are implicit in the VORTEX model. To the degree that these biological and mathematical assumptions are unrealistic in terms of the actual ecology and biology of whooping cranes, they will add uncertainty to the model’s outputs. The most notable of these assumptions are described below.

Individuals in the founder population (the initial population specified for VORTEX simulations) and any supplemental animals are assumed to be unrelated. This assumption is not valid for the current world population of whooping cranes, all of which are derived from less than 14 (probably 6–8) founder individuals. This assumption results in an underestimate of inbreeding depression in the model simulations, if inbreeding depression is selected as a parameter.

When the inbreeding depression option is selected, VORTEX models inbreeding depression as reduced survival in the first year of life only. This assumption also results in an underestimate of inbreeding depression. Moreover, for each modeling year, breeding partners are randomly reshuffled by VORTEX. This assumption is not valid for whooping cranes, which generally mate for life. This assumption results in increased genetic diversity in a population, and thus underestimates inbreeding depression, if the inbreeding depression parameter is selected.

Most inputs into VORTEX cannot be varied during the modeling interval (except randomly within the specified range of environmental variation). That is, values for mortality, productivity, and catastrophes are assumed to be fixed during the 100- or 200-year simulations. (An exception is carrying capacity, K , for which an increasing or decreasing trend can be entered). Averages derived from existing data were typically used for the fixed model inputs; however, this approach does not account for steadily increasing or decreas-

ing trends. For example, data for the AWP show that both mortality and reproduction have been decreasing over time. As for the FP, trends in demographic data are not unexpected as the number of experienced birds hatched in the wild increases or inoculations for disease lose their effectiveness. Finally, economic or environmental trends that may affect the probability or severity of catastrophes cannot be accounted for directly. The use of fixed values will underestimate or overestimate population sizes depending on the trends and the values used. Therefore, variations in these parameters must be tested in separate experimental runs.

VORTEX assumes that the effects of a catastrophe are felt only in the year in which the catastrophe occurs. This assumption most likely is inappropriate for some catastrophes which may befall whooping cranes. For example, hurricanes and major chemical spills may have lasting effects (e.g., effects on food supply, habitat, reproduction) which apply to more than 1 year.

Finally, in VORTEX, survival is assumed to be density independent up to the point that carrying capacity, K , is reached. Thus, there is no negative feedback mechanism on survival as the population size increases towards K . Based on ecological principles, this type of population growth is unlikely for whooping cranes. If mortality increases as population size approaches K (e.g., at the wintering grounds) then VORTEX overestimates population sizes for later years and underestimates the time until K is reached.

RESULTS AND DISCUSSION

Analysis of AWP VORTEX Simulation Results

This discussion focuses on the most notable results of the VORTEX analyses for the AWP. The results of all runs appear in Table 3.

Check Runs.—Prior to carrying out the population viability assessment for the AWP, we ran 2 retrospective simulations from 1975 to 1995 to confirm the accuracy of the standard inputs. These runs used the AWP 1975 population size of 49 cranes and the standard inputs, simulating for 20 years to the present. When compared against the actual AWP of spring 1995 (132 cranes), the outcomes of the retrospective runs were remarkably accurate. Use of the stable age distribution and the actual age distribution in the simulations resulted in population sizes of 131.9 and 129.3, respectively. With the accuracy of the standard inputs established, the population viability analysis was carried out.

Standard Run.—The standard run, with an estimated carrying capacity of 500, resulted in a mean population size of 487.8 after 100 years. As illustrated in Figure 1, use of the standard set of parameters leads to a projection of rapid

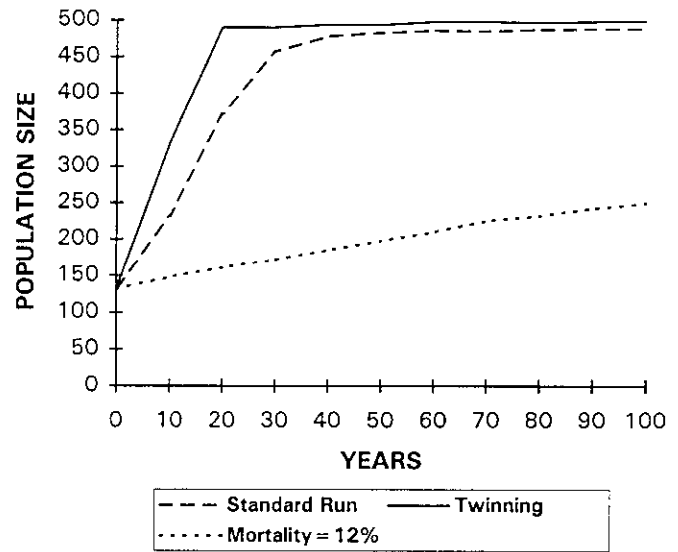


Fig. 1. VORTEX simulation showing effects of twinning and high mortality on the future of the Aransas/Wood Buffalo whooping crane population.

growth for the next 30 years, at which time the population approaches the established carrying capacity of the habitat. It is the carrying capacity "lid" that causes the growth rate to level off at this point. The average rate of growth for the population before bumping into the carrying capacity lid was $r = 0.0498$, with a 0% probability of extinction over the 100 years of the simulation. These outcomes indicate that, if the standard parameters are fairly accurate, the AWP will remain viable.

In the VORTEX program, 2 unique alleles are assigned to each individual animal that is present in the population at the beginning of a simulation. The last 2 columns of Table 3 present the data on loss of allelic diversity for each simulation. For the standard run, there were 131 animals in the starting population (see Appendix B); therefore, there were 262 unique alleles in the starting population. By the end of 100 years, there were only 71 of these unique alleles remaining in the population. This result suggests that loss of allelic diversity may be a potential problem for the AWP. The implications of this finding will be discussed later.

Single Parameter Variations of the Standard Run.—**Stable Age Distribution:** A stable age distribution was used in place of the estimated actual age distribution but yielded very similar results.

Inbreeding Depression: Introducing inbreeding depression into the population had no serious effects on the population's viability. However, given the species' susceptibility to disease, it is suspected that loss of genetic diversity is in actuality affecting this population in combination with genetic

Table 3. VORTEX simulation of the Aransas/Wood Buffalo whooping crane population over 100 years. Refer to Table 1 for parameter values in standard run.

Description ^a	Final population		Intrinsic growth rate (<i>r</i>)	<i>P</i> of extinction	Expected heterozygosity	Observed heterozygosity	Original unique founder alleles	Final alleles ^b
	<i>N</i>	SD						
20-year check runs (1975-95)								
Actual age distribution	129.32	48.19	0.0448	0	0.9697	0.9855	98	51.56
Stable age distribution	131.91	49.15	0.0456	0	0.9701	0.9855	98	51.99
Standard run (1,000 simulations)								
Actual age distribution	487.79	35.99	0.0498	0	0.9746	0.9773	262	70.68
Stable age distribution	481.87	47.11	0.0492	0	0.9750	0.9778	264	71.62
Inbreeding depression								
Heterosis; 3 lethal equivalents	489.04	35.09	0.0489	0	0.9746	0.9784	262	70.81
Age of first breeding								
M=5, F=5	487.23	27.57	0.0378	0	0.9756	0.9784	262	72.21
Maximum age								
M=30, F=30	485.06	35.78	0.0462	0	0.9726	0.9753	262	68.21
Brood size								
Decrease, 0=60%, 1=40%	479.62	46.37	0.0367	0	0.9741	0.9759	262	70.11
Decrease, 0=67%, 1=33%	402.73	113.67	0.0159	0.001	0.9644	0.9688	262	55.41
Twinning								
0=41.7%, 1=50.8%, 2=7.5%	499.22	10.74	0.0842	0	0.9735	0.9760	262	68.15
0=41.7%, 1=50.8%, 2=7.5% (1,000 sims.)	491.83	32.54	0.0830	0	0.9733	0.9763	262	67.38
0=52.4%, 1=41.5%, 2=6.1% (1,000 sims.)	491.10	31.35	0.0614	0	0.9735	0.9765	262	68.47
0=52.4%, 1=45.6%, 2=2%	482.04	45.85	0.0544	0	0.9746	0.9772	262	70.68
0=52.4%, 1=37.6%, 2=10%	495.62	21.73	0.0681	0	0.9729	0.9753	262	67.02
Mortality								
Mortality = 6%	490.14	37.23	0.0711	0	0.9764	0.9794	262	76.08
Mortality = 10%	465.62	59.17	0.0277	0	0.9688	0.9716	262	59.25
Mortality = 12%	249.02	139.96	0.0045	0.011	0.9351	0.9450	262	33.20
57-year, 10% (no catastrophes)	447.89	69.05	0.0411	0	0.9699	0.9732	262	61.12
57-year, 11% (no catastrophes)	422.94	92.74	0.0307	0	0.9641	0.9677	262	54.01
Catastrophes (vars. re: chemical spill)								
<i>P</i> = 5%, survivorship = 0.90, <i>K</i> = 500	486.53	35.01	0.0464	0	0.9737	0.9761	262	69.00
<i>P</i> = 5%, survivorship = 0.50, <i>K</i> = 500	315.10	176.94	0.0188	0	0.9364	0.9489	262	39.34
<i>P</i> = 5%, survivorship = 0.90, <i>K</i> = 300	288.58	26.70	0.0472	0	0.9648	0.9688	262	49.91
<i>P</i> = 5%, survivorship = 0.50, <i>K</i> = 300	192.89	101.89	0.0162	0.04	0.9273	0.9414	262	29.61
<i>P</i> = 2%, survivorship = 0.75, <i>K</i> = 500	477.92	52.13	0.0469	0	0.9732	0.9761	262	68.37
<i>P</i> = 2%, survivorship = 0.50, <i>K</i> = 500	445.35	98.47	0.0379	0	0.9672	0.9696	262	58.45
<i>P</i> = 2%, survivorship = 0.75, <i>K</i> = 300	290.14	22.17	0.0450	0	0.9633	0.9677	262	48.35
<i>P</i> = 2%, survivorship = 0.50, <i>K</i> = 300	255.89	68.59	0.0370	0	0.9563	0.9620	262	42.04
Carrying capacity								
<i>K</i> = 300	285.20	32.94	0.0492	0	0.9645	0.9690	262	49.87
<i>K</i> = 1,000	964.05	100.99	0.0489	0	0.9799	0.9813	262	92.27
Decrease of 0.16%/yr for 50 yrs, SD = 0	445.75	35.04	0.0509	0	0.9735	0.9775	262	68.24
Decrease of 1.00%/yr for 50 yrs, SD = 0	245.31	14.82	0.0500	0	0.9622	0.9677	262	46.55
Decrease of 0.16%/yr. for 50 yrs; SD=50	421.56	47.60	0.0490	0	0.9717	0.9743	262	64.05
Decrease of 1.00%/yr for 50 yrs, SD = 50	194.60	41.35	0.0501	0	0.9536	0.9586	262	38.80
Decr., 1.00%/yr; 50 yrs, mortality up 20%	231.13	23.53	0.0309	0	0.9581	0.9659	262	42.73
Decr., 1.00%/yr, 50 yrs; recruit. down 20%	229.89	35.50	0.0271	0	0.9606	0.9670	262	45.93
Supplementation								
5M + 5F/year, years 5-24	482.37	47.40	0.0495	0	0.9802	0.9834	262	91.15
57-year data								
With catastrophes	446.02	71.03	0.0405	0	0.9664	0.9684	262	58.56
No catastrophes	462.96	56.43	0.0522	0	0.9718	0.9749	262	65.43
Mortality = 12%	362.74	143.72	0.0180	0	0.9447	0.9539	262	42.78
Mortality = 6%	479.86	38.64	0.0875	0	0.9760	0.9775	262	75.17

^a All scenarios were run for 100 simulations and for 100 years unless otherwise noted.

^b Due to supplementation, the final alleles value has only relative meaning.

drift (e.g., loss of genetic diversity such as Major Histocompatibility Complex, MHC, genes).

Age of First Breeding: Increasing the age of first breeding from 4 to 5 years old decreased r by nearly 25% but did not have a significant impact on the viability of the population within the 100-year timeframe.

Maximum Age: The maximum age for the cranes was reduced from the standard 40 to 30, but this had little effect on the results. This is because cranes in the higher age classes are few in number and are therefore not making a large contribution to the flock productivity.

Brood Size/Productivity: The percent of brood size 0 was increased to 60 and then to 67 (with brood size 1 decreased to 40 and 33, respectively) to examine the effects of lower recruitment rates on the population. The first level of reduction in productivity had only minor impacts on the population ($N = 479.62$, $r = 0.0367$). The second level of reduced productivity led to a decrease in N (402.73), a large decrease in r (0.0159), and a 0.001 probability of extinction. These results indicate that the percentage of successful nests is an important parameter in maintaining the flock's growth. Therefore, if the cranes experience sustained decreased recruitment in the future (e.g., during drought years), management strategies must address the issue of productivity (see twinning below).

Twinning: In these variations, it was assumed that the flock is allowed to have twins instead of the current practice of removing surplus eggs from the nests of breeding pairs. For the first twinning variation, inputs were based on actual twinning data from 1938 to 1967 where the estimated brood size percentages were 0 = 41.7%, 1 = 50.8%, and 2 = 7.5%. As illustrated in Fig. 1, in this simulation the population reaches the set carrying capacity of 500 very quickly (about 20 years), and r shows a substantial increase from the standard run (0.0842 vs. 0.0498). This simulation was repeated for 1,000 iterations with very similar results.

In a second series of twinning variations, the standard run value for brood size 0 (52.4%) was used so that the effect of twinning could be compared to the standard run with all other variables held constant. Under these conditions, when brood size 2 was set at 6.1% (the expected value based on the historic twinning ratio), the growth rate of the population was 0.0614 as compared to the standard run value of $r = 0.0498$. This result indicates that allowing twinning may result in a notable increase in the rate of population growth. Other parameters such as final population size and genetic diversity did not change appreciably from the standard run. The sensitivity runs, varying the brood size 2 percentage, had predictable effects (see Table 3). With low twinning (brood size 2 = 2%), the growth rate ($r = 0.0544$) was higher than the standard run but lower than the run with the best estimate

of the twinning rate if twinning were allowed. With high twinning (brood size 2 = 10%), the growth rate was predictably higher ($r = 0.0681$). Again, in all twinning variations, parameters other than growth rate did not change appreciably from the standard run.

Mortality: Simulations were run varying the level of mortality from the standard 8% down to 6%, and up to 10% and 12% to determine the population's sensitivity to this parameter. A notable result from these simulations was that at 12% mortality, $r = 0.0045$, which was the lowest growth rate for any scenario in the AWP population viability assessment. This outcome indicates that, given the other standard parameters, mortality rates cannot be allowed to increase much beyond 12% if the flock is to remain viable. At 12% mortality, allelic diversity decreases much farther than in the standard run.

Catastrophes: The probability of a chemical spill catastrophe was increased from 2% to 5% with no remarkable changes in outcome. When the probability of a chemical spill is maintained at the standard (2%), but survivorship is decreased to 0.5, r decreases to 0.0379. When the 2 parameters are combined (an increase in catastrophe probability and a decrease in survivorship), the resultant population size decreases to 315, and r decreases still further to 0.0188. However, even in the latter case, r remains positive and the management goal of maintaining 40 breeding pairs is still achievable. (Also see the results of multiple parameter variations below). VORTEX assumes no long-term effects of catastrophes. That is, the effects on reproduction and mortality are felt only in the year in which the catastrophe occurs.

Carrying Capacity: A decrease in the carrying capacity from the standard of 500 down to 300 resulted in a final population size of 285.2. In this simulation, the average growth rate (0.0492) was almost exactly the same as in the standard run (0.0498). The major negative effect of the reduced carrying capacity (other than placing a cap on the population size) was the loss of allelic diversity (49.87 final alleles vs. 70.68 final alleles for the standard run). When the carrying capacity was increased to 1,000, the final population reached 964.05, there was no notable change in r from the standard run, and retained allelic diversity was maximized (final alleles = 92.27). [Note: the r calculated by VORTEX is based on population growth prior to truncation due to limited carrying capacity, so unless K becomes very small, r is not usually affected by changes in carrying capacity.]

Trend in Carrying Capacity: A series of simulations was conducted incorporating a trend of decreased carrying capacity over time (e.g., if the amount of fresh water decreases in the cranes' wintering grounds). None of the decreases in K modeled over time produced any noteworthy

impacts on the viability of the flock. That is, although final population sizes decreased with the decreasing K , population growth rates (r) remained as high as with the standard run. There were, however, negative impacts on allelic diversity in the simulations that included a 1% per year decrease in carrying capacity for a period of 50 years. Predictions about carrying capacity and its trends are extremely hard to make because, over time, additional wintering habitat may become more or less suitable and the cranes may or may not expand into alternative areas from those they currently occupy.

Supplementation: Supplementing the AWP showed no notable differences in the population size, or in the rate of growth, by the end of 100 years when compared to the standard run. Also, the apparently higher level of preservation of genetic diversity (both heterozygosity and unique alleles) in this simulation is misleading because, as previously noted, VORTEX treats supplemental animals as if they were unrelated to the receiving population and, in the case of the AWP, this assumption is not true. In general, the results of the supplementation simulation support the current management decision not to supplement the AWP.

Multiple Parameter Variations of the Standard Run.—Based on the results of the standard run and the initial variations, combinations of parameters were varied within single simulations.

Catastrophe and Carrying Capacity: When the effects of an increased chemical spill catastrophe probability ($P = 5\%$) were combined with a lower carrying capacity ($K = 300$), the final population size dropped to 288.58 but r remained high (0.0472). Another variation on this scenario was simulated with the assumption of a greater impact on survivorship (value = 0.5) in addition to increased probability. This combination produced the following results: final population size dropped to 192.89, r decreased to 0.0162, there was a 4% probability of extinction, and final unique alleles dropped to 29.61. The combined effects of increased probability and severity of catastrophe and lowered carrying capacity clearly impact the population in terms of lowering both N and r , and decreasing genetic diversity. This result suggests that the flock is put at substantial risk if the impacts of catastrophes are greater than expected and if the carrying capacity of the wintering grounds is reduced.

Trend in Carrying Capacity and Increasing Mortality or Decreasing Recruitment: When increased mortality (by 20%) or decreased recruitment (by 20%) were modeled simultaneously with an annual 1% decrease in K (over 50 years), there were noticeable reductions in the growth rate of the population from the standard of $r = 0.0498$ to $r = 0.0309$ and $r = 0.0271$, respectively. In addition, both of these simulations resulted in notably decreased allelic diversity and heterozygosity. However, even with these negative effects,

the population remained viable.

Simulations Based on the 57-year Data Set.—The standard run is based on the 20-year data set (1975–95) for the AWP. Simulations were run by substituting some of the standard inputs with values derived from the 57-year data. As noted earlier, there was a logical rationale for either excluding or including catastrophes in these simulations. Therefore, simulations were run both ways. The results of these runs were fairly consistent with those of the standard run. Without catastrophes, the growth rate with the 57-year data set was somewhat higher ($r = 0.0522$) than in the standard run. When catastrophes were included, the growth rate with the 57-year data set was somewhat lower ($r = 0.0405$) than the standard run. The impacts of varying mortalities, with the 57-year data set, were similar to those variations with the 20-year data set.

Observations on Heterozygosity.—A general goal for the management of endangered species is to maintain 90% of the original population's genetic diversity for 100 years (Soulé et al. 1986). All of the variations modeled in this analysis appear to meet this goal; however, the VORTEX program assumes that the 1995 population begins with 100% heterozygosity, whereas in actuality it begins with only approximately 87% heterozygosity (87% is the final value derived from the 1991 PVA, which included the effects of the 1941 bottleneck, see Mirande et al. 1991). The resultant values of observed heterozygosity were converted into values reflecting the number of autozygous alleles remaining in the population by calculating 1 minus the inbreeding coefficient (F). The range of values for F falls between 0.0665 and 0.0141. A value of 0 implies that there is no inbreeding; a value of 1 implies that the population is totally inbred. The results in this analysis remain very close to 0, indicating that the population is not significantly inbred. Based on this PVA, the genetic diversity of the AWP appears to be in good standing. VORTEX underestimates inbreeding however (see Methods). The simulations are based on the assumption that the AWP starts with 131 unique lines in year 1 rather than the less than 14 unique lines that survived the population bottleneck of 1941.

Observations on Allelic Diversity.—The founding population in this analysis—the 131 cranes of the AWP in the spring of 1995 (see Appendix B)—are assigned 262 unique founder alleles in the VORTEX program. All variations carried out on the population revealed great losses in the number of alleles over time. The parameter variations such as severe catastrophes and high mortality rates had particularly devastating effects on allelic diversity. Carrying capacity set at 1,000 as well as the supplementation scenario resulted in the greatest maintenance of unique alleles, but even these numbers were less than one-half of the founder alleles (and, as noted above, the supplementation simulation

overestimates diversity because of the false assumption that the supplemental birds are not related to the receiving population). These low values for final alleles can be expected due to the genetic drift associated with small populations and the fact that small populations are more sensitive to stochastic variation and therefore more likely to lose individuals with unique alleles. The loss in allelic diversity may explain the high vulnerability of the species to disease (e.g., the EEE outbreak in the captive flock and tuberculosis in the Gray's Lake population and the AWP). [Note again: VORTEX assumes that the 131 birds in the starting population are unrelated; therefore, 262 unique alleles are possible at any 1 locus. In fact, if less than 14 unique lines survived the 1941 bottleneck, the maximum number of unique alleles at any 1 locus would be 28.]

Analysis of FP VORTEX Simulation Results

As with the AWP analysis, this discussion covers only those simulations which reveal notable outcomes. Table 4 presents the results of all simulations.

Standard Run.—As expected, the FP exhibits a steady increase in flock size during the years of supplementation. However, as soon as supplementation is terminated at year 20, the growth rate decreases, leaving the final population at one-half the designated carrying capacity (162 individuals, $SD = 90.51$), with an average post-supplementation growth rate of 0.0026, and with a 1.1% chance of extinction over 100 years. In light of these findings, another simulation was run using the standard inputs, but this time for 200 years, to gain more insight into the population trends. The 200-year simulation showed a 17% chance of extinction over those years and a final population size of 136 individual cranes, with the average r becoming negative (-0.0001). Based on the outcomes of these standard runs, the post-supplementation population growth rate is an issue of great concern. Much of the analysis using the following variations focuses on which parameters can be varied to achieve positive growth rates beyond the supplementation years.

Single Parameter Variations on the Standard Run.—Because the years of supplementation have positive values for r in every simulation (as would be expected), the discussion of results for each variation focuses on the years following supplementation.

Inbreeding Depression: Incorporating inbreeding depression into the model produces a negative growth rate for the population by the end of 100 years. The negative value, however, is only slightly below the standard run final r value, as are the resultant levels of genetic and allelic diversity. From this simulation, it appears that inbreeding depression produces mild effects on the population which can be

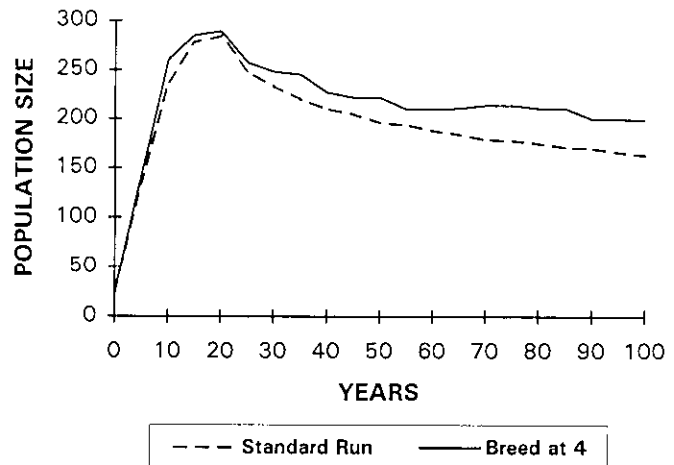


Fig. 2. VORTEX simulation showing effect of early breeding on the future of the Florida whooping crane population.

significant if growth rates are low.

Age of First Breeding: Lowering the age of first breeding from 5 to 4 years increases the growth rate of the population notably above the r of the standard run (0.0152 vs. 0.0026). On the other hand, raising the breeding age from 5 to 7 has a clearly detrimental effect on the growth rate ($r = -0.0196$). These results indicate that breeding age is a variable that can have significant impacts on the population (Fig. 2).

Maximum age: Reducing the maximum age from 40 to 30 to 20 had a slightly adverse impact on the number of individuals remaining in the population at the end of 100 years. A maximum age of 20 leaves the population with only 129 cranes. However, these variations did not notably impact the growth rates, or amounts of genetic or allelic diversity as compared to those of the standard run. For these reasons, maximum age was ruled out as a sensitive parameter.

Productivity: This parameter exhibited a great deal of sensitivity on the down side. Decreasing productivity by 10% dropped the growth rate to -0.0117 and the final population size to 108 individuals. Under these conditions, the flock had a 7% probability of going extinct. Alternatively, increasing the productivity by 10% produced negligible positive effects on the final population size and growth rate, suggesting that investing in techniques to increase productivity will not yield great rewards.

Mortality: Reducing adult mortality from 10% to 8% produced a notably positive growth rate ($r = 0.0279$). This was the highest growth rate exhibited in a single parameter variation. This scenario was re-run for 200 years to confirm the longevity of this growth rate, and similar results were achieved. On the other hand, increasing the adult mortality to 12% reduced the population's growth rate to $r = -0.0223$.

Table 4. VORTEX simulation of the Florida whooping crane population over 100 years (or 200 years as indicated). Refer to Table 2 for parameter values in standard run.

Description ^a	Final population		Growth rate (<i>r</i>)		<i>P</i> of extinction	Expected heterozygosity	Observed heterozygosity	Final alleles ^b
	<i>N</i>	SD	With supplementation	Without supplementation				
Standard run (1,000 simulations)								
100-year run	162.58	90.51	0.1529	0.0026	0.011	0.9406	0.9572	36.83
200-year run	136.40	85.91	0.1502	-0.0001	0.17	0.8627	0.8769	14.99
Inbreeding depression								
Heterosis, 3 lethal equivalents	122.37	86.30	0.1539	-0.0053	0.02	0.9270	0.9517	32.21
Age of first breeding								
M=4, F=4	199.16	79.33	0.1658	0.0152	0	0.9519	0.9604	39.52
M=7, F=7	89.47	80.62	0.1362	-0.0196	0.11	0.9180	0.9500	27.60
Maximum age								
M=20, F=20	129.66	86.96	0.1530	-0.0081	0.03	0.9286	0.9457	29.05
M=30, F=30	150.07	91.79	0.1552	-0.0003	0.03	0.9363	0.9558	33.76
Productivity								
Low (decreased 10%)	108.87	75.65	0.1522	-0.0117	0.07	0.9258	0.9510	29.80
High (increased 10%)	169.53	85.95	0.1593	0.0067	0.01	0.9425	0.9557	37.26
Mortality								
Non-chick mortality = 8% (100 year run)	252.86	56.18	0.1683	0.0279	0	0.9679	0.9740	55.60
Non-chick mortality = 8% (200 year run)	255.67	58.89	0.1647	0.0279	0	0.9330	0.9396	27.81
Non-chick mortality = 12%	65.74	66.40	0.1408	-0.0223	0.06	0.8812	0.9236	20.65
Chick mortality = 10%	231.63	70.26	0.1608	0.0212	0	0.9588	0.9689	44.27
Non-chick mortality = 8%; chick mort. = 10%	261.30	48.17	0.1717	0.0391	0	0.9659	0.9708	51.34
Catastrophes								
No catastrophes	256.61	42.94	0.1717	0.0327	0	0.9693	0.9752	56.45
Disease, <i>P</i> = 20%, survivorship = 0.75	45.00	46.10	0.1380	-0.0309	0.17	0.8463	0.9200	15.34
Disease, <i>P</i> = 5%, survivorship = 0.75	218.40	72.79	0.1655	0.0148	0	0.9588	0.9698	45.99
Disease, <i>P</i> = 10%, survivorship = 0.90	239.26	63.88	0.1620	0.0239	0	0.9651	0.9714	51.75
Hurricane, <i>P</i> = 0.66%, survivorship = 0.90	160.05	84.92	0.1518	-0.0018	0.06	0.9408	0.9561	35.48
Stable age distribution	165.43	86.42	0.1563	0.0009	0.02	0.9477	0.9627	36.74
Carrying capacity								
<i>K</i> =150	75.40	45.22	0.1913	-0.0037	0.04	0.8744	0.9118	17.30
<i>K</i> =500	270.86	139.94	0.1472	0.0030	0	0.9611	0.9749	58.57
<i>K</i> =800	419.61	230.99	0.1444	0.0047	0	0.9735	0.9765	81.05
<i>K</i> =1,000	510.85	301.41	0.1458	0.0052	0.01	0.9715	0.9807	94.62
Supplementation								
30 birds per year for 5 years	130.95	93.64	0.3449	-0.0029	0.09	0.8973	0.9180	23.15
20 birds per year for 10 years	155.51	92.64	0.1927	0.0019	0.04	0.9192	0.9373	27.65
30 birds per year for 10 years	151.84	89.42	0.2289	0.0016	0.02	0.9285	0.9480	30.88
30 birds per year for 20 years (standard run)	162.58	90.51	0.1529	0.0026	0.011	0.9406	0.9572	36.83
40 birds per year for 20 years	166.40	88.70	0.1770	0.0036	0	0.9464	0.9580	38.25
Combination scenario: best case								
Non-chick mortality = 8%, breeding age = 4, catastrophic disease probability = 5%, high productivity (+10%), suppl. with 40/yr	290.93	22.79	0.2218	0.0661	0	0.9691	0.9736	56.93
Combination scenario: low mortality with worst case for other parameters								
Non-chick mortality = 8%, breeding age = 7, catastrophic disease probability = 20%, low productivity (-10%), suppl. with 30 for 5 years	21.67	21.74	0.3381	-0.0405	0.54	0.7749	0.8778	9.20
Combination scenario: best case, but 12% adult mortality								
Non-chick mortality = 12%, breeding age = 4, catastrophic disease probability = 5%, high productivity (+10%), suppl. with 40/yr	230.52	66.74	0.1858	0.0201	0	0.9580	0.9642	43.14
Combination scenario: best case, but 15% adult mortality								
Non-chick mortality = 15%, breeding age = 4, catastrophic disease probability = 5%, high productivity (+10%), suppl. with 40/yr	101.97	85.33	0.1702	-0.0146	0.06	0.9088	0.9446	24.00

^a All scenarios were run for 100 simulations and for 100 years unless otherwise noted.

^b Due to supplementation, the final alleles value has only relative meaning.

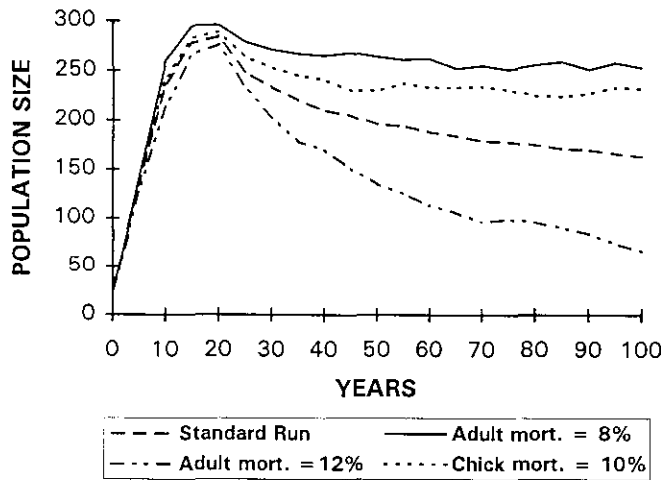


Fig. 3. VORTEX simulation showing effects of variation in mortality on the future of the Florida whooping crane population.

Reducing chick mortality from 26.7% to 10% increased the growth rate from 0.0026 to 0.0212, and the final population size increased from 162.58 to 231.63. With chick mortality at 10% and adult mortality at 8%, the growth rate climbed to 0.0391, and the final population size was 261.30. From these results, it appears that chick and adult mortality rates are variables of the FP that should receive intensive monitoring and close management attention (Fig. 3).

Catastrophes: The probability and severity of disease in the FP are issues of great concern. When the probability of a disease catastrophe is increased from 10 to 20 times in 100 years, the flock has a 17% chance of extinction. Alternatively, decreasing the probability to 5% yields positive results as compared with the standard run ($N = 218.40$, $r = 0.0148$). Also, decreasing severity of catastrophic disease impact from 25% mortality to 10% mortality has an even more positive effect than reducing the probability of disease ($N = 239.26$, $r = 0.0239$). It appears that disease is a very significant variable for the FP. Hurricanes, on the other hand, do not have as severe an impact on the viability of the population when the probability of their occurrence is increased. When a simulation is conducted with no catastrophes included, the results are very positive for the FP: the final population size is 256.61 and the population growth rate is 0.0327 after supplementation has ceased (Fig. 4).

Stable Age Distribution: This variation was run to verify that inputting the actual age distribution of this population did not hinder the ability of VORTEX to model the population accurately. The results were very similar to those of the standard run.

Carrying Capacity: Varying the carrying capacity

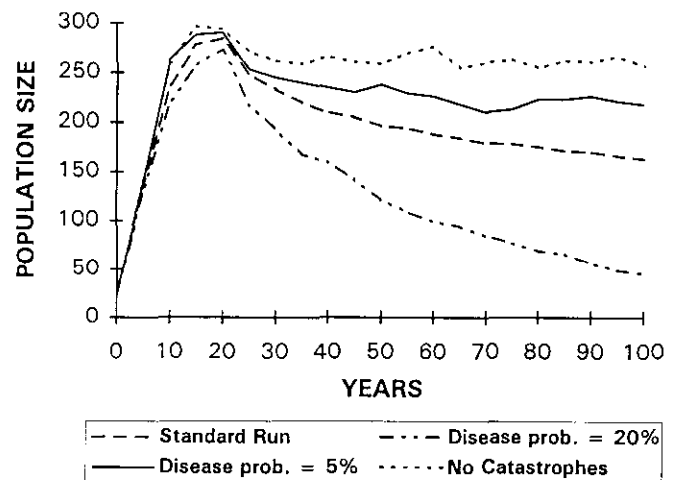


Fig. 4. VORTEX simulation showing effects of catastrophes on the future of the Florida whooping crane population.

produced fairly predictable results. Decreasing K yielded a smaller final population with a negative growth rate, and increasing K yielded larger final populations with slightly higher growth rates than the standard run. It is interesting to note that, in all these scenarios, the population grew only to approximately one-half of the designated carrying capacity. This outcome was probably due to the large standard deviations in the distributions of final population sizes in these simulations. The large standard deviations, in themselves, constitute an index of the instability of final population size.

Supplementation: Variations in the supplementation scenario yielded negligible differences over the long run (Fig. 5). Varying supplementation to take place over longer or shorter periods of time had immediate effects on the population within the first 5 to 20 years but did not have notable positive or negative effects on the population by the end of 100 years. These results, and those of the adult mortality variations, suggest that if adult mortality is high, supplementation will not be helpful over the long run. However, if adult mortality is low, supplementing at low levels over 5, 10, or 20 years will be helpful in establishing a viable flock. Supplementation may also be an important insurance strategy during particular periods of high mortality or during periods when there are insufficient data to discern clear trends in other critical parameters. For example, supplementation may sustain the population during an initial period until adult mortality can be reduced.

Multiple Parameter Variations on the Standard Run.—Results from the single parameter variation simulations indicate that adult mortality rate was one of the most significant parameters for the FP. Therefore, the

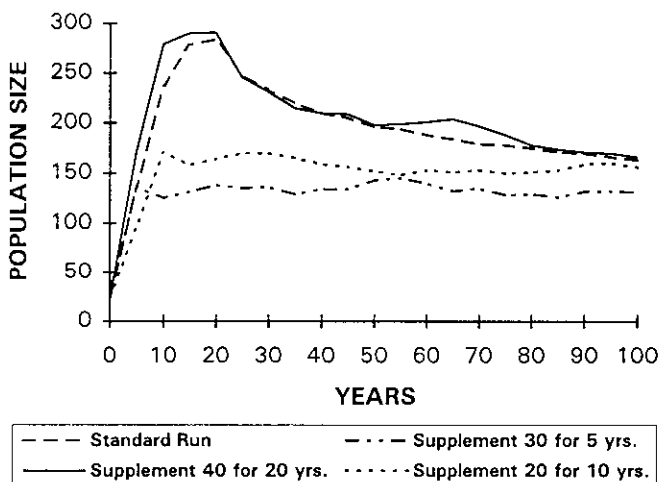


Fig. 5. VORTEX simulation showing effects of variation in supplementation rate on the future of the Florida whooping crane population.

multiple parameter variations were designed to test scenarios centering around variations in the adult mortality rate (Fig. 6). The “best case” scenario was to model adult mortality at 8% with an age of first breeding of 4, disease catastrophe probability at 5%, productivity increased by 10%, and supplementing 40 birds per year for 20 years. The impacts of these variations were strongly positive. The final population came within 10 cranes of the carrying capacity ($K = 300$). The growth rate following supplementation was 0.0661, and there was a 0% probability of extinction. This scenario was also modeled using all of the “best case” parameters except for adult mortality, which was set at 12%. In this simulation, the population remained viable over the 100-year time period with a final population size of 230.52 and an average growth rate of 0.0201. However, when mortality was increased to 15%, in combination with all the other “best case” parameters, the simulation resulted in a negative growth rate (-0.0146) with a 6% chance of extinction. The results of this series of simulations indicate that under certain conditions, the negative effects of high adult mortality rates can be overcome; however, there is a threshold at which point adult mortality rates dominate.

One final simulation was run which included a “best case” adult mortality rate (8%) and “worst case” values for the other 4 parameters listed above (i.e., age of first breeding = 7, disease catastrophe probability = 20%, productivity decreased by 10%, and supplementing 30 birds per year for 5 years). It is apparent from these results ($N=21.67$, $r = -0.0405$) that a low adult mortality rate is not enough to save the population if other important parameters are at values significantly worse than the expected values. The probability of extinction in this case was 54%.

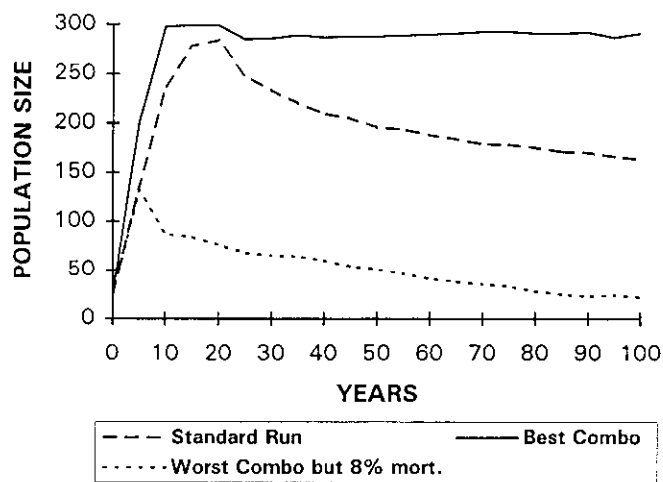


Fig. 6. VORTEX simulation showing effects of combination scenarios (see Table 4) on the future of the Florida whooping crane population.

CONCLUSIONS

AWP Viability Assessment

The 1991 PVA concluded that the “population is projected to have a very low (less than 1%) probability of extinction within the next 100 years,” with a growth rate of 0.028 when surplus eggs are removed and a growth rate of 0.046 when they are not (Mirande et al. 1991:4,28). The findings of the present analysis, which took into account new data available since 1991, additional expert opinions on parameters, and new information on environmental scenarios, also indicate that the AWP has a very low probability of extinction with a growth rate of 0.0498 with continued egg removal and a growth rate of 0.0842 when twinning is allowed. If the selected standard parameters of this PVA are indeed accurate and will continue to be accurate in the coming years, the AWP should clearly meet the recovery goal of a minimum of 40 breeding pairs for 10 years or more before the year 2020 (Fig. 1).

In the simulations described here, the most notable positive effects on population growth were caused by twinning and by decreased mortality. If historic rates of twinning re-occur, discontinuing the current practice of egg removal could have a significant impact on the rate of population increase. If mortality rates are reduced, the population will also reap the benefits of a higher growth rate.

The most negative impacts on the population are realized when the severity and probability of a chemical spill catastrophe are increased, when the carrying capacity is lowered to 300, and when mortality rates increase or recruitment rates decrease. Under no conditions, however,

did the population experience a negative growth rate, and only when mortality was increased to 12%, or when increased probability and severity of catastrophe were combined with decreased carrying capacity, did the results show a notable probability of extinction.

As they have in the past, human actions can strongly influence the future prospects of the AWP. Following are some actions that can keep the odds stacked in favor of AWP survival and growth: protecting against catastrophic losses, maintaining potential for expanded habitat, reducing mortality (e.g., marking powerlines and securing/restoring safe stop-over locations for migrating birds), and increasing recruitment (e.g., allowing twinning and managing the blue crab population at Aransas). If these actions can yield even more favorable parameters than were assumed in the best estimates used for this analysis, the AWP will reach carrying capacity more quickly, with less loss of heterozygosity and rare alleles, and the flock will have even better chances of maintaining a self-sustaining viable population in the future.

FP Viability Assessment

Two major questions concerning the potential success of the Florida reintroduction experiment are: (1) Can adult mortality from predation and disease be reduced? and (2) Will the captive-reared birds breed naturally in the wild? Concerning the first question, changing release sites to avoid concentrations of bobcats (*Lynx rufus*) has already produced a notable drop in early mortality (Nesbitt et al. 1997), and it is hoped that these gains will endure as the birds reach adulthood. Also, research is currently underway to assess the effects of pre-release inoculations against disease. (Inoculations may be only a stop-gap measure because chicks hatched in the wild will not be protected and titers in released birds may drop over time).

Concerning the second question, at this writing, there are two rays of hope already on the horizon: the pairing of 2-year-olds and the nesting attempt of 3-year-old whooping cranes during the spring of 1995 at Kissimmee (Nesbitt et al. 1997) and the natural breeding behavior that has been observed in released, captive-reared sandhill cranes (Duan 1994).

Even if the introduced whooping cranes breed successfully, the simulations reported here indicate that the Florida project has borderline prospects for long-term success (Fig. 2). If our standard ("best-estimate") parameters are close to correct, growth of the flock will be very slow (or even negative) after supplementation efforts have ceased. As Table 4 indicates, each of several key variables has the potential to "make or break" the Kissimmee experiment. In positive combination, these key variables will provide a

strong base for success in Florida. If adult mortality is 1 or 2 percentage points lower than our best-estimate scenario, prospects are favorable as long as breeding (i.e., productivity and age of first breeding) and disease risk remain at or near best-estimate values. Even if adult mortality is at, or slightly above, the standard value, as long as breeding and disease risk are somewhat better than the standard, the outcome appears good. On the negative side, if mortality rates for young birds are higher than our best estimate, or if adult mortality approaches 12% annually, then all other key variables will have to be at better-than-standard values to avoid extinction of the experimental population.

The amount and duration of supplementation have only minimal effects on the prospects for success in Florida. It is the enduring rates of mortality, breeding, and disease risk that will determine the outcome of the experiment. Fortunately, there are some management actions that may have an influence on the values of these key variables. As noted above, careful selection of release sites can affect the mortality resulting from bobcat predation. Release site selection can also consider the proximity of other birds that may function as role models for introduced cranes in terms of where to roost safely and where to find food, for example. Ongoing research on vaccines and health monitoring may help to minimize the risk of a catastrophic disease outbreak, and selective releases of new birds can help to balance the sex ratio, increase the genetic diversity, and bolster the flock against periods of high adult mortality. All of these management actions have the potential to push the odds in favor of success. Thus, with careful monitoring of the key variables, and creative interventions to influence them positively, the Florida reintroduction experiment could provide a major boost to the prospects for long-term recovery and survival of the whooping crane.

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Appendix A. Numbers, mortality, and recruitment of whooping cranes in the Aransas/Wood Buffalo population. Data collected during 57 years at Aransas National Wildlife Refuge, Texas.

Year	Total cranes arriving at ANWR	Cranes not returning next fall	Mortality rate (non-chicks)	Adults arriving	Chicks arriving	Recruitment (chicks/total cranes)
1938/39	18	3	0.16666667	14	4	0.22222222
1940	22	1	0.04545455	15	7	0.31818182
1941	26	12	0.46153846	21	5	0.19230769
1942	16	1	0.0625	14	2	0.125
1943	19	3	0.15789474	15	4	0.21052632
1944	21	6	0.28571429	16	5	0.23809524
1945	18	0	0	15	3	0.16666667
1946	22	0	0	18	4	0.18181818
1947	25	0	0	22	3	0.12
1948	31	4	0.12903226	25	6	0.19354839
1949	30	0	0	27	3	0.1
1950	34	8	0.23529412	30	4	0.11764706
1951	31	11	0.35483871	26	5	0.16129032
1952	25	6	0.24	20	5	0.2
1953	21	0	0	19	2	0.0952381
1954	24	3	0.125	21	3	0.125
1955	21	1	0.04761905	21	0	0
1956	28	6	0.21428571	20	8	0.28571429
1957	24	2	0.08333333	22	2	0.08333333
1958	26	3	0.11538462	22	4	0.15384615
1959	32	1	0.03125	23	9	0.28125
1960	33	3	0.09090909	31	2	0.06060606
1961	36	2	0.05555556	30	6	0.16666667
1962	39	7	0.17948718	34	5	0.12820513
1963	32	6	0.1875	32	0	0
1964	33	1	0.03030303	26	7	0.21212121
1965	42	6	0.14285714	32	10	0.23809524
1966	44	6	0.13636364	36	8	0.18181818
1967	43	4	0.09302326	38	5	0.11627907
1968	48	4	0.08333333	39	9	0.1875
1969	50	2	0.04	44	6	0.12
1970	56	5	0.08928571	48	8	0.14285714
1971	57	3	0.05263158	51	6	0.10526316
1972	59	13	0.22033898	54	5	0.08474576
1973	51	4	0.07843137	46	5	0.09803922
1974	49	2	0.04081633	47	2	0.04081633
1975	49	0	0	47	2	0.04081633
1976	57	0	0	49	8	0.14035088
1977	69	7	0.10144928	57	12	0.17391304
1978	72	4	0.05555556	62	10	0.13888889
1979	75	5	0.06666667	68	7	0.09333333
1980	76	4	0.05263158	70	6	0.07894737
1981	78	7	0.08974359	72	6	0.07692308
1982	73	6	0.08219178	71	2	0.02739726
1983	73	5	0.06849315	67	6	0.08219178
1984	75	4	0.05333333	68	7	0.09333333
1985	86	5	0.05813953	71	15	0.1744186
1986	97	8	0.08247423	81	16	0.16494845
1987	110	1	0.00909091	89	21	0.19090909
1988	134	15	0.1119403	109	25	0.18656716
1989	138	12	0.08695652	119	19	0.13768116
1990	146	13	0.0890411	126	20	0.1369863
1991	146	22	0.15068493	133	13	0.0890411
1992	132	11	0.08333333	124	8	0.06060606
1993	136	9	0.06617647	121	15	0.11029412
1994	143	18	0.12587413	127	16	0.11188811
1994/95	132 ^a	?	?	125	7	0.0530303
Totals	3,151	295	5.71041907	2,870	413	7.81716469

Weighted mean mortality (295/3,151) = 0.09362107

Weighted mean recruitment (413/3,283) = 0.12579957

^a Not included in column total.

Appendix B. Estimated actual age distribution of the Aransas/Wood Buffalo whooping crane population in 1994-95.

Year	Age	VORTEX age class	No. of chicks	(A) Annual survival rate ^a	(B) Previous years' survival product ^{a,b}	(C) Cumulative survival (A × B) ^a	Live birds (C × No. of chicks) ^a	Rounding remainder ^c	Adjusted total ^c
1995	0	1	7	1.00	NA	1.00	7.00	0.00	7
1994	1	2	16	0.87	1.00	0.87	13.92	0.00	14
1993	2	3	15	0.93	0.87	0.81	12.14	-0.08	12
1992	3	4	8	0.92	0.81	0.74	5.96	0.06	6
1991	4	5	13	0.85	0.74	0.63	8.18	0.02	8
1990	5	6	20	0.91	0.63	0.58	11.47	0.20	12
1989	6	7	19	0.91	0.58	0.52	10.03	-0.33	10
1988	7	8	25	0.89	0.52	0.47	11.57	-0.30	11
1987	8	9	21	0.99	0.47	0.46	9.77	0.27	10
1986	9	10	16	0.92	0.46	0.42	6.77	0.04	7
1985	10	11	15	0.94	0.42	0.40	5.92	-0.19	6
1984	11	12	7	0.95	0.40	0.38	2.66	-0.27	2
1983	12	13	6	0.93	0.38	0.35	2.12	0.40	3
1982	13	14	2	0.92	0.35	0.32	0.64	-0.48	0
1981	14	15	6	0.91	0.32	0.30	1.75	0.16	2
1980	15	16	6	0.95	0.30	0.28	1.71	-0.09	2
1979	16	17	7	0.93	0.28	0.26	1.82	-0.38	1
1978	17	18	10	0.94	0.26	0.25	2.44	0.44	3
1977	18	19	12	0.90	0.25	0.22	2.70	-0.12	3
1976	19	20	8	1.00	0.22	0.22	1.76	-0.42	1
1975	20	21	2	1.00	0.22	0.22	0.44	0.34	1
1974	21	22	2	0.96	0.22	0.21	0.42	-0.22	0
1973	22	23	5	0.92	0.21	0.19	0.97	0.20	1
1972	23	24	5	0.78	0.19	0.15	0.74	0.17	1
1971	24	25	6	0.95	0.15	0.14	0.86	-0.09	1
1970	25	26	8	0.91	0.14	0.13	1.02	-0.23	1
1969	26	27	6	0.96	0.13	0.13	0.75	-0.21	1
1968	27	28	9	0.92	0.13	0.12	1.08	-0.46	1
1967	28	29	5	0.91	0.12	0.11	0.55	-0.48	0
1966	29	30	8	0.86	0.11	0.09	0.76	0.07	1
1965	30	31	10	0.86	0.09	0.08	0.77	-0.17	1
1964	31	32	7	0.97	0.08	0.08	0.54	-0.40	0
1963	32	33	0	0.81	0.08	0.06	0.00	0.14	0
1962	33	34	5	0.82	0.06	0.05	0.25	0.14	0
1961	34	35	6	0.94	0.05	0.05	0.28	0.39	1
1960	35	36	2	0.91	0.05	0.04	0.09	-0.33	0
1959	36	37	9	0.97	0.04	0.04	0.35	-0.24	0
1958	37	38	4	0.88	0.04	0.04	0.14	0.11	0
1957	38	39	2	0.92	0.04	0.03	0.07	0.25	0
1956	39	40	8	0.79	0.03	0.03	0.19	0.32	1
1955	40	41	0	0.95	0.03	0.03	0.00	-0.49	0
1954	41	42	3	0.88	0.03	0.03	0.08	-0.49	0
1953	42	43	2	1.00	0.03	0.03	0.06	-0.41	0
1952	43	44	5	0.76	0.03	0.02	0.11	-0.35	0
1951	44	45	5	0.65	0.02	0.01	0.07	-0.24	0
1950	45	46	4	0.76	0.01	0.01	0.03	-0.17	0
1949	46	47	3	1.00	0.01	0.01	0.03	-0.14	0
1948	47	48	6	0.87	0.01	0.01	0.05	-0.11	0
1947	48	49	3	1.00	0.01	0.01	0.03	-0.08	0
1946	49	50	4	1.00	0.01	0.01	0.04	-0.04	0
1945	50	51	3	1.00	0.01	0.01	0.03	-0.01	0

^a Rounded.

^b B calculated as follows: e.g., for 1993, (1.00×0.87)=0.87; for 1992, (1.00×0.87×0.93)=0.81; for 1991, (1.00×0.87×0.93×0.92)=0.74; etc.

^c Rounding procedure suggested by R. C. Lacy (pers. commun.).

Appendix C. Mortality and recruitment in the Aransas/Wood Buffalo whooping crane population during 20 years, 1975-95.

Year	Total cranes arriving at ANWR	Cranes not returning next fall	Mortality rate (non-chicks)	Adults arriving	Chicks arriving	Recruitment (chicks/ total cranes)
1975	49	0	0	47 ^a	2 ^a	0.040816 ^a
1976	57	0	0	49	8	0.140351
1977	69	7	0.101449	57	12	0.173913
1978	72	4	0.055556	62	10	0.138889
1979	75	5	0.066667	68	7	0.093333
1980	76	4	0.052632	70	6	0.078947
1981	78	7	0.089744	72	6	0.076923
1982	73	6	0.082192	71	2	0.027397
1983	73	5	0.068493	67	6	0.082192
1984	75	4	0.053333	68	7	0.093333
1985	86	5	0.05814	71	15	0.174419
1986	97	8	0.082474	81	16	0.164948
1987	110	1	0.009091	89	21	0.190909
1988	134	15	0.11194	109	25	0.186567
1989	138	12	0.086957	119	19	0.137681
1990	146	13	0.089041	126	20	0.136986
1991	146	22	0.150685	133	13	0.089041
1992	132	11	0.083333	124	8	0.060606
1993	136	9	0.066176	121	15	0.110294
1994	143	18	0.125874	127	16	0.111888
1995	132 ^a	? ^a	? ^a	125	7	0.053030
20-year total	1,965	156	1.4338	1,809	239	2.3216
20-year mean		7.8	0.0717	90.45	11.95	0.1161
20-year SD		5.7149	0.0376	27.958	6.0537	0.0461
Weighted mean			0.0794			0.1167

^a Not included in 20-year means and standard deviations.