Population Viability Analysis (PVA) Report for the Species Meta-Population of Whooping Cranes (*Grus americana*)

Photo courtesy of Calgary Zoo

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Cover photo: Calgary Zoo

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A contribution of the IUCN/SSC Conservation Planning Specialist Group, in collaboration with the Whooping Crane International Recovery Team, the United States Fish and Wildlife Service, the Canadian Wildlife Service, and workshop participants.

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Section 1. Executive Summary

Population viability analyses (PVAs) were conducted for four distinct whooping crane populations using a stochastic, individual-based population model developed in the *VORTEX* 10.2.15 (Lacy and Pollak 2017) software program. Individual PVAs were conducted for the following populations:

1) Aransas-Wood Buffalo wild migratory population (AWBP)
2) Eastern migratory population (EMP)
3) Louisiana non-migratory population (LNMP)
4) Captive population (SSP)

Each of these populations has its own demographic rates, initial population structure, and management options (see Appendix II). Models were used to project population status under best estimated future conditions, conduct sensitivity testing, and examine viability under alternative management scenarios for each of these whooping crane populations. These results were combined to evaluate the potential for these four populations collectively to meet down-listing criteria and contribute to recovery of this species.

Population-specific PVA results
The *Aransas-Wood Buffalo population (AWBP)* is a large, wild self-sustaining migratory population of 400-500 cranes with historical annual growth of ~3.7% over the past 40 years. Potential changing future conditions that may impact these rates lead to some uncertainty in future population viability projections. An exploration of these factors over plausible values suggests that the two most influential impacts may be potential lower recruitment related to climate change and potentially higher mortality during migration due to increased development and other anthropogenic threats. If historical (past 40 years) and current conditions continue into the future, model projections indicate strong positive growth that is cyclic and includes some years of population decline. Inclusion of probable future threats predicted across its range, including Canadian breeding grounds, wintering grounds along the U.S. Gulf Coast, and semi-annual migration between these areas, project a gradual reduction in future annual growth rate to ~1.2%

The *Eastern migratory population (EMP)* is a reintroduced population of ~100 cranes established from captive-reared released cranes beginning in 2001. This relatively young reintroduced population winters in the Southeastern US and summers in Wisconsin, and has experienced relatively good survival but low reproductive success with no population growth since 2009 despite continued releases. Future survival and reproduction of these birds and their wild-hatched descendants is uncertain, which limits the value of PVA projections. Population projections based on the best estimates of demographic rates and incorporating this uncertainty exhibit high variability in population size, viability, and progress toward recovery, ranging from a large, viable population that meets down-listing criteria to a declining population with high risk of extinction. Most projections suggest the EMP may level off or decline for ~25 years once releases cease. Reproductive rates of mixed-origin and wild-hatched breeding pairs are a key factor impacting future EMP growth and viability. Even small, consistent losses of adult cranes due to human-related or other threats may have significant impacts on the population. Additional releases may improve the viability of the population provided overall reproductive rates improve.

The *Louisiana non-migratory population (LNMP)* is a newly established reintroduced population of ~60 cranes in Louisiana developed via annual releases of captive-reared juvenile cranes beginning in 2011. Some of these cranes have recently reached breeding age, and the first chicks were hatched in 2016. Given the young age and short history of this population, it is challenging to predict future demographic rates. Early nesting attempts by young pairs have been high but with a high rate of nest failure, with some improvement seen in 2018. With no further releases, the projected demographic and genetic viability of the LNMP is moderate and involves significant variation across the uncertainty in demographic rates with 9% risk of extinction over 100 years. Like the EMP projections, the population is projected to show some decline and a period of no growth for about 30 years once releases end; if the population persists it is projected to grow provided that reproductive success and survival of wild-hatched cranes is good. PVA results suggest that continued release of juveniles for at least several more years can provide short- and long-term benefits to the population and improve viability measures, provided that overall reproductive success improves and adult survival is good.

The *captive population* of ~160-200 cranes (depending upon season) was established from eggs collected from the Aransas-Wood Buffalo Population from 1967-1998 and is managed demographically and genetically by the Species Survival Plan® (SSP®) of the Association of Zoos and Aquariums (AZA). Most breeding and rearing has occurred at the five long-term breeding centers, which have produced cranes for release to establish the two reintroduced populations (EMP and LNMP). The recent closing of the largest breeding center at Patuxent limits the breeding and rearing capacity of the SSP until additional zoos expand to fill this gap. This population meets the genetic and demographic requirements to serve its two conservation roles as an insurance population against extinction and as a source population to provide juveniles for release, although it may not be able to meet the optimal number of juveniles desired for release for the next several years.

Recovery objectives and criteria for down-listing

The 2007 International Recovery Plan (CWS & USFWS 2007) outlines two primary objectives and measurable criteria for species down-listing for whooping cranes. This include:

- Objective 1: Establish and maintain self-sustaining populations of whooping cranes in the wild that are genetically stable and resilient to stochastic environmental events (by meeting Criterion 1, 1A or 1B).
- Objective 2: Maintain a genetically stable captive population to ensure against extinction of the species (by meeting Criterion 2).

These objectives can be met in one of three different ways. Criterion 1 for Objective 1 specifies the establishment of 160 cranes in the AWBP, and 100 cranes each in the EMP and LNMP, provided all three populations are self-sustaining at these levels for at least 10 years. Alternatively, down-listing can occur under Alternative Criterion 1A with self-sustaining populations of 400 cranes in the AWBP and 120 cranes in one additional (reintroduced) population. The final down-listing option, under Alternative Criterion 1B, is to establish a single, self-sustaining population of 1000 cranes in the AWBP. For all three scenarios, down-listing also requires that the SSP maintain 153 captive cranes to provide an insurance and source population for conservation purposes (Criterion 2) (see Section 6 for full text for Objectives and Criteria).

Down-listing under Criteria 1&2 (three wild populations, plus captive population) would provide multiple viable crane populations across the widest landscape and provide redundancy as protection against local catastrophic events. The AWBP already meets Criteria 1, and the SSP meets Criteria 2 as an insurance population. The two reintroduced populations are not currently self-sustaining, and will need better reproductive success and continued good survival to meet down-listing Criteria 1. Future releases will improve the probability of down-listing but are not sufficient without good survival and reproductive success. Management actions that improve these demographic rates are important components for population viability and eventual down-listing. The SSP is projected to be able to provide sufficient releases to contribute positively to the establishment of both reintroduced populations provided improved demographic rates in the future, with LNMP given priority if release numbers are limited.

Down-listing under Alternative Criteria 1A&2 (two wild populations, plus captive population) would provide a secondary viable crane population that extends the geographic distribution of the species and provides redundancy as protection against local catastrophic events. The AWBP already meets Criteria 1, and the SSP meets Criteria 2 as an insurance population. Neither of the two reintroduced populations are currently self-sustaining, and both of them will need better reproductive success and good adult survival to meet down-listing Alternative Criterion 1A. Future releases will improve the probability of down-listing but are not sufficient without good survival and reproductive success. Management actions that promote these demographic rates are important components for population viability and eventual down-listing. The SSP is projected to be able to provide the optimal number of releases to one reintroduced population to contribute to down-listing under this higher target, although it is not clear which of the two populations has the better probability of meeting down-listing criteria. An alternative strategy is to manage both populations for viability and with releases as under Criteria 1 until such time that future demographic rates are better understood and future realistic viability projections more reliable.

Down-listing under Alternative Criteria 1B&2 (single wild population, plus captive population) is an option if the establishment of additional wild self-sustaining populations through reintroduction is not successful. This would require the significant expansion of the original wild population in Aransas-Wood Buffalo National Park to buffer this single population against stochastic risks such as catastrophes or genetic drift. A genetically and demographically viable captive population as insurance against species extinction also is required and is already met by the SSP. PVA projections suggest that the AWBP will meet the down-listing target size of 1000 cranes, on average, in ~33 years, with 90% confidence within 54 years. Estimated future effective population size (Ne) under estimated future range-wide threats is 474, approaching that suggested for genetic stability (see Section 6). Mitigation efforts to improve recruitment to offset future threats can reduce the time to down-listing to that projected based on historical conditions, which is ~22 years, or alternatively to address higher levels of future threats than estimated. Threat reduction would also lead to higher Ne. Actual time to down-listing will be dependent upon actual future threats, management actions, and cyclicity in population numbers.

These PVA results are based on the best available data at the time of these analyses (November 2018). Historical data for the AWBP provided good demographic data for a self-sustaining, growing crane population. These data, however, are not directly applicable to the two reintroduced populations that currently demonstrate low reproductive success. In addition, future threats may be different for any or all crane populations due to various climate change effects and expanding human activities, especially as crane populations expand and utilize a wider landscape mosaic. These uncertainties limit precise viability projections but provide valuable guidance regarding key factors affecting viability, important data gaps, and management actions that will promote viability, down-listing and eventual recovery. It would be valuable to revisit these analyses as more data become available.

Section 2. Whooping Crane Population Viability Analysis (PVA) Report: Aransas-Wood Buffalo Population Base Model and Alternative Scenario Results

This report describes the final whooping crane baseline *VORTEX* model and results for the wild Aransas-Wood Buffalo migratory population (AWBP). This population model and scenarios were developed in conjunction with the 2015 and 2016 Population Viability Analysis workshops in Calgary, and were informed by additional electronic and telephone discussions through 2018 with recovery team members and workshop participants. Detailed information on model development can be found in Appendix II.

Objective

The objective of the overall whooping crane modeling effort is to develop a representative population simulation model and conduct a Population Viability Analysis (PVA) for the whooping crane (*Grus americana*), incorporating all existing wild and captive populations of this species meta-population. A PVA using this model will provide long-term viability projections for each population and for the species meta-population under current and potential future threat and management conditions. These projections also can be used to estimate the probability of reaching program goals under current management. Additional uses of this model include: 1) to evaluate the impact of alternative management strategies; 2) to inform discussions of revising program goals; 3) to provide an estimate of the type and degree of management needed to reach program goals; 4) to identify the role of various populations within the management of this meta-population (particularly that of the captive population); and 5) to identify criteria or thresholds for action.

Model Inputs

A stochastic, individual-based population model was developed for the whooping crane using the *VORTEX* 10.2.17 (Lacy and Pollak 2017) software program. *VORTEX* is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild or captive small populations. A one-year time step was implemented, with most events (e.g., breeding) occurring once per year. Two mortality events occur in the model each year so that summer vs winter events can be altered separately in the model. The model begins each 'year' in spring just prior to breeding. Model scenarios were run for 100 years with 500 iterations each (instead of 1000 for other whooping crane PVA models in this report) due to model complexity and larger population size.

<u>Base Model Using Historical Data</u>

Demographic rates to parameterize the AWBP model were derived from Gil-Weir *et al.* 2012, Moore *et al*. 2012, Butler *et al*. 2014, Servanty *et al*. 2014, Wilson *et al*. 2016, Butler *et al*. 2017 and other sources, as well as expert opinion from conference calls and PVA workshops. This included inputs to match historical and current conditions, along with exploration of projected future changes in environmental conditions and human-related threats, under current management. Sensitivity testing explored some of the uncertainty around these input estimates. A summary of inputs is provided below; see Appendix II for details. Note that inputs are entered as mean rates; these means fluctuate annually based on environmental variation (EV), and observed rates vary due to demographic variation in this individual-based model.

Reproduction

The mating system was modeled as long-term monogamous pairs, with reproduction beginning as early as age 4. Mean female breeding rate (probability of producing a clutch that year) is 91.9% and is age specific, with essentially all females age 7-23 laying eggs and rates declining slightly in older females. Successful breeding pairs produce one clutch with typically two eggs (96% of clutches), although both chicks seldom survive. Rates were based primarily on Gil-Weir *et al*. 2012 and Wilson *et al.* 2016. Environmental variation (EV) for reproduction was set at CV = 10% based on partitioning of EV from observed variance in AWB nesting data.

Mortality

Mortality rates were based on Wilson *et al*. 2016, Gil-Weir *et al*. 2012 and raw data tables, and were implemented as two mortality events per year (summer vs winter mortality). The resulting annual mortality rates for cranes $\geq$ 1 year old were: 10.8% (1 and 2 year olds); 15% (3 year olds); and 5.6% (adults 4 years and older), with no sex-specific differences. Maximum lifespan was set at 30 years. EV was set at CV=10% and was partially correlated (0.5) with EV in reproduction to account for most EV occurring in the summer breeding grounds.

Modeling first-year mortality was more complex. Mortality during the first six months included mortality from egg through fledging through autumn migration to arrival at the wintering grounds (~59% for the first egg and ~95% for second egg, see below); an additional 10% mortality was applied to surviving 6-month-old birds during the remainder of the first year (first winter and first spring migration).

Cyclicity in Recruitment

Whooping crane demographic rates, primarily recruitment and population growth, fluctuate in a cyclic pattern, which has been reported to correlate with ~10-year cyclic patterns observed in boreal snowshoe hare-Canadian lynx and other boreal predator populations (Boyce *et al*. 2005; Wilson *et al*. 2016; Butler *et al*. 2017). Butler *et al*. 2017 also reported evidence of 11-year solar (sunspots) cycles affecting climatic conditions and demographic rates for whooping cranes. Weather on the breeding grounds and during autumn migration both likely influence juvenile mortality (directly or via increased predation risk) and therefore affect recruitment. While the proximate mechanism is uncertain, evidence suggests cyclicity in boreal species may be a product of complex interactions among food supply, predator abundance, hydrology and weather patterns influenced by the solar cycle (Butler *et al*. 2017). Cyclic recruitment data were provided by M. Butler and used to incorporate matching cyclicity (11-yr cycle) into first 6-month mortality in the AWBP *VORTEX* model ($\text{mean}_{\text{Egg1}}$ = 59.6%, $\text{range}_{\text{Egg1}}$ = 49.5-69.7%; $\text{mean}_{\text{Egg2}}$ = 94.8%, $\text{range}_{\text{Egg2}}$ = 86.4-100%; see Table A1 in Appendix II). No additional EV was imposed for the first 6-month mortality.

Environmental variation

Demographic stochasticity is an inherent property of the model, while EV, or environmental variation (annual fluctuation in demographic rates), must be explicitly added. EV for reproduction (% females breeding) was set at CV = 10% based on partitioning of EV from observed variance in AWB nesting data. EV for mortality was set at CV=10% for most mortality rates to match that used for breeding and by Tischendorf 2004. No EV was specified for first-year mortality, as this was accounted by cyclic rates. EV for reproduction and mortality were partially correlated in the model (0.5) to account for most EV occurring in the summer breeding grounds.

Catastrophes

Two catastrophic events were incorporated into the base model, based in part upon general trends in catastrophic declines observed in 88 species of wild vertebrates by Reed *et al*. 2003. Risk of a high mortality event in the wintering grounds was incorporated as a 0.5% risk (~ once every 200 years) of a 50% reduction in survival for all age classes over winter. The risk of a poor breeding season (90% reduction in fledgling production) was given a 5% risk of occurrence (~ once every 20 years) based upon a conservative estimate of similar historical population declines.

Population Regulation

There is no growth regulation in demographic rates, i.e., no density-dependency or limitation of nesting sites or resources (i.e., no carrying capacity limitations) on the breeding grounds. Rather, population size is limited in the model by carrying capacity (K) in the wintering grounds and by general demographic rates. Probabilistic truncation to K is implemented if population size exceeds K at the end of each year and is applied only to non-breeding birds (i.e., immature or nulliparous birds) in the model.

Sensitivity Testing
Recognizing that there is some uncertainty around model input parameters, sensitivity testing (ST) was conducted by varying a single parameter at a time to assess the sensitivity of the model results to different variables. This can be useful not only in assessing the impact of uncertainty in model results but also valuable in estimating which threats or management actions may have the greatest effect on population viability. All ST scenarios were run for 100 years with an initial population of 500 birds to avoid small population effects in the results. Stochastic growth rate (r), calculated prior to truncation to K, was selected as the most appropriate measure of population viability and model results. A brief summary of ST results is provided here (detailed information on sensitivity testing can be found in Appendix II). Historical data are most robust for demographic rates (age-specific reproduction and mortality) for the AWBP. Growth rate was found to be most sensitive to adult survival, followed by sub-adult survival and juvenile survival, when these rates are varied by equal proportions. Historically, most observed variation in demographic rates in the field has occurred in the survival of early age classes, while adult survival is high with relatively little variation. Changes in breeding rate (i.e., egg production) have little effect over the range of values tested, possibly as the proportion of females breeding is high in this population. Wilson *et al*. 2016 similarly noted that fledging rate had the greatest influence on annual growth rate, followed by breeding propensity (% females nesting), given the relatively low variation in adult survival for the AWBP. Factors that affect hatching and fledging rates and juvenile survival are likely to drive viability *as long as* sub-adult and adult survival remain high. Increases in adult (and to a lesser extent, sub-adult) mortality in the future, however, could reduce population viability. This suggests the importance of minimizing the loss of adult cranes from the population.

Other model inputs relied more heavily on estimation and harbor greater uncertainty. Values tested for environmental variation (EV), inbreeding sensitivity, and maximum age had little to no effect. Allowing three-year-old birds to breed slightly improved growth. Catastrophes do have some effect on growth rate, but populations of 500 grow well with no extinction risk even if the risk of both catastrophes is doubled. These results suggest that model results are not particularly sensitive to the uncertainty in these parameters for populations of several hundred birds. Population size was also explored (N = 50 to 1000) to determine its relative impact on population viability. While small populations show reduced viability, relative gains in growth rate with increased size begin to taper with populations of 300 or more birds.

Validation of Historical Demographic Rates
Retrospective modeling of the AWBP was conducted by using this base model to project the trend of this population over the past 38 years (from 1977 to 2015); the estimate for 2016 was not included due to different survey resolution. The model was initiated with 72 individuals. The severe winter mortality catastrophe (see below) was not incorporated, as this rare, extreme event was not observed during this period. Model results show cyclic positive growth of stochastic r = 0.0368 (SD = 0.052) and mean N_{2015} = 313 (SD = 70), approximately matching field observations (average lambda $\geq$ 1.035; 2015 survey count = 329) (see Figure 1). In the *VORTEX* model the population experienced a negative or zero growth rate (r $\leq$ 0) on average in 7.7 years of the 38 years, comparable to the model developed by Wilson *et al*. 2016 (n=8 years) and to field observations (n=7 years). Cyclicity in stochastic growth rate and recruitment was similar to that presented by Butler *et al*. 2017, although peak values were higher. An effort was made to initiate the model at the point in the solar cycle that best matches observed cycles in field observations, recognizing that actual solar cycle length varies around an average of 11 years and does not follow a rigid 11-year pattern. Overall the model is a reasonable representation of the whooping crane AWBP with an improved fit to historical data over a non-cyclic model.

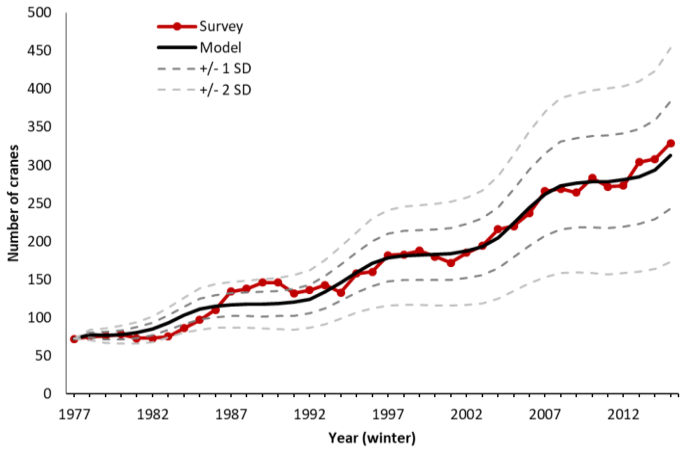

Fig. 1. Retrospective model projection of the AWB whooping crane population from 1977 to 2015 (black line) and USFWS survey results (red line).

Parameter Inputs for AWBP Future Projections

Initial Population Size

The *VORTEX* model yearly cycle begins at the point just prior to production of eggs and chicks (i.e., early spring). The initial population of 414 cranes used for the AWBP model was based on results from the December 2016 survey (USFWS 2017) and adjusted to account for winter and spring migration mortality to estimate the pre-breeding population in spring 2017 (331 adults, 83 sub-adults age 1-3yrs). The model was initiated at the point in the 11-year solar cycle that best fit historical data in Figure 1. It is possible that the model cycle may be slightly out of synch with the actual cycle impacting wild cranes due to variation in the natural solar cycle (i.e., not always exactly 11 years). Thus, model results may project a slight shift in cyclicity compared to wild crane population number peaks and valleys, but long-term projected trends remain the same.

Genetics

Initially a small genetic load (3 lethal equivalents, 1 as a lethal allele and 2 as non-lethal effects) was incorporated into the model and applied as lower juvenile survival in inbred individuals, based on conservative estimates for wild vertebrate populations suggested by O'Grady *et al.* 2006 and taking into account the likelihood of purging effects due to the historical bottleneck and population expansion experienced by this species. Preliminary results indicated that the AWBP remains large enough such that this level of inbreeding depression did not affect model results (see Appendix I). Final AWBP scenarios reported here were run without this genetic component to greatly reduce computing time; however, inbreeding effects will be incorporated into scenarios for other, smaller whooping crane populations.

Estimation of Future Conditions and Threats: Climate change impacts

While there is substantial historical demographic data to inform the development of the AWBP base model, estimating future conditions and threats involves greater uncertainty. It is unlikely that future conditions will exactly mirror those in the past. Changing environmental conditions due to climate change and expanding human development and activities may impose additional threats in the future, especially as whooping crane populations expand and utilize new areas. Ignoring such changes may be a more erroneous assumption than incorporating the best available predictions into the model. The following factors were examined, discussed and incorporated into various alternative scenarios of the AWBP model, and their impacts evaluated to determine the sensitivity of model results across this uncertainty.

Current and Projected K in Wintering Grounds

Revised estimates for the potential carrying capacity (K) of the whooping crane wintering grounds in the expanded Aransas National Wildlife Refuge (ANWR) area, including both protected and unprotected lands, were provided by K. Metzger (unpublished data, pers. comm.). Protected lands include all public protected areas, which extend beyond ANWR. Current K is estimated at 2550 cranes (774 in protected lands, 1776 in unprotected lands in the study region).

Estimates of future K were provided by Metzger for scenarios with a sea level rise of 0.6m (K=3317), 1m (K=2505) and 2 m (K=2115) by the year 2100. These estimates are based on habitat changes and do not include human-related threats that may be higher in non-protected lands. Note that potential K for whooping cranes *increases* initially and peaks at 0.6m but then decreases with additional sea level rise. The shape of the curve for K over time was approximated using habitat types (especially regularly-flooded marsh) as a proxy, and assumed no further rise above 1m after 2100 (Fig. 2). This results in essentially no net loss of winter carrying capacity for whooping cranes in 100 years. These K projections assume that habitat utilization by cranes will be similar to that observed in the past and that there are no behavioral or other density-dependent effects. The 1m rise scenario was chosen as a conservative estimate of sea level rise with low climate change impact and was incorporated into some model scenarios.

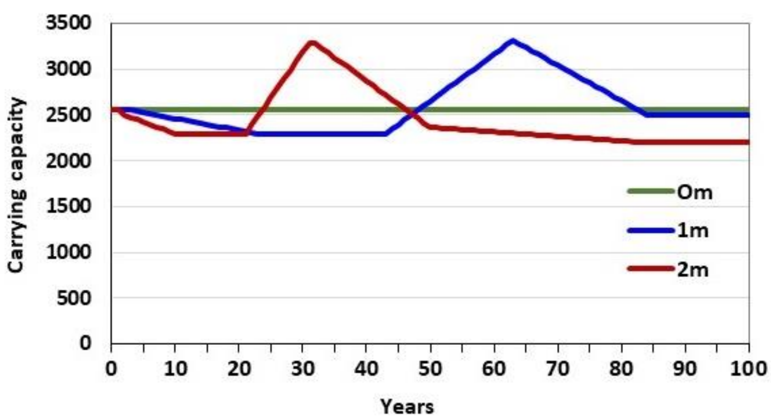

Fig. 2. Projected carrying capacity for whooping cranes (AWBP) in the winter grounds with no sea level rise, 1m rise or 2m rise by 2100. Note that the loss in K with 2m rise is almost entirely within currently protected lands.

Greater degrees of sea level rise (i.e., > 1m) will likely result in some loss of K for cranes, especially in protected areas. For example, estimated K in protected areas in 2100 is K_{1m}= 738 with 1m sea level rise and K_{2m}= 368 with 2m sea level rise; however, there is almost no anticipated impact in non-protected lands (K_{1m}= 1767 vs K_{2m}= 1747) (Metzger, pers. comm.). Sea level rise is not likely to be a major impact on the whooping crane wintering population *unless* mortality is significantly higher in non-protected areas or if sea level rise is greater than 2m.

Impacts of Increasing Atmospheric CO_2

Butler *et al.* 2017 propose a reduction in recruitment with the expected rise in atmospheric CO_2 to 500ppm by 2050. Increased atmospheric CO_2 may alter temperatures and precipitation in the breeding grounds and during autumn migration that reduce recruitment (~1.37% decrease observed per 10ppm increase in CO_2; Butler, pers. comm.) and result in reduced population growth and loss of demographic resiliency. Data for estimated recruitment under atmospheric CO_2 conditions of 400ppm and 500ppm were provided by Butler (unpublished data) and used to develop a model scenario to evaluate the potential impact of increasing CO_2 levels. This scenario incorporates a steady small increase in first 6-month mortality to match the corresponding degree of impact by year 2050; model conditions were then held at that level with no further atmospheric CO_2 increases (although some climatic models project a continued increase in CO_2 to 700ppm by 2100). The resulting stochastic growth in the AWBP model leads to 5-6 years spent in negative growth at the valley of each cycle under 500ppm (similar to Butler *et al.* 2017; see Fig. A6). Mean growth rate declines over time but averages higher than that modeled by Butler *et al*. 2017.

Inclusion of this factor in the model has a substantial impact on future crane population growth, reducing overall growth rate by ~44%, which could potentially affect time to recovery and the ability of the population to withstand other threats. This model scenario assumes that atmospheric CO_2 will continue to increase at a constant rate until 500ppm is reached; that CO_2 levels will not rise beyond 500ppm; and that the impact on whooping cranes will exhibit the same trends in the future as those observed historically.

Increased Frequency of Major Hurricanes

Hurricanes likely are a lower threat to migratory (vs non-migratory) whooping crane populations such as the AWBP, as the hurricane season typically coincides with those months when the cranes are in the northern inland breeding grounds. Impacts on food supply and habitat are hypothesized to be localized and temporary, and fall within EV (environmental variation) model values. A potential additional consequence of intense hurricanes that was proposed may be chemical contamination. Such events would likely be local but could have a major effect on cranes in the affected area. Little risk of contamination exists in current crane wintering grounds; however, this threat is anticipated to increase if the AWBP expands up the coast into more developed areas.

Current hurricane frequency was estimated to be ~every 30 years (3.1% annual risk) based on estimates by the National Hurricane Center for Category 4 and 5 hurricanes impacting beach mouse (*Peromyscus polionotus*) habitat along the Gulf Coast to the east of whooping crane habitat (Traylor-Holzer *et al*. 2005). These estimates were based on past trends (1886-2002); however, tropical storm event trends may be impacted by climate change. A recent technical report from the National Center for Atmospheric Research (NCAR) (Bruyère *et al*. 2017) investigated the impact of climate change on hurricanes in the Gulf of Mexico and concluded that average storm intensity will increase, resulting in an increased proportion of Category 3, 4 and 5 storms associated with increased precipitation and damage potential. Modeling by NCAR showed a 2- to 4.5-fold increase in frequency of storm events characteristic of major hurricanes.

Based on these reports, an alternative scenario was developed for the AWBP model to include a specific risk of major hurricanes impacting cranes wintering outside of protected areas. The impact of a major hurricane was modeled as a loss of ~5% of cranes living outside of protected areas, with hurricane frequency (annual risk) starting at 3.1% and increasing to 6.2% (twice as frequent) by 2085 (mid-point of NCAR model). This scenario was compared to that without this hurricane-related contamination risk to assess the relative impact of such events. Inclusion of this factor in the model has only a slight effect on future population size. This threat is modeled as only affecting cranes outside of protected areas, as it is hypothesized to be a factor only when crane populations are large and expanding into developed areas.

Cumulative Effects of Projected Climate Change Impacts

Model results suggest that the combined effects of sea level rise (to 1m by 2100), rise in atmospheric CO_2 (to 500ppm by 2050), and increased frequency of intense hurricanes and associated risk of contamination events (in non-protected lands) may negatively affect AWBP population growth and size over the next 50-60 years (Fig. 3). Of these three factors, CO_2 level is the primary driver of population growth at the levels and rates modeled. While increasing CO_2 levels may be a realistic projection, there is some uncertainty regarding the precise impacts this factor may have on whooping cranes in the future.

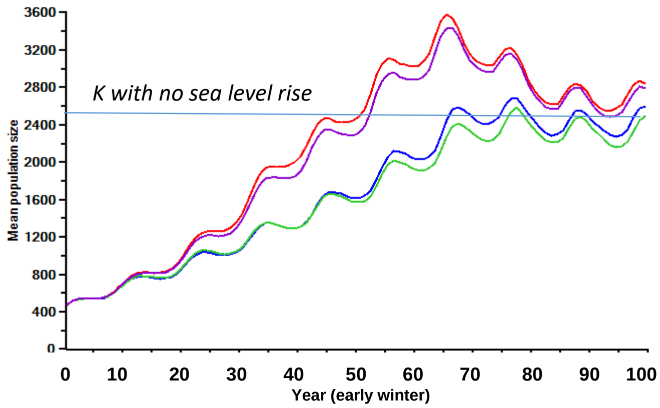

Fig. 3. Projected mean population size for AWBP over 100 years assuming 1m sea level rise, under four scenarios. Results with no sea level rise exhibit similar trends for the first 50-65 years until the population reaches K and levels off (~2500 cranes).

-400ppm CO_2, no hurricane impact (**red**)
-400ppm CO_2, with hurricanes (**purple**)

-500ppm CO_2, no hurricane impact (**blue**)
-500ppm CO_2, with hurricanes (**green**)

The primary differing impact of these factors is the rate at which the population grows to carrying capacity and the projected time to recovery. All scenarios project positive growth, high retention of genetic variation, and no extinction risk over 100 years, with final mean population sizes over 2200 cranes (Table 1). These model projections suggest that modest sea level rise of 1m by 2100, risk of contamination events due to increased frequency of intense hurricanes, and increased atmospheric CO_2 levels to 500ppm combine to reduce population growth and size for the AWB whooping crane population, increase stochasticity in population size, and increase time to recovery; however, in isolation and without additional risk factors, these factors are not projected to severely reduce AWBP viability over the next 100 years. Reduced growth and size, however, increase the vulnerability of the population to additional threats that reduce survival or reproduction and increase the time to reach certain downlisting criteria.

Table 1. Model results over 100 years for AWBP under 400 vs 500ppm atmospheric CO_2, and with and without hurricane contamination events (N=population size, GD=gene diversity retained, stoch r = stochastic r, PE=probability of extinction, TTT=mean time to target of $N \geq 1000$). All scenarios assume 1m sea level rise by 2100.

Scenario	Mean N_{100}	Mean GD_{100}	Stoch r	PE_{100}	$TTT_{N \geq 1000}$
400ppm/No hurricanes	2467 (SD=177)	0.994	0.0427	0	22
400ppm/With hurricanes	2437 (SD=220)	0.994	0.0382	0	22
500ppm/No hurricanes	2335 (SD=397)	0.993	0.0237	0	31
500ppm/With hurricanes	2263 (SD=436)	0.993	0.0214	0	31

Estimation of Future Conditions and Threats: Human-related mortality

Increased Mortality in Non-Protected Areas

It is reasonable to assume that mortality, particularly human-caused deaths, may be higher in non-protected areas than in Aransas NWR. As the AWB crane population increases, cranes will increasingly move into non-protected areas over winter, which may raise overall winter mortality. Unlike the previous climate change-related model revisions described above, there are little data on which to base an estimate of these future threats. Historical data separating mortality between the two land protection types is not available, and estimates of future K made by Metzger do not account for changes in mortality across the landscape. There was a suggestion among contributors to this project that any increase likely would be modest but this is based on few observations. A small amount of additional mortality in non-protected areas was tested (1.1x current mortality) to assess the sensitivity of the results to this parameter, along with higher levels (1.2x – 1.5x base value) for sensitivity testing. In the model cranes were assumed to utilize protected areas exclusively until they reach protected area capacity and then move into unprotected lands as the population expands. This assumption is not realistic, but is a simplification of this non-spatially explicit model, and may potentially underestimate the impact of this source of mortality to the degree that cranes will utilize non-protected areas with higher threats when protected habitat is available.

Increased Mortality During Migration

Migration mortality is believed to likely increase in the future due to the increase in wind farms, agro-conversion, the Athabasca Oil Sands development, and similar emerging threats along migration routes. Like increased winter mortality in non-protected lands, there are scant data to inform estimates of future increases in mortality during migration above the historic level. An estimate of 15% increase of the current level (i.e., 1.15x current level) was suggested, and levels above and below that (1.0x -1.3x current values) were tested to assess the sensitivity of model results to this parameter. These increases were applied to all cranes and during both spring and autumn migration. These scenarios were run in combination with varying winter mortality in non-protected lands.

Partitioning Annual Mortality

In order to modify winter and migration mortality rates as described above, it was necessary to separate out the components of annual mortality rates into summer, autumn migration, winter, and spring migration. This was handled differently for the first 6 months of age than for older birds that have completed their first migration. Juvenile mortality from egg to 6 months was partitioned to attribute 90% to egg-to-fledgling mortality on breeding grounds and 10% to their first autumn migration based in part on Wilson *et al*. 2016. All other age classes were handled as described below.

Two sources exist to inform the partitioning of rates during the annual cycle, both of which have limitations. Stehn and Haralson-Strobel (2014) expanded the previous analysis by Lewis *et al*. 1992 to examine whooping crane mortality for the AWBP from 1950 to 2010. Winter mortality represented about 20% of total mortality; other seasonal rates were estimated, with migration mortality believed to comprise a significant proportion of annual mortality. It was suggested by contributors to this PVA that a reasonable partitioning based on these data might be 20/30/20/30 for summer/autumn migration/winter/ spring migration mortality percentages, respectively. Telemetry results for 17 satellite tagged cranes suggest a different conclusion (40/10/40/10) (Pearse, pers. comm.), but may have limited applicability due to small number of tagged birds, restricted temporal scale, poor winter conditions for these years relative to average, and possible bias since most observed mortalities occurred in birds <3 years old. It was suggested that a 'best estimate' approach for this PVA modeling effort would be a compromise (intermediate rate) between these two results, which was applied using the following partitioning for annual mortality: 30% summer, 20% autumn migration, 30% winter, 20% spring migration.

Results of Mortality Rate Sensitivity Exploration

The 14 scenarios resulting from testing seven levels of additional migration mortality (base value, plus increases of 1.05x - 1.3x base value) times two levels of additional mortality in non-protected lands (base value, 1.1x base value) using intermediate distribution rates result in a range of population trajectories, with growth rates varying from 2-4% (Fig. 4). These mortality rates have substantial impacts on time to recovery and growth to K, but have smaller impacts on long-term mean population size (~2400-2800 after 100 years). Population growth in the model is more sensitive to the values chosen for additional mortality during migration than for added risk in non-protected areas during winter. This is due to two reasons: migration mortality is modeled as a greater percentage of annual mortality (~40%, vs 30% for winter mortality), and migration mortality affects all individuals in all years whereas additional winter mortality only affects cranes spending winter outside the refuge and so has an impact only as the population expands beyond protected area K. While the precise impact of additional mortality risks during migration or living in non-protected lands is unknown, these anticipated risks have the potential to significantly impact population growth rate and time to recovery. Adding additional potential threats, i.e. hypothesized climate change impacts of increasing CO_2 and increasing risk of mortality due to intense hurricanes, results in lower growth rates, with essentially no population growth at migration mortality at 1.3x base value.

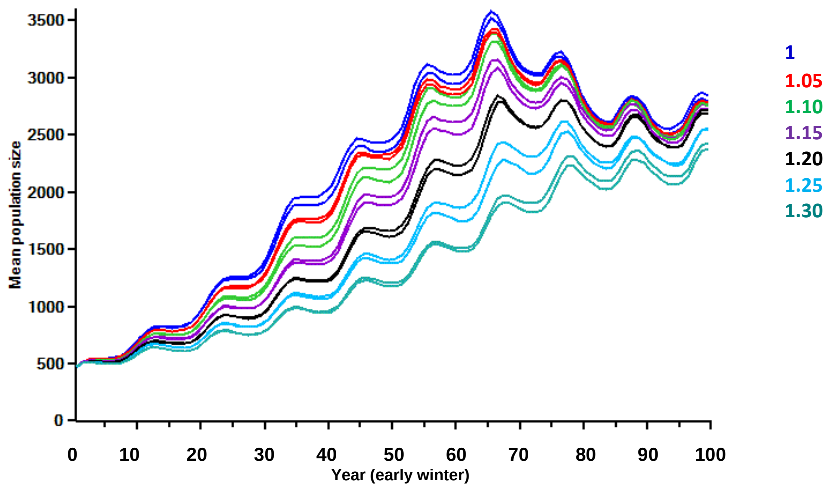

Fig. 4. Projected mean size of AWBP for 100 years for 14 ST scenarios varying migration and non-protected lands winter mortality. Numbers on the right indicate migration mortality base value multiplier; within each of these is a set of two same-colored lines representing 0% and 10% additional winter mortality in non-protected lands. Scenarios assume 1m sea level rise and no impacts of rising CO_2 or more frequent intense hurricanes.

Model results suggest that increased mortality during migration can have a significant impact on crane population growth and time to recovery, depending upon the degree of increase and other mortality rates. The distribution of annual mortality (i.e., proportion occurring during migration vs on breeding/wintering grounds) affects specific projections for specific mortality rates. If higher mortality proportions for migration are used (i.e., based on analyses by Stehn and Haralson-Strobel), the impact of migration mortality is higher; if telemetry data estimates (20% total) are used, the impact is lower. While the proportioning of seasonal mortality influences the magnitude of the effect for a particular level of additional mortality, it is clear that additional migration mortality, if high enough, has the potential to significantly reduce growth and time to recovery.

Summary of Mortality Rate Sensitivity Results

Several factors related to climate change and/or human activities have been suggested to impact the AWB whooping crane population in the future, either through increased mortality or through reduced habitat capacity for cranes. These impacts may combine to reduce growth and population size, with increasing consequences after several decades. Figures 5a-c illustrate the projected mean stochastic growth rate (a), mean time to reach down-listing target (b), and mean final population size at 100 years (c), that result from varying each of five factors independently (input values used are given in ()):

1) sea level rise by year 2100 (0, 1m, 2m);
2) inclusion of hurricane contamination events (no/yes);
3) impacts of rising atmospheric CO_2 to 500ppm by 2050 (no/yes);
4) additional mortality in non-protected lands (1.0-1.3x base value at 0.1 intervals); and
5) additional migration mortality (1.0-1.3x base value at 0.05 intervals).

The base scenario (in orange) represents sea level rise of 1m but no additional migration mortality, no additional mortality in non-protected lands, and no impacts of atmospheric CO_2 or increasing hurricane events.

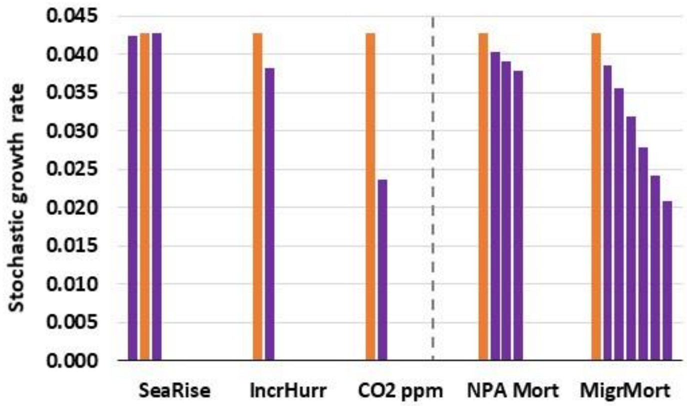

Fig. 5a. Projected mean stochastic growth rate (r) of AWBP over 100 years for ST scenarios varying climatic change-related factors (left of the dashed line) and human-related mortality (on right). Orange bars represent base values of 1m rise in sea level (SeaRise), no hurricane impacts (IncrHurr), no rising CO_2 impacts (CO2 ppm), no addition mortality in no-protected lands (NPA Mort), and no additional migration mortality (MigrMort).

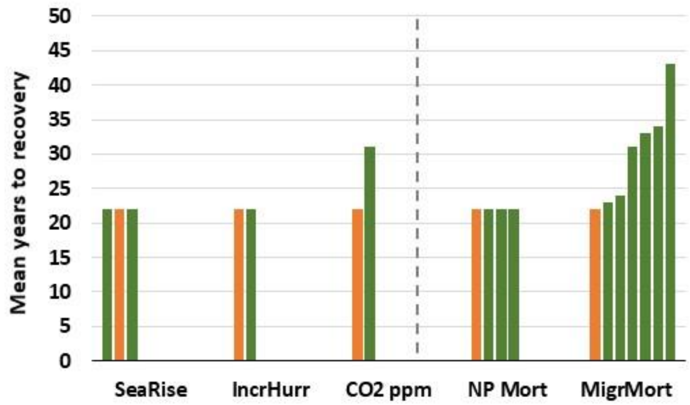

Fig. 5b. Projected mean years to down-listing (i.e., > 1000 cranes sustained, winter census) for ST scenarios varying climatic change-related factors (left of the dashed line) and human-related mortality (on right). Orange bars represent base value as described for Fig. 5a.

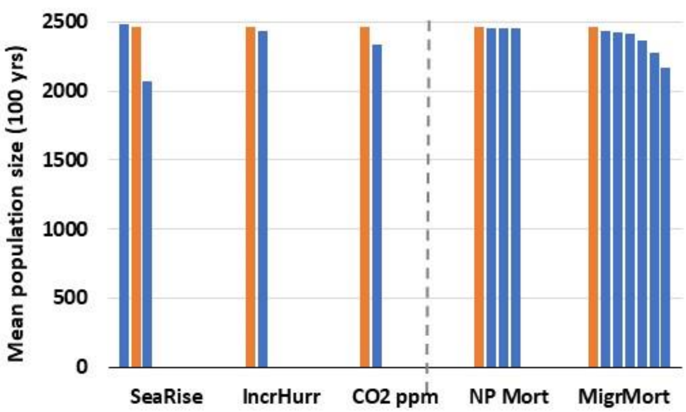

Fig. 5c. Projected mean population size at 100 years for ST scenarios varying climatic change-related factors (left of the dashed line) and human-related mortality (on right). Orange bars represent base value as described for Fig. 5a.

In the model, atmospheric CO_2 and migration mortality have the largest impact on growth rate, and therefore on time to recovery, over the range of values tested. Mortality in non-protected lands, either through overall higher risk or through risks associated with hurricanes, has comparative little impact as modeled, *provided* core protected areas provide a refuge with continued low mortality. While growth rates vary, all show positive growth toward carrying capacity of the habitat. Sea level rise ($\geq$2m) has an impact on final population size (at 100 years) due to loss of K especially in protected lands.

Across scenarios that explore all combinations of these five factors (at the specified values), none of the scenarios result in overall negative growth. The only scenarios that result in a final mean population size < 1000 at year 100 are scenarios with 25-30% migratory mortality using either intermediate or Stehn and Haralson-Strobel seasonal mortality proportions. No scenarios indicated a risk of extinction in 100 years (with extinction defined as only one sex remaining in the population).

AWBP PVA Model Results

The future viability projection for the AWBP is dependent upon decisions made to incorporate additional future risks in the model due to climatic change and to increasing human-related mortality. While consensus views are that some mortality risks will increase in the future, there is uncertainty regarding the magnitude of these risks and their specific impact on cranes. If all of these additional risks are omitted, the AWB population is projected to grow rapidly (r=0.0423, SD=0.068) and reach the down-listing target of >1000 cranes on average in ~21 years, depending upon solar year cyclicity (Fig. 6; also see Section 6). This mean growth rate is a bit higher than historically observed growth. Past growth may have been influenced more heavily by stochastic processes due to smaller population size in the past, while current and future anticipated population sizes are large enough to be substantially buffered from these effects.

Note that Figure 6 depicts the mean projected AWB population size plotted as N directly following autumn migration and before any truncation to K due to winter habitat limitations, allowing population size to exceed K. In the model, N is then truncated back approximately to K at the end of the year via higher mortality in non-breeding birds. If reproduction is not density dependent, this suggests that in reality either there may be higher winter mortality as the population reaches K due to limited resources in wintering grounds and/or the population might expand beyond the habitat designated in the model.

Incorporating potential changing future threats alters these projections. Five alternative scenarios were modeled, in addition to the baseline of no additional future threats, using the best estimate for each:

<u>Current</u>: Historical rates with no additional climate change or human development impacts

<u>Alternate 1</u>: Breeding ground impacts only (lower recruitment with rising CO_2 to 500ppm by 2050)

<u>Alternate 2</u>: Migratory route impacts only (increased mortality during migration at 1.15x base rate)

<u>Alternate 3</u>: Wintering ground impacts only (1m sea level rise by 2100; increased mortality in non-protected areas, including direct mortality (1.1x base rate), and increased rate of major hurricanes (twice as frequent by 2085, resulting in 5% mortality in non-protected areas))

<u>Alternate 4</u>: Range-wide impacts (all impacts in Alternates 1-3 combined)

<u>Alternate 5</u>: Higher impacts (same as Alternate 4, except migratory mortality= 1.3x base rate and non-protected area winter mortality = 1.5x base rate in protected areas).

It is difficult to provide a true 'worse case' projection, as future risks during migration can have a significant influence on population growth but are difficult to predict. Scenario Alternate 5 represents higher rates of migratory and non-protected area mortality that lead to zero population growth once other factors are in full effect (i.e., sea level rise and increased atmospheric CO2). Figure 6 presents the results for the Current and Alternate scenarios 1-5.

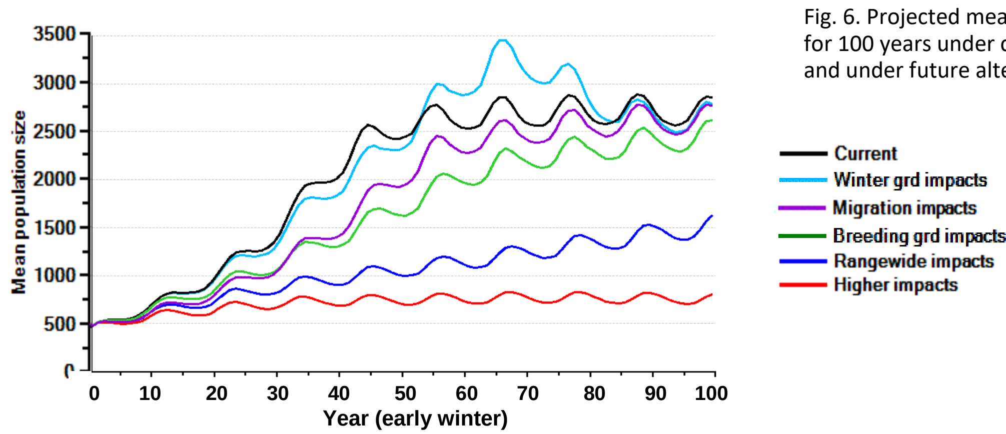

Fig. 6. Projected mean size of AWBP for 100 years under current conditions and under future alternate conditions.

All six projections suggest a demographic sustainable and genetically robust population under the conditions modeled, with high genetic retention and no risk of extinction over 100 years. Wintering ground impacts have little negative effect, with the same mean time to N>1000 (~21 years) and similar final population size (~2800). Population size actually increases temporarily with wintering ground impacts as K increases with modest sea level rise (0.6m) but then returns to the current level. Migration route and breeding ground impacts each independently reduce growth and time to target (~31 years) at the values modeled, with a small reduction in final population size with breeding ground impacts.

When all range-wide threats are combined, overall growth is significantly reduced to 1.2%, leading to longer time to down-listing target of N>1000 (~45 years) and substantially small population size over time. Higher range-wide impacts modeled to lead to no growth (0.47%) result in the population fluctuating on average between 700-800 cranes across the solar cycle. The reduction in growth and population size observed in Alternate 5 is driven primarily by the increased migratory mortality.

Given the slow overall growth rate under the two range-wide threats scenarios, this AWB population could be vulnerable to additional threats (e.g., CO_2 >500ppm, sea level rise >2m, higher migration mortality than modeled, more severe catastrophic impacts) that could interact to lower recruitment and survival. Model results suggest that under climate change impacts (primarily increasing CO_2 levels to 500ppm), population growth rate approaches zero and recovery is not achieved in 100 years at an increase in migration mortality of ~1.3x base value. This translates into an additional ~0.7% annual mortality for adults and ~1.5% mortality for birds 1-3 years old. For example, this would translate into an additional 2 adults and 1 sub-adult lost per year during migration for the current AWBP population of ~400 cranes.

All scenarios explored suggest that the AWB whooping crane population is likely to demonstrate positive growth, retain high levels of current genetic diversity, and have little risk of extinction under current or foreseeable future conditions. Additional threats in the future have the potential to significantly reduce population growth and increase the time to down-listing, primarily through decreased survival as supported by sensitivity testing results. Management actions that either prevent additional threats and/or mitigate their effects are likely to shorten the time to recovery for this species. The extent to which such management actions are needed will depend upon future threats and the desired balance between more rapid recovery and amount of effort and resources applied.

Two scenarios – Current Conditions and Range-wide Impacts – were chosen as reasonable benchmarks to bracket the exploration of alternative management scenarios. These projections are presented in Figure 7 with accompanying standard deviations to indicate the degree of variability around the mean projected population sizes. These scenarios project a range of time to reaching down-listing target of 19-30 years (mean = 21) under current conditions, and 23 to >100 years (mean = 45) with range-wide impacts. In some cases, the Higher Impacts scenario was also included in the exploration of management impacts.

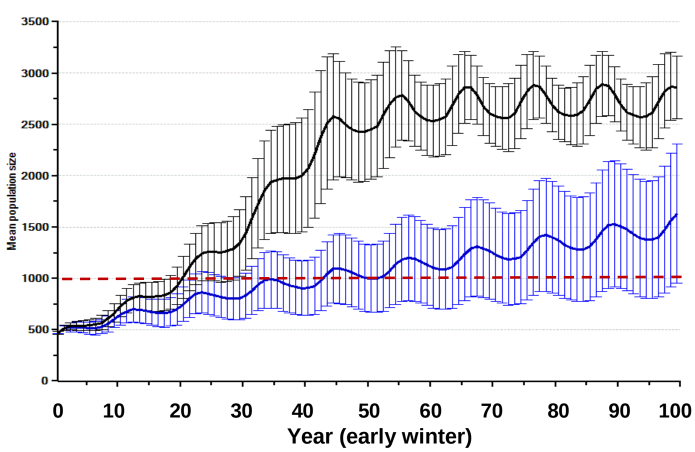

Fig. 7. Projected mean size of AWBP for 100 years under current conditions (black line) and with range-wide impacts (blue line). Bars indicate SD. Red dashed line indicates N=1000.

Exploration of Alternative Management Options

Exploration of the future viability of the AWBP suggests that population size and growth potentially could be limited due to lower recruitment and/or higher mortality in the future. Five priority alternative management options were identified to explore the relative impacts of potential management actions using the Current Conditions and Range-wide Impacts (Alternate 4) scenarios. All five management options address mortality and/or recruitment. Modeling results for these scenarios are presented below.

<u>Option 1: Reduce the rate of future higher migration mortality</u>.

Sensitivity testing suggests that migration (or other comparable) mortality may be an important consideration for AWB population size and viability. There is concern that migration mortality risks may increase in the future. Clark *et al* (2017) suggest that many anthropogenic mortality risks to adult cranes, such as power line collisions, oil spills, and accidental or illegal hunting, have the potential to be minimized. A management option was proposed to model the reduction of migration mortality by actions that might include encouraging cranes' use of expanded habitat areas along migration routes through prescribed burns, improved freshwater access, and other methods to reduce mortality.

Precise modeling of this management alternative is not possible given the uncertainty in expected increase in migration mortality in the future. Participants in this PVA suggested that it would be difficult to reduce migration mortality beyond its current level; therefore, a 'no additional mortality' scenario may be the best scenario that is feasible. Table 2 provides results for several levels of migratory mortality with or without other threats included. While future migration mortality levels are uncertain, model results suggest that management actions to reduce migration mortality (or comparable levels of mortality in other parts of the AWBP's range) are likely to have demographic benefits leading to more rapid growth and larger population size for the AWBP and more rapid achievement of down-listing criteria.

Table 2. Model results over 100 years for AWBP with increased migratory migration, under current conditions and with rangewide impacts (N=population size, GD=gene diversity, stoch r = stochastic r, PE=probability of extinction).

Migration mortality relative to base value	Current Conditions					Range-wide Impacts				
	Mean N_{100}	Mean GD_{100}	Stoch r	Mn Yrs to $N \geq 1000$	PE_{100}	Mean N_{100}	Mean GD_{100}	Stoch r	Mn Yrs to $N \geq 1000$	PE_{100}
1.00	2481	0.994	0.0423	22	0	2234	0.993	0.0200	23	0
1.05	2498	0.994	0.0388	22	0	2038	0.992	0.0170	32	0
1.10	2477	0.993	0.0355	23	0	1832	0.991	0.0145	33	0
1.15	2440	0.993	0.0317	30	0	1531	0.990	0.0120	45	0
1.20	2424	0.992	0.0285	31	0	1273	0.989	0.0102	65	0
1.25	2350	0.992	0.0245	33	0	1006	0.987	0.0074	>100	0
1.30	2171	0.991	0.0210	42	0	828	0.986	0.0054	--	0

<u>Option 2: Reduce winter mortality through drought management</u>.

This management option was suggested to simulate the impact of drought management actions along the Texas coast to reduce starvation mortality. Drought events are not explicitly modeled in the AWBP model but are incorporated as part of environmental variation (EV) in mortality rates to fit the historical data. Butler *et al.* 2014 examined 61 years (1950-2011) of demographic rates and winter drought data for the AWBP and found that annual mortality remained relatively constant across drought conditions on the wintering grounds. Cranes were found to use upland areas more during extreme drought conditions. Temporary movement of cranes to other areas, and/or compensatory decreases in other forms of mortality, may be the mechanism resulting in little net reduction in population growth due to drought. These conclusions suggest that there is no utility in modeling this management option unless more data are available to propose how this situation might change in the future as the crane population expands.

<u>Option 3: Expand areas in protected status in the wintering grounds</u>.
This management option simulates an increase in winter habitat quality and survival by increasing the amount of protected areas in wintering grounds. The value of this scenario depends upon differential mortality in protected vs non-protected lands. Currently, any increase in mortality in non-protected lands is assumed to be relatively small. A reduction of additional mortality in non-protected (vs protected) lands from 10% to 0% under current conditions results in very modest demographic benefits for the AWBP (r=0.0409 to r=0.0423), with no change in final population size, time to down-listing, gene diversity or risk of extinction. Growth is modestly lower if winter mortality rates are as much as 1.5x higher in non-protected lands (r=0.0343). A similar pattern was observed under range-wide impacts, with modest reductions in growth rate and final population size between no additional mortality (r=0.0132, N_{100}=1681), 1.1x (r=0.0120, N_{100}=1531), and 1.5x (r=0.0107, N_{100}=1287) higher mortality in non-protected lands.

Additional winter mortality in non-protected lands, as modelled, does not appear to be a primary contributor of population viability. This is not surprising, as the current winter mortality rate is small and even a 50% increase resolves to the loss of 3% (first winter), 1.7% (1 and 2 year olds), 3% (3 year olds), and 0.86% (adults) cranes each winter, and is applied only to cranes that expand out of saturated protected areas. However, this factor may have greater impact if rising sea levels significantly reduce protected habitat for cranes, if cranes do not preferentially use protected (vs non-protected) lands or if additional winter habitat loss or threat factors occur, such as increased human development.

<u>Option 4: Improve fledging rate through management</u>.
This represents alternative management actions in the breeding grounds that lead to an increase in fledging rate. This could include predator management, construction of nest platforms, egg swapping, or other actions. Specific management actions were not modeled *per se*; rather a range of juvenile survival rates were explored to determine the rate needed to offset estimated impacts of future threats.

Figure 8 illustrates an increase in juvenile survival (egg to pre-migration, on summer breeding grounds) of 5%, 10% and 15% above the Range-wide Impacts model (blue line). An increase in survival of 15% (1.15x base value, purple line) or more counteracts most of the range-wide impacts and enables the population to reach habitat carrying capacity within 100 years. While population growth is slower compared to growth under current conditions (black line), time to down-listing is about the same. This scenario translates into approximately 6-11 additional fledglings in the population for each of the first few years, depending upon the stage of solar cycle. The number of additional fledglings represented by this projection increases over time as the population grows, with about 19 extra fledglings by year 10, 33 by year 20, and 40 by year 30, assuming these fledglings have the same post-fledging survival rates as other wild whooping cranes. Higher fledgling survival may be required to counteract greater degrees of threat. Figure 9 shows the impacts of a 5% to 30% increase in fledgling survival under the Higher Impacts scenario (30% increase in migration mortality, 50% increase in mortality in non-protected lands, and hurricane impact). A 25% increase in fledgling survival is required to counteract these effects with respect to time to down-listing, and 30% or more increase is needed to reach carrying capacity in 100 years. Predator management has proven useful for increasing sandhill crane (*Grus canadensis*) recruitment, doubling late summer recruitment at Malheur National Wildlife Refuge, OR (Littlefield 2003). The use of artificial nesting islands along the Copper River Delta, AK increased nest survival by 50% (compared to nests in the surrounding landscape) of dusky Canada geese (*Branta canadensis*) (Miller *et al.* 2007; Maggiulli and Dugger 2011). A modest increase in whooping crane fledgling rates (5-15% increase in egg to late summer survival) has the potential to significantly increase population growth and time to down-listing, if such an improvement would be feasible through some type of management action.

This management option increases recruitment and thus has the potential to positively impact population growth, but may bring implementation challenges. An alternate strategy for increasing recruitment is to increase the survival of second fertile eggs through headstarting (see Option 5 below).

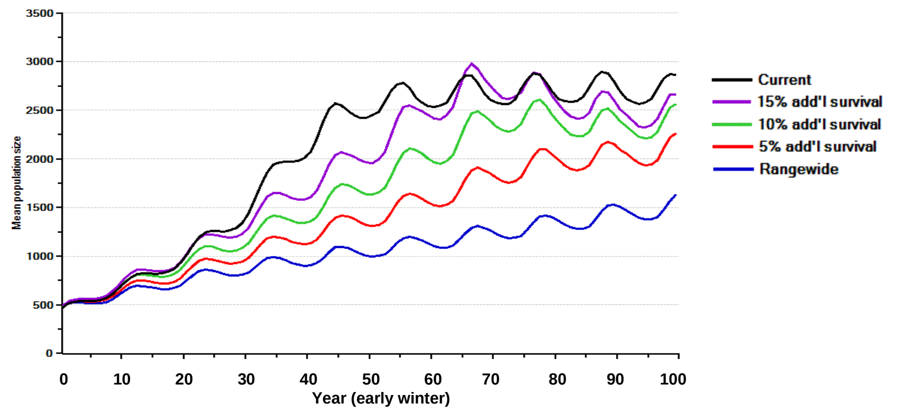

Fig. 8. Projected mean size of AWBP for 100 years for the Range-wide Impacts scenario with current fledgling survival (blue) and with increased fledgling survival of 5%, 10% and 15%. Black line represents Current Conditions (no impacts of CO_2, sea rise, hurricanes or added mortality).

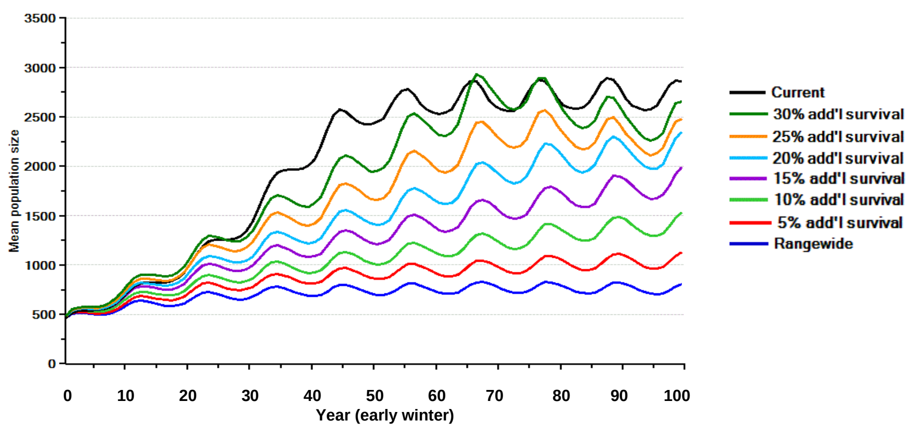

Fig. 9. Projected mean size of AWBP for 100 years with 30% added migration mortality, 50% added mortality in non-protected lands, and with hurricane impacts, with current fledgling survival (blue) and with increased fledgling survival of 5%, 10%, 15%, 20%, 25% and 30%. Black line represents Current Conditions (no impacts of CO_2, sea rise, hurricanes or added mortality).

<u>Option 5: Improve recruitment through headstarting</u>.

This management option explores another method to improve recruitment and represents the collection of second wild-laid eggs from a portion of nests in Wood Buffalo National Park (WBNP) with two fertile eggs, hatching and headstarting (HS) of these chicks in captivity, and release of headstarted juveniles back into WBNP. This scenario includes the following parameters:

- Eggs would be collected from nests with two fertile eggs in WBNP. Egg collection is assumed to have no impact on the survival of the remaining egg (Boyce *et al*. 2005; Clark *et al*. 2017).
- Eggs would be reared by crane pairs at the Calgary Zoo (with an estimated 12 suitable foster adult pairs available per year). One scenario assumes 1 chick reared per pair, while an alternative scenario assumes that some pairs may raise two chicks, for a total of 18 chicks raised by 12 pairs.
- Estimated mortality from collected egg to released juvenile is 30% (considered to be a reasonable but conservative estimate; mortality may be lower).
- Headstarted juveniles are released back to WBNP in late autumn prior to migration to Aransas.
- Collection, headstarting and releases occur annually until program termination.

<u>Headstarting to Mitigate Impacts of Future Threats</u>
Model scenarios (n=108) were developed using the Range-wide Impacts scenario to explore the ability of headstarting to offset future threats, similar to the approach taken in Alternative Management Option 4. These scenarios were based on combinations of the following four variables:

<u>Number of eggs collected</u> for headstarting each year: 12 vs 18

<u>Survival of released juveniles</u> (from release to 12 months old): 100%, 75% or 50% of the survival of wild-hatched birds of the same age (same survival as wild-hatched birds after reaching 1 year of age)

<u>Reproduction</u> (production of fledglings) by adult pairs: 100%, 50% or 15% of wild reproductive rate (i.e., two wild-hatched mates), applied to all breeding pairs consisting of two released birds; reproductive rate for pairs with one wild-hatched bird and one released bird were tested with released rates (pessimistic) and with wild rates (optimistic)

<u>Length of HS program</u>: 100 years vs 20 years

Interaction of survival and reproduction in released cranes
The impact of egg collection and headstarting on the AWBP is influenced by an interaction of survival and reproductive rates of released birds, which is best illustrated by examining scenarios in which headstarting is conducted annually over the entire 100-year projection to observe cumulative effects over time. Tables 3 and 4 give model results using the Range-wide Impacts scenario as a basis and assuming a pessimistic (conservative) view that reproductive success is lower for any released crane regarding of whether its mate is wild-hatched or released. The results are color coded as follows to indicate the degree of change (based on final N and stochastic r) from Range-wide Impacts projection results:

- Bright green: >20% improvement over Range-wide Impacts projection
- Medium green: 10-20% improvement
- Light green: 5-10% improvement
- No shading: Similar to range-wide impacts ($\pm$ 5%)
- Yellow: 5-10% decrease
- Light orange: 10-20% decrease
- Bright orange: 20-30% decrease
- Red: Over 30% decrease; final population < 1000 birds

Model results for egg collection and headstarting over the entire 100 years under these assumptions suggest that headstarting results in increased population growth and size *as long as* reproduction of released birds is good (Table 4). Increased population viability is highest when survival and reproduction of released birds is the same as wild-hatched birds; if 18 eggs are collected annually, this scenario slightly exceeds that projected with a 5% increase in recruitment as modeled in Alternative Option 4 (Figure 8). The population benefits from headstarting efforts even if immediate post-release survival (to 1 year of age) is only 50% of that of wild-hatched birds. As long as reproduction in these birds is high, there is benefit to headstarting, as essentially this greatly improves the survival of 12-18 second eggs each year and thus overall recruitment.

Reproductive rates of released birds have a much larger impact on the population than their immediate post-release survival. If released birds always show reproductive rates at 50% of wild-hatched birds, regardless of the origin of their mate, the population shows slight improvements in status, with essentially no impact at 50% of normal survival (to age 1) and 50% of normal reproduction. If reproduction is very poor (15% of the rate of wild-hatched birds, similar to that observed in reintroduced whooping crane populations to date), regardless of the origin of their mate, then population growth can be negatively affected especially if survival is high (Table 3). This is because, in this scenario, released birds may pair with wild-hatched birds, reducing the reproductive rates of more breeding pairs under the conditions modelled. In the most extreme case (18 headstarted eggs per year for 100 years, with normal survival and 15% of normal reproduction), the final population is projected to be <1000 birds (Fig. 10, red line). None of these scenarios result in a risk of extinction over 100 years, and all retain a high level of gene diversity.

Under a continuous (100-year) headstarting program, the number of headstarted birds in the population grows for ~30 years and then stabilizes (N_{HS}=~55 cranes with 50% of normal survival, ~85 cranes with 75% of normal survival, and ~120 cranes with normal survival). Released birds represent from 4-17% of the population after 100 years, depending upon their post-release survival, total population size and trend.

Realistically, headstarting activities are not likely to continue for 100 years. Two additional sets of scenarios were modelled with the same inputs but with headstarting implemented only for the first 20 years or only when the population was < 1000 birds (one year and older). The results between these two implementation options were very similar, so only the results for headstarting for 20 years are presented here. Conducting the program for only 20 years tempers the impacts of headstarting, whether positive or negative (Table 4). Even in the worst case scenario, the population shows overall positive growth with a final population > 1000 (Fig. 10, purple line), but performs worse than without headstarting. Almost all scenarios with a 20-year headstart program result in ≤10% change in final population size and growth rate compared to no headstarting, the exception being cases in which reproduction of released birds is high.

Under a 20-year headstarting program, both the number and proportion of released birds in the AWBP peaks at about 20 years and then slowly declines as headstarting ceases. The peak proportion of HS birds is approximately 9-14% (with normal survival), 7-11% (with 75% survival), and 4-7% (with 50% survival), depending on 12 or 18 HS eggs. (Fig. 11).

The overall conclusion is that headstarting has the potential to benefit the AWBP if survival and reproduction of released birds is good (e.g., at least 50% of survival rates and reproductive rates for wild-hatched birds under the conditions modeled). Releasing HS birds has the potential to reduce population viability, however, if reproduction of released birds remains poor throughout their lives, is not influenced by having wild mates, and especially if their survival concurrently is high.

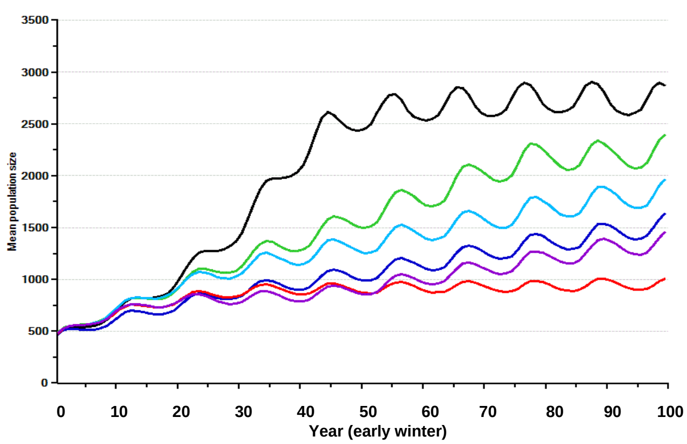

Fig. 10. Projected mean size of AWBP for 100 years under four headstarting scenarios with 18 HS eggs per year and normal survival: best HS projections, with 100% reproduction for 100 (green) and 20 (light blue) years; and worst HS projections, with 15% reproduction for 100 (red) and 20 (purple) years. Dark blue line represents the Range-wide Impacts; black line represents Current Conditions.

Table 3. Model results for AWBP based on the Range-wide Impacts scenario, with headstarting 12 or 18 eggs per year <u>for 100 years</u>, with varying survival and reproduction relative to wild-hatched (N=population size at 100 years, GD=gene diversity retained, r = stochastic r; TTT=mean time to target of N≥1000). Mixed breeding pairs have HS reproductive rates.

Range-wide Impacts scenario: N = 1538; r = 0.0121; GD = 0.990; TTT=45yrs						
	12 HS eggs			**18 HS eggs**		
	100% of normal repro	**50% of normal repro**	**15% of normal repro**	**100% of normal repro**	**50% of normal repro**	**15% of normal repro**
100% of normal survival	N=2113 r=0.0171 GD=0.992 TTT: 30yrs	N=1653 r=0.0130 GD=0.991 TTT: 42yrs	N=1181 r=0.0092 GD=0.989 TTT: 65yrs	N=2195 r=0.0184 GD=0.993 TTT: 22yrs	N=1658 r=0.0132 GD=0.991 TTT: 32yrs	N=954 r=0.0068 GD=0.987 TTT: >100yrs
75% of normal survival	N=1969 r=0.0157 GD=0.992 TTT: 32yrs	N=1571 r=0.0124 GD=0.990 TTT: 44yrs	N=1260 r=0.0096 GD=0.989 TTT: 64yrs	N=2099 r=0.0171 GD=0.992 TTT: 23yrs	N=1575 r=0.0125 GD=0.990 TTT: 42yrs	N=1090 r=0.0081 GD=0.988 TTT: 86yrs
50% of normal survival	N=1860 r=0.0148 GD=0.991 TTT: 32yrs	N=1598 r=0.0128 GD=0.991 TTT: 44yrs	N=1345 r=0.0104 GD=0.989 TTT: 64yrs	N=1929 r=0.0155 GD=0.992 TTT: 32yrs	N=1573 r=0.0125 GD=0.990 TTT: 43yrs	N=1224 r=0.0093 GD=0.988 TTT: 65yrs

Table 4. Model results for AWBP based on the Range-wide Impacts scenario, with headstarting 12 or 18 eggs per year <u>for 20 years</u>, with varying survival and reproduction relative to wild-hatched (N=population size at 100 years, GD=gene diversity retained r = stochastic r; TTT=mean time to target of N≥1000). Mixed breeding pairs have HS reproductive rates

Range-wide Impacts scenario: N = 1538; r = 0.0121; GD = 0.990; TTT=45yrs						
	12 HS eggs			**18 HS eggs**		
	100% of normal repro	**50% of normal repro**	**15% of normal repro**	**100% of normal repro**	**50% of normal repro**	**15% of normal repro**
100% of normal survival	N=1759 r=0.0139 GD=0.991 TTT: 32yrs	N=1595 r=0.0124 GD=0.990 TTT: 43yrs	N=1436 r=0.0113 GD=0.989 TTT: 55yrs	N=1826 r=0.0144 GD=0.992 TTT: 22yrs	N=1577 r=0.0124 GD=0.990 TTT: 44yrs	N=1376 r=0.0109 GD=0.989 TTT: 65yrs
75% of normal survival	N=1694 r=0.0134 GD=0.991 TTT: 32yrs	N=1592 r=0.0126 GD=0.990 TTT: 43yrs	N=1465 r=0.0115 GD=0.989 TTT: 54yrs	N=1772 r=0.0139 GD=0.991 TTT: 32yrs	N=1585 r=0.0125 GD=0.990 TTT: 43yrs	N=1423 r=0.0112 GD=0.989 TTT: 65yrs
50% of normal survival	N=1657 r=0.0130 GD=0.991 TTT: 33yrs	N=1540 r=0.0122 GD=0.990 TTT: 44yrs	N=1512 r=0.0120 GD=0.990 TTT: 54yrs	N=1670 r=0.0132 GD=0.991 TTT: 32yrs	N=1538 r=0.0120 GD=0.990 TTT: 44yrs	N=1539 r=0.0122 GD=0.990 TTT: 54yrs

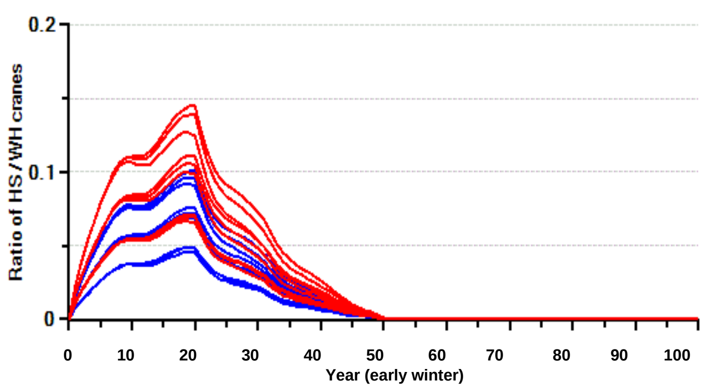

Fig. 11. Projected mean proportion of HS cranes in the AWBP for 100 years with HS for the first 20 years. Red lines represent the 9 scenarios with 18 HS eggs per year; blue lines represent 9 scenarios with 12 HS eggs per year. Each set of 9 scenarios vary survival and reproduction of HS birds.

Impact of reproductive success of mixed-origin breeding pairs
Model results presented above assume that reproductive rates of released birds do not improve over time or with reproductive experience, and that the reproductive success of a wild-hatched (WH) x HS pair combination is reduced by the HS mate and is the same as HS-HS pairs. However, observations of captive-reared released Mississippi sandhill cranes suggest that breeding pairs with *at least* one wild-hatched mate are twice as likely to fledge a chick as breeding pairs comprised of two released birds (Brooks, pers. comm.). This could be interpreted as both wild pairs and WH-HS pairs (i.e., all pairs with at least one WH mate) have normal (wild) success rates, while HS x HS pairs have 50% reduction in success compared to wild rates. To simulate this more optimistic situation for whooping cranes, model scenarios were tested in which HS-HS pairs had lower reproduction, but WH-HS pairs reproduce at the same average rate as wild pairs.

Results suggest that the reproductive success of mixed origin breeding pairs (i.e., one wild-hatched bird and one released bird) can have a significant influence on the impact of headstarting programs. If mixed origin pairs (WH-HS pairs) have the same reproductive success as wild pairs, then the reproductive success of HS-HS pairs does not influence the long-term results; population growth rate, final size, genetic diversity and time to down-listing are similar whether HS-HS success is 100%, 50% or 15% of wild birds. This holds true for the AWBP model likely because only a few birds are being released into a large wild population, and therefore many released birds may be pairing with wild mates in the model (i.e., there may be relatively few HS-HS pairs). In the model, pairs are formed between young, unpaired (i.e., available) birds, with no preference with respect to origin. All scenario combinations result in higher growth and shorter time to down-listing compared with no headstarting, with better results observed with more effort (18 HS eggs annually) and with length of program (100 years) (Table 5, Figure 12).

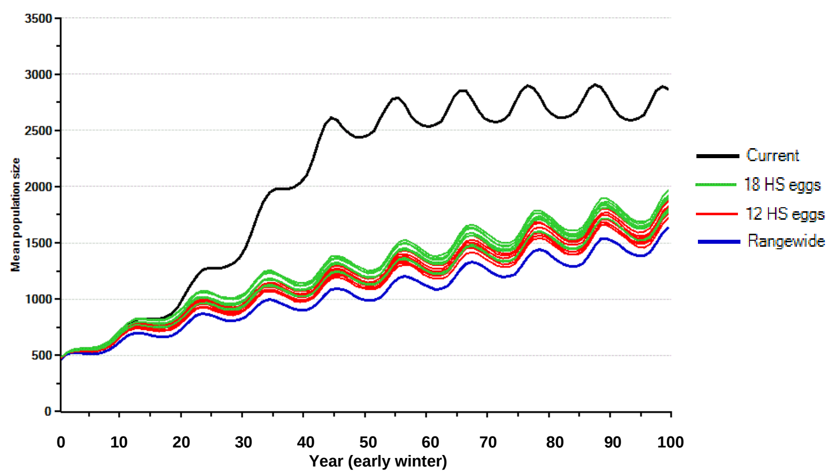

Fig. 12. Projected mean size of AWBP for 100 years with first 20 years of headstarting, varying post-release survival and reproductive rate of HS-HS pairs (see Table 10). Green lines = 18 HS eggs/year; red lines = 12 HS eggs/year. Dark blue line represents the Range-wide Impacts; black line represents Current Conditions.

Understanding reproduction in mixed pairs is important, as it influences projections for headstarting programs for augmentation of wild populations (e.g., AWBP) that creates mixed WH-HS pairs. This also may influence how quickly reintroduced populations with mostly released HS birds will 'take off' as new wild-hatched birds are produced and reach breeding age. The relative impact of reproductive success in mixed pairs is greatest when reproductive success in released HS birds is low and when headstarting efforts are high and long term. To explore this range further, model scenarios were developed to test intermediate success rates of mixed pairs to estimate the point at which headstarting becomes beneficial.

Table 5. Model results for AWBP based on the Range-wide Impacts scenario, with headstarting 12 or 18 eggs per yr for 100 or 20 yrs, with varying survival and reproduction relative to wild-hatched (N=population size at 100 yrs; GD=gene diversity; r = stochastic r; TTT=mean time to N≥1000). Mixed breeding pairs have wild crane reproduction.

Range-wide Impacts scenario: N = 1538; r = 0.0121; GD = 0.990; TTT=45yrs				
	HS for 100 years		**HS for 20 years**	
	12 HS eggs	**18 HS eggs**	**12 HS eggs**	**18 HS eggs**
	15 to 100% of normal repro	**15 to 100% of normal repro**	**15 to 100% of normal repro**	**15 to 100% of normal repro**
100% of normal survival	N=2014-2113 r=0.0165-0.0171 GD=0.992 TTT: 30-31yrs	N=2152-2195 r=0.0180-0.0184 GD=0.993 TTT: 22yrs	N=1707-1759 r=0.0136-0.0139 GD=0.991 TTT: 32yrs	N=1783-1830 r=0.0141-0.0144 GD=0.992 TTT: 22-23yrs
75% of normal survival	N=1955-1969 r=0.0156-0.0157 GD=0.992 TTT: 32yrs	N=2039-2099 r=0.0165-0.0171 GD=0.992 TTT: 23-30yrs	N=1683-1694 r=0.0132-0.0134 GD=0.991 TTT: 32-33yrs	N=1772-1784 r=0.0139-0.0142 GD=0.991-0.992 TTT: 31-32yrs
50% of normal survival	N=1833-1860 r=0.0146-0.0148 GD=0.991 TTT: 32-33yrs	N=1929-1958 r=0.0155-0.0157 GD=0.992 TTT: 32yrs	N=1610-1657 r=0.0127-0.0131 GD=0.991 TTT: 33-42yrs	N=1663-1690 r=0.0132 GD=0.991 TTT: 32-33yrs

Reproductive success for mixed pairs was varied from 15% to 100% of normal base rates for wild pairs, while maintaining low reproductive success for HS x HS pairs (15% of wild value). Headstarting was modeled as the collection and headstarting of 18 eggs annually for 100 years to maximize the impact of varying mixed pair success under range-wide impacts. *Results suggest that, under these conditions, headstarting has no impact when reproductive success of mixed pairs is ~ 45% of base wild rates (Fig. 13). Headstarting benefited the population when mixed pair success was higher (e.g., ≥60%), and was detrimental to the population when mixed pair success was lower (e.g., ≤30%). The same result was observed regardless of the survival rate of released birds (100%, 75% or 50% of base rate).*

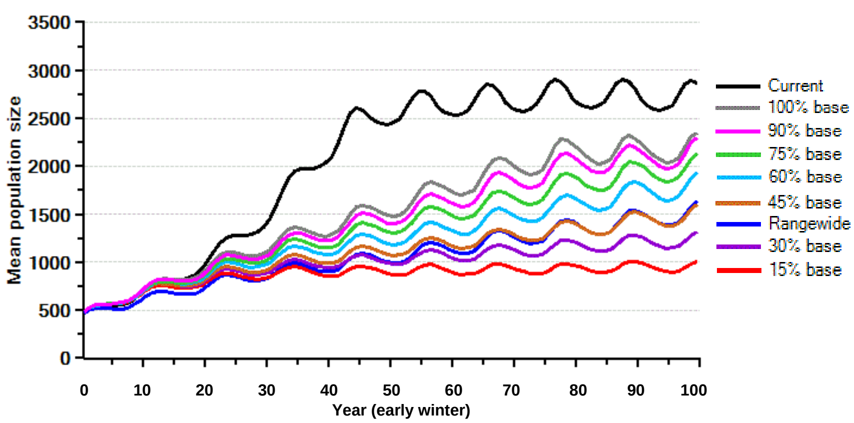

Fig. 13. Projected mean size of AWBP with headstarting 18 eggs annually, varying reproductive rate of WH-HS pairs. HS pairs at 15% of wild reproduction; survival of released birds same as wild. Dark blue line (partially obscured by 45% base rate line) represents the Range-wide Impacts; black line represents Current Conditions.

The results presented in this PVA bracket the extreme cases of mixed origin pairs performing as poorly as released pairs and as optimally as wild pairs as well as intermediate values between these extremes. In addition, demographic rates and therefore outcomes may be different depending upon the location and conditions where birds are released, or may change over time for individuals as birds gain reproductive experience. Given the complex interaction of survival and reproductive rates of released cranes, monitoring survival and reproduction of released birds and the factors that influence these rates will be important to evaluate the impacts of headstarting and to effectively revise strategies based on new information. Management actions, either during the *ex situ* headstarting process or during or following release, that promotes good reproductive success of released HS birds should be considered.

Headstarting in the Absence of Future Threats

The above analyses were based on the Range-wide Impacts scenario and provide guidance on the level of effort and conditions under which headstarting might be used to mitigate the impact of future threats. Additional scenarios were tested using the Current Conditions scenario as a base to evaluate how headstarting might be used short term to reduce time to down-listing if the AWBP continues to exhibit strong growth in the absence of future threats. Scenarios were run for 20-year headstart programs only.

As seen above, the reproductive success of mixed origin breeding pairs greatly influenced the impacts of headstarting in the Range-wide Impacts models. This factor has less influence under Current Conditions. This may be because population growth is currently strong, and releases quick account for smaller proportions of the wild population and have less influence.

If mixed breeding pairs (WH x HS pairs) have the same reproductive success as pairs of released birds (HS x HS pairs), i.e., pessimistic values, all scenarios result in strong growth of at least 4% and time to down-listing from 18-22 years, and retain high levels of gene diversity with no risk of extinction in 100 years. Some headstarting scenarios result in lower growth than in the absence of headstarting, in a pattern similar to Table 4 under Range-wide Impacts. However, these impacts are more modest ($\pm$ 10%) under Current Conditions, and result in mean growth rates of r = 0.0412-0.0440 (12 eggs) and r = 0.0404-0.0453 (18 eggs). Time to reaching down-listing target size varied from 18-22 years across all scenarios.

If mixed origin pairs (WH x HS pairs) have the same reproductive success as wild pairs, then a 20-year headstarting program has a positive impact on the AWBP across all survival and reproductive values modeled. Growth rates range from r=0.043 to 0.047, and time to target size from 20-21 years with 12 HS eggs, and from r=0.044 to 0.050, and time to target size from 18-20 years with 18 HS eggs. These scenarios most closely compare to headstart models developed by Clark *et al*. 2017, which are based on historical data and assume no future threats. While numerous differences in model structure and inputs do not allow for direct comparison of scenarios in these two models, both this PVA and the Clark *et al.* model suggest that the AWBP will reach the down-listing criterion of >1000 birds on average in 2038 with no augmentation and under current conditions. Headstarting projections may be in some cases more optimistic in Clark *et al.* models; for example, under annual release of 11-13 juveniles exhibiting wild demographic rates, down-listing to >1000 birds is projected to be achieved on average by 2030 by Clark *et al*., whereas this PVA projects 2034 as the average year to reach >1000 birds. The inclusion of cyclicity in this PVA may account for this difference, as the AWBP is projected to reach ~950 birds by 2030 but then experiences several years in the 'trough' of the solar cycle rather than a steady increase as modeled by Clark *et al*. The assumptions of no future threats and no reduced reproduction in released birds in Clark *et al*.'s model may lead to optimistic projected impacts of headstarting and augmentation if these assumptions are not upheld.

Impacts of retaining some HS birds in the SSP

An alternative version of the headstarting scenarios would be to retain one juvenile per year for a total of 10 juveniles over a period of 10-15 years to genetically supplement the Species Survival Plan (SSP) captive population. Model results suggest that the retention of one juvenile per year in the SSP for the first 10 years has very little to no long-term effect on the AWB population comparing to releasing all HS juveniles. Separate modeling will be conducted to assess the impact of this strategy on the SSP *ex situ* population.

AWBP PVA Summary and Implications for Recovery Objectives

PVA Model Summary

A VORTEX population simulation model was developed for the wild Aransas-Wood Buffalo population (AWBP) of whooping cranes. Extensive historical survey and research data as well as expert opinion from whooping crane managers and researchers enabled the development of a robust model that represents past conditions and trends, including 11-year cyclicity in population size and growth rate. Retrospective modeling suggests that this model is a good representation of historical trends. Sensitivity testing suggests that recruitment (egg production and fledging rate) and adult survival are primary factors in population growth and size.

Demographic rates have been positive in the past, leading to ~3.7% annual growth and expanding the population from 72 to over 400 cranes over the past 40 years. Potential changing future conditions that may impact these rates lead to some uncertainty in future population viability projections. An exploration of these factors over plausible values suggests that the two most influential impacts may be potential lower recruitment related to climate change and potentially higher mortality during migration due to increased development and other anthropogenic threats.

If historical and current conditions continue into the future, model projections indicate strong positive growth (r=0.0423, SD=0.0684) that is cyclic and includes some years of population decline. Estimated time to reach the target for down-listing under Alternative Criterion 1B (i.e., sustained population of at least 1000 cranes) is approximately 21 years (ranging from 19-30 years), and the population reaches carrying capacity on average in 55-65 years. Mean population size in 100 years is 2481 (SD=228), with high retention of current gene diversity (99.4%) and no risk of extinction over 100 years. If the best estimates of range-wide threats are incorporated into the model, projections suggest overall gradual (lower) positive growth (r=0.0120, SD=0.0708). Projected population size in 100 years is variable (N_{100}=1538, SD_{100}=627) but is significantly lower than modeled habitat carrying capacity (K_{100}=2505). This is attributable to low overall growth rate due to projected additional mortality sources in the future (due to climate change and/or human activities). Loss of existing genetic variation is minimal (~1%) and there is no projected risk of extinction over 100 years. Average time to down-listing target is ~45 years under current management conditions (range from 23 to over 100 years).

Uncertainty and Assumptions

While consensus views are that some mortality risks will increase in the future, there is uncertainty regarding the magnitude of these risks and how they will impact whooping cranes. The range of outcomes over the values explored for climate change and anthropogenic mortality impacts is large in terms of future population size and growth; however, all scenarios tested resulted in overall stable or positive growth, high retention of genetic variation, and no risk of extinction in 100 years. These scenarios assume that mortality rates during migration will not exceed 130% of estimated historical rates for the AWB migratory population (and that all birds would be equally vulnerable), that sub-adult and adult survival remains high in protected areas of the wintering grounds and in the breeding grounds, that changes in available wintering habitat do not exceed the projections for a 2m sea level rise, and that negative effects of rising atmospheric CO_2 levels do not exceed those modeled for 500ppm.

Impacts of Management Alternatives

Five alternative management options were explored, three targeting winter or migration mortality and two enhancing recruitment. Higher mortality risks during migration have the potential to significantly impact the population; thus, actions that minimize additional migration risks (or additional risks to adults in general at any time or location) would be beneficial. Actions that improve recruitment rate also will help compensate for additional mortality and for climate change impacts on recruitment. Increasing fledging rate (survival from egg to fledging) in the wild can be effective but may be challenging to implement. An alternative approach is to increase recruitment through headstarting chicks in captivity from wild-collected eggs and releasing juveniles back to the AWBP. This can be effective if reproduction of released cranes is good but may not produce significant results if program length is short and/or reproduction of released cranes is poor. In some instances, headstarting activities could negatively affect the population (i.e., survival is high but reproduction is poor for released birds through their lives, even when paired with wild mates). Headstarting or other forms of augmentation are likely to have greater impact when the population is small or under threat.

PVA Results and Recovery Objectives

The current international recovery plan (CWS & USFWS 2007) includes two recovery objectives for down-listing of whooping cranes, one for the wild population and one for the captive population. Objective 1 is to "establish and maintain self-sustaining populations of whooping cranes in the wild that are genetically stable and resilient to stochastic environmental events." Down-listing Criteria 1 and 1A relate to the development and maintenance of a whooping crane wild meta-population of 2-3 sub-populations and will be addressed in separate modeling efforts. This PVA is relevant in particular to Alternative Criterion 1B that specifies only one large wild population and would require the AWBP to be self-sustaining and remain above 1,000 individuals (i.e., 250 productive pairs).

The 'range-wide impacts' scenario suggests that the AWBP can meet down-listing Alternative Criterion 1B on average in about 45 years; however, projected population size is considerably variable and could lead to shorter or longer times to actual down-listing. Under the conditions modeled, the population will likely reach and maintain at least 1000 cranes (and at least 250 productive pairs) with high retention of existing genetic variation. Timeline to meeting this criterion varies significantly not only stochastically but also depending upon model assumptions and future estimated threats. In the 'current conditions' scenario (i.e., no future climate change or additional anthropogenic threats), the AWBP may reach meet this criterion in half the time (~21 years). Some scenarios with higher future mortality (e.g., migratory mortality >125% of AWBP historical rates) are not projected to meet this criterion within 100 years. While uncertainty in future conditions make it difficult to precisely predict time to meeting down-listing criteria, the scenarios explored in this PVA can guide management actions that will promote down-listing sooner.

Objective 2 to "maintain a genetically stable captive population to ensure against extinction of the species" is being modelled separately to evaluate the projected genetic and demographic status of the SSP population. As none of the AWBP scenarios project a risk of extinction of the AWBP over the next 100 years, this suggests that the captive population may not be required to augment or re-establish the wild AWB population. However, the captive population may provide headstarting or augmentation services that could reduce the time to down-listing for the AWB population. The captive population may play a critical role for the development of additional reintroduced populations, for example by parent fostering wild-laid eggs or producing additional birds for release. In addition, given the uncertainty of future climate change impacts and anthropogenic threats, there may be a risk of population decline or extinction in the presence of greater threats than modeled and increasing the need for a back-up captive insurance population.

Acknowledgements

This PVA model was developed in consultation with the Whooping Crane International Recovery Team and numerous crane biologists and managers who participated through workshops and/or electronic discussion in 2015-2018. Additional PVA work was conducted in 2018 to assess the captive and reintroduced whooping crane populations and full meta-population. These PVA models and results will serve as a basis to evaluate potential management actions to increase whooping crane viability and to evaluate recovery goals for this species, and will inform species conservation planning discussions scheduled in October 2019.

Section 3. Whooping Crane Population Viability Analysis (PVA) Report: Eastern Migratory Population Model and Sensitivity Testing of Management Options

This report describes the whooping crane baseline *VORTEX* model and results for the wild Eastern migratory population (EMP). This population model and scenarios were developed in conjunction with the 2015 and 2016 Population Viability Analysis (PVA) workshops in Calgary, and were informed by additional electronic and telephone conference discussions through 2018.

Releases of captive-reared juvenile cranes began in 2001 to establish this migratory population, which has breeding grounds in Necedah National Wildlife Refuge and other wildlife areas in central Wisconsin and that winters in or on the flyway to the Gulf coast of Florida. As of spring 2017 (the point at which this model is initiated), 278 young cranes had been released for 16 consecutive years (2001-2016) in cohorts of 10-29 birds per year. Reproduction began in 2005 and has been consistent since 2009. Pairing, mating and egg production rates are high, along with sub-adult and adult survival. A high rate of nest abandonment results in low recruitment (production of fledglings) that is currently insufficient for population sustainability. While this reintroduced population has a longer history than the Louisiana non-migratory population (LNMP), it is challenging to predict future demographic rates.

Model Inputs

A stochastic, individual-based population model was developed for the whooping crane using the *VORTEX* 10.2.15 (Lacy and Pollak 2017) software program. *VORTEX* is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild or captive small populations. A one-year time step was implemented, with most events (e.g., breeding) occurring once per year. Two mortality events occur in the model each year so that summer vs winter events can be altered separately in the model. The model begins each 'year' in spring just prior to breeding. Model scenarios were run for 100 years with 1000 iterations each.

Demographic rates to parameterize the EMP model were derived from a combination of field data for the Aransas-Wood Buffalo population (AWBP) and the EMP, as well as expert opinion on conference calls and at the PVA workshops This includes projected future changes in environmental conditions and human-related threats under current management actions. Sensitivity testing was used to explore some of the uncertainty around these input estimates and the resulting viability projections. A summary of inputs is provided below; see AWBP PVA report for more details.

Initial Population

The model was initiated with 104 surviving birds as of spring 2017 prior to breeding. Age and sex of these individuals were taken from census and studbook data and include 54 males and 50 females ranging in age from 1-15 years. Pedigree data from the 2017 studbook were used to set kinships among the initial birds (Peregoy 2017). Individual birds were marked in the model as either released or wild-hatched birds according to their origin, which influences the demographic rates attributed to them in the model. The additional 17 birds released in 2017 were added as juveniles to the first year of the model simulation.

Carrying Capacity

Carrying capacity was discussed at the PVA workshop and was estimated by the participants to be 2000 birds (summer K), with ~1350 breeding adults (675 pairs).

Reproduction (Egg Production)

The mating system was modeled as long-term monogamous pairs, with reproduction beginning as early as age 4. In the model, female breeding rate is defined as the probability that an adult female will produce eggs that year (hatch rate and juvenile survival are modeled separately – see below). Female reproductive rates (egg production) for the EMP were varied based on female reproductive experience, with nulliparous adult females having a 50% chance of producing a clutch, and proven females (i.e., those that had produced eggs in the past) having a 95% chance of producing a clutch, based on Servanty *et al.* (2014). These rates approximate those observed in the young adult cranes released into the LNMP to date (54% for nulliparous females; 91% in females that had nested in a previous year). A small decline in breeding rates (down to 81-88%) was incorporated for older females (>23 years old) to match that used in the AWBP model. Environmental variation (EV) for reproduction was set at CV = 8%.

All nesting attempts in the same year were collapsed to represent one 'clutch' in the model, as breeding pairs that hatch a chick do not produce an additional clutch and so never produce multiple successful clutches. Most clutches consist of two eggs (96% of clutches, as used in the AWBP and LNMP models), although both chicks seldom survive. Rates above were based primarily on Gil-Weir *et al*. 2012, Wilson *et al.* 2016 and Whooping Crane Eastern Partnership (WCEP) reports.

Mortality
Mortality is implemented in the model as two mortality events per year (summer vs winter mortality), with no sex-specific differences in mortality. First-year mortality was divided into six-month mortality from egg through fledging to late fall, with additional mortality during the remainder of the first year. Mortality rates used for other age classes were similarly applied to each six-month summer/fall or winter/spring period. Maximum lifespan was set at 30 years. This model structure matches that of the AWBP and LNMP PVA models.

Future age-specific mortality rates are challenging to estimate for this relatively young population currently composed primarily of released captive-reared birds. Data are available regarding the reproductive success (nesting, egg production, hatch rate, fledge rate) and survival of these captive-reared released birds; however, data are not yet available on the reproductive success of wild-hatched pairs or pairs of mixed origin in this population, nor on the survival of cranes past ~16 years of age.

Hatching and fledging rates vary significantly between the three whooping crane populations (AWBP, EMP, LNMP), with both rates much lower in the two reintroduced populations that are composed primarily of captive-reared (CR) released cranes than in the AWBP comprised of wild-hatched (WH) birds. The EMP has experienced high mortality from hatching to fledging due in part to abandonment, while the LNMP to date has experienced few hatches but good parental care for those few chicks.

Given the observations to date for the reintroduced populations compared to the wild AWBP, mortality from egg to fledging may depend upon the origin of the parents, i.e., released captive-reared birds vs wild-hatched birds. Observations of captive-reared released Mississippi sandhill cranes suggest that breeding pairs with at least one wild-hatched mate are twice as likely to fledge a chick as breeding pairs comprised of two released birds (Brooks, pers. comm.). This hypothesis was incorporated into the PVA models for both the EMP and LNMP. Offspring survival and parental care were assumed to be static for each pair and was not modeled as improving over time. The following juvenile mortality rates (egg to ~6 months old) were incorporated into the EMP base model based in part on PVA discussions, and is similar to the modeling strategy used for the LNMP (also see Table 6):

> <u>Captive-reared pairs (CR-CR)</u>: If both parents are captive-reared released birds, EMP rates from 2014-2017 were used. This time period was chosen as it represents a period of relatively consistent management and when the population was relatively large and reproducing regularly. Default rates were based on non-manipulated nesting attempts (i.e., data were excluded for pairs that were forced to renest due to egg collection of their first clutch).

Wild-hatched pairs (WH-WH): If both parents are wild-hatched and reared in the wild, then AWBP egg-to-fledging mortality rates were used, unless otherwise noted.

Mixed-origin pairs (WH-CR): If one parent is wild-reared and one is captive-reared, three different rates were explored:

- Default rate: EMP survival rate x 2
- Optimistic rate: mean (midpoint) of AWBP and EMP rates
- Pessimistic rate: same rate as captive-reared (CR-CR) pairs

An additional scenario was explored in which wild-hatched and mixed-origin pairs both have marginally better reproductive success than captive-reared pairs. This scenario (Poor Wild Success) represents the scenario in which all pairs have low reproductive success, for example, if black fly infestation causes high rates of nest abandonment.

Table 6. Egg to six-month mortality rates used for the EMP base model. Wild-reared = natural reproduction in the wild. Captive-reared = either captive-produced and captive-reared juveniles, or wild-collected eggs that are hatched and reared (headstarted) in captivity and returned to the wild as juveniles at ~6 months of age. Mixed origin = one wild-reared and one captive-reared parent. Default rates given in blue.

Pair success	Wild-reared parents		Mixed origin parents		Captive-reared parents	
	Egg 1	Egg 2	Egg 1	Egg 2	Egg 1	Egg 2
Optimistic (mixed)	58.15%	95%	76.33%	97%	94.5%	99%
	AWBP rates		*Midpoint of WH & CR*		*EMP rates*	
Default (mixed)	**58.15%**	**95%**	**89%**	**98%**	**94.5%**	**99%**
	AWBP rates		*CR-CR survival x2*		*EMP rates*	
Pessimistic (mixed)	58.15%	95%	94.5%	99%	94.5%	99%
	AWBP rates		*CR-CR survival*		*EMP rates*	
Poor wild success	89%	98%	89%	98%	94.5%	99%
	EMP rates		*EMP rates*		*EMP rates*	

Mortality rates for sub-adult and adult cranes in the EMP are not significantly different from those observed for the wild AWB population (Servanty *et al*. 2014). While human-related mortality may account for a greater proportion of identified causes of death in the EMP, it is not known whether such deaths are additive or compensatory with deaths due to natural mortality causes. To account for potentially higher human-related mortality in this population, AWBP mortality rates were increased by 5% and used as the default rate for cranes over 6 months of age. Additional scenarios were tested with AWBP rates (Optimistic) and 10% increase in AWBP mortality (Pessimistic) (see Table 7).

EV for mortality rates was set at COV=10% and was partially correlated (0.5) with EV in reproduction as in the AWBP model. No cyclicity related to the solar cycle and no impacts of increased atmospheric CO_2 was included in juvenile recruitment for this population.

Table 7. Mortality rates used for the EMP base model for cranes over 6 months old. Default rates given in blue.

Adult mortality	6 months to 1 year	1 and 2 yrs olds (annually)	3 yr old	Adult (4+ yrs) (annually)
Optimistic	10.5%	11.34%	15.75%	5.6%
		AWBP rate x 1.05		*AWBP rate*
Default	**10.5%**	**11.34%**	**15.75%**	**5.88%**
		AWBP rate x 1.05		*AWBP rate x 1.05*
Pessimistic	10.5%	11.34%	15.75%	6.16%
		AWBP rate x 1.05		*AWBP rate x 1.1*

Population Size Regulation

There is no growth regulation in demographic rates, i.e., no density-dependency or limitation of nesting sites or resources. Rather, population size is limited in the model by carrying capacity (K) and by general demographic rates. Probabilistic truncation to K is implemented if population size exceeds K at the end of each year and is applied only to non-breeding birds.

Catastrophes

Two catastrophic events were incorporated in the base model, based in part upon general trends in catastrophic declines observed in wild vertebrate populations by Reed *et al*. 2003. Risk of a high mortality event in the wintering grounds was incorporated as a 0.5% risk (~once every 200 years) of a 50% reduction in survival for all age classes over winter. The risk of a poor breeding season (90% reduction in fledgling production) was given a 5% risk of occurrence (~ once every 20 years). While these catastrophes were developed for the AWBP model, they were considered reasonable to apply to the EMP model given the potential for severe flooding, tropical storms or other extreme events to impact survival.

Genetics

A small genetic load (3 lethal equivalents, 1 as a lethal allele and 2 as non-lethal effects) was incorporated into the model and applied as lower juvenile survival in inbred individuals. This is lower than the genetic load suggested by O'Grady *et al.* (2006) of 12.29 lethal equivalents for wild vertebrate populations, as it is assumed that some of the initial genetic load may have been purged due to the historical bottleneck and population expansion experienced by this species. The model tracked pedigree relatedness and applied inbreeding effects on any future additional inbreeding. Any supplementation was modeled as unrelated birds except for the 2017 releases.

Ex Situ Management Options

Several population management strategies that involve *ex situ* components are available to support the establishment of reintroduced whooping crane populations. These may result in different demographic rates for reproduction and mortality, as hypothesized in Table 6. Some of these options have been implemented in the past and were explored in different modeling scenarios for their potential impact.

Supplementation: Releases

The EMP was established through the release of juvenile captive-reared whooping cranes. The EMP PVA model was initialized at the point of pre-breeding season in 2017 to match with other whooping crane population models in this PVA. The 17 juveniles that were released in late 2017 were incorporated into the first year of modeling to match actual management to date. Incorporation of future releases (i.e., releases in 2018 and later) were varied in different scenarios (see below).

Headstarting and/or Forced Renesting

Another management option to address poor egg and juvenile survival is to collect fertile eggs from a portion of the first clutches in the EMP population, hatch and rear these chicks under breeding pairs in captivity, and return these same juveniles at some stage back to the EMP. This could greatly increase the survival of these chicks compared to survival if reared in the EMP but may have consequences for their future reproduction. If all eggs are collected from a nest, the pair may produce an additional (second) clutch, which may partially compensate for the loss of the first clutch from the population. This represents the current management practice and is referred to as "forced re-nesting" by WCEP.

A related management option is to collect fertile eggs from some of the first clutches in the EMP population and rear these chicks under breeding pairs in captivity (as described above), but not return surviving juveniles to the EMP. Instead, these juveniles could be used to supplement another population such as the LNMP. This could benefit the LNMP but may have consequences for the EMP depending upon how many clutches are collected and the success rate of renesting attempts.

Validation of Historical Trends

Retrospective demographic modeling of the EMP since its establishment in 2001 was conducted, using studbook data and WCEP annual reports to inform the schedule of captive-reared juvenile releases by sex and year (pedigree information was not included in this model). Model projections track survey data closely until 2010, after which model projections continue to grow in 2010-2011 before leveling off. The 2014 WCEP annual report noted an emerging concern regarding lower survival than expected among 2011-2013 releases for both ultralight-led (UL) and Direct Autumn Release (DAR) birds. Model results represent population numbers in approximately late fall, while survey data represent numbers in December-February, possibly contributing to the discrepancy. Although the model results are higher, they are within approximately one standard deviation (SD) of the mean and represent the same overall trend of population stabilization for the past ~5-6 years. Given the small population size and other considerations, this appears to a reasonable representation of this reintroduced Eastern migratory population under past conditions. The reproductive rates and survival of wild-born descendants in the future is less understood, as is the future rate and impact of shooting and other human-caused threats on survival.

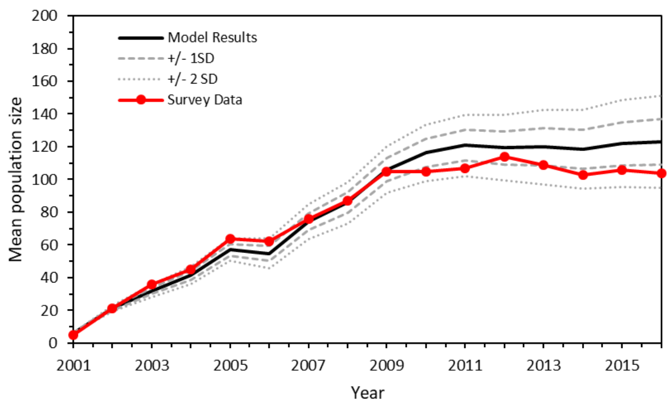

Fig. 14. Retrospective model projection of the Eastern migratory whooping crane population from fall 2001 to fall 2016 (black line) and survey results (red line).

Measures of Population Viability and Progress toward Down-listing

Most of the following simulations project a period of population decline (and in some instances, extinction), followed by a period of continued growth. This is related to assumptions in most scenarios of lower reproductive success among captive-reared released cranes and their long lifespan, allowing for stronger growth once all released birds have died and the population consists solely of wild-hatched birds with higher reproductive rates. Population projections over the next 30-40 years are influenced by assumptions in demographic rates of released birds and are not necessarily indicative of long-term trends.

Mean population size (N) and mean gene diversity (GD) reported here represent ending population status for iterations in which the population did not go extinct (i.e., status of populations that persist). Probability of extinction (PE) is calculated over 100 years (unless otherwise specified). Together these measures convene likely population status at 100 years and are an indication of long-term viability.

The stochastic growth rate *r* reported here represents the mean stochastic growth rate over the entire 100-year projection (incorporating both population decline and expansion) and not the ending growth rate or trend. Thus, a negative *r* does not *necessarily* indicate a long-term declining population in this long-lived species that might experience improved growth in future wild-hatched generations. Stochastic *r* is presented here to aid relative comparisons on overall growth among different management scenarios.

Mean time to reaching down-listing target (TTT) represents the year at which the mean population size meets the down-listing criterion (under Objective 1, Criterion 1; CWS & USFWS 2007) of at least 100 or 120 cranes and being self-sustaining for at least a decade. This may be a more useful indicator of population status than *r*.

All values for N, GD, *r* and TTT represent means around which there is a high degree of variation. This means, for example, that TTT represents the point at which the population meets the down-listing criteria about ~ 50% of the time, provided it did not go extinct. In reality, this means there is some probability that the population will meet down-listing criteria sooner, and a significant probability that the population will not meet down-listing criteria until substantially later. A useful metric is the probability that the population will reach a certain population size by a given year; this measure is also provided in some of the following results.

Exploration of Future Viability under Uncertainty

Sensitivity analysis of the AWBP model indicated that population growth rate is most sensitive to adult survival, followed by sub-adult survival and juvenile survival, when these rates are varied by equal proportion. Historically, most observed variation in wild whooping crane demographic rates has been in the survival of early age classes while adult survival is high with relatively little variation. Given this Wilson *et al*. 2016 noted that fledging rate had the greatest influence on annual growth rate. Factors that affect hatching and fledging rates and juvenile survival are likely to drive viability as long as sub-adult and adult survival remain high. Higher mortality in adult (and to a lesser extent, sub-adult) mortality, however, can reduce population viability. Population size is another factor due to increased stochastic impacts in smaller populations. Sensitivity testing of the AWBP model showed reduced viability in populations with fewer than 300 cranes (refer to the AWBP PVA report for more information).

For the EMP there is substantial uncertainty regarding future demographic rates, in particular with respect to future survival and reproductive success of wild-hatched cranes. It is also unclear how rearing history affects demographic rates. Multiple scenarios were explored to examine the range of future projections for the EMP under this uncertainty, and the level of management needed to prevent population decline.

Projected Viability and Growth: No further supplementation

Using the model input values outlined above (with the default settings for all mortality rates) and with no further supplementation, the projected viability of the EMP is moderate (with respect to the viability categories presented in this report) and involves significant uncertainty. Recruitment of wild-hatched juveniles may be insufficient to balance deaths and maintain the population, leading on average to a slowing declining population. Once most or all released cranes have died (after ~25 years), then breeding pairs consist of wild-reared birds with higher reproductive success (in the model) and thus allow the potential for positive growth (Fig. 15). At this point the population is likely to be under 100 birds (mean=78, SD=30). A small risk of extinction develops over time after about 35 years, with PE_{50yr}=0.004 and PE_{100yr}=0.02. Projected population size is highly variable (Fig. 16).

In those iterations (98%) in which the population persists, average population size is 128 (SD=75) in 50 years and 402 (SD=344) in 100 years, with a mean time to down-listing of 43 years (TTT_{N100}) and 51 years (TTT_{N120}), respectively. Although the population reaches these thresholds on average at 43-51 years, about one half of the time the population will reach these thresholds earlier and one half of the time later. Figure 17 shows how the probability of the EMP falling short of these population size criteria changes over time. Note that the probability of not reaching 100 cranes in 100 years is 19.4% (23.1% for 120 cranes).

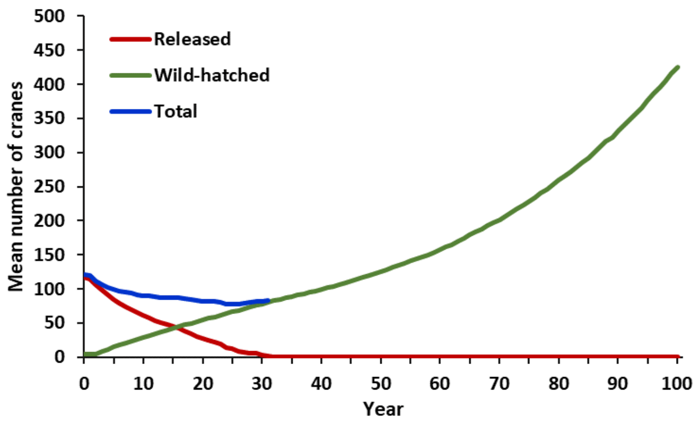

Fig. 15. Projected mean number of captive-reared released cranes (red line), wild-hatched cranes (green line), and total cranes in the EMP over 100 years for model runs in which the population did not go extinct (98% of iterations).

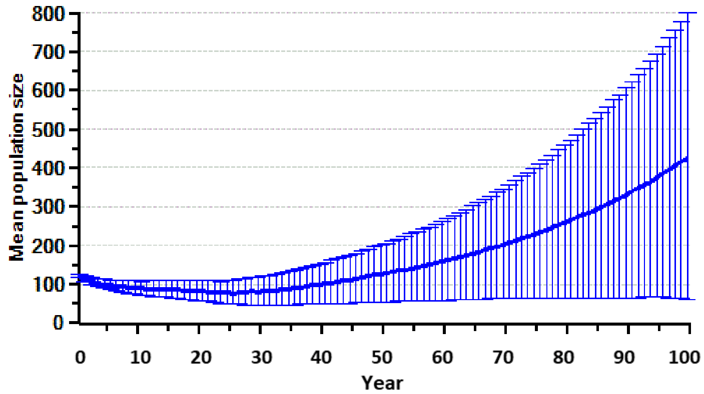

Fig. 16. Projected total cranes in the EMP over 100 years (for runs that did not go extinct). Bars indicate $\pm$ 1 SD.

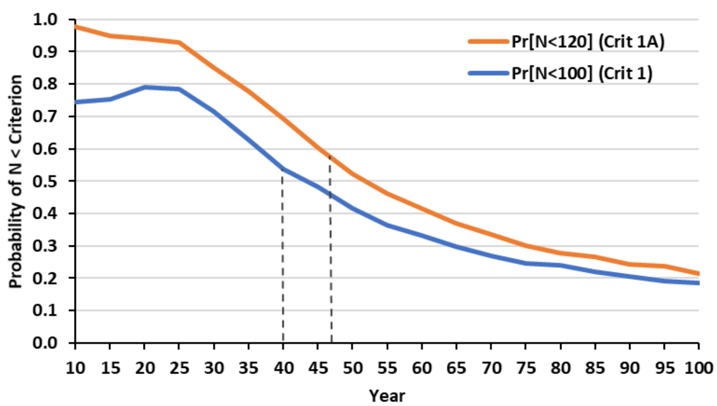

Fig. 17. Probability over time that EMP will consist of less than 100 (blue line) or less than 120 (orange line) cranes at winter count. Dashed lines indicate the year in which mean N reaches 100 or 120, respectively.

Impact of rearing success of mixed-origin breeding pairs

It is uncertain how the rearing success of mixed-origin breeding pairs (one wild-hatched (WH) bird and one captive-reared (CR) bird) compares to that of wild pairs (WH-WH) or breeding pairs of released birds (CR-CR). Observations of captive-reared released Mississippi sandhill cranes suggest that breeding pairs with at least one wild-hatched mate are twice as likely to fledge a chick as breeding pairs comprised of two released birds (Brooks, pers. comm.). The default rate modeled for the EMP (Figs. 15-17) represents twice the survival from egg to six months of age for mixed-origin pairs (11%) vs CR-CR pairs (5.5%) for the first egg in the nest, and 2% vs 1% for the second egg. While this may be a reasonable estimate, mixed-pair success rates may in fact be higher or lower. Three alternative scenarios were explored:
1) more optimistic intermediate survival rate (WH-CR rates = midpoint of WH-WH and CR-CR rates);
2) pessimistic rate (WH-CR rates = CR-CR rates); and 3) poor survival rates for wild-hatched parents (WH-WH = WH-CR default rates) (see Table 6).

The reproductive success of mixed-origin pairs can have a significant impact on the future viability of the EMP. With no future supplementation (releases), some CR released cranes may live up to 30 years and may form mixed-origin pairs. The default values result in a slowly declining mean population size during this period. More optimistic (midpoint) values lead to population growth, while pessimistic (CR-CR) values lead to faster population decline (Fig. 18). While mixed-origin pairs cannot exist past year 31 and therefore all subsequent pairs are WH-WH pairs with higher success rates, poor recruitment and resulting small population size during the first 31 years has long-term impacts on demographic and genetic viability and extinction risk (Fig. 19; Table 8). Gene diversity declines quickly between years 22-32 for the pessimistic scenario, suggesting that many released birds had little to no successful reproduction (i.e., little genetic representation in the next generation). Optimistic rates lead to a high probability (97-98%) of meeting down-listing criteria within 100 years, while pessimistic rates have less than 50% probability of meeting these criteria. If wild-hatched pairs also demonstrate poor reproductive success, population decline and extinction are likely in the absence of interventions such as supplementation. Again, population size is highly variable within each scenario.

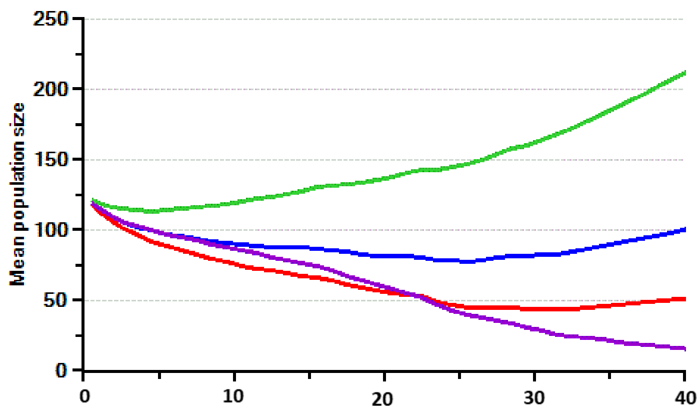

Fig. 18. Projected total cranes in the EMP over 40 years (for runs that did not go extinct) using different reproductive success rates for mixed-origin pairs.

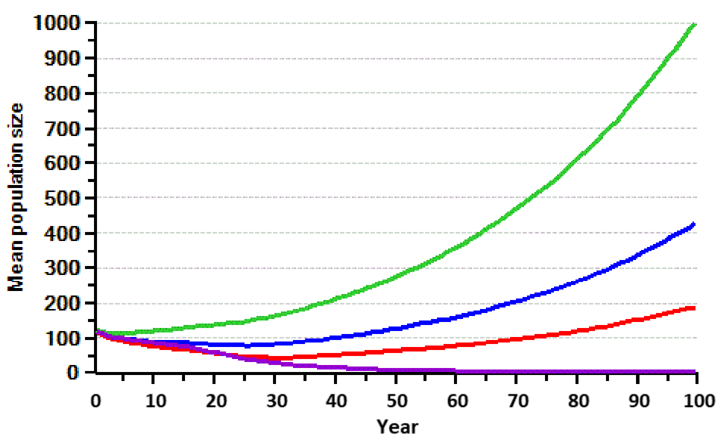

Fig. 19. Projected total cranes in the EMP over 100 years (for runs that did not go extinct) using different reproductive success rates for mixed-origin pairs.

Table 8. Model results for EMP for 100 years with different first six-month (egg to post-fall migration) mortality rates for mixed-origin breeding pairs and wild-hatched pairs. Stoch r=stochastic growth rate; N=mean population size; GD=mean gene diversity; PE=probability of extinction; TTT=mean time to target size for down-listing.

	First 6-mo. mortality (WH-CR parents)		First 6-mo. mortality (WH-WH parents)			Mean (SD)			Mean	Mean
Scenario	**Egg 1**	**Egg 2**	**Egg 1**	**Egg 2**	**Stoch r**	**N_{100yr}**	**GD_{100yr}**	**PE_{100yr}**	**TTT_{100}**	**TTT_{120}**
Optimistic	76.33%	97%	58.15%	95%	0.0179	926 (556)	0.935	0.002	11yrs	15yrs
Default	89%	98%	58.15%	95%	0.0067	402 (344)	0.895	0.020	43yrs	51yrs
Pessimistic	94.5%	99%	58.15%	95%	-0.0074	177 (195)	0.831	0.141	81yrs	89yrs
Poor wild success	89%	98%	89%	98%	-0.0594	2.7 (0.6)	0.607	0.997	--	--

Improvement in rearing success

Model results presented in this PVA assume that the parental rearing success (measured by successful survival of offspring from egg to fledging) is a fixed characteristic of a pair and does not improve over time or with reproductive experience. Females that have laid previous clutches are more likely to produce a clutch in subsequent years (95% vs 45% for first-time nesters), but hatching and fledging success rates of eggs are not affected in the model. If reproductive experience has an effect in crane pairs in the wild, this effect is incorporated in a general manner for wild-hatched pairs by using the average historical AWBP rates. For newly established reintroduced populations it is possible that hatching and/or fledging rates may improve over time with increasing years in the wild and increasing number of reproductive pairs in the population, and/or rates may improve once a pair successfully fledges a chick. The lack of data on these variables combined with the complex model structure required to explore these factors make it impractical to address in this PVA. However, it is possible that reproductive rates of released pairs may increase in the future beyond those observed in the past.

Uncertainty in future survival rates

The EMP is a relatively new crane population comprised primarily of captive-reared birds and is subject to different conditions and threats than other existing whooping crane populations. There is substantial uncertainty not only with respect to reproductive success but also regarding future adult mortality rates, especially of released birds. Survival of released cranes to date has been similar to that of cranes in the AWBP cranes (Servanty *et al*. 2014; B. Hartup, pers. comm.). However, this population inhabits and migrates through different areas than the AWBP and may be subjected to different threats. The relative proportion of deaths with known causes that are attributable to human-related causes is higher in the EMP than the AWBP, but it is unknown whether such mortality is compensatory or additive to natural deaths. In addition, threats may change in the future and/or if the population expands into new areas. Previous sensitivity analyses suggest that crane populations may be impacted by increased adult mortality, and thus this represents a potentially important area of uncertainty.

Scenarios were modeled with three different adult mortality rates for all adult cranes (both released and wild-hatched) by applying AWBP rates (Optimistic), 5% increase of AWBP mortality (Default), and 10% increase of AWBP mortality (Pessimistic) (see Table 7 for rates used). The results are presented in Table 9 and are color coded as follows to indicate the relative demographic and genetic viability of the EMP for these 12 sensitivity scenarios exploring adult mortality:

- Dark blue: N≥600, GD≥0.96, PE≤0.005, ≥2.5% mean growth, >99% of 100
- Light blue: N≥500, GD≥0.94, PE≤0.01, ≥2% mean growth, >95% chance of reaching N=100
- Bright green: N≥300, GD≥0.88, PE≤0.05, ≥1% mean growth, >90% chance of reaching N=100
- Light green: N≥200, GD≥0.85, PE≤0.10, positive growth, >70% chance of reaching N=100
- Yellow: N≥100, GD≥0.82, PE≤0.20, no decline, >50% chance of reaching N=100
- Light orange: N≥100, GD≥0.78, PE≤0.30, ≤ 1% mean decline, >30% chance of reaching N=100
- Bright orange: N≥70, GD≥0.75, PE≤0.40, ≤ 2% mean decline, >10% chance of reaching N=100
- Red: N≤70, GD≤0.75, PE>0.40, ≥ 2% mean decline, <10% chance of reaching N=100

The definitions of these categories is to some extent arbitrary and can be classified differently. The purpose is to visually illustrate general clustering of categories of long-term viability measures.

As expected, higher adult mortality impacts population growth and size, and therefore time to down-listing and recovery. A 5% increase in mortality over AWBP (i.e., from 5.6% to 5.88% annual mortality) has relatively little impact across the reproductive success rates explored. An additional 5% increase above AWBP annual adult mortality (i.e., to 6.16%) has a greater impact, roughly halving mean population size and in some cases affecting time to down-listing and extinction risk. This suggests that the EMP (and possibly other whooping crane populations) are vulnerable to additional threats to adult birds.

Mixed-origin pair reproductive success has a significant and similar impact across all three adult mortality rates, and has a greater impact over the matrix of values tested. While mixed-origin pairs are possible during the first 30 years of model projections, low success rates lead to population decline and increasing stochastic risks associated with small population size. Poor reproductive success of wild-hatched birds perpetuates this situation and prevents the population from potential growth and recovery in the future, resulting in continued population decline and eventual extinction (Table 9).

Table 9. Model results for EMP for 100 years, with varying adult mortality of all cranes and reproductive success of mixed-origin breeding pairs (N=mean population size (SD); r = stochastic r; GD=mean gene diversity; PE=probability of extinction; TTT=mean time to down-listing target size(100/120 cranes); Pr=probability of reaching down-listing size (100/120 cranes)). Mean N, GD and TTT calculated only for iterations that did not go extinct.

	Optimistic adult mortality (5.6%) AWBP rate	Default adult mortality (5.88%) AWBP rate x 1.05%	Pessimistic adult mortality (6.16%) AWBP rate x 1.1%
Optimistic mixed pair success	N_{100}=1111 (595) r=0.0202 GD_{100}=0.938 PE_{100}=0.002 $TTT_{100/120}$=11y/13y $Pr_{100/120}$=0.981/0.974	N_{100}=926 (556) r=0.0179 GD_{100}=0.935 PE_{100}=0.002 $TTT_{100/120}$=11y/15y $Pr_{100/120}$=0.977/0.969	N_{100}=419 (312) r=0.0086 GD_{100}=0.916 PE_{100}=0.007 $TTT_{100/120}$=11y/30y $Pr_{100/120}$=0.862/0.850
Default mixed pair success	N_{100}=507 (392) r=0.0097 GD_{100}=0.907 PE_{100}=0.022 $TTT_{100/120}$=38y/45y $Pr_{100/120}$=0.867/0.843	N_{100}=402 (344) r=0.0067 GD_{100}=0.895 PE_{100}=0.020 $TTT_{100/120}$=43y/51y $Pr_{100/120}$=0.806/0.769	N_{100}=176 (162) r=0.0030 GD_{100}=0.864 PE_{100}=0.057 $TTT_{100/120}$=65y/78y $Pr_{100/120}$=0.571/0.505
Pessimistic mixed pair success	N_{100}=200 (217) r= -0.0054 GD_{100}=0.841 PE_{100}=0.129 $TTT_{100/120}$=75y/83y $Pr_{100/120}$=0.492/0.456	N_{100}=177 (195) r= -0.0074 GD_{100}=0.831 PE_{100}=0.141 $TTT_{100/120}$=81y/89y $Pr_{100/120}$=0.465/0.407	N_{100}=75 (87) r= -0.0199 GD_{100}=0.787 PE_{100}=0.285 $TTT_{100/120}$=>100y $Pr_{100/120}$=0.183/0.144
Poor wild pair success	N_{100}=3.5 (1.3) r= -0.0579 GD_{100}=0.602 PE_{100}=0.987 DL not possible	N_{100}=2.7 (0.6) r= -0.0594 GD_{100}=0.607 PE_{100}=0.997 DL not possible	N_{100}=2 (0) r= -0.0679 GD_{100}=0.510 PE_{100}=0.999 DL not possible

<u>Summary Results: No future supplementation</u>

The EMP is a relatively young reintroduced population composed primarily of captive-reared released cranes that have experienced relatively good survival but low reproductive success. Future survival and reproduction of these birds and their wild-hatched descendants is uncertain. Population projections based on the best estimates of demographic rates and incorporating this uncertainty exhibit high variability in population size, viability, and progress toward recovery, ranging from a large, viable population that meets down-listing criteria to a declining population with high risk of extinction (Fig. 20). Most projections suggest the EMP may level off or decline for ~25 years and may be take decades to reach down-listing criteria, if at all, in the absence of additional future supplementation. Reproductive rates of mixed-origin and wild-hatched breeding pairs are a key factor impacting future EMP growth and viability. Even small, consistent losses of adult cranes may have significant impacts on the population.

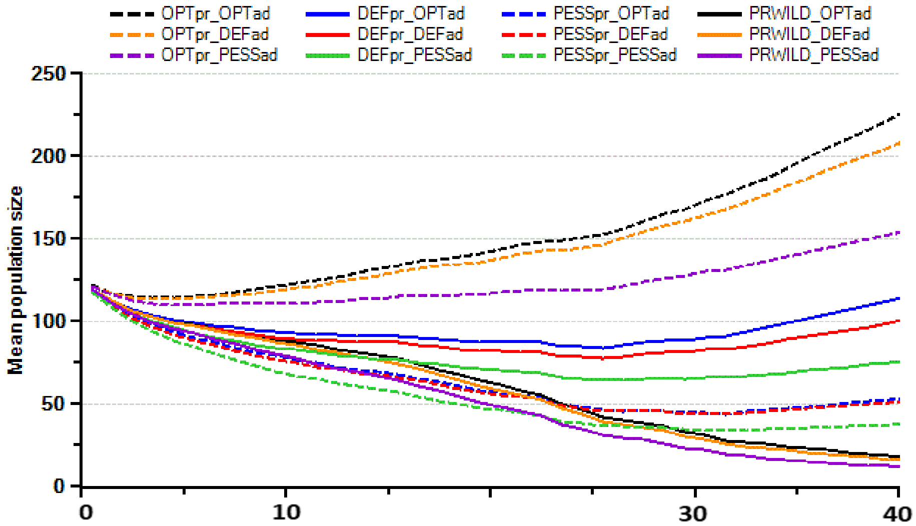

Fig. 20. Projected mean total cranes in the EMP over 40 years (for runs that did not go extinct) for 12 combinations of different reproductive success rates and adult mortality. OPT=Optimistic; DEF=default; PESS=pessimistic; PRWILD=poor wild success; pr=pair success; ad=adult mortality.

Projected Viability: Improved fledging success

Poor survival from egg to fledging hinders past and potential future population growth in the EMP. Only a few wild-laid eggs have led to surviving descendants thus far. Several different management actions may be considered that may improve future fledging rates. These may include releases or population expansion to other regions (e.g., outside of Necedah), impoundment management, or other actions. Such options may differ with respect to feasibility.

A series of scenarios was developed to explore the potential benefit of improved fledging rates of released cranes, regardless of the method by which this might be achieved. Model results can be used to assess the level of effort required for a certain result and weighed together with practical and other considerations. These scenarios used the default values for released (CR-CR) pair success as a base, explored across the three adult mortality schedules in Table 7. Fledging rate (i.e., survival from egg to fledging) was modeled as 2x, 3x, 4x and 5x the base rate for CR-CR pairs and applied to both captive-reared and mixed-origin pairs (Table 10). Wild-hatched pairs were modeled with the default AWBP fledging rates (41.85% and 5% for the first and second egg, respectively), which equates to ~7.6x base rate.

Table 10. Survival and mortality rates (egg to fledging) used in fledging success scenarios. Default rates in blue.

Scenario	Default		2xBase		3xBase		4xBase		5xBase	
	Egg 1	Egg 2	Egg 1	Egg 2	Egg 1	Egg 2	Egg 1	Egg 2	Egg 1	Egg 2
CR-CR pairs										
Survival	**5.5%**	**1%**	11%	2%	16.5%	3%	22%	4%	27.5%	5%
Mortality	**94.5**	**99%**	89%	98%	83.5%	97%	78%	96%	72.5%	95%
WH-CR pairs										
Survival	**11%**	**2%**	11%	2%	16.5%	3%	22%	4%	27.5%	5%
Mortality	**89%**	**98%**	89%	98%	83.5%	97%	78%	96%	72.5%	95%

Doubling the survival rate from 5.5% to 11% had little effect compared to the default scenario, as it only effectively impacts CR-CR pair success. Additional increases in egg-to-fledging survival (3x-5x) have substantial positive impacts for the EMP, even under Pessimistic adult mortality rates (i.e., 1.1x AWBP mortality). In comparison, tripling egg-to-fledging survival (from 5.5% to 16.5%) provides a relatively large benefit (Fig. 21). Benefits with additional increases in survival have the most impact when adult (or other age class) mortality is higher. These results assume that wild-laid and reared eggs will have good (AWBP) survival rates to fledging.

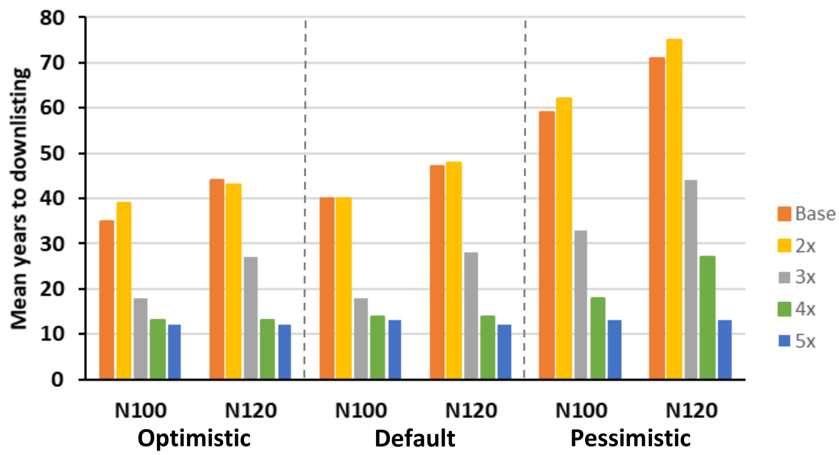

Fig. 21. Mean time to meeting down-listing criteria (for N≥100 or 120 and self-sustaining) across increasing fledging rates (1-5x base value) and for three adult mortality rates (Optimistic, Default, Pessimistic).

Projected Viability: Additional future supplementation

Juvenile recruitment is a primary issue for this newly established population, both for sustainability and to quickly grow the population size to reduce the impacts of stochastic processes. Historically the EMP was established via annual release of juvenile cranes reared in captivity. The continued release of additional cranes into the population for the next few years can help buffer against small population risks. However, if reproduction success is low for CR-CR and mixed-origin pairs, continued releases have the potential to delay population growth driven by more successful wild-hatched pairs. This may be especially true if the survival of released cranes is high, as noted in the LNMP PVA. It is also valuable to assess the relative benefit of various release strategies against effort required as well as ability to meet recovery objectives.

Measuring Time to Target size for down-listing under supplementation

It is difficult to measure if populations are self-sustaining while supplementation is underway. The population may reach and maintain over 100 cranes during and after supplementation but may not be eligible as 'self-sustaining for a decade' (per down-listing Criterion 1) until a minimum of 10 years after releases have ended. In some cases, the population may show some decline following termination of releases until a balance is reached in the age structure and between released and wild-hatched birds; however, population size may remain high and soon stabilizes. Such cases are indicated in the results.

Continued annual release of captive-reared juveniles

Two release rates (5 vs 10 releases per year, equal sex ratio) and two release schedules (annually for 5 or 10 years) were combined to model four release strategies. These release strategies were evaluated against uncertainty in mixed-origin pair reproductive success and adult mortality of released birds. Nine scenarios were developed for each of these release strategies by varying mixed-origin pair success (optimistic, default, and pessimistic rates) and adult mortality (optimistic, default, and pessimistic rates). This resulted in 36 scenarios that allow comparison of how different release strategies perform against this uncertainty.

Model results are presented in Table 11. Management (release) strategies are represented by rows, with columns representing a range of uncertainty in key demographic rates of released birds. As in Table 9, color coding represents approximate categorization of viability and is provided to illustrate relative different impact among strategies, acknowledging that different definitions could be used. Releases were modelled as unrelated individuals (to each other and to existing EMP cranes); thus, GD is not an accurate reflection of heterozygosity but is useful as a relative comparison of gene diversity retention over time of different management strategies. Scenarios to the left of the thick black line are ones that maintain an average of >100 birds for the duration of the projection, starting at Year 1.

Table 11. Model results for EMP for 100 years with supplementation of released juveniles (5-10 per year for 5-10 years), with varying adult mortality and reproductive success of mixed-origin breeding pairs (N=mean population size at 100 years (SD); r = stochastic r; GD=mean gene diversity; PE=probability of extinction in 100 years; TTD = years to down-listing (N100 or 120); Pr=probability of reaching down-listing criteria (N100 or 120) in 100 years. Mean N and GD calculated only for iterations that did not go extinct. AM=adult mortality. Scenarios to the left of the thick line maintain mean N > 100 birds starting at Year 1.

	Optimistic Repro			**Default Repro**			**Pessimistic Repro**		
	5.6% AM	**5.88% AM**	**6.16% AM**	**5.6% AM**	**5.88% AM**	**6.16% AM**	**5.6% AM**	**5.88% AM**	**6.16% AM**
No further releases *Min. 11yrs to down-list*	N=1111 (595) r=0.0202 GD=0.938 PE=0.002 TTT_{100}=11y TTT_{120}=13y Pr_{100}=0.981 Pr_{120}=0.974	N=926 (556) r=0.0179 GD=0.935 PE=0.002 TTT_{100}=11y TTT_{120}=15y Pr_{100}=0.977 Pr_{120}=0.969	N=419 (312) r=0.0086 GD=0.916 PE=0.007 TTT_{100}=11y TTT_{120}=30y Pr_{100}=0.862 Pr_{120}=0.850	N=507 (392) r=0.0097 GD=0.907 PE=0.022 TTT_{100}=38y TTT_{120}=45y Pr_{100}=0.867 Pr_{120}=0.843	N=402 (344) r=0.0067 GD=0.895 PE=0.020 TTT_{100}=43y TTT_{120}=51y Pr_{100}=0.806 Pr_{120}=0.769	N=176 (162) r=0.0030 GD=0.864 PE=0.057 TTT_{100}=65y TTT_{120}=78y Pr_{100}=0.571 Pr_{120}=0.505	N=200 (217) r= -0.0054 GD=0.841 PE=0.129 TTT_{100}=75y TTT_{120}=83y Pr_{100}=0.492 Pr_{120}=0.456	N=177 (195) r= -0.0074 GD=0.831 PE=0.141 TTT_{100}=81y TTT_{120}=89y Pr_{100}=0.465 Pr_{120}=0.407	N=75 (87) r= -0.0199 GD=0.787 PE=0.285 TTT_{100}=>100y TTT_{120}=>100y Pr_{100}=0.183 Pr_{120}=0.144
5 years **5 per year** (25 released) *Min. 16yrs to down-list*	N=1354 (589) r=0.0236 GD=0.951 PE=0.001 TTT_{100}=16y TTT_{120}=16y Pr_{100}=0.991 Pr_{120}=0.988	N=1136 (579) r=0.0209 GD=0.949 PE=0.001 TTT_{100}=16y TTT_{120}=16y Pr_{100}=0.992 Pr_{120}=0.989	N=545 (374) r=0.0121 GD=0.936 PE=0.003 TTT_{100}=16y TTT_{120}=16y Pr_{100}=0.931 Pr_{120}=0.910	N=635 (477) r=0.0124 GD=0.923 PE=0.013 TTT_{100}=35y TTT_{120}=37y Pr_{100}=0.991 Pr_{120}=0.986	N=515 (410) r=0.0103 GD=0.918 PE=0.009 TTT_{100}=35y TTT_{120}=40y Pr_{100}=0.876 Pr_{120}=0.852	N=210 (184) r= -0.0004 GD=0.886 PE=0.040 TTT_{100}=51y TTT_{120}=62y Pr_{100}=0.632 Pr_{120}=0.584	N=273 (274) r= -0.0070 GD=0.868 PE=0.082 TTT_{100}=58y TTT_{120}=65y Pr_{100}=0.626 Pr_{120}=0.577	N=230 (256) r= -0.0043 GD=0.857 PE=0.119 TTT_{100}=62y TTT_{120}=70y Pr_{100}=0.627 Pr_{120}=0.584	N=103 (119) r= -0.0147 GD=0.823 PE=0.222 TTT_{100}=95y TTT_{120}=>100y Pr_{100}=0.264 Pr_{120}=0.217
5 years **10 per year** (50 released) *Min. 16yrs to down-list*	N=1472 (563) r=0.0254 GD=0.959 PE=0 TTT_{100}=16y TTT_{120}=16y Pr_{100}=0.996 Pr_{120}=0.995	N=1296 (598) r=0.0229 GD=0.956 PE=0.001 TTT_{100}=16y TTT_{120}=16y Pr_{100}=0.992 Pr_{120}=0.989	N=679 (432) r=0.0146 GD=0.946 PE=0.001 TTT_{100}=16y TTT_{120}=16y Pr_{100}=0.959 Pr_{120}=0.942	N=770 (518) r=0.0152 GD=0.936 PE=0.007 TTT_{100}=33y TTT_{120}=33y Pr_{100}=0.944 Pr_{120}=0.932	N=622 (467) r=0.0127 GD=0.931 PE=0.005 TTT_{100}=34y TTT_{120}=34y Pr_{100}=0.920 Pr_{120}=0.895	N=272 (226) r=0.0028 GD=0.906 PE=0.028 TTT_{100}=40y TTT_{120}=50y Pr_{100}=0.733 Pr_{120}=0.684	N=345 (346) r=0.0027 GD=0.884 PE=0.053 TTT_{100}=51y TTT_{120}=59y Pr_{100}=0.706 Pr_{120}=0.658	N=269 (269) r=0.0003 GD=0.880 PE=0.062 TTT_{100}=55y TTT_{120}=63y Pr_{100}=0.671 Pr_{120}=0.617	N=119 (129) r= -0.0118 GD=0.840 PE=0.184 TTT_{100}=85y TTT_{120}=96y Pr_{100}=0.323 Pr_{120}=0.280
10 years **5 per year** (50 released) *Min. 21yrs to down-list*	N=1446 (590) r=0.0249 GD=0.959 PE=0 TTT_{100}=21y TTT_{120}=21y Pr_{100}=0.994 Pr_{120}=0.990	N=1241 (582) r=0.0223 GD=0.957 PE=0.001 TTT_{100}=21y TTT_{120}=21y Pr_{100}=0.993 Pr_{120}=0.993	N=651 (415) r=0.0142 GD=0.945 PE=0.001 TTT_{100}=21y TTT_{120}=21y Pr_{100}=0.958 Pr_{120}=0.945	N=762 (522) r=0.0152 GD=0.937 PE=0.005 TTT_{100}=35y TTT_{120}=35y Pr_{100}=0.949 Pr_{120}=0.935	N=644 (460) r=0.0130 GD=0.933 PE=0.008 TTT_{100}=35y TTT_{120}=35y Pr_{100}=0.923 Pr_{120}=0.902	N=270 (218) r= 0.0029 GD=0.907 PE=0.0300 TTT_{100}=39y TTT_{120}=50y Pr_{100}=0.725 Pr_{120}=0.678	N=341 (330) r=0.0027 GD=0.888 PE=0.058 TTT_{100}=52y TTT_{120}=59y Pr_{100}=0.696 Pr_{120}=0.653	N=265 (260) r= -0.0002 GD=0.877 PE=0.060 TTT_{100}=57y TTT_{120}=65y Pr_{100}=0.621 Pr_{120}=0.576	N=122 (126) r= -0.0115 GD=0.845 PE=0.178 TTT_{100}=95y TTT_{120}=>100y Pr_{100}=0.343 Pr_{120}=0.295
10 years **10 per year** (100 released) *Min. 21yrs to down-list*	N=1635 (502) r=0.0282 GD=0.969 PE=0 TTT_{100}=21y TTT_{120}=21y Pr_{100}=0.997 Pr_{120}=0.997	N=1488 (569) r=0.0257 GD=0.967 PE=0 TTT_{100}=21y TTT_{120}=21y Pr_{100}=0.993 Pr_{120}=0.993	N=870 (499) r=0.0175 GD=0.960 PE=0.002 TTT_{100}=21y TTT_{120}=21y Pr_{100}=0.975 Pr_{120}=0.968	N=1008 (574) r=0.0191 GD=0.953 PE=0.001 TTT_{100}=34y TTT_{120}=34y Pr_{100}=0.975 Pr_{120}=0.969	N=842 (550) r=0.0165 GD=0.949 PE=0.002 TTT_{100}=35y TTT_{120}=35y Pr_{100}=0.956 Pr_{120}=0.947	N=384 (290) r=0.0074 GD=0.932 PE=0.014 TTT_{100}=35y TTT_{120}=35y Pr_{100}=0.843 Pr_{120}=0.811	N=453 (409) r=0.0069 GD=0.911 PE=0.030 TTT_{100}=44y TTT_{120}=50y Pr_{100}=0.792 Pr_{120}=0.759	N=355 (330) r=0.0046 GD=0.907 PE=0.030 TTT_{100}=47y TTT_{120}=54y Pr_{100}=0.768 Pr_{120}=0.721	N=154 (150) r= -0.0054 GD=0.873 PE=0.083 TTT_{100}=72y TTT_{120}=85y Pr_{100}=0.490 Pr_{120}=0.419

Several conclusions can be gleaned from this analysis:

1) All release strategies tested lead to improved viability compared to no future releases.
2) The total number of releases has more impact than the timing of those releases. Specifically, there is little difference in long-term viability between releasing 10 cranes for 5 years or 5 cranes for 10 years. Having more releases sooner may promote slightly shorter time to down-listing.
3) Releasing at least 50 birds promotes a viable population that has a good probability of meeting down-listing criteria within 100 years across almost of the demographic uncertainty tested. Increased levels of supplementation further improve viability.
4) Despite the benefits of additional releases, the uncertainty in future demographic rates is a greater driver of future population size and growth, viability and progress toward down-listing and recovery over the supplementation schedules modeled.

Examining the first 40 years of model projections is useful to identify the impact of the release strategy on mean time to down-listing target and time to reach 100 cranes. Figure 22 shows EMP population projections for 40 years for each release strategy using the default demographic values. At modest supplementation levels (i.e., additional 50 released juveniles), the population on average maintains at least 100 birds. Doubling releases to 100 cranes maintains, on average, at least 120 cranes.

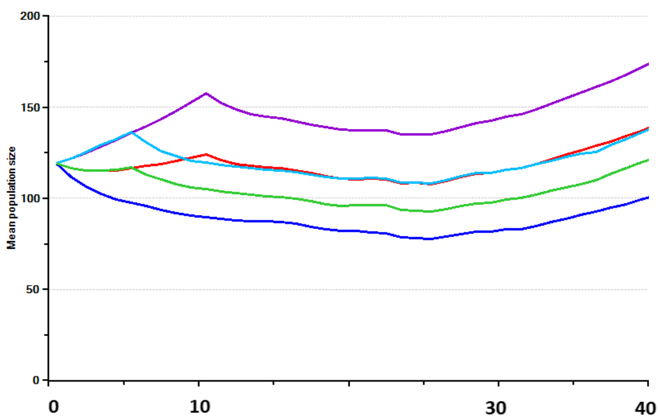

Fig. 22. Projected total cranes in the EMP over 40 years (for runs that did not go extinct) under different release strategies for captive-reared juveniles. Default demographic rates used.

The management strategy used to establish the EMP was to release captive-reared juvenile birds. Although different rearing and release methods have been explored, there is still some uncertainty regarding how age or rearing may affect survival and reproductive rates of released birds. The continued exploration of rearing and release techniques might lead to improved 'quality' of released birds that will lead to higher reproductive success, moving the population from its current (uncertain) state to better long-term viability aspects.

Headstarting EMP eggs

The above analysis modeled the release of juveniles into the EMP essentially as if from another source, such as chicks produced by captive pairs. Some of the released birds that established the EMP were derived from the captive population. Another method for increasing juvenile recruitment is to collect eggs from the EMP, rear the chicks in captivity, and return these chicks to the EMP (headstarting). This method also has been used in the past for the EMP. Beginning in spring 2014, a portion of first clutches have been removed for headstarting, with the hypothesis that many of these EMP breeding pairs will renest and produce a second clutch that they may rear themselves (forced renesting, FN). This could potentially lead to increased production of juveniles from these pairs.

Data for the 2014-2017 breeding seasons were examined to estimate the impact of this practice on renesting, hatching and fledging rates (see Fig. 23 below). Overall, about 30% of first clutches were removed for rearing. Renesting rate for these pairs has been 69%. While hatching rates have been much higher in second clutches (both forced and natural), survival to fledging has been low especially for forced renesting attempts. This means that production of wild-hatched juveniles by FN pairs is lower than pairs allowed to incubate their first clutch. Egg-to-fledging survival is higher in captivity than in the EMP, so more juveniles are added to the population through headstarting. However, if future reproductive success is significantly lower for captive-reared birds, the overall impacts of this method are uncertain.

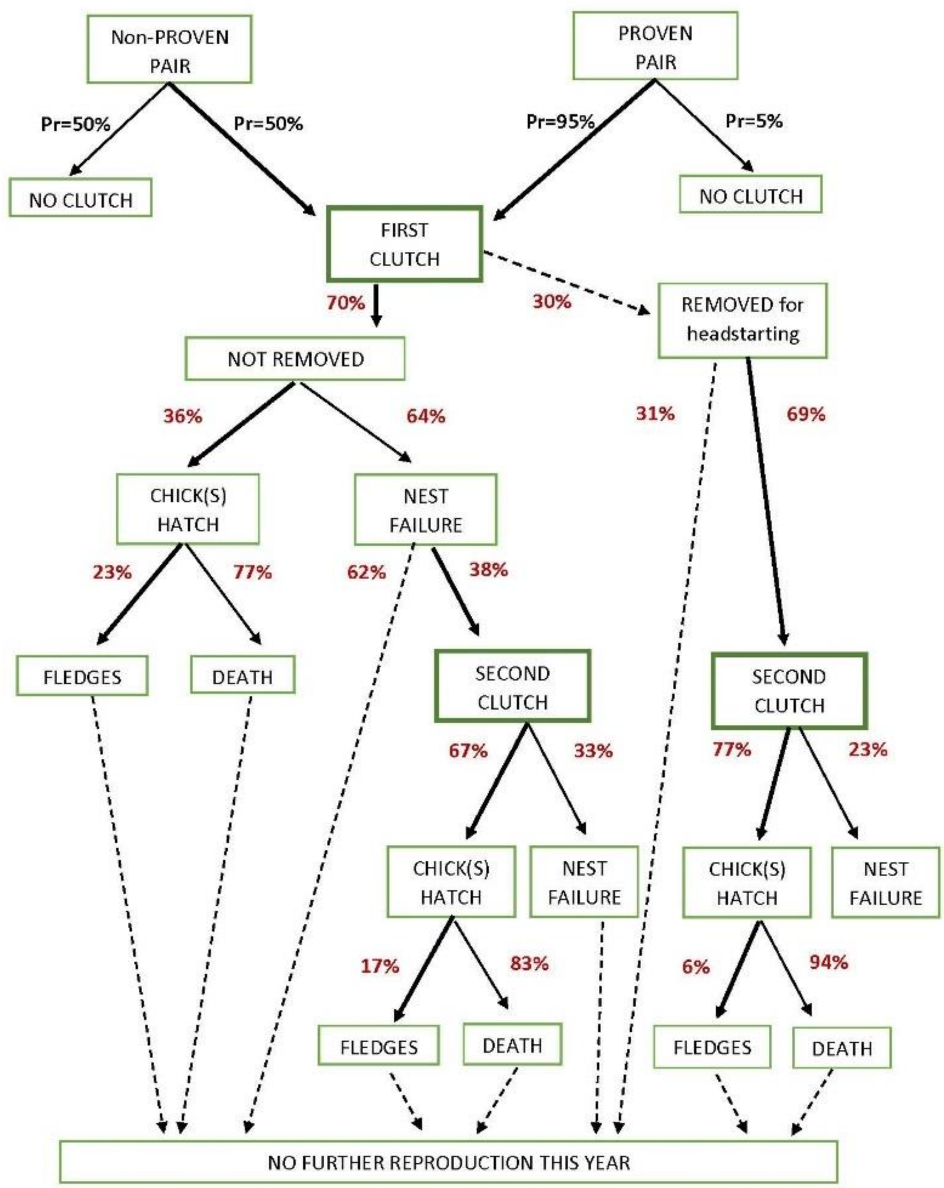

Fig. 23. Proportion of pairs producing eggs, chicks, and fledglings in the EMP from 2014 to 2017, including forced renesting (n=32 removed first clutches and 73 non-removed first clutches).

Headstarting scenarios were modeled across the same demographic uncertainty as the release scenarios (three reproductive success rates x three adult mortality rates), with 5, 10 or 15 first clutches collected and headstarted for either 5 or 10 consecutive years. *Ex situ* survival from collected egg to release was modeled as 70%, which was considered to be a conservative estimate by SSP representatives. This results in the release of 7 headstarted (HS) juveniles from eggs collected from 5 clutches, 14 releases from 10 clutches, and 21 releases from 15 clutches, assuming the collection of all eggs (up to 2) from collected nests and equal sex ratio of releases. Pairs were allowed to renest in the model, with rates from Figure 10 applied to renesting and substantial hatching and fledging from these nests.

Model results show little difference in population size and growth between similar supplementation (release) and headstarting scenarios. Both strategies include the potential addition of captive-reared (released) juveniles (either headstarted or captive-laid eggs) and wild-hatched juveniles by all EMP pairs but in different numbers and proportions. Headstarting increases survival of first clutches (*ex situ*) but results in a greater proportion of captive-reared juveniles in the population, which may have implications for future reproductive success. These tradeoffs appear to balance under those conditions modeled in this PVA. These results relate to demographic considerations and do not take into consideration any genetic management options offered by either approach.

Similar to the release results in Table 11, all headstarting scenarios improve population size and viability, with greater total numbers of HS birds having the largest impact. Figure 24 illustrates 50-year projections for 12 scenarios of headstarting 0, 5, 10 or 15 clutches per year for five years, using combined optimistic, default and pessimistic rates as benchmarks. The smallest gains are observed when both reproductive success and adult survival rates are low, as supplementation is insufficient to promote growth. Under much of the range of uncertainty modeled, headstarting has the ability to increase population size, promote positive growth, and reduce time to down-listing.

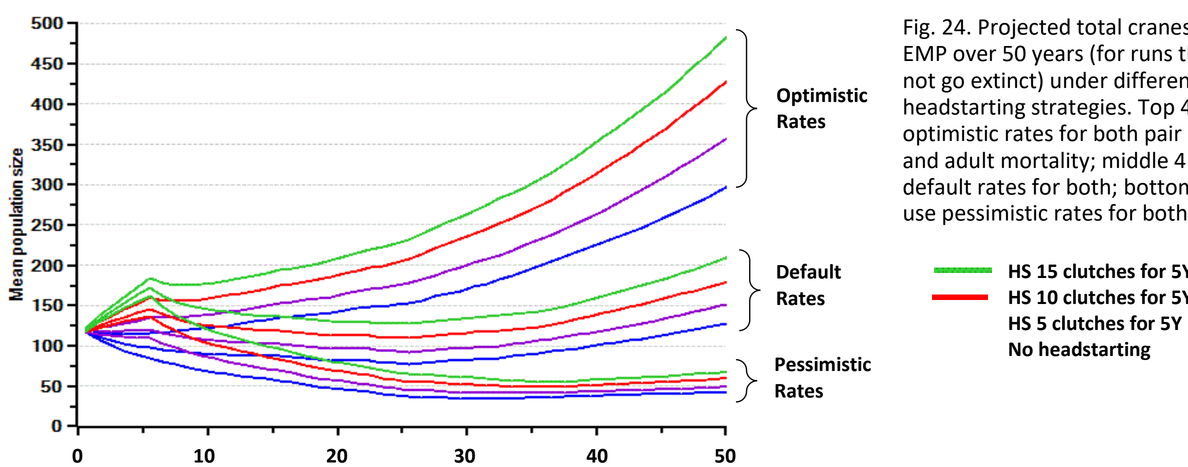

Fig. 24. Projected total cranes in the EMP over 50 years (for runs that did not go extinct) under different 5-year headstarting strategies. Top 4 lines = optimistic rates for both pair success and adult mortality; middle 4 lines use default rates for both; bottom 4 lines use pessimistic rates for both.

Forced renesting without releases

A potential metapopulation strategy would be to implement forced renesting in the EMP, headstart these eggs to produce juveniles for release, but release them into the Louisiana non-migratory population rather than back into the EMP. This could provide any alternative source of juveniles for release to boost the younger LNMP. However, since all FN pairs do not renest, and those that do thus far have experienced low fledging rates, it is likely that this strategy would impose a demographic cost to the EMP. The same HS scenarios described above were modeled for the EMP, but with no HS juveniles returning to the population.

Using historical rates from 2014-2017, limited forced renesting (i.e., collection of first clutches from some EMP breeding pairs) has little effect when demographic rates are poor (i.e., pessimistic rates), with a modest impact as rates improve (i.e., optimistic rates) (Fig. 25). While the impact is larger with optimistic rates, the population still maintains positive growth. Returning a portion of the HS juveniles could offset this effect (e.g., 2 of the 7 HS juveniles produced from 5 clutches). This provides an option that might be used sparingly for periodic demographic and/or genetic management of other populations.

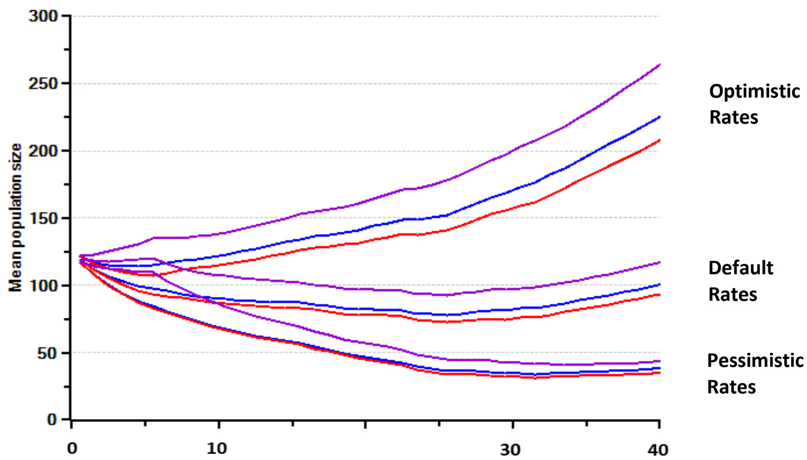

Fig. 25. Projected total cranes in the EMP over450 years (for runs that did not go extinct) under three conditions: headstarting, forced renesting with no releases, and no intervention. Top 3 lines = optimistic rates for both pair success and adult mortality; middle 3 lines use default rates for both; bottom 3 lines use pessimistic rates for both.

<u>Summary Results: Additional future supplementation/population management</u>

Demographic supplementation to the EMP, either through headstarting and/or release of juveniles from the captive population, is likely to improve population size, growth, and viability, and reduce the time to down-listing. An additional 50-100 released juveniles may provide substantial benefits. Low reproductive success of released birds, and the potential for additional adult mortality, however, are overriding factors that may contribute more heavily to the viability and down-listing/recovery of the EMP. Management actions that significantly improve the fledging rate can provide benefits and may be especially valuable if adult mortality is higher than AWBP rates.

EMP PVA Summary and Implications for Recovery Objectives

PVA model summary

A V*ORTEX* population simulation model was developed for the Eastern migratory population (EMP) of whooping cranes, using the Aransas-Wood Buffalo population (AWBP) model as a foundation. Demographic rates were estimated based on data from the EMP, AWBP and Louisiana non-migratory population (LNMP). Retrospective modeling suggests that this model is a reasonable representation of historical trends to date in this young population. Sensitivity testing of the model suggests that recruitment (egg production, hatching and fledging rate) and adult survival are primary factors in population growth and size and therefore time to down-listing and recovery.

There is substantial uncertainty regarding future demographic rates in this reintroduced population, in particular with respect to the reproductive success of released cranes as they pair with wild-hatch mates, and also with respect to adult mortality rates as compared to rates observed in the AWBP. It is also unclear how rearing history may affect these rates. This uncertainty limits the value of the population projections. While quantitative results are presented in this PVA report, these model results should not be considered as precise viability projections. PVA results, however, can help identify important data gaps for understanding and managing the EMP and can be useful in making relative comparisons among alternative management strategies. Multiple scenarios were explored to examine the range of future projections for the EMP under major areas of uncertainty, and the type of level of supplementation that might be needed to promote growth and achieve down-listing criteria for this population.

Assumptions

Primary assumptions built into this PVA model include that wild-hatched EMP cranes will have similar reproductive rates as wild cranes in the AWBP (except when paired with a captive-reared mate); that historical demographic rates for released, captive-reared birds will continue into the future; and that the reproductive success of pairs does not improve with experience or with population density.

Viability projections in the absence of future supplementation

Demographic rates from the EMP and other whooping crane populations were incorporated to provide a best estimate for EMP future viability. With no further supplementation, the projected viability of the EMP is moderate and involves significant variation in population measures. Most projections suggest the EMP may level off or decline for ~25 years and may be take decades to reach down-listing criteria, if at all, in the absence of additional future supplementation. Projections for population size over time are highly variable. Using default demographic rates the projected mean population size in 100 years is 402 (SD=344), with a 77-81% probability of reaching down-listing size with a mean time to down-listing of 43-51 years, and a 2% risk of population extinction.

Varying the reproductive success of mixed-origin pairs (those comprised of one wild-hatched mate and one captive-reared mate) can significantly alter these projections. Default values result in a relatively stable mean population size over the next several decades, while higher and lower values tested result in population growth or decline, respectively, in subsequent decades. Higher adult mortality negatively impacts population viability; even small, consistent losses of adult cranes may have significant impacts on the population. Actions that improve fledging success and reduce adult mortality will benefit the EMP.

Impacts of future supplementation

All release strategies explored in this PVA lead to improved viability compared to projections under which there are no further releases. Results suggest that continued release of juveniles for at least several more years can provide short- and long-term benefits to the population. The total number of releases has more impact than the timing of those releases (over the ranges tested). However, the timing of releases affects the number of years to down-listing; the earlier the releases occur, the more quickly the population grows to target size. Releasing an additional 50-100 juveniles over the next 5-10 years provides greatest relative gain in future viability across the range of uncertainty explored in vital rates of released birds.

These specific results for supplementation strategies are contingent upon many assumptions in the survival and reproductive success of captive-reared and wild-hatched released and resident birds, and should be considered only as general trends. Examining the trends in these results may be useful to illustrate the potential benefit of different release strategies. These scenarios assume no disease transmission risk, no negative behavioral consequences, or other potential risks to be considered in release programs; inclusion of any risk factors is important and will affect the impacts on the population.

The reproductive success of captive-reared released cranes is a key factor that drives population growth and viability. Management strategies or actions that improve reproductive success of released cranes would improve the status of the EMP under any scenarios explored here.

PVA results and recovery objectives

The current international recovery plan (CWS & USFWS 2007) includes two recovery objectives for down-listing of whooping cranes, one for the wild population and one for the captive population. Objective 1 is to "establish and maintain self-sustaining populations of whooping cranes in the wild that are genetically stable and resilient to stochastic environmental events." This PVA is relevant to the down-listing Criteria 1 and 1A related to the development and maintenance of a whooping crane wild meta-population of 2-3 sub-populations. Criterion 1 requires the maintenance of at least 160 cranes in the AWBP and two additional populations of at least 100 cranes each, with all three populations being self-sustaining at these levels for a decade before down-listing. Alterative Criterion A1 requires an AWBP of at least 400 cranes and one additional population of at least 120 cranes, both of which are self-sustaining at this level for a decade. The AWBP already exceeds 400 cranes and is projected to increase in size.

The best estimates for the expected length of time until the EMP reaches and maintains at least 100 cranes for a decade ranges, in the absence of further supplementation, from 11 years to over 100 years across the uncertainty explored in this PVA. Growth to at least 120 cranes would take longer. Additional supplementation likely will be required to significantly shorten time to meeting down-listing criteria. Continuing the release of ~10 juvenile cranes each year for 5-10 more years is projected to have significant positive impacts on all population measures. Other management actions, such as those that improve fledging success, can also contribute toward viability and down-listing. While the high degree of uncertainty in demographic rates make it difficult to predict the precise time to meeting down-listing criteria under these management strategies, the scenarios explored in this PVA can guide management actions that will promote quicker recovery. More details are provided in Section 6.

A similar PVA was developed to explore similar questions and scenarios for the second reintroduced population – the Louisiana non-migratory population (LNMP). The success of this population will impact the importance of and down-listing criteria for the EMP.

Objective 2 to "maintain a genetically stable captive population to ensure against extinction of the species" is being modelled separately to evaluate the projected genetic and demographic status of the SSP population. As none of the AWBP scenarios project a risk of extinction of the AWBP over the next 100 years, this suggests that the captive population may not be required to augment or re-establish the AWBP population. However, the captive population may provide important headstarting or supplementation services that could reduce the time to down-listing for the AWB population and to establish viable reintroduced populations (EMP and LNMP). The captive population may play a critical role for the development of additional reintroduced populations, for example by parent fostering wild-laid eggs, producing eggs for cross-fostering to wild parents, and producing additional birds for release. In addition, given the uncertainty of future climate change impacts and anthropogenic threats, there may be a risk of

AWB population decline or extinction in the presence of greater threats than modeled and increasing the need for a back-up captive insurance population.

Acknowledgements
This PVA model was developed in consultation with the Whooping Crane International Recovery Team and numerous crane biologists and managers who participated through workshops and/or electronic discussion in 2015-2018. Additional PVA work was conducted in 2018 to assess the other whooping crane populations and full meta-population. These PVA models and results will serve as a basis to evaluate potential management actions to increase whooping crane viability and to evaluate recovery goals for this species, and will inform species conservation planning discussions scheduled in October 2019.

Section 4. Whooping Crane Population Viability Analysis (PVA) Report: Louisiana Non-Migratory Population Model and Sensitivity Testing of Management Options

This report describes the whooping crane baseline *VORTEX* model and results for the wild Louisiana non-migratory population (LNMP). This population model and scenarios were developed in conjunction with the 2015 and 2016 Population Viability Analysis (PVA) workshops in Calgary, and were informed by additional electronic and telephone conference discussions through 2018.

This non-migratory population is a newly established reintroduced population based on annual releases of captive-reared juvenile cranes beginning in 2011. As of spring 2017 (the point at which this model is initiated), 102 young cranes (5-9 months old) had been released for six consecutive years (2011-2016) in cohorts of 10-26 birds per year. The oldest surviving birds only recently reached breeding age. The first chicks hatched and a fledgling produced in 2016, which survived just over one year. An additional chick hatched in 2017.

Given the young age and short history of this population, it is challenging to predict future demographic rates. Demographic rates for other wild whooping crane populations (Aransas-Wood Buffalo and Eastern Migratory populations) differ most substantially from each other on the survival of offspring from egg to arrival on the wintering grounds approximately six months later (higher survival for AWBP), followed by smaller differences in breeding rates (i.e., mating and egg production). As a non-migratory population, the LNMP may be exposed to fewer threats, although there is a local threat of shooting (accounting for at least some of the mortality of released birds). Early nesting attempts by young pairs (age 3-6 years) have been high but with a high rate of nest failure due to infertility, embryo death and other causes.

Model Inputs

A stochastic, individual-based population model was developed for the whooping crane using the *VORTEX* 10.2.15 (Lacy and Pollak 2017) software program. *VORTEX* is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild or captive small populations. A one-year time step was implemented, with most events (e.g., breeding) occurring once per year. Two mortality events occur in the model each year so that summer vs winter events can be altered separately in the model. The model begins each ‘year’ in spring just prior to breeding. Model scenarios were run for 100 years with 1000 iterations each.

Demographic rates to parameterize the LNMP model were derived from a combination of field data for the Aransas-Wood Buffalo (AWBP), Eastern Migratory (EMP) and LNMP populations (see AWBP and EMP reports for details on data sources for those populations), as well as expert opinion on conference calls and at the PVA workshops This includes projected future changes in environmental conditions and human-related threats under current management actions. Sensitivity testing was used to explore some of the uncertainty around these input estimates and the resulting viability projections. A summary of inputs is provided below; see AWBP PVA report for more details.

Initial Population

The model was initiated with 56 surviving birds as of spring 2017 prior to breeding. Age and sex of these individuals were taken from census and studbook data and include 28 males and 28 females ranging in age from 1-6 years. Pedigree data from the 2017 studbook were used to set kinships among the initial birds (Peregoy 2017). All birds were marked in the model as released birds, which influences the demographic rates attributed to them in the model.

Carrying Capacity

Allen's 1952 historical estimate of K=2500 for tallgrass prairie was expanded to include coastal marsh that potentially could support an additional 500-1000 cranes as a conservative estimate (W. Selman, pers. comm.). Carrying capacity was set at 3000 as a conservative estimate for this population with no change over time.

Reproduction (Egg Production)

The mating system was modeled as long-term monogamous pairs, with reproduction beginning as early as age 4. In the model, female breeding rate is defined as the probability that an adult female will produce eggs that year (hatch rate and juvenile survival are modeled separately – see below). PVA workshop participants recommended using the EMP rate for the percent of females breeding (laying eggs) given that both are reintroduced populations. This annual rate is 50% chance for nulliparous females and 95% for proven breeders (i.e., females that have previously nested and laid eggs). These rates approximate those observed in the young adult cranes released into the LNM population to date (54% for nulliparous females; 91% in females that had nested in a previous year). A small decline in breeding rates (down to 81-88%) was incorporated for older females (>23 years old) to match that used in the AWBP model. Environmental variation (EV) for reproduction was set at CV = 8%.

All nesting attempts in the same year were collapsed to represent one 'clutch' in the model, as breeding pairs that hatch a chick do not produce an additional clutch and so never produce multiple successful clutches. Most clutches consist of two eggs (96% of clutches, as used in the AWBP and EMP models), although both chicks seldom survive. Rates above were based primarily on Gil-Weir *et al*. 2012, Wilson *et al.* 2016 and WCEP reports.

Mortality

Mortality is implemented in the model as two mortality events per year (summer vs winter mortality), with no sex-specific differences in mortality. First-year mortality was divided into six-month mortality from egg through fledging to winter, with additional mortality during the remainder of the first year. Mortality rates used for other age classes were similarly applied to each six-month summer or winter period. Maximum lifespan was set at 30 years. This model structure matches that of the AWBP and EMP PVA models.

Future age-specific mortality rates are challenging to estimate for this population. The population is newly established, currently consists primarily of captive-reared released birds, and is subject to different threats and environmental conditions than migratory crane populations (AWBP and EMP). Past observations suggest that early survival may vary not only according to age but also origin (wild-reared vs captive-reared released birds). Hatching and fledging rates also vary significantly between the three populations, with both rates much lower in the reintroduced populations that are composed primarily of captive-reared released cranes than in the wild AWBP. The EMP has experienced high mortality from hatching to fledging due in part to abandonment, while the LNMP to date has experienced few hatches (5.36% of eggs laid) but good parental care for those few chicks. Allowing for very small number of nesting pairs and nesting years to date for the young LNMP, fledging rates are comparable between the two populations but may be influenced by different factors and challenges, although preliminary data available after PVA development suggest improved fledge rates in 2018.

Given the experience to date in the reintroduced populations compared to the wild AWBP, mortality from egg to fledging may depend upon the origin of the parents (released birds vs wild-hatched birds). Observations of captive-reared released Mississippi sandhill cranes suggest that breeding pairs with at least one wild-hatched mate are twice as likely to fledge a chick as breeding pairs comprised of two released birds (Brooks, pers. comm.). This hypothesis was incorporated into the PVA model. Offspring survival (and parental care) was assumed to be static for each pair and not improve over time.

The following rates were incorporated into the base model based in part on PVA discussions:

- Egg to 6 months (which incorporates hatch and fledge rates):
    - if both parents are captive-reared, then use EMP rates from 2014-2017 (two options):
        - Default: excludes data for breeding pairs whose eggs were removed and were forced to re-nest
        - Alternate values: based on data from all breeding pairs and attempts, including forced renesting
    - if both parents are wild-reared, then use AWBP rates
    - if one wild-reared and one captive-reared parent, use intermediate rate (two alternatives):
        - Default: EMP survival rate x 2
        - Alternate values: mean of AWBP and EMP rates

    Exploring all combinations above led to four alternatives for first six-month survival (see Table 12).

- Six months through age 3:
    - If wild-reared, use mortality rates from the reintroduced EMP
    - If released, use mortality rates from LNMP 2011-2016 cohorts
- Adults (age $\geq$ 4 years, regardless of origin): mortality rates used for EMP and AWBP models

The resulting rates used are given in Table 12. EV was set at COV=10% and was partially correlated (0.5) with EV in reproduction as in the AWBP model. No cyclicity related to the solar cycle and no impacts of increased atmospheric CO_2 was included in juvenile recruitment for this population.

Table 12. Age-specific mortality rates used for the LNMP base model. Wild-reared = either natural reproduction in the wild or captive-produced egg cross-fostered to wild parents for hatching and rearing. Captive-reared = either captive-produced and reared juveniles or wild-collected eggs that are hatched and reared (headstarted) in captivity and returned to the wild as juveniles at ~6 months of age.

	Wild-reared (either wild- or captive-laid egg)			**Captive-reared (released juvenile)**
Age class	**Wild-reared parents**	**Mixed origin parents**	**Captive-reared parents**	**Parent-reared in captivity**
First 6 months (egg 1; egg 2)	58.15%; 95% AWBP rates	89%; 98% (default) 76.33%; 97% (midpoint)	94.5%; 99% EMP rates (default)	n/a
		90.4%; 98% (default) 76.68%; 97% (midpoint)	95.2%; 99% EMP rates (alternate)	
6 months to 1 year	8.1% EMP rate	8.1% EMP rate	8.1% EMP rate	11% (release to age 1) LNMP rate
Sub-adults (annual)	10.8% for ages 1 & 2; 15% for age 3 AWBP rates	10.8% for ages 1 & 2; 15% for age 3 AWBP rates	10.8% for ages 1 & 2; 15% for age 3 AWBP rates	22% for age 1; 10.8% for ages 2 & 3 LNMP rates
Adults ($\geq$ 4yrs) (annual)	5.6% AWBP rate	5.6% AWBP rate	5.6% AWBP rate	12% for age 4 LNMP rate 5.6% >age 4 AWBP rate

Population Size Regulation

There is no growth regulation in demographic rates, i.e., no density-dependency or limitation of nesting sites or resources. Rather, population size is limited in the model by carrying capacity (K) and by general demographic rates. Probabilistic truncation to K is implemented if population size exceeds K at the end of each year and is applied only to non-breeding birds.

Catastrophes

Two catastrophic events were incorporated in the base model, based in part upon general trends in catastrophic declines observed in wild vertebrate populations by Reed *et al*. 2003. Risk of a high mortality event during winter was incorporated as a 0.5% risk (~ once every 200 years) of a 50% reduction in survival for all age classes over winter. The risk of a poor breeding season (90% reduction in fledgling production) was given a 5% risk of occurrence (~ once every 20 years). While these catastrophes were developed for the AWBP model, they are reasonable to apply to the LNMP model given the potential for severe flooding or tropical storms to impact survival especially for juveniles.

Genetics

A small genetic load (3 lethal equivalents, 1 as a lethal allele and 2 as non-lethal effects) was incorporated into the model and applied as lower juvenile survival in inbred individuals. This is lower than the genetic load suggested by O'Grady *et al.* (2006) of 12.29 lethal equivalents for wild vertebrate populations, as it is assumed that some of the initial genetic load may have been purged due to the historical bottleneck and population expansion experienced by this species. The model tracked pedigree relatedness and applied inbreeding effects on any future additional inbreeding. Any supplementation was modeled as unrelated birds except where specific cranes from the Florida non-migratory population were included in the model.

Ex Situ Management Options

Several population management strategies that involve *ex situ* components are available to support the establishment of reintroduced whooping crane populations. These may result in different demographic rates for reproduction and mortality, as hypothesized in Table 12. Some of these options have been implemented in the past and were explored in different modeling scenarios for their potential impact.

Supplementation: Releases

The LNMP was established through the release of juvenile whooping cranes at ~5-6 months of age. The LNMP PVA model was initialized at the point of pre-breeding season in 2017 to match with other whooping crane population models in this PVA. The 23 juveniles that were released in December 2017 were incorporated into the first year of modeling to match actual management to date. Incorporation of future releases (representing 2018 and later) were varied in different scenarios (see below).

Supplementation: Cross-Fostering

A different method for supplementation was initiated in the field in 2017, with cross-fostering of captive-laid eggs (or potentially eggs collected from a different wild population) to nesting LNMP crane pairs with non-viable eggs. If successful, this would result in juveniles that were parent-reared in the wild, potentially improving their future survival and reproduction over captive-reared juvenile releases. This management strategy is sometimes referred to as 'egg swapping'.

Headstarting

Another management option to address poor egg and juvenile survival is to collect fertile eggs from the LNMP population (e.g., second fertile eggs in a nest, eggs from captive-reared pairs), hatch and rear these chicks under breeding pairs in captivity, and return these same juveniles at some stage back to the LNMP. This could greatly increase the survival of these chicks but may have consequences for their future reproduction and offers little advantage over the release of captive-bred and reared juveniles. Headstarting was not modeled in this PVA but was explored in the AWBP and EMP PVAs (Sections 1 & 2).

Supplementation: Adults

The LNMP can be supplemented by translocating cranes from other wild populations (e.g., AWBP, Florida NMP) or from the *ex situ* population. This might involve translocation of established pairs. This offers another option for quickly increasing the number of wild-hatched chicks.

Validation of Historical Trends

Retrospective modeling of the LNMP was limited due to the short historical timeline and was conducted using the base model to project the trend of this population over the past 6 years (from spring 2012 to spring 2018). The initial 2010 cohort was not included, as high mortality was observed with this first release and led to changes in release procedures and timing. The model was initiated with 14 one-year-old birds (6 males, 8 females) representing the 2011 cohort still living prior to the 2012 breeding season. Additional yearlings were added each year to match annual releases that occurred in 2012 through 2017. Alternate EMP mortality rates were used, as forced re-nesting was in practice during the reproductive years of this time period. Higher intermediate mortality rates were used, but have no effect, as mixed breeding pairs were unlikely in this timespan.

Model results indicate a stochastic r = 0.274 (SD = 0.147), which is driven by releases and not reproduction, and final mean N = 72.6 (SD = 5.3) that represents the population size in spring 2018 just prior to breeding. This is close to the 2018 field count in early March (69 birds) (Figure 26). The model predicts an average of 71.2 released cranes and 1.3 living wild-hatched cranes in spring 2018. This is in line with the one living wild-hatched crane in the population prior to the 2018 breeding season. Removing all reproduction from the model leads to very similar projections (final N = 70.8). These results suggest that little successful reproduction is expected in this population prior to the 2018 breeding season given the rates used as model inputs. While model results indicate slightly higher survival of released cranes than that observed for the LNMP, survey results fall within one SD of model projections.

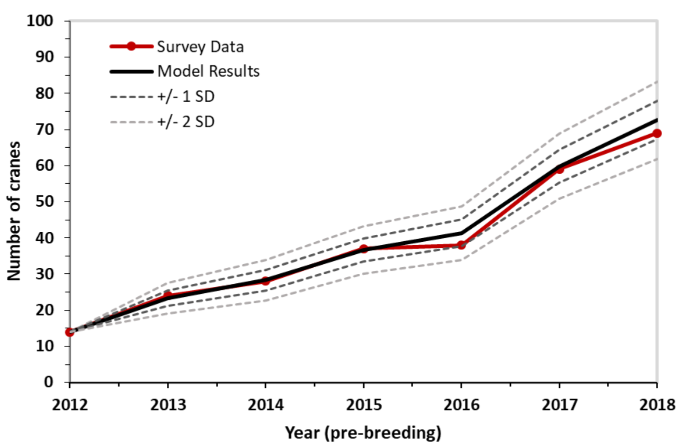

Fig. 26. Retrospective model projection of the LNM whooping crane population from spring 2012 to spring 2018 (black line) and survey results (red line).

Overall the model appears to be a reasonable representation of the Louisiana whooping crane population with respect to the survival of young released birds for several years following release; however, future adult survival and reproductive rates and survival of wild-born descendants is much less understood. There is substantial uncertainty regarding the reproductive success of these cranes as they age, primarily in terms of hatching and fledging rates (i.e., mortality from egg to ~6 months), which will greatly influence future growth rates. The survival rate of next generation wild-hatched birds is also uncertain, and it is unclear if survival rates from other crane populations are appropriate for LNMP projections. Finally, the future rate and impact of shooting and other human-caused threats on survival is unknown.

Exploration of Future Viability Projections

Sensitivity analysis of the AWBP model indicated that population growth rate is most sensitive to adult survival, followed by sub-adult survival and juvenile survival, when these rates are varied by equal proportion. Historically, most observed variation in wild whooping crane demographic rates has been in the survival of early age classes while adult survival is high with relatively little variation. Given this Wilson *et al*. 2016 noted that fledging rate had the greatest influence on annual growth rate. Factors that affect hatching and fledging rates and juvenile survival are likely to drive viability as long as sub-adult and adult survival remain high. Higher mortality in adult (and to a lesser extent, sub-adult) mortality, however, can reduce population viability. Population size is another factor due to increased stochastic impacts in smaller populations. Sensitivity testing of the AWBP model showed reduced viability in populations with fewer than 300 cranes (refer to the AWBP PVA report for more information).

For the LNMP there is substantial uncertainty regarding future demographic rates, in particular with respect to future survival and reproductive success of released cranes. It is also unclear how rearing history affects these rates. Multiple scenarios were explored to examine the range of future projections for the LNMP under this uncertainty, and the level of management needed to prevent population decline.

A note about population measures of viability

Most of the following simulations project a period of population decline (and in some cases, extinction), followed by a period of continued growth. Mean population size (N) and mean gene diversity (GD) reported here represent ending population status for iterations in which the population did not go extinct, and probability of extinction (PE) is calculated over 100 years (unless otherwise specified). Together these measures convene population status at 100 years. The stochastic growth rate *r* reported here represents the mean stochastic growth rate over the entire 100-year projection and not the ending growth rate. Thus, a negative *r* does not necessarily indicate a declining population. Stochastic *r* is presented here to aid relative comparisons on overall growth among different management scenarios. Time to target (TTT) represents the year at which the population meets the down-listing criterion for the LNMP (under Objective 1, Criterion 1; CWS & USFWS 2007) of at least 100 cranes and being self-sustaining for at least a decade. This may be a more useful indicator of population status than *r*. For some scenarios involving supplementation, TT_{N100} is reported in addition to TTT (see supplementation results). All values for N, *r*, GD, TTT and TT_{N100} represent means around which there is a high degree of variation.

<u>Projected Viability: No future supplementation</u>

Using the model input values outlined above (with the default settings for first six-month mortality) and with no further supplementation, the projected viability of the LNMP is moderate and involves significant uncertainty. Recruitment of wild-hatched juveniles may be sufficient to balance deaths and maintain a population of ~45 cranes, but is generally insufficient for population growth. Once all released cranes have died (after 30-35 years), then all breeding pairs consist of wild-reared birds with higher reproductive success and allow the potential for positive growth (Fig. 27). At this point the population is likely to be very small (mean=41, SD=23) and there is a small risk of extinction (PE_{32yr}=0.007). Extinction risk rises over time, with PE_{50yr}=0.024 and PE_{100yr}=0.09. Projected population size is highly variable (Fig. 28). In those iterations in which the population persists, average population size is 61(SD=44) in 50 years and 195 (SD=197) in 100 years, with a mean time to target (TTT) of 72 years. If slightly higher juvenile mortality rates are used (i.e., based on all EMP pairs, include those forced to re-nest), projections show a similar pattern with slightly less growth (N_{100yr}=181, SD=185; PE_{100yr}=0.12).

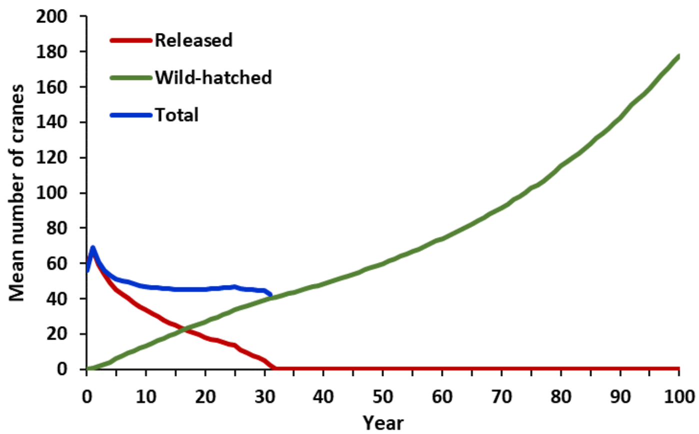

Fig. 27. Projected mean number of captive-reared released cranes (red line), wild-hatched cranes (green line), and total cranes in the LNMP over 100 years for model runs in which the population did not go extinct (91% of iterations).

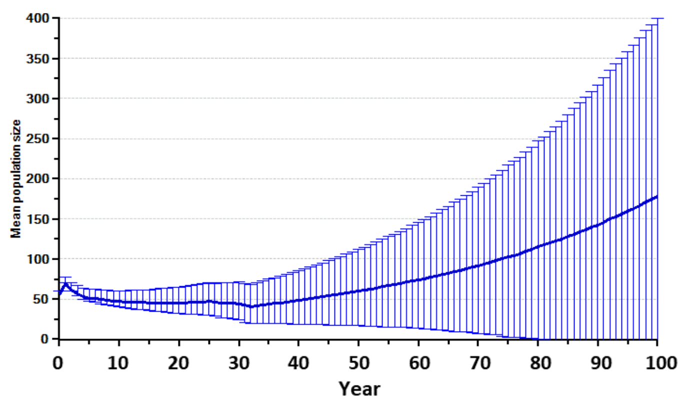

Fig. 28. Projected total cranes in the LNMP over 100 years (for runs that did not go extinct). Bars indicate $\pm$ 1 SD.

Impact of rearing success of mixed-origin breeding pairs

It is uncertain how the rearing success of mixed-origin breeding pairs (one wild-hatched (WH) bird and one captive-reared (CR) bird) compares to that of wild pairs (WH-WH) or breeding pairs of released birds (CR-CR). Observations of captive-reared released Mississippi sandhill cranes suggest that breeding pairs with at least one wild-hatched mate are twice as likely to fledge a chick as breeding pairs comprised of two released birds (Brooks, pers. comm.). The default rate modeled for the LNMP (Figs. 27 & 28) represents twice the survival from egg to six months of age for mixed-origin pairs (11%) vs CR-CR pairs (5.5%) for the first egg in the nest, and 2% vs 1% for the second egg (Table 12). While this may be the most reasonable estimate, mixed-pair success rates may in fact be higher or lower. Two alternative scenarios were explored: 1) higher intermediate survival rate (WH-CR rates = midpoint between WH-WH and CR-CR rates); and pessimistic (WH-CR rates = CR-CR rates).

The reproductive success of mixed-origin pairs may have a significant impact on the future viability of the LNMP. With no future supplementation (releases), some CR released cranes may live up to 30 years and may form mixed-origin pairs during this time. The default values result in a stable mean population size during this period. Higher intermediate (midpoint) values lead to population growth, while pessimistic (CR-CR) values lead to population decline (Fig. 29). While mixed-origin pairs cannot exist past year 31 and therefore all subsequent pairs are WH-WH pairs with higher success rates, poor recruitment and resulting small population size during the first 31 years has long-term impacts on demographic and genetic viability and extinction risk (Fig. 30; Table 13). Gene diversity declines sharply between years 25-32 for the pessimistic scenario, suggesting that many released birds had little to no successful reproduction (i.e., little genetic representation in the next generation) (Fig. 31).

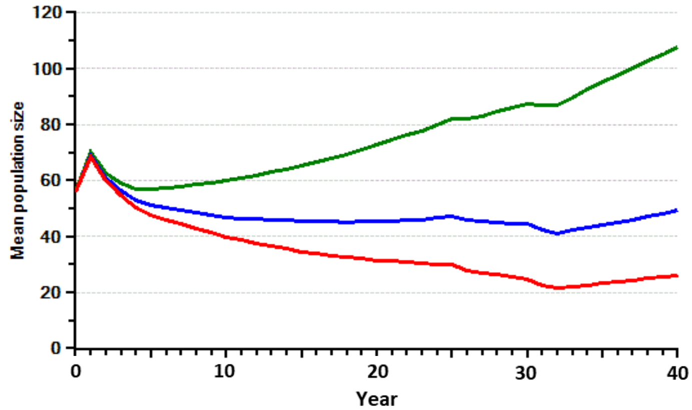

Fig. 29. Projected mean number of cranes in the LNMP over 40 years (for runs that did not go extinct) using different reproductive success rates for mixed-origin pairs.

Intermediate (midpoint)
Intermediate (default)
Pessimistic (CR-CR)

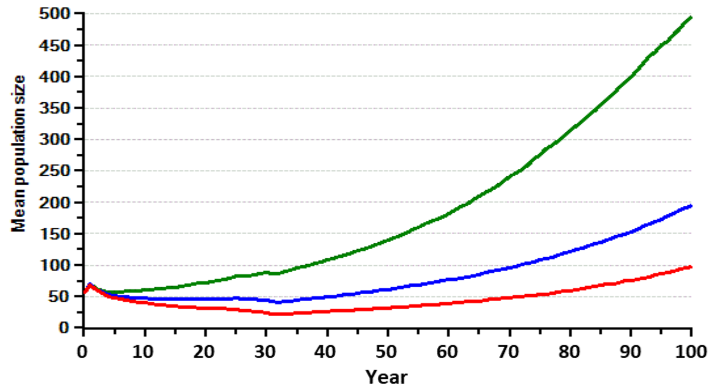

Fig. 30. Projected mean number of cranes in the LNMP over 100 years (for runs that did not go extinct) using different reproductive success rates for mixed-origin pairs.

Intermediate (midpoint)
Intermediate (default)
Pessimistic (CR-CR)

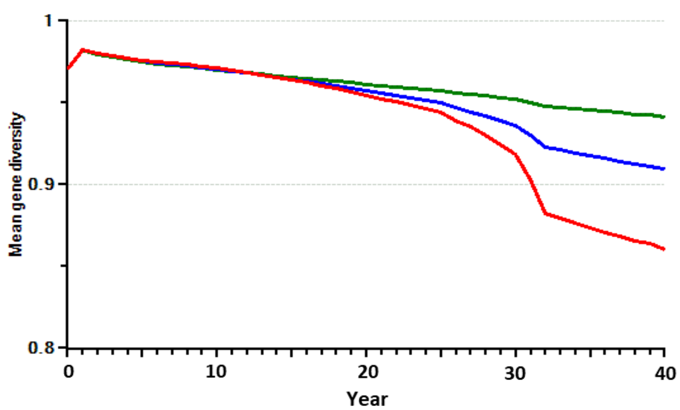

Fig. 31. Projected mean gene diversity retained in the LNMP over 40 years (for runs that did not go extinct) using different reproductive success rates for mixed-origin pairs.

Intermediate (midpoint)
Intermediate (default)
Pessimistic (CR-CR)

Table 13. Model results for LNMP for 100 years with different first six-month (egg to post-fall migration) mortality rates for mixed-origin breeding pairs (one wild-hatched mate and one released mate). Stoch r=stochastic growth rate; N=mean population size; GD=mean gene diversity; PE=probability of extinction; TTT=time to target.

	First 6-mo. mortality						
Scenario	**Egg 1**	**Egg 2**	**Stoch r**	**N_{100yr}**	**GD_{100yr}**	**PE_{100yr}**	**TTT**
Intermediate (mid-point)	76.33%	97%	0.019	496 $\pm$ 312	0.916	0.011	37yrs
Intermediate (default)	89%	98%	0.004	195 $\pm$ 197	0.848	0.089	72yrs
Pessimistic (same as CR-CR pairs)	94.5%	99%	-0.013	98 $\pm$ 123	0.775	0.379	>100yrs

Improvement in rearing success

Model results presented in this PVA assume that the parental rearing success (measured by successful survival of offspring from egg to fledging) is a fixed characteristic of a pair and does not improve over time or with reproductive experience. Females that have laid previous clutches are more likely to produce a clutch in subsequent years (95% vs 45% for first-time nesters), but hatching and fledging success rates of eggs are not affected in the model. If reproductive experience has an effect in crane pairs in the wild, this effect is incorporated in a general manner for wild-hatched pairs by using the average historical AWBP rates. For newly established reintroduced populations it is possible that hatching and/or fledging rates may improve over time with increasing years in the wild and increasing number of reproductive pairs in the population, and/or rates may improve once a pair successfully fledges a chick. The lack of data on these variables combined with the complex model structure required to explore these factors make it impractical to address in this PVA. However, it is possible that reproductive rates of released pairs may increase in the future beyond those observed in the past.

Uncertainty in future survival rates

The LNMP is a new crane population comprised of young captive-reared birds and is subject to different conditions and threats than other existing whooping crane populations. There is substantial uncertainty not only with respect to reproductive success but also regarding adult mortality rates, especially of released birds. Survival of released cranes (at ~6 months) to 5 years of age has been lower (~49%) in the LNMP than similar age span for AWBP cranes (~59%). The default LNMP model assumes that adult mortality (starting at age 5) is the same for LNMP releases as for wild migrating AWBP cranes (Table 12). This may or may not be the case. Some released LNMP cranes have migrated, and there have been some instances of human-caused mortality (shooting). Higher adult mortality of released cranes may be another mechanism that could slow early population growth and have long-term consequences.

Alternative scenarios were modeled with higher adult mortality rates for released cranes, with 1% increments from 5.6% to 11.6% (~ 12% rate observed in LNMP 4-year-old birds). As with reproductive success, higher adult mortality in released cranes impacts growth for the first ~30 years as well as long-term viability measures such as final population, gene diversity retained, and probability of extinction. However, mixed-origin pair reproductive success has a relatively greater impact over the range of values tested. The results in Table 14 are color coded as follows to indicate the relative demographic and genetic viability of the LNMP for these 21 sensitivity scenarios exploring adult mortality:

- Dark blue: Mean $N_{100} \geq 600$, GD$\geq$0.96, PE$\leq$0.005, $\geq$2.5% mean growth
- Light blue: Mean $N_{100} \geq 500$, GD$\geq$0.94, PE$\leq$0.01, $\geq$2% mean growth
- Bright green: Mean $N_{100} \geq 300$, GD$\geq$0.88, PE$\leq$0.05, $\geq$1% mean growth
- Light green: Mean $N_{100} \geq 200$, GD$\geq$0.85, PE$\leq$0.10, positive growth
- Yellow: Mean $N_{100} \geq 100$, GD$\geq$0.82, PE$\leq$0.20, no decline
- Light orange: Mean $N_{100} \geq 100$, GD$\geq$0.78, PE$\leq$0.30, $\leq$ 1% mean decline
- Bright orange: Mean $N_{100} \geq 70$, GD$\geq$0.75, PE$\leq$0.40, $\leq$ 2% mean decline
- Red: Mean $N_{100}<70$ or GD<0.75 or PE>0.40 or >2% mean decline

The definitions of these categories are to some extent arbitrary and can be classified differently. The purpose is to visually illustrate general clustering of categories of long-term viability measures.

Table 14. Model results for LNMP for 100 years, with varying adult mortality of released cranes and reproductive success of mixed-origin breeding pairs (N= mean population size at 100 years ± 1 SD, GD=gene diversity, r = stochastic r, PE=probability of extinction; TTT=time to target). Mean N and GD calculated only for iterations that did not go extinct.

	5.6% AWBP rate	**6.6%**	**7.6%**	**8.6%**	**9.6%**	**10.6%**	**11.6%**
Intermediate (midpoint)	N=496 ±312 r=0.019 GD=0.916 PE=0.011 TTT=37y	N=455 ±311 r=0.018 GD=0.909 PE=0.009 TTT=41y	N=406 ±293 r=0.015 GD=0.898 PE=0.020 TTT=45y	N=363 ±272 r=0.014 GD=0.892 PE=0.035 TTT=49y	N=310 ±243 r=0.011 GD=0.883 PE=0.047 TTT=54y	N=288 ±250 r=0.010 GD=0.874 PE=0.059 TTT=58y	N=254 ±230 r=0.008 GD=0.863 PE=0.052 TTT=61y
Intermediate (default)	N=195 ±197 r=0.004 GD=0.848 PE=0.089 TTT=72y	N=189 ±188 r=0.002 GD=0.841 PE=0.127 TTT=74y	N=162 ±166 r=0.000 GD=0.828 PE=0.149 TTT=80	N=133 ±138 r= -0.004 GD=0.812 PE=0.219 TTT=89y	N=128 ±143 r= -0.005 GD=0.802 PE=0.226 TTT=91y	N=110 ±119 r= -0.008 GD=0.784 PE=0.278 TTT=96y	N=94 ±105 r= -0.011 GD=0.774 PE=0.329 TTT>100y
Pessimistic (CR-CR)	N=98 ±123 r= -0.013 GD=0.775 PE=0.379 TTT>100y	N=73 ±84 r= -0.016 GD=0.755 PE=0.413 TTT>100y	N=79 ±91 r= -0.017 GD=0.757 PE=0.445 TTT>100y	N=71 ±86 r= -0.023 GD=0.742 PE=0.551 TTT>100y	N=59 ±72 r= -0.025 GD=0.717 PE=0.551 TTT>100y	N=58 ±68 r= -0.028 GD=0.720 PE=0.607 TTT>100y	N=52 ±69 r= -0.030 GD=0.701 PE=0.637 TTT>100y

Projected Viability: Additional future supplementation

Another factor that will influence the size and viability of the LNMP is the continued release of additional cranes into the population in the future. Future releases have the potential for a variety of impacts. Continued releases for the next few years can help buffer against risks associated with small population size until the population can reach a larger, less vulnerable size. However, if reproduction success is low for CR-CR pairs and mixed-origin pairs, continued releases have the potential to delay higher population growth driven by more successful wild-hatched pairs. This may be especially true if the survival of released cranes is high. It is also valuable to assess the relative benefit of various release strategies against effort required as well as ability to meet recovery objectives.

Measuring time to down-listing target under supplementation

It is difficult to measure if populations are self-sustaining while supplementation is underway. The population may reach and maintain over 100 cranes during and after supplementation but may not be eligible as 'self-sustaining for a decade' (per recovery Criterion 1) until a minimum of 10 years after releases have ended. In some cases, the population may show some decline following termination of releases until a balance is reached in the age structure and between released and wild-hatched birds; however, population size may remain high and soon stabilizes. In such cases, an additional population measure, TT_{100}, is reported. TT_{100} is the year at which the population reaches and maintains over 100 cranes into the future and exhibits positive growth in the last ≥50 years of the simulation; in some cases, the population may decline when supplementation ends but eventually becomes self-sustaining.

Continued annual release of captive-reared juveniles

Two release rates (10 vs 20 releases per year, equal sex ratio) and two release schedules (annually for 5 or 10 years) were combined to model four release strategies. An additional scenario for 10 releases annually for 20 years was added to evaluate the impact of timing vs number of releases; however, releases in practice are not expected to continue for this long. These five release strategies were evaluated against uncertainty in the reproductive success of mixed-origin pairs and in the adult mortality of released birds. Six scenarios were developed for each of these release strategies by varying mixed-origin pair success (intermediate midpoint, intermediate default, and pessimistic rates) and adult mortality for released birds

(5.6% and 11.6%) – analogous to the first and last column in Table 14. This resulted in 30 scenarios that allow comparison of how different release strategies perform against this uncertainty.

In addition, four variable-schedule release strategies were modeled. Three variable strategies begin with a large number of releases (20-30 cranes) in the short term (5 years) and taper to fewer releases (0 or 10). The fourth strategy considers that fewer cranes may be available for release in the short term due to the loss of *ex situ* potential to rear chicks, and is modeled as 10 releases annually for 5 years followed by 20 annually for another 5 years. These scenarios represent the release of 120-200 total cranes respectively and were also explored across uncertainty in demographic rates for an additional 24 scenarios.

Model results are presented in Table 15. Management (release) strategies are represented by rows, with columns representing a range of uncertainty in key demographic rates of released birds. The four variable schedule strategies are presented at the bottom of the table. As in Table 14, color coding represents approximate categorization of viability and is provided to illustrate relative different impact among strategies, acknowledging that different definitions could be used. Releases were modelled as unrelated individuals (to each other and to existing LNMP cranes); thus, GD is not an accurate reflection of heterozygosity but is useful as a *relative comparison* of gene diversity retention over time of different management strategies. As mentioned earlier, the stochastic growth rate *r* reported here represents the mean stochastic growth rate over the entire 100-year projection and not the ending growth rate. Thus, a negative *r* does not necessarily indicate a declining population. Stochastic *r* is presented here to aid relative comparisons on overall growth among different management scenarios.

Several conclusions can be gleaned from this analysis:

1) All release strategies tested lead to improved viability compared to no future releases.
2) The total number of releases has more impact than the timing of those releases (over the ranges tested). In most cases, releasing a greater number of cranes in total leads to higher viability.
3) There are some conditions under which too much supplementation can be detrimental, i.e., if reproductive success (of mixed pairs) is poor and adult survival is also poor. Additional modeling of higher rates of supplementation (e.g., 20 releases per year for 20 years) supported this effect.
4) In most cases the timing of the releases has little impact on long-term population size and viability. For example, there is relatively little difference in long-term viability between releasing 10 cranes for 10 years or 20 cranes for 5 years; the same is true for 20 cranes for 10 years vs 10 cranes for 20 years.
5) The timing of releases can impact more immediate results, including the time to reach and maintain a population size of 100 (i.e., time to down-listing).
6) Releasing at least 100 birds promotes a viable population that can meet recovery goals within 100 years across most of the demographic uncertainty tested. Increased levels of supplementation further improve viability and in some cases can significantly reduce time to down-listing.
7) The variable schedule release strategies produced similar results as the constant schedule strategies that released the same total number or cranes, but they were slightly less robust across uncertainty in demographic rates when CR adult reproduction and mixed-origin pair reproduction is poor.

Table 15. Model results for LNMP for 100 years with supplementation of released juveniles (10-30 per year for 5-20 years), with varying adult mortality of released cranes and reproductive success of mixed-origin breeding pairs (N=mean population size at 100 years ±SD, GD=gene diversity, r = stochastic r, PE=probability of extinction, TTT = years to target; TT_{N100}=time to N=100). Mean N and GD calculated only for iterations that did not go extinct.

		Intermediate (midpoint)		Intermediate (default)		Pessimistic (CR-CR)	
		5.6% AM	11.6% AM	5.6% AM	11.6% AM	5.6% AM	11.6% AM
	No future releases	N=496 ±312 r=0.019 GD=0.916 PE=0.011 TTT=37y	N=254 ±230 r=0.008 GD=0.863 PE=0.052 TTT=61y	N=195 ±197 r=0.004 GD=0.848 PE=0.089 TTT=72y	N=94 ±105 r= -0.011 GD=0.774 PE=0.329 TTT<100y	N=98 ±123 r= -0.013 GD=0.775 PE=0.379 TTT<100y	N=52 ±69 r= -0.030 GD=0.701 PE=0.637 TTT<100y
CONSTANT SCHEDULE RELEASES	**5 yrs x 10 birds** (50 released in 5 years)	N=735 ±301 r=0.027 GD=0.949 PE=0.001 TTT=18y	N=476 ±307 r=0.018 GD=0.917 PE=0.022 TTT=41y	N=368 ±287 r=0.014 GD=0.906 PE=0.031 TTT=51y	N=178 ±186 r=0.001 GD=0.839 PE=0.131 TTT=76y	N=134 ±193 r= -0.002 GD=0.836 PE=0.199 TTT=79y	N=88 ±122 r= -0.017 GD=0.768 PE=0.460 TTT>100y
	5 yrs x 20 birds (100 released in 5 years)	N=843 ±243 r=0.031 GD=0.964 PE=0 TTT=18y TT_{N100}=4y	N=634 ±315 r=0.023 GD=0.941 PE=0.006 TTT=30y	N=530 ±264 r=0.020 GD=0.934 PE=0.007 TTT=38y	N=280 ±253 r=0.009 GD=0.881 PE=0.053 TTT=60y	N=242 ±237 r=0.005 GD=0.873 PE=0.097 TTT=66y	N=125 ±149 r= -0.008 GD=0.807 PE=0.294 TTT=92y
	10 yrs x 10 birds (100 released in 10 years)	N=848 ±241 r=0.031 GD=0.964 PE=0 TTT=21y TT_{N100}=8y	N=627 ±315 r=0.023 GD=0.940 PE=0.003 TTT=30y	N=522 ±319 r=0.019 GD=0.933 PE=0.006 TTT=38y	N=291 ±257 r=0.010 GD=0.888 PE=0.056 TTT=60y	N=235 ±229 r=0.006 GD=0.873 PE=0.090 TTT=68y	N=122 ±142 r= -0.008 GD=0.806 PE=0.292 TTT=93y
	10 yrs x 20 birds (200 released in 10 years)	N=911 ±189 r=0.036 GD=0.977 PE=0 TTT=22y TT_{N100}=4y	N=822 ±254 r=0.030 GD=0.964 PE=0.003 TTT=28y TT_{N100}=5y	N=746 ±293 r=0.027 GD=0.960 PE=0.002 TTT=28y TT_{N100}=5y	N=478 ±304 r=0.018 GD=0.929 PE=0.006 TTT=42y	N=394 ±298 r=0.014 GD=0.920 PE=0.035 TTT=50y	N=205 ±207 r=0.003 GD=0.863 PE=0.117 TTT=72y
	20 yrs x 10 birds (200 released in 20 years)	N=918 ±176 r=0.036 GD=0.977 PE=0 TTT=31y TT_{N100}=8y	N=810 ±264 r=0.029 GD=0.964 PE=0 TTT=31y TT_{N100}=13y	N=721 ±295 r=0.026 GD=0.962 PE=0.002 TTT=31y TT_{N100}=11y	N=457 ±295 r=0.018 GD=0.932 PE=0.016 TTT=45y	N=374 ±292 r=0.014 GD=0.922 PE=0.022 TTT=53y	N=195 ±200 r=0.003 GD=0.869 PE=0.108 TTT=74y
VARIABLE SCHEDULE RELEASES	**2yrs x 30 birds** **3yrs x 20 birds** (120 released in 5 years)	N=874 ±221 r=0.032 GD=0.966 PE=0 TTT=15y TT_{N100}=3y	N=659 ±317 r=0.024 GD=0.942 PE=0.003 TTT=28y	N=547 ±334 r=0.020 GD=0.932 PE=0.013 TTT=38y	N=299 ±264 r=0.009 GD=0.889 PE=0.092 TTT=60y	N=240 ±247 r=0.004 GD=0.868 PE=0.127 TTT=70y	N=125 ±154 r= -0.009 GD=0.802 PE=0.324 TTT>100y
	5yrs x 10 birds **5yrs x 20 birds** (150 released in 10 years)	N=889 ±214 r=0.033 GD=0.971 PE=0 TTT=20y TT_{N100}=7y	N=731 ±304 r=0.026 GD=0.953 PE=0.004 TTT=20y TT_{N100}=8y	N=600 ±331 r=0.022 GD=0.944 PE=0.009 TTT=20y TT_{N100}=8y	N=325 ±267 r=0.012 GD=0.899 PE=0.043 TTT=57y	N=261 ±256 r=0.007 GD=0.883 PE=0.077 TTT=66y	N=144 ±183 r= -0.006 GD=0.818 PE=0.248 TTT=98y
	2yrs x 30 birds **3yrs x 20 birds** **5yrs x 10 birds** (170 released in 10 years)	N=895 ±213 r=0.034 GD=0.972 PE=0.001 TTT=20y TT_{N100}=3y	N=775 ±291 r=0.028 GD=0.955 PE=0.002 TTT=20y TT_{N100}=3y	N=630 ±328 r=0.023 GD=0.947 PE=0.007 TTT=20y TT_{N100}=3y	N=377 ±296 r=0.014 GD=0.906 PE=0.030 TTT=51y	N=301 ±273 r=0.008 GD=0.890 PE=0.085 TTT=61y	N=161 ±184 r= -0.003 GD=0.833 PE=0.228 TTT=91y
	5yrs x 20 birds **10yrs x 10 birds** (200 released in 15 years)	N=918 ±174 r=0.035 GD=0.975 PE=0 TTT=25y TT_{N100}=4y	N=790 ±276 r=0.029 GD=0.961 PE=0.001 TTT=25y TT_{N100}=5y	N=677 ±313 r=0.024 GD=0.954 PE=0.007 TTT=25y TT_{N100}=5y	N=409 ±303 r=0.015 GD=0.915 PE=0.025 TTT=48y	N=312 ±270 r=0.010 GD=0.902 PE=0.061 TTT=60y	N=176 ±194 r= -0.001 GD=0.850 PE=0.183 TTT=86y

Examining the first 40 years of model projections is useful to identify the impact of release strategy on mean time to down-listing and time to reach 100 cranes. Figure 32 shows LNMP population projections for 40 years for each fixed release strategy using the default demographic values. At modest supplementation levels (i.e., additional 100 released juveniles), the population on average does not maintain 100 birds until ~38 years, although likely a small increase in releases might hasten this. Doubling releases to 200 cranes reduces mean time to reaching 100 cranes to ~5 years (20 per year for 10 years) to ~11 years (10 per year for 20 years). It is difficult, however, to meet the existing down-listing criteria as they are currently defined (and assuming default demographic rates) in less than ~30 years.

Figure 33 shows LNMP population projections for 40 years for the four variable schedule release strategies using default demographic rates. As with the fixed schedule releases, the population may decline slightly when supplementation ceases and as the population moves from one of mixed-origin cranes to wild-hatched cranes. More early releases grow the population faster, and more total releases lead to larger mean population size.

The management strategy used to establish the LNMP was to release captive-reared juvenile birds (~6 months of age). It is uncertain how age or rearing may affect survival and reproductive rates of released birds. The continued exploration of rearing and release techniques might lead to improved 'quality' of released birds that will lead to higher reproductive success, moving the population from its current (uncertain) state to better long-term viability aspects.

Cross-fostering of eggs to LNMP nesting pairs
An alternative supplementation option is to cross-foster full-term fertile (possibly pipped) eggs to nesting LNMP pairs, swapping out their own eggs. From a demographic viewpoint, this essentially increases hatch rate and leads to more parent-reared birds in the wild, which may confer higher reproductive success to these birds as adults. This would provide demographic and potentially also genetic benefits. This strategy is being tested in the field, with 2 eggs cross-fostered in 2017.

To investigate this supplementation strategy, two model scenarios were developed. Each scenario simulated the cross-fostering of 1 hatching egg to each of 3 adult pairs in the LNMP each year for 5 years. Survival of cross-fostered chicks from hatching to fledging was assumed to be the same as the pair's natural offspring, and varied dependent upon the rearing origin of the parents. Post-fledging demographic rates were assumed to be the same for cross-fostered cranes as for wild-hatched cranes. Application of these rates resulted on average in the production of 1 fledging surviving to at least 6 months of age every other year. An alternative scenario was created using a higher (2x) success rate (i.e., 1 juvenile surviving to 6 months each year). Both success rates also were run with cross-fostering implemented for 10 years.

Cautionary note: This strategy required a complex modeling effort to project its impacts on population viability. All attempts were made to validate these model scenarios, which appear to function correctly. However, caution should be exercised when interpreting the results of these scenarios.

Preliminary modeling suggests that cross-fostering may on average lead to larger final population size and shorter time to down-listing. However, this strategy may possibly incur a higher risk of population extinction (Table 16). It is unclear if increased extinction risk is probable or if it is an undetected artificial artifact of model construction. Population growth is slightly lower if cross-fostering is extended from 5 to 10 years, again suggesting some short-term impact, real or artificial, in the cross-fostering model scenarios. Growth is improved with higher survival of cross-fostered eggs to 6 months of age, although overall growth is lower than that observed in scenarios modelling juvenile supplementation (Fig. 34). Field data regarding the survival of cross-fostered eggs, the impact of cross-fostering on future reproductive success of foster parents, and other areas of uncertainty regarding the impacts of cross-fostering would be valuable to better access the value and risks of this approach.

Release of adult pairs
Another supplementation strategy is to translocate and release adult whooping cranes, potentially reproductive pairs, into the LNM population. The source of the translocated birds, as well as their individual physical and behavioral attributes, could have implications for their success in and impact on the LNMP. Additional modeling was conducted to explore the relative impact of this strategy, assuming translocated pairs would have the same reproductive success as wild-hatched resident pairs. Releasing reproductive adult pairs has the potential to lead to increased population viability. Under the conditions modeled, more benefit was derived from adding young wild breeding adult pairs than adding the same number of captive-reared juveniles. This is expected, as not all released juveniles will survive to breeding age and those that do were estimated to have lower reproductive success. Releasing 10 juveniles has a similar effect as releasing one young adult pair given the assumptions for this scenario. While potentially beneficial, this strategy currently is considered to have low feasibility.

Translocation of cranes from Florida
The Florida non-migratory population (FNMP) was initiated through the release of 289 young whooping cranes from 1993 through 2006 into central Florida. High mortality and poor reproduction of this population led to the decision to discontinue releases after 2006 (Folk 2013). Protocols were developed to address survival challenges such as high predation, disease, and metal toxicosis and other human-related threats, and led to improved survival. Power line collisions contributed to male-biased mortality that led to a female-based sex ratio, limiting the number of breeding pairs. Limited reproduction has been observed, with the first fledging reared to independence in 2002 and 9 fledglings produced by 2008 (Folk *et al.* 2010). Spalding *et al.* 2010 found extreme annual variability in fertility and hatchability (0-62%) that suggests a disease or environmental influence. Low rainfall and marsh water levels may limit reproduction in this population below levels required for a sustainable population.

Discussions are underway regarding the potential translocation of cranes from the remnant FNMP to the LNMP. As of May 2018 the FNMP consists of 4 adult pairs plus 3 unpaired adult females (12-20 years old) and three young birds (age 2-3 years). All pairs plus the 20-year-old female are captive reared; all others are wild hatched. Current plans under discussion are to translocate the 6 unpaired cranes to the LNMP as a first priority. This scenario was modeled, using default demographic rates and assuming no translocation-associated mortality and that all 6 translocated cranes exhibited wild demographic rates. An additional scenario modeled the transfer of all 14 cranes in the FNMP (6 above, plus 4 breeding pairs).

Given these assumptions, model results suggest that transferring cranes from the non-viable FNMP to the LNMP offer potential positive demographic and genetic benefits. All long-term viability measures are improved compared to a "no translocations" scenario (Table 16). This improves the color-coded viability classification for the LNMP. Translocations from the FNMP are insufficient to allow the population, on average, to reach the down-listing criteria for ~50 years (Fig. 35). This scenario assumes no disease transmission risk, no negative behavioral consequences or other potential risks to be considered.

Mixed Supplementation Strategies
The most probable management for the LNMP will be a mix of supplementation types and schedules. This is occurring already, with both the release of captive-reared juveniles and the swapping of wild-laid eggs with captive-laid ones (i.e., cross-fostering) being implemented beginning in 2017. Short-term, higher intensity supplementation that quickly boosts population size may be the preferred strategy from a practical viewpoint. While many combinations of supplementation method and schedule are possible, two scenarios were requested and modeled. These incorporated the following management:

1) Release of juveniles annually for 5 years (either 10 or 20 per year)
2) Translocation of all 14 cranes from Florida
3) Cross-fostering of eggs to 3 pairs each year for 5 years (normal success)

Two additional mixed strategy scenarios were modeled that comprised the same juvenile releases and translocation of cranes from Florida (#1&2 above) but omitted the cross-fostering of eggs (#3).

All four mixed supplementation strategies lead to increased overall growth, larger population size, higher genetic diversity and shorter time to down-listing compared to no additional supplementation. However, strategies that include cross-fostering have higher extinction risk that those with no cross-fostering (Table 16). In those iterations in which the population did not go extinct, strategies that include cross-fostering lead to a shorter time until population growth begins to increase (~15 years) vs those without cross-fostering (~32 years), and is related to the proportion of wild-hatched cranes in the population (Fig. 36). The two mixed strategies that include annual releases of 20 (vs 10) juveniles lead to significantly shorter time to recovery. All four strategies lead to significantly larger mean population size over 100 years provided the population does not go extinct.

The combination of juvenile releases and translocations from Florida provide benefits over either single strategy. The impacts of adding cross-fostering of eggs is less certain. This strategy has the potential to boost population growth and size, but is associated with higher extinction risk as modelled in this PVA. The realized impacts on the LNMP will depend upon a variety of demographic factors associated with this management strategy. Close monitoring of the LNMP will enable any potential negative impacts to be detected and appropriate management adjustments made, and will enable more precise PVA modeling that includes this strategy.

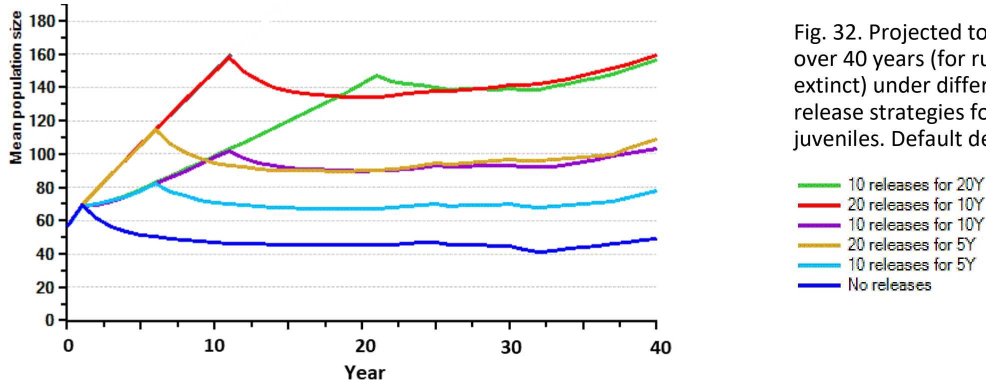

Fig. 32. Projected total cranes in the LNMP over 40 years (for runs that did not go extinct) under different fixed schedule release strategies for captive-reared juveniles. Default demographic rates used.

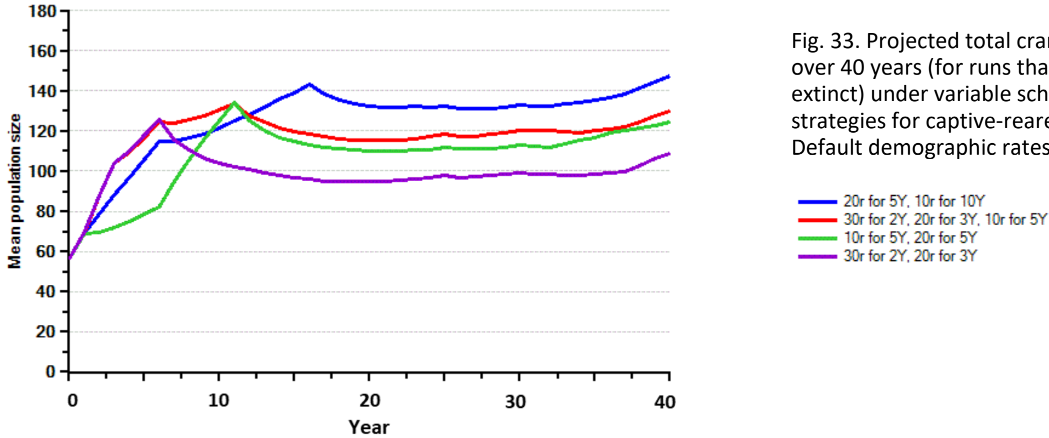

Fig. 33. Projected total cranes in the LNMP over 40 years (for runs that did not go extinct) under variable schedule release strategies for captive-reared juveniles. Default demographic rates used.

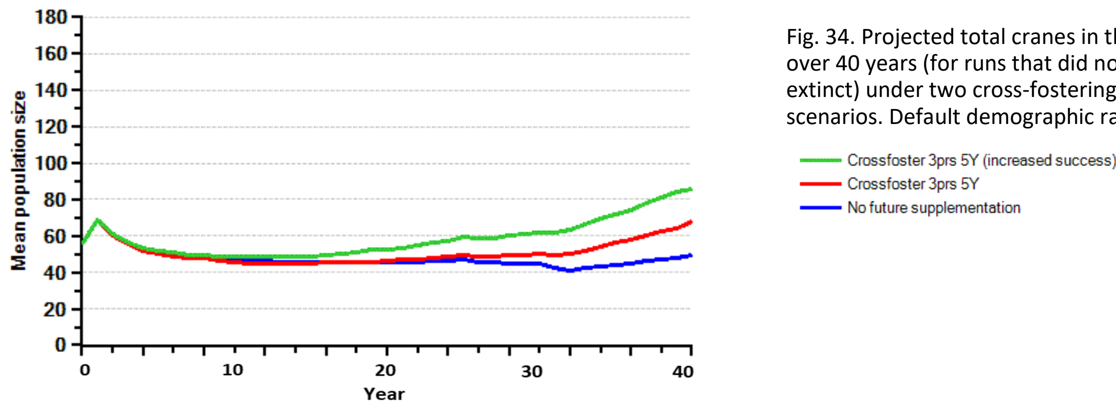

Fig. 34. Projected total cranes in the LNMP over 40 years (for runs that did not go extinct) under two cross-fostering scenarios. Default demographic rates used.

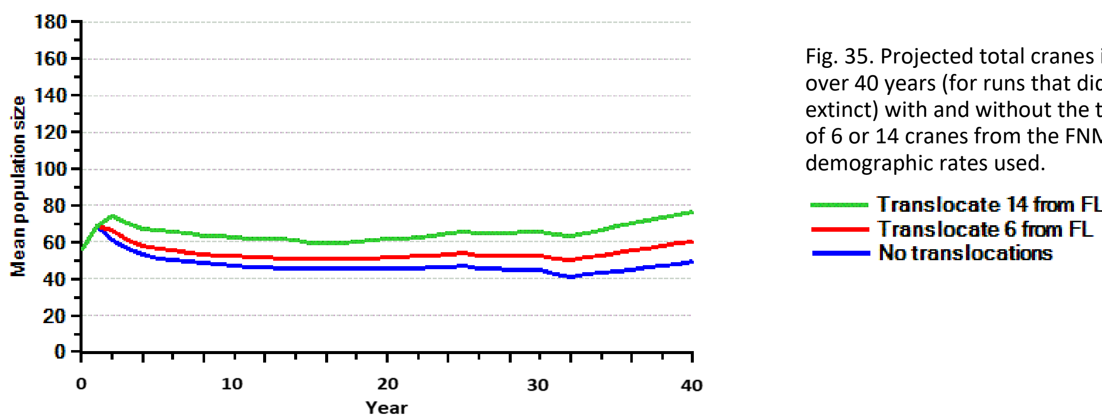

Fig. 35. Projected total cranes in the LNMP over 40 years (for runs that did not go extinct) with and without the translocation of 6 or 14 cranes from the FNMP. Default demographic rates used.

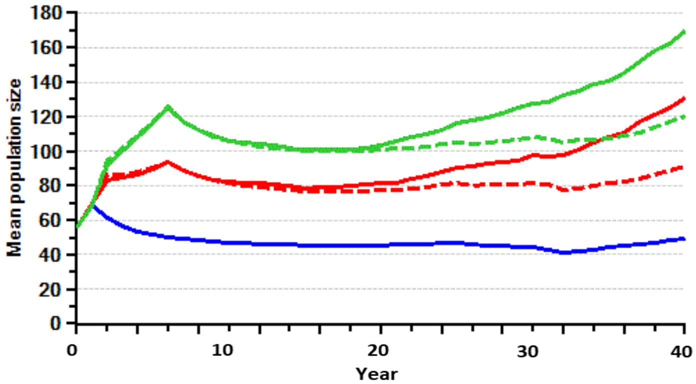

Fig. 36. Projected total cranes in the LNMP over 40 years (for runs that did not go extinct) under four mixed-supplementation strategies. Default demographic rates used.

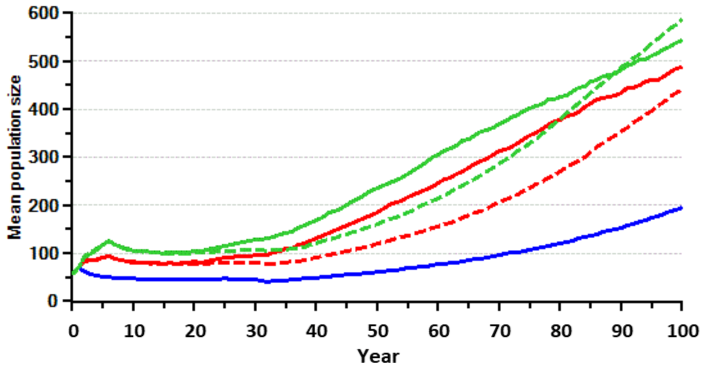

Fig. 37. Projected total cranes in the LNMP over 100 years (for runs that did not go extinct) under four mixed-supplementation strategies. Default demographic rates used.

Table 16. Model results for LNMP for 100 years with cross-fostering and with no supplementation. Stoch r=stochastic growth rate; N=mean population size ±1 SD; GD=mean gene diversity; PE=prob. of extinction; TTT=time to target.

Scenario	Stoch r	N_{100yr}	GD_{100yr}	PE_{100yr}	TTT
No further releases	0.004	195 ± 197	0.848	0.089	72yrs
Juvenile releases					
Release 10 juveniles annually for 5 years	0.014	368 ± 287	0.906	0.031	51yrs
Release 20 juveniles annually for 5 years	0.020	530 ± 324	0.934	0.070	38yrs
Cross-fostering eggs					
Cross-foster 3 pairs for 5 years (1 juvenile surviving to 6 months per 2 years)	0.004	325 ± 325	0.860	0.227	52yrs
Cross-foster 3 pairs for 10 years (1 juvenile surviving to 6 months per 2 years)	0.002	304 ± 315	0.849	0.226	54yrs
Cross-foster 3 pairs for 5 years (1 juvenile surviving to 6 months per year)	0.008	378 ± 342	0.873	0.173	45yrs
Cross-foster 3 pairs for 10 years (1 juvenile surviving to 6 months per year)	0.006	352 ± 332	0.869	0.180	50yrs
Translocation from FL					
Translocation of 6 cranes (no pairs)	0.008	255 ± 229	0.867	0.050	63yrs
Translocation of all 14 cranes	0.013	327 ± 257	0.885	0.033	52yrs
Mixed (multiple) supplementation types					
Cross-foster 3 pairs for 5 years FNMP translocation (14 cranes) Release 10 juveniles/yr for 5 yrs	0.016	488 ± 354	0.914	0.114	33yrs
Cross-foster 3 pairs for 5 years FNMP translocation (14 cranes) Release 20 juveniles/yr for 5 yrs	0.021	545 ± 343	0.932	0.079	15yrs
FNMP translocation (14 cranes) Release 10 juveniles/yr for 5 yrs	0.017	442 ± 306	0.919	0.017	44yrs
FNMP translocation (14 cranes) Release 20 juveniles/yr for 5 yrs	0.021	587 ± 331	0.941	0.012	15yrs

LNMP PVA Summary and Implications for Recovery Objectives

PVA model summary
A VORTEX population simulation model was developed for the Louisiana non-migratory population (LNMP) of whooping cranes, using the Aransas-Wood Buffalo population (AWBP) model as a foundation. Demographic rates were estimated based on data from the AWBP, LNMP and Eastern migratory population (EMP). Retrospective modeling suggests that this model is a reasonable representation of historical trends to date in this young population. Sensitivity testing of the model suggests that recruitment (egg production, hatching and fledging rate) and adult survival are primary factors in population growth and size and therefore time to down-listing and recovery.

There is substantial uncertainty regarding future demographic rates in this reintroduced population, in particular with respect to survival and reproductive success of released cranes. It is also unclear how rearing history may affect these rates. This uncertainty limits the value of the population projections. While quantitative results are presented in this PVA report, these model results should not be considered as precise viability projections. PVA results, however, can help identify important data gaps for understanding and managing the LNMP and can be useful in making relative comparisons among alternative management strategies. Multiple scenarios were explored to examine the range of future projections for the LNMP under major areas of uncertainty, and the type of level of supplementation that might be needed to promote growth and achieve recovery goals for this population.

Assumptions
Primary assumptions built into this PVA model include that wild-hatched LNMP cranes will have similar reproductive and mortality rates as wild cranes in the AWBP (except when paired with a captive-reared mate); that captive-reared released juvenile cranes will have similar reproductive rates as cranes in the reintroduced EMP; and that the reproductive success of pairs does not improve with experience or with population density.

Viability projections in the absence of future supplementation
Demographic rates from other whooping crane populations were incorporated to provide a best estimate for LNMP future viability. With no further supplementation, the projected viability of the LNMP is moderate and involves significant variation in population measures. The population is projected to fluctuate around a mean of about 40-50 cranes for about 30 years (until all released cranes die) and then, on average, to grow, provided that reproductive success and survival of wild-hatched cranes is similar to that observed in the AWBP. Projections for population size over time are highly variable, with a mean of 195 (SD=197) in 100 years, mean time to down-listing of 72 years, and a 9% risk of population extinction.

Varying the reproductive success of mixed-origin pairs (those comprised of one wild-hatched mate and one captive-reared mate) can significantly alter these projections. Default values result in a relatively stable mean population size over the next several decades, while higher and lower values tested result in population growth or decline, respectively, in subsequent decades. Higher adult mortality in released cranes negatively impacts population viability. However, mixed-origin pair reproductive success has a relatively greater impact over the range of values tested.

Impacts of future supplementation
All release strategies explored in this PVA lead to improved viability compared to projections under which there are no further releases. Results suggest that continued release of juveniles for at least several more years can provide short- and long-term benefits to the population. The total number of releases has more impact than the timing of those releases (over the ranges tested). However, the timing of releases affects the number of years to down-listing; the earlier the releases occur, the more quickly the population

grows to target size. Releasing an additional 100-200 juveniles over the next 5-10 years provides greatest relative gain in future viability across the range of uncertainty explored in vital rates of released birds.

Adding wild reproductive pairs while the population is still small can greatly improve long-term viability, leading to larger population size, greater genetic diversity and reduced risk of extinction over 100 years. The largest relative gain can be achieved with the addition of as few as two pairs per year, with additional pairs providing additional benefits. As with juvenile releases, releasing the same number of birds sooner allows population size to increase more quickly and leads to a shorter time to down-listing. More benefit is derived from adding young wild breeding adults than adding the same number of captive-reared juveniles. This is logical, as young adults have survived to breeding age and, being wild hatched, have a higher probability of fledging a chick (at least in the model) than captive-reared cranes.

Translocating cranes from the current non-viable reintroduced Florida non-migratory population to the LNMP offers potential positive demographic and genetic benefits but is insufficient alone to allow the population, on average, to reach the down-listing criteria until ~50 years. Combining these translocations with the continued release of juveniles provides a more robust and effective management strategy and shortens time to down-listing.

Cross-fostering of soon-to-hatch eggs to wild LNMP pairs may provide benefits but also is associated with higher extinction risk as modeled in this PVA. More data regarding the impacts of cross-fostering is needed to better understand potential benefits and risks and to develop more useful PVA models for this strategy.

Population projections in this PVA are highly variable. In addition, the specific results for these supplementation strategies are contingent upon many assumptions in the survival and reproductive success of captive-reared and wild-hatched released and resident birds, and should be considered only as general trends. Examining the trends in these results may be useful to illustrate the potential benefit of different release strategies. These scenarios assume no disease transmission risk, no negative behavioral consequences, or other potential risks to be considered in release programs; inclusion of any risk factors is important and will affect the impacts on the population.

The reproductive success of captive-reared released cranes is a key factor that drives population growth and viability. Management strategies or actions that improve reproductive success of released cranes would improve the status of the LNMP under any scenarios explored here. Reports of improved fledging rates for the 2018 breeding season (not available at the time of PVA development) are encouraging.

PVA results and recovery objectives

The current international recovery plan (CWS & USFWS 2007) includes two recovery objectives for down-listing of whooping cranes, one for the wild population and one for the captive population. Objective 1 is to "establish and maintain self-sustaining populations of whooping cranes in the wild that are genetically stable and resilient to stochastic environmental events." This PVA is relevant to the down-listing Criteria 1 and 1A related to the development and maintenance of a whooping crane wild meta-population of 2-3 sub-populations. Criterion 1 requires the maintenance of at least 160 cranes in the AWBP and two additional populations of at least 100 cranes each, with all three populations being self-sustaining at these levels for a decade before down-listing. Alterative Criterion A1 requires an AWBP of at 400 cranes and one additional population of at least 120 cranes, both of which are self-sustaining at this level for a decade. The AWBP already exceeds 400 cranes and is projected to increase in size.

The best estimates for the expected length of time until the LNMP reaches and maintains at least 100 cranes for a decade ranges, in the absence of further supplementation, from 37 years to over 100 years across the uncertainty explored in this PVA. Growth to at least 120 cranes would take longer. Additional supplementation likely will be required to significantly shorten time to meeting down-listing criteria. Continuing the past practice of releasing ~ 20 juvenile cranes each year for 10 more years is projected to have significant positive impacts on all population measures. Releasing adult cranes can have similar positive impacts. Combining these two strategies can provide a strong management option to increase population viability and shorten time to down-listing. The impacts of cross-fostering eggs/chicks to wild pairs is less certain and should be monitored to ensure positive benefit. While the high degree of uncertainty in demographic rates make it difficult to predict the precise time to meeting down-listing criteria under these management strategies, the scenarios explored in this PVA can guide management actions that will promote quicker recovery.

A separate PVA is underway to explore similar questions and scenarios for the second reintroduced population – the Eastern migratory population (EMP). The success of this population will impact the importance of and down-listing criteria for the LNMP.

Objective 2 to "maintain a genetically stable captive population to ensure against extinction of the species" is being modelled separately to evaluate the projected genetic and demographic status of the SSP population. As none of the AWBP scenarios project a risk of extinction of the AWBP over the next 100 years, this suggests that the captive population may not be required to augment or re-establish the AWBP population. However, the captive population may provide important headstarting or supplementation services that could reduce the time to down-listing for the AWB population and to establish viable reintroduced populations (LNMP and EMP). The captive population may play a critical role for the development of additional reintroduced populations, for example by parent fostering wild-laid eggs, producing eggs for cross-fostering to wild parents, and producing additional birds for release. In addition, given the uncertainty of future climate change impacts and anthropogenic threats, there may be a risk of AWB population decline or extinction in the presence of greater threats than modeled and increasing the need for a back-up captive insurance population.

Acknowledgements
This PVA model was developed in consultation with the Whooping Crane International Recovery Team and numerous crane biologists and managers who participated through workshops and/or electronic discussion in 2015-2018. Additional PVA work was conducted in 2018 to assess the other whooping crane populations and full meta-population. These PVA models and results will serve as a basis to evaluate potential management actions to increase whooping crane viability and to evaluate recovery goals for this species, and will inform species conservation planning discussions scheduled in October 2019.

Section 5. Whooping Crane Population Viability Analysis (PVA) Report: Species Survival Plan Model and Sensitivity Testing of Management Options

This report describes the baseline *VORTEX* model and results for the captive managed population of whooping cranes. This population model and scenarios were developed in conjunction with the 2015 and 2016 Population Viability Analysis (PVA) workshops in Calgary for all whooping crane populations, and were informed by additional electronic and telephone conference discussions through 2018.

The captive population was established at the Patuxent Wildlife Research Center (PXT) from eggs collected from the Aransas-Wood Buffalo Population (AWBP) between 1967 and 1998. In 1989, some of the population was transferred to the International Crane Foundation (ICF), with Calgary Zoo, San Antonio Zoo, and Audubon Zoo joining the program soon after (Peregoy 2017). This captive population is managed collectively as a Species Survival Plan® (SSP®) of the Association of Zoos and Aquariums (AZA). A studbook database is maintained (by S. Liu, Dallas Zoo) for the captive and reintroduced populations, and the SSP is coordinated by K. Boardman, ICF.

Historically, most breeding and rearing has occurred at the five long-term breeding centers (PXT, ICF, and Calgary, San Antonio and Audubon zoos). Most breeding occurs between cranes within each center, with occasional inter-facility transfers of eggs or cranes. These primary breeding centers have produced cranes for release to establish the two reintroduced populations (Eastern migratory population (EMP) and Louisiana non-migratory population (LNMP)) and have also reared chicks from eggs collected from the EMP and released them back to the EMP as juveniles (a process known as headstarting).

This SSP population is managed both demographically and genetically to meet its goals of serving as a source of birds for release as part of reintroduction efforts and as a long-term insurance population against species extinction, as specified in Objective 2 of the recovery plan (CWS & USFWS 2007). Adults are paired behaviorally but artificial insemination is often used, providing increased opportunities for genetic management in this monogamous species. The breeding centers also contribute to the establishment of reintroduced population by headstarting wild-collected eggs to produce juveniles for release.

The Patuxent Wildlife Research Center played a large role historically in breeding and headstarting young cranes for release but announced in 2017 that the program was terminating due to funding issues. To address this loss of capacity, several zoos plan to expand their breeding capacity and efforts. Cranes at PXT are being distributed to other zoos, and may experience lower reproductive rates in the short term. It is unclear if other zoos will be able to provide the headstarting capacity once provided by PXT.

This PVA explores the projected ability for the captive SSP population to meet its population and conservation roles to support the recovery of wild whooping crane populations under different conditions.

Model Inputs

A stochastic, individual-based population model was developed for the whooping crane using the *VORTEX* 10.2.15 (Lacy and Pollak 2017) software program. *VORTEX* is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild or captive small populations. A one-year time step was implemented, with events (e.g., breeding, mortality, releases) occurring once per year. The model begins each 'year' in spring prior to breeding and tallies population numbers at this time. Model scenarios were run for 100 years with 1000 iterations each.

Demographic rates to parameterize the SSP model were derived primarily from studbook data for the SSP as well as expert opinion on conference calls and at the PVA workshops. The SSP also provided projected future changes in capacity or management. There are two main differences between the SSP model and the PVA models developed for the wild and reintroduced populations (AWBP, EMP, LNMP):

1) Only one mortality event per year is applied in the SSP model, instead of two different seasonal mortality events in the wild populations; and

2) Reproduction is defined as the hatching of chicks instead of the production of eggs as in the wild population models. This is because only hatched eggs are recorded in the studbook. Reproductive events that produce 1-2 chicks are referred to as "broods" and are used to define reproduction in the SSP PVA model, whereas reproductive events that produce 1-2 eggs are termed "clutches" and are used in the wild population models. Inputs and considerations for modeling broods is different than rates associated with clutches.

Initial Population
The population was initiated with cranes living prior to the 2017 breeding season (n=160). Age, sex, reproductive history, and parentage (pedigree) for each crane was taken from the 2017 studbook (Peregoy 2017). Empirical kinships derived from molecular genetic data (provided by K. Jones) were overlaid on the population's pedigree to estimate relationships among genetic founders. The SSP was modeled as one panmictic population with no separation into institutions or breeding centers.

Carrying Capacity
Carrying capacity (K) for the entire SSP population was set at 165. If population size (N) exceeds K at the end of a model year, excess juveniles (N-K) are probabilistically removed. Details are provided below under *Population Size Regulation*.

Reproduction (Production of Broods with Chicks)
Studbook data were analyzed for the captive population to determine age- and sex-specific reproductive and mortality rates. Reproductive lifespan was set from age 4-30 years for females and 4-35 years for males, with a maximum lifespan of 40 years (longer lifespan than that of 30 years used for wild PVAs).

Reproductive parameters were calculated based primarily on data from 2001 to 2016. This period represents years during which the SSP was well established in multiple breeding centers and zoos and was producing juveniles per year for release. Some estimates excluded data for 2014-2016, during which some reproductive pairs were used to rear eggs collected from the wild (EMP) for headstarting efforts.

While cranes form behavioral reproductive pairs in the SSP, genetic mating is sometimes done by artificial insemination (AI). Thus this long-term monogamous species was modeled as polygynous, with females having a 30% chance of retaining their same genetic mate for the subsequent breeding season. Males were limited to siring broods with a maximum of two female 'mates' per year. All broods produced by a female in the same breeding season were sired by the same genetic mate.

Reproduction is controlled in the model by setting a maximum number of broods per year for the SSP. The determination of this number is influenced by SSP capacity (number of pairs and facilities available for rearing of chicks) and by the demographic goals of the population for maintenance of the SSP and production of juveniles for release. For this PVA, broods are defined as reproductive events that produce at least one hatched chick (i.e., clutches of only infertile or fertile eggs that do not hatch are not included).

From 2001 to 2014 there was an average of approximately 24+ broods per year estimated from studbook data). Issues in hatch dates prevented accurate determination of broods in the historical data. The number of broods was likely underestimated from the data and required calibration in the model with chick production and releases (see below). An average of approximately 28 juveniles were released and 6 juveniles retained in the SSP each year, with annual variation in release and retention rates.

Genetic management was modeled based on the SSP's strategy of minimizing mean kinship (MK) in the population, which has been demonstrated to slow the rate of loss of gene diversity due to genetic drift (Ballou and Lacy 1995). The mean kinship value (to the SSP living population) was calculated for each individual prior to breeding season. Low MK values indicate priority birds for breeding as they represent underrepresented genetic lines.

Annual reproduction was modeled for each adult female (pair) as follows:

1. Adult female with the lowest MK value is selected for potential breeding.
2. Probability of producing at least one chick that year is calculated based on the female's age and reproductive history; if successful, she is given a mate and produces chicks(s).
3. Female is not allowed to breed if the maximum number of broods for the year has been reached.
4. If reproductive that year, the number of broods (and number of chicks per brood) is determined.
5. Sire is selected for chicks (either the female's same mate as previous year, or the most genetic valuable available male). Genetic pairings with male-female kinships of 0.125 or higher (i.e., level of half-sibling mating) are rejected, and a different male mate is selected.

The impact of a female's past reproductive history was taken from studbook data from 2001-2013 for all adult females age 4-30 years at one of the five breeding facilities (ICF, PXT, Calgary, San Antonio, Audubon). Proven breeders (i.e., females that had produced at least one chick in the past) were given a higher probability of success (64%) for that year than nulliparous females (10%). This probability was reduced for older females (ages 26 and over) to 43% for proven breeders and 0% for nulliparous females. Partitioning of variance in these data indicated that yearly variance observed in these rates can be explained by demographic stochasticity, so no annual environmental variation (EV) was added to reproduction (hatches). EV is commonly low or absence in controlled captive conditions.

Selection of females for breeding and application of these success rates is applied to all adult females in the model, not just those at breeding institutions. However, as long as there are few breeding age females in non-breeding facilities and only those of low genetic values, the above modeling process and inputs should be a reasonable representation of breeder selection and success.

Females can have up to three broods per year, with the following distribution based upon 2001-2013 studbook data and ICF data: 1 brood (55%); 2 brood (36%); and 3 broods (9%), with the caveat that the number of true broods may be underestimated. The number of hatchlings per brood were modeled as 37% for one chick and 63% two chicks for first broods, and 54% for one chick and 46% for two chicks for second and third broods. Older females were modeled with a lower number of hatchlings (mostly one chick per brood). These allocations result in an average of 2.42 chicks per successful female (1.7 chicks for females over 25 years), which matches these calculations from 2001-2013 studbook data.

Note: Several differences can be noted between how breeding occurs in the model compared to the actual SSP breeding plans. The model attempts to breed females in prioritized genetic order (i.e., most valuable females first) and will therefore stochastically assign more broods from genetically valuable females. In reality, valuable females may not reproduce due to factors including health, behavior and location; thus, while stochastic, the model is likely to apply stricter genetic management than observed in the SSP. The model also does not differentiate proven breeders except by genetic value. "Good breeders" are not preferentially selected as might occur in reality, and therefore the model is more likely to breed more different individual cranes. Also, SSP breeding plans and allocation of offspring to the SSP and reintroduced populations occurs biannually and well ahead of time, and therefore is not as immediately responsive to changes in population status as the model.

Population Size Regulation
SSP population size is regulated in three ways in this PVA model. First, the number of broods produced is restricted, with breeders selected based on their genetic value to the SSP. Excess offspring (i.e., those above carrying capacity) are removed from the population, with the restriction that they are not of high genetic value to the SSP (i.e., juvenile MK > (population MK/3), using a static MK list). During release program years, these excess offspring are tallied in a virtual holding pen to track releases and then removed from model the following year. In non-release years, the number of broods is set to maintain the target size. In all years, if N > K at the end of the year, additional juveniles are probabilistically removed to bring the population to target size.

Mortality
Unlike the PVA models for wild and reintroduced crane populations, the SSP model applied mortality once each year, using sex- and age-specific rates gleaned from the studbook and smoothed to produce survivorship curves for maximum age of ~40. Female mortality was higher for sub-adults (1-3 years old), generating a slightly male-biased population (see Table 17 for mortality rates using in the SSP model).

First-year mortality was calculated and applied in a different manner, as some juvenile cranes were reared in captivity and released before reaching their first year. Most first-year mortality in the SSP occurs within the first three months; all juveniles were used in this calculation. Only juveniles retained in the SSP were considered in the calculation of the remaining first-year mortality (4-12 months). In the model, this mortality was applied during the 1-2 age class to prevent its application to juveniles destined for release (as releases occur after first-year mortality in the model). Partitioning of variance in mortality rates led to the inclusion of small environmental variation (EV) in first three-month mortality rates but not for other age classes. This simulates annual variation in early mortality.

Table 17. Age- and sex-specific mean mortality rates (given as %) used in the SSP model. EV given in parenthesis.

Age class	Males	Females
Hatch to ~4 months	17.7 (2.75)	17.7 (2.75)
~4-12months	6	6
1 – 2 yrs	1	5
2 – 3 yrs	1	5
3 – 4 yrs	1	5
4 – 27 years (annual rate)	2.5	2.5
28 – 30 years (annual rate)	2.5	12
31-40 years (annual rate)	12	12

Catastrophes
One catastrophe is included in the SSP model. Disease (e.g., avian influenza) is modeled as an institutional-level outbreak (2% annual risk of hitting a large breeding center, 75% survival affecting 20% of the SSP population). Adverse weather (e.g., hurricane, blizzard, tornado, depending upon location) was also considered to be a risk, occurring about every 10 years and resulting in reduced reproductive success. This was considered to be included in the EV observed and added to chick mortality as described above.

Genetics
A small genetic load (3 lethal equivalents, 1 as a lethal allele and 2 as non-lethal effects) was incorporated into the model and applied as lower juvenile survival in inbred individuals. This is lower than the genetic load suggested by O'Grady *et al.* (2006) of 12.29 lethal equivalents for wild vertebrate populations, as it is assumed that some of the initial genetic load may have been purged due to the historical bottleneck and population expansion experienced by this species.

Validation of Historical Trends

A model was constructed to provide a retrospective analysis of the SSP population for the period of 2001 to 2013. During this time the SSP population was slowly expanded while providing juveniles for release to establish three reintroduced populations, in Florida, Wisconsin and Louisiana.

The retrospective model was initiated from studbook data with 121 cranes living in the SSP just prior to the 2001 breeding season. Since SSP population growth was controlled during this time while surviving juveniles were prioritized for release, a shifting carrying capacity was used to match SSP population size and match management. The release of 8 yearling cranes in 2001 was added to match actual releases; otherwise, releases were modeled as juveniles under 1 year of old and were generated by the model. The model was tested to determine its ability to approximate chick production and juvenile releases given the SSP's size, and to better assess the number of broods of chicks that match these conditions.

All model results matched the SSP size closely. The model underestimated actual chick production in the first three model years, with actual hatches falling about 1 SD above the projected model mean. The proportion of adult females that were experienced breeders was lower in the model during these years than that experienced by the SSP, perhaps due to better than average adult female survival and/or reproduction in the SSP. The proportion of proven females better matched SSP levels by year 4. Given this initial inconsistency, the first three years of modeling were ignored, and the 10-year period of 2004-2013 was used for model validation to align chick production with number of estimated broods.

Studbook data for 2004-2013 averaged ~ 24 broods per year, with the caveat that distinct true broods are not clear in the studbook data and so this is likely an underestimate of true broods as defined for modeling purposes. The current SSP rearing capacity (number of chicks) was estimated by SSP representatives as 12-15 chicks at ICF, 5 chicks (expanding to 8 in the future) at Calgary, and 5 at Audubon SSC, for a total of 22-28 chicks. Patuxent reared an additional 25-30 chicks, included headstarted chicks. Studbook data show an average of 43 hatches per year during 2001-2013. After neonatal deaths an average of 28 juveniles were released each year and an average of 6 retained in the SSP. Yearly variation in releases vs juveniles retained in the program may have been influenced by specific reintroduction needs, which was not incorporated into the retrospective model.

The model scenario with a maximum of 28 broods (17% over the 24-brood estimation from studbook data) performed best in comparison to studbook data. This scenario resulted in an average of 42 chicks hatched per year (SD=2.8) during this period (1.5 hatches/brood), with an average of 25 juveniles released (SD=4.3) and 9.7 juveniles retained (SD=2.7). Figure 38 depicts a comparison of annual actual and model data for total chicks (hatches), releases and surviving chicks retained in the SSP (note that model data are plotted as means only for visual clarity but are stochastic inputs with associated variance around those means). The model retained an average of ~3-4 more juveniles each year than actually occurred (Fig. 38). A possible explanation is that the model determined the number of juveniles to retain just prior to the following breeding season and thus incorporated the mortality of sub-adult and adult cranes for the year into this calculation, whereas SSP decisions were made and juveniles released much earlier or with different priorities.

Overall the model is a reasonable representation of SSP demographic and breeding system. Using the empirical kinships combined with studbook pedigree data, the model projects the mean gene diversity in 2013 to be 0.971 for the entire SSP population. A similar calculation for the SSP in 2016 that excludes 10 permanent non-breeders is 0.968 (Boardman *et al*. 2017).

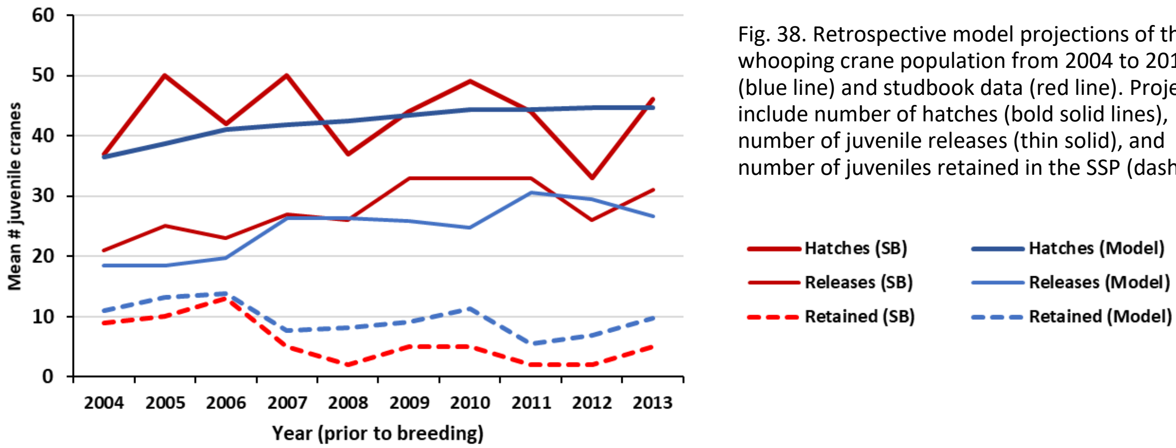

Fig. 38. Retrospective model projections of the SSP whooping crane population from 2004 to 2013 (blue line) and studbook data (red line). Projections include number of hatches (bold solid lines), number of juvenile releases (thin solid), and number of juveniles retained in the SSP (dashed).

Projected Viability Under Estimated Future Conditions

The PVA model was used to investigate the ability of the SSP population to serve as a demographically sustainable and genetically viable captive population as insurance against species extinction and to provide juveniles for release to establish reintroduced populations. Future management may differ from historical management both in the short term and long term for this population. Contributing factors include the recent loss of the Patuxent Wildlife Research Center as a major holder and breeder of captive whooping cranes and as a resource for headstarting wild-collected eggs. Another factor may be the potential downscaling of reproduction and population size when release efforts are discontinued. Other management options in terms of genetic management and rearing method may also have impacts. Model scenarios were developed to explore the future projected demographic and genetic status of the SSP in light of these changing conditions and potential management options.

Closing of the Patuxent breeding facility is not anticipated to lead to the loss of those cranes housed there, as these birds are being redistributed to other SSP facilities, or to reduction in SSP capacity of 160-170 cranes, as some facilities are expanding their capacity and new ones may be added to the program. The current capacity for 22-25 chicks is expected to increase to ~26-29 chicks by 2019, ~30-33 chicks by 2020, up to ~35-38 chicks in the next few years and possibly as high as 50 chicks. Redistributed females are expected to experience lower reproduction initially but are expected to be back to normal reproduction by 2020. It is uncertain whether headstarting of wild-collected eggs will continue or to what extent.

It is likely that release programs will run for a maximum of 20 years. Once releases cease, significantly fewer broods will be required to maintain the target population size. About 6-7 broods (with chicks) would be needed to maintain about 160-165 cranes in the SSP, given model parameters.

Model scenarios were developed to examine future projected viability under these new conditions.

1. Target population size (carrying capacity) was set at 165.
2. Reproduction was limited to 28 broods in 2017 (prior to PXT closing), and then decreased to 16 broods in 2018, with an incremental increase in maximum allowed broods of 2 per year until a 28-brood limit is reached in 2024 (historical level with release program). This level was maintained through year 2037, simulating a 20-year release program (2018-2037).
3. Females at Patuxent in 2017 were marked and given no ability to produce chicks in 2018, 50% chance of reproduction (if attempted) in 2019, and normal reproductive rates starting in 2020.
4. Releases cease after 20 years (i.e., last releases in 2037), and reproduction is limited to 7 broods per year and a maximum of 2 broods per breeding female for the remainder of the simulation.

Impact of estimated future conditions
Projections using the inputs outlined in #1-4 above suggest that the SSP is demographically sustainable and genetically viable under these conditions. The population maintains a mean of 163.8 cranes (SD=2.7) with 95.4% gene diversity after 100 years under strong genetic management. Estimated effective population size (Ne) is 206, calculated from the loss of gene diversity over 100 years and using a generation time (T) of 14.5 years. Once releases cease, the population hatches about 11-14 chicks annually (~2 more than needed to maintain the target population size) if 7 broods are allowed. Mean growth rate (r) after releases cease is 0.0125 prior to truncation to K.

While the model cannot accurately output the number of productive pairs as defined in the recovery objectives, it can track the number of pairs reproducing each year and the number of proven females. Results suggest an average of 21 breeding pairs per year (SD= ~4) once breeding centers have been expanded, dropping to ~16 breeding pairs per year (SD= ~3.5) once releases cease. The mean number of female proven breeders is 31-35 (SD= ~4) during the release program, and 24 (SD= ~3) once releases cease. If managed intensively, this population size appears demographically and genetically viable.

Under the inputs and conditions modeled, there is no long-term impact on SSP population size and gene diversity associated with the loss of the Patuxent facility. There are several short-term effects, however, most of which affect chick production and therefore the number of juveniles potentially available for release. The number of chicks produced is substantially reduced for the first 3-5 years after PXT closing. If priority is given to maintaining the SSP target size (default model), this results in significantly fewer juveniles available for release (Fig. 39). This impact is greatest in the first year (i.e., 2018), provided that no transferred females reproduce and that there is capacity for only about 24 chicks. As transferred females gain full reproductive potential and as facilities expand their reproductive capability, the number of broods, chicks and releases increase to levels before closing of the Patuxent facility. Most of this reduction is due to reduced breeding capacity in the SSP rather than reduced reproductive behavior of transferred females, provided that these females are distributed among the breeding centers. A scenario modeling zero reproduction in transferred females leads to an average loss of 4.5 releases in 2018 and 2 releases in 2019; after that point, projected capacity of the SSP is the determining factor for production.

If priorities are shifted to releases such that all juveniles (up to 12 males and 12 females) are released each year, then releases only drop on average to about 16 in the first year and 20 in the second year post-PXT closing. SSP population is impacted under this strategy, as few juveniles are retained in the SSP for the first several years. This in turn affects age structure and future growth, with the SSP declining to ~140-145 cranes until releases cease. The population is then able to grow back to capacity in an average of ~14 years (Fig. 40). Gene diversity is still high after 100 years (GD=0.953), with an estimated Ne of 188.

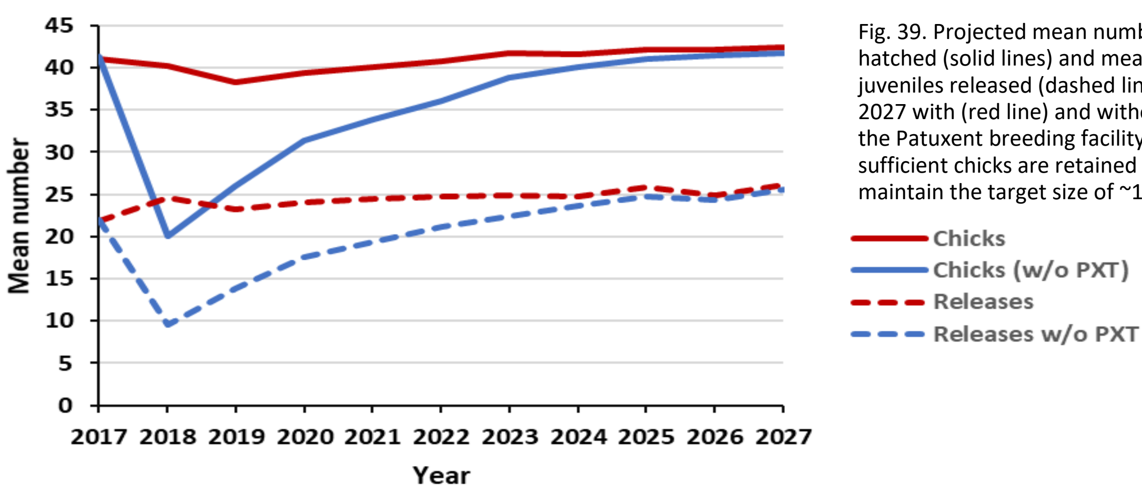

Fig. 39. Projected mean number of chicks hatched (solid lines) and mean number of juveniles released (dashed lines) for 2017-2027 with (red line) and without (blue lines) the Patuxent breeding facility. Assumes sufficient chicks are retained in the SSP to maintain the target size of ~165 cranes.

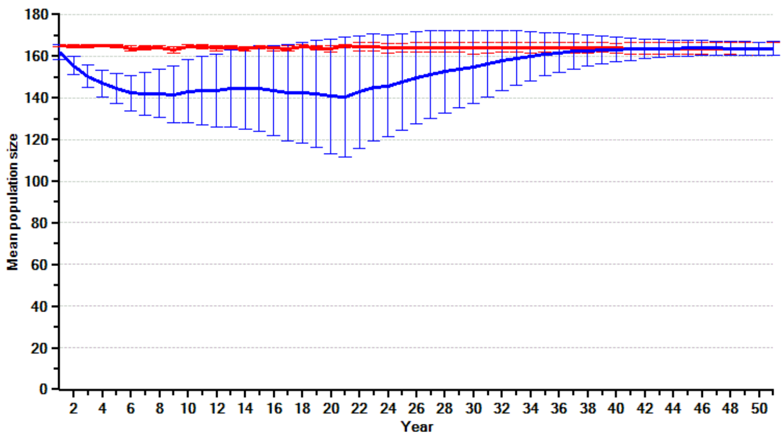

Fig. 40. Projected mean population size for the SSP for the next 50 years with priority given to releases for the next 20 years (blue line). Red line indicates mean size of SSP either with Patuxent facility retained, or if priority is to maintain 165 cranes. Bars indicate 1 SD.

Impact of increased single broods (as a proxy for parent-rearing)

It is hypothesized that parent-reared juveniles may be more suitable for release, as they may experience improved reproduction and/or survival in the wild. Rearing method is not explicitly modeled in the SSP PVA model and has no impact in the model on survival in captivity before release or on demographic rates of cranes that remain in the SSP. Parent rearing may be one of the methods by which increased reproductive success of released cranes is achieved in the EMP and LNMP PVA models. For the SSP PVA model, the primary difference in increased parent rearing may be an increase in the proportion of single vs multi-broods for breeding pairs. This might be the case whether the pair raises their own chicks or those from wild-collected eggs as part of a headstarting program. For example:

- If a pair is allowed to incubate eggs from its first clutch and rear chicks, they would only produce one brood.
- If eggs from a pair's first clutch are removed and the pair is allowed to rear chicks from any subsequent eggs (their own or wild-collected), these pulled eggs may not hatch (e.g., ICF hatch rate for 244 eggs from 2011 to 2016 was 23%); in this case, the pair produces only one brood of chick(s).
- If eggs from a first clutch are swapped for wild-laid eggs for headstarting, a maximum of only one brood is raised in the SSP.
- Not all single broods are necessarily parent reared, however; for example, pulled eggs from the first clutch may result in costume-reared chicks and the second clutch may fail, resulting in the production of only one brood from the pair.

Allowing captive pairs to raise chicks, be it their own or wild-collected eggs as part of a headstarting program, means that reproduction of these pairs in many cases may be limited to one brood of chicks. Two model scenarios was developed to compare SSP population viability and production of juveniles for release when single brood contribute a greater proportion to the reproductive output of the SSP. The default scenario attributes single broods to 55% of successfully breeding pairs. An 'increased parent rearing' scenario was run with 75% as single broods (25% of pairs with two broods). In addition, a scenario was run with all reproduction occurring from a single brood to assess the impact of such a strategy while recognizing that this would not likely be implemented. SSP population size and gene diversity retained over 100 years remained the same under all three scenarios, with no risk of extinction. If no multiple broods are produced, on average about 16-23% fewer chicks are hatched. Assuming that the SSP target size is maintained, this leads to ~30% reduction in the number of juveniles available for release (~6-7 fewer releases per year). The intermediate strategy of increased single broods and limited second broods (25% of pairs have 2 broods) led to better availability of juveniles for release, resulting in only ~11% reduction in juveniles released (~2.5 fewer releases per year) over the historical reproductive management while potentially promoting more parent rearing for released juveniles (Fig. 41). In this case, the mean number of juveniles from single broods is approximately the same as the mean number available for release. Note that these mean numbers of juveniles available for release each year is highly variable. In addition, differences in how reproduction occurs in the model vs real world mean that these means should not be taken as precise and exact figures. However, these scenarios provide an approximation of the tradeoffs between the quantity and 'quality' of chicks produced.

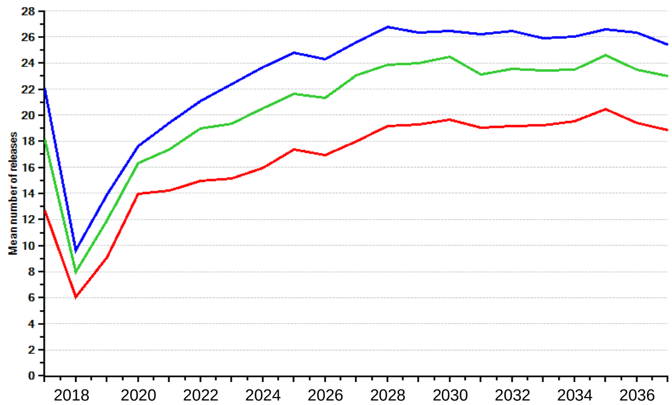

Fig. 41. Projected mean number of juveniles available for release over 20 years (from 2017 to 2038), under the default historical management of 55% single brood (blue line), 75% single broods (green line), and 100% single broods (red line).

Impact of genetic management

The SSP is projected to maintain high levels of gene diversity under the genetic management strategy modeled. This is accomplished by maximizing reproduction from genetically valuable (underrepresented) individuals. Selecting less genetically valuable juveniles for release can also contribute to the retention of genetic variation in the SSP, minimizing selection to captivity and inbreeding effects and promoting its role as a genetic insurance population. The PVA model structure likely overestimates the extent to which genetic management can be practically achieved. A scenario was run in which genetic management was removed. Breeding adults and pairs were chosen randomly (except for prevention of inbred pairs with $F \geq 0.125$). Breeding pairs remained together until one mate died, allowing the remaining crane to re-pair.

This scenario results in an almost 3-fold increase in the rate of loss of gene diversity due to genetic drift at a target population size of 165. The projected gene diversity at 100 years under random mating is 92.8%, representing a rate of loss that translates Ne = 79.8. Random mating should not be considered a worse-case or no-management scenario, as this scenario assumes that the only factors affecting reproductive success are age and reproductive history. In reality, not all adults have an equal probability of breeding successfully due to differences in location (i.e., housed at non-breeding facilities), behavior, health and other traits that may cause it to be a 'good breeder' vs a poor or difficult breeder. The preferential breeding of 'good breeding pairs' may perform worse than random mating. However, the results of this scenario suggest that the SSP has a good probability of retaining over 90% gene diversity for 100 years and will retain more genetic variation under genetic management.

Impacts of reduced population size

The SSP is able to serve its conservation roles of a source population for reintroduction and as an insurance population with a target population size of 165. Model scenarios were developed to explore the demographic and genetic impacts of reducing the SSP's target population size from 165 to 150, 135, 120 or 105 following termination of the release program. These scenarios assume no changes in demographic rates (survival and reproductive success) and include continued strong genetic management. Population decline was achieved through reduction in reproduction to 6 broods annually with a maximum of two broods per year per pair, removal of excess juveniles not needed to maintain the target population size, and through natural attrition of aging adults.

All scenarios are able to achieve and maintain the target population size with no risk of extinction. Gene diversity retention is slightly lower with smaller population size, but all scenarios maintain >94% mean gene diversity (Table 18). Model results are based on the quickest route to population reduction, which is to not retain juveniles until the population approaches its new lower target. This creates a gap in the age structure that spans several age classes, creating a top-heavy age pyramid and setting up a slowly oscillating pattern in both age structure (e.g., juvenile-to-adult ratio) and reproduction (e.g., number of breeding pairs, proportion of proven females). Maintaining the current target of 165 requires only small adjustments once releases stop, while large population reductions take significantly longer to stabilize (Fig. 42). The long reproductive lifespan of this species enables it to potentially handle such oscillations with little impact as long as the population is carefully managed demographically and genetically.

Model results do not address any potential negative consequences of reduced or delayed reproduction on future reproductive success. Delayed or infrequent reproduction has been observed to affect future success in several species (Penfold *et al*. 2014). It will be important to maintain reproductive potential in adult birds both physiologically and behaviorally during population reduction or whenever reproductive rates are lowered. Currently 47% of adult females are proven breeders, but proportionally fewer breeders will be needed once releases cease and during any reduction in population size (Table 18).

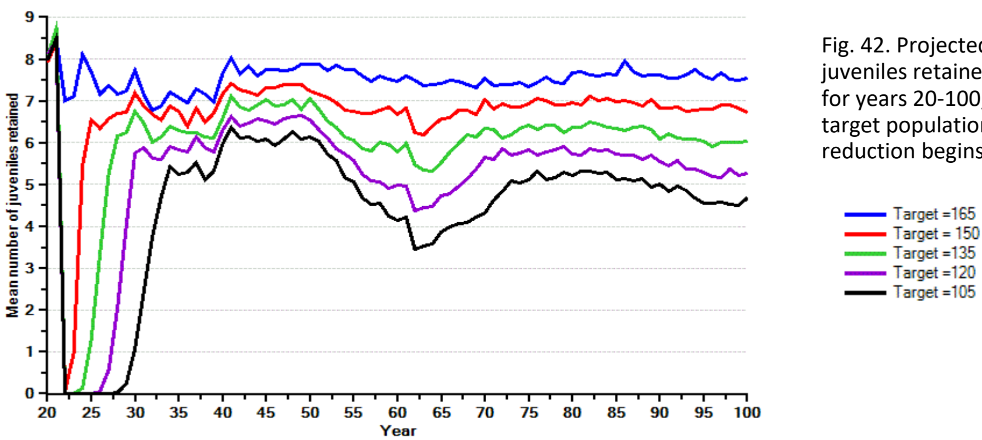

Fig. 42. Projected mean number of juveniles retained in the SSP population for years 20-100, across a range of target population sizes. Population reduction begins in Year 22 (2028).

Table 18. Model results for reduced target population size starting in Year 22 (after 20-year release program). SD given in parenthesis. FFs=adult females.

Target size (K)	Mean N_{100}	Mean Yrs to Target	Mean GD_{100}	Estimated Ne	Mean # juveniles	Mean # proven FFs	Prop. Proven FFs
165	163.8 (2.7)	0	0.954	206	7.6 (2.7)	23.9 (3.3)	0.367
150	148.5 (3.0)	3	0.952	184	6.7 (2.4)	21.7 (3.1)	0.367
135	134.3 (2.2)	5	0.950	165	6.0 (2.5)	20.3 (3.0)	0.377
120	119.7 (1.8)	8	0.948	144	5.3 (2.6)	19.0 (2.8)	0.396
105	104.9 (1.5)	11	0.944	123	4.7 (2.6)	17.3 (2.8)	0.413

SSP PVA Summary and Implications for Recovery Objectives

PVA model summary
A VORTEX population simulation model was developed for the captive managed population (SSP) of whooping cranes, using data from the 2017 studbook for demographic rates and other relevant inputs as well as input from SSP representatives and whooping crane *ex situ* experts. Model structure was revised from that used for wild and reintroduced crane populations to accommodate differences both in data and management. Intensive captive population management is complex and is only approximated by the model structure; however, PVA results can provide guidance on the impact of various management options and on the potential for this population to contribute to species recovery objectives.

Assumptions
This model assumes successful strong genetic management (including the use of AI to allow males to have two female 'mates', if needed), all adults are capable of reproduction, no genetically valuable breeding age adults are in non-breeding facilities, there are no differences in the survival of chicks within a brood or between broods, and that the priority for the allotment of juveniles is to maintain SSP target population size before providing juveniles for release.

PVA results and recovery objectives
The current international recovery plan (CWS & USFWS 2007) includes two recovery objectives for down-listing of whooping cranes, one for the wild population and one for the captive population. Both objectives are dependent upon the SSP and correspond to its two identified conservation roles.

Objective 1 is to "establish and maintain self-sustaining populations of whooping cranes in the wild that are genetically stable and resilient to stochastic environmental events." This PVA is relevant to the down-listing Criteria 1 and 1A related to the development and maintenance of a whooping crane wild meta-population of 2-3 sub-populations. Criterion 1 requires the maintenance of at least 160 cranes in the AWBP and two additional populations of at least 100 cranes each, with all three populations being self-sustaining at these levels for a decade before down-listing. Alterative Criterion A1 requires an AWBP of at 400 cranes and one additional population of at least 120 cranes, both of which are self-sustaining at this level for a decade. Based on PVAs conducted for the two reintroduced populations (EMP and LNMP), both populations will require additional supplementation to meet either of these criteria.

The captive SSP population may provide important headstarting or supplementation services vital to the establishment of viable reintroduced populations and/or reduce the time to down-listing. The SSP can contribute by producing cranes for release, by producing eggs for cross-fostering to wild parents, and/or by parent-fostering wild-laid eggs for later release (headstarting). These services could potentially be provided to the wild AWB population as well to reduce time to down-listing, if needed.

Objective 2 is to "maintain a genetically stable captive population to ensure against extinction of the species". Criterion 2 specifies the maintenance of 153 cranes (21 productive pairs) in the captive population to retain 90% of its gene diversity for 100 years. None of the AWBP scenarios project a risk of extinction of the AWBP over the next 100 years, which might suggest that the captive population may not be required to augment or re-establish the AWBP population. Given the uncertainty of future climate change impacts and anthropogenic threats, however, there may be a risk of AWB population decline or extinction in the presence of greater threats than modeled and supporting the need for a back-up captive insurance population to reinforce any of the wild or reintroduced populations.

Ability to serve as a long-term insurance population
The loss of a major holding and breeding facility (PXT) for whooping cranes provides a challenge for the SSP. Provided that all birds remain in the SSP and that breeding capacity is expanded in other facilities as

projected, the SSP should be able to maintain its target size with no long-term demographic or genetic impacts. The current target size of 160-170 birds is sufficient for a demographically self-sustaining population and to retain high levels of existing gene diversity, even if excess juveniles are produced and released. Once this population is no longer needed as a regular source population, it may be possible to reduce population size and still function this conservation role of an insurance population, although this reduction is likely to occur slowly and may come with some genetic cost. Maintaining some level of juvenile recruitment during any intentional population reduction is advised. Caution should be used when considering this option, as the PVA provided here does not incorporate potential behavioral, physiological or other effects that may occur when reproductive rates are reduced or age structure becomes unstable.

Ability to serve as a source for release

The SSP has demonstrated its ability to provide captive-hatched and reared juveniles for release to establish and reinforce reintroduced crane populations. The number of juveniles available for release is expected to be lower than historical levels for the next 5-6 years as breeding capacity expands following the closing of the Patuxent breeding facility. The exact number of releases available each year is both stochastic and dependent upon the relative priority of maintaining SSP target population size vs maximizing the number of releases. Maintaining SSP population size will produce, on average, ~ 94 juveniles for release over the next 5 years (2019-2023) and about ~219 juveniles over the next 10 years (2019-2028), with slightly lower averages if all juveniles are parent reared (~83 and 193, respectively). If SSP population size is sacrificed, the SSP may be able to produce, on average, 111 juveniles for release over the next 5 years and 227 over the next 10 years. The next few years will be the greatest challenge until the population can restore its reproductive potential. If this is accomplished as anticipated, then the SSP population should be able to effectively serve its conservation role of a source population for reinforcement of reintroduced populations. Without expansion of reproductive capacity to replace that lost with Patuxent's closing, it may be difficult for this captive population to adequately meet this role in a timely manner.

Acknowledgements

This PVA model was developed in consultation with the Whooping Crane International Recovery Team, the AZA Whooping Crane SSP and numerous crane biologists and managers who participated through workshops and/or electronic discussion in 2015-2018. Additional PVA work was conducted to assess the full whooping crane meta-population. These PVA models and results will serve as a basis to evaluate potential management actions to increase whooping crane viability and to evaluate recovery goals for this species, and will inform species conservation planning discussions scheduled in October 2019.

Section 6. Whooping Crane Population Viability Analysis (PVA) Report: Meta-Population Assessment in Relation to Species Recovery Objectives

Population viability analyses (PVAs) were conducted for four distinct whooping crane populations using a stochastic, individual-based population model developed in the *VORTEX* 10.2.15 (Lacy and Pollak 2017) software program. Individual PVAs were conducted for the following populations:

1) Aransas-Wood Buffalo wild migratory population (AWBP)
2) Eastern migratory population (EMP)
3) Louisiana non-migratory population (LNMP)
4) Captive population (SSP)

Each of these populations has its own demographic rates, initial population structure, and management options. Models were initiated at the point of early spring 2017 prior to breeding season, and run for 100 years. Sections 2-5 and Appendix II of this report outline model inputs and results for best estimated future conditions, sensitivity testing, and alternative management scenarios for each of these whooping crane populations. These results can be combined to evaluate the potential for these four populations collectively to meet down-listing criteria and contribute to recovery of this species.

Recovery Objectives and Criteria for Down-listing

The 2007 International Recovery Plan (CWS & USFWS 2007) outlines two primary objectives and measurable criteria for species down-listing. Text from the 2007 plan specifying these is provided below:

Objective 1: Establish and maintain self-sustaining populations of whooping cranes in the wild that are genetically stable and resilient to stochastic environmental events.

Criterion 1: Maintain a minimum of 40 productive pairs in the AWBP for at least 10 years, while managing for continued increase of the population. Establish a minimum of 25 productive pairs in self-sustaining populations at each of 2 other discrete locations. A productive pair is defined as a pair that nests regularly and has fledged offspring. The two additional populations may be migratory or non-migratory. Population targets are 160 in the AWBP, and 100 each in the Florida non-migratory population and the eastern migratory population. All 3 populations must be self-sustaining for a decade at the designated levels before down-listing could occur.

Alternative Criterion 1A: If only one additional wild self-sustaining population is reestablished, then the AWBP must reach 400 individuals (i.e. 100 productive pairs), and the new population must remain above 120 individuals (i.e. 30 productive pairs). Both populations must be self-sustaining for a decade at the designated levels before down-listing could occur. This alternative is based on the principle that with the reestablishment of only one additional population separate from the AWBP, then crane numbers must be higher in both populations than if there are three distinct populations.

Alternative Criterion 1B: If establishment of second and third wild self-sustaining populations is not successful, then the AWBP must be self-sustaining and remain above 1,000 individuals (i.e. 250 productive pairs) for down-listing to occur. 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. This higher number ensures a better chance for survival of the AWBP in the event of a catastrophic event within its extremely limited range. The target of 1,000 is reasonable for down-listing given the historical growth of the AWBP and theoretical considerations of minimum population viability. To ensure sufficient genetic variability, the AWBP must increase to the level where the creation of new alleles through genetic mutation will offset the loss of genetic diversity. After reaching the goal of 250 pairs, the population should gain genetic variation faster than the population loses genetic material.

Objective 2: Maintain a genetically stable captive population to ensure against extinction of the species.

Criterion 2: Maintain 153 whooping cranes in captivity (21 productive pairs). Genetic analysis suggests that 90% of the genetic material of the species can be sustained for 100 years at this population size (Jones and Lacy 2003). To achieve this, 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 SAZ. A breeder pair (as differentiated from a productive pair) is defined as a pair that breeds or is intended to breed in the future. Production from PWRC, ICF, CZ, SSC and SAZ will be the principal source of birds for release to the wild for reintroduced populations. However, sources of release birds should be based on the optimal genetic mix to ensure long-term population viability.

Results of the individual crane population PVAs were examined to determine the relative probability, timeline and conditions under which both down-listing objectives could be met. Tables in this section provide two measures. The mean number of years to reach the numeric down-listing target (both size and sustainability) is given; however, since this is an average, there is a good chance that this population size may not be reached until much later. Therefore, a second metric is provided, which is the year at which there is $\geq$90% chance that the population will not fall below the down-listing target size in the future. This lends some insight on the confidence of the down-listing timeline.

Down-listing Under Criteria 1 and 2

The first option for achieving down-listing (i.e., meeting Objective 1, Criterion 1; and Objective 2, Criterion 2) would require the establishment of three self-sustaining wild crane populations, comprised of the original wild population in Aransas-Wood Buffalo National Park and two reintroduced populations, as well as a genetically and demographically viable captive population as a source for cranes for release and insurance against species extinction. Specific numerical criteria are:

Criterion 1:
AWBP: Maintain a population of $\geq$160 cranes (40 productive pairs).
EMP & LNMP: Establish a minimum of 25 productive pairs at each location, with a population target of $\geq$100 cranes for each population.
All 3 populations must be self-sustaining for a decade at the designated levels before down-listing could occur.

Criterion 2: Maintain 153 whooping cranes in captivity (21 productive pairs). Genetic analysis suggests that 90% of the genetic material of the species can be sustained for 100 years at this population size.

Meeting Criterion 1 for AWBP

This population has demonstrated strong positive growth in the past but may face additional challenges in the future that could potentially slow growth. Potential future threats include increased atmospheric CO_2, which may lead to reduced juvenile recruitment, and increased adult mortality, for example from increased human-related threats along migration routes. All projections that encompassed estimates of future increased threats indicate a demographically sustainable and genetically robust population with no extinction risk over 100 years. Three scenarios bracket the primary uncertainty in future conditions and are presented below along with the projected ability of the AWBP to meet down-listing criteria:

Historical conditions: Demographic rates similar to those observed in the past; no climate change impacts or increased human-related mortality

Range-wide threats: Best estimate at this time of future threats across the population's range, including climate change impacts on the breeding and wintering grounds (i.e., increased atmospheric CO_2 to 500ppm; 1m sea level rise; increase risk of hurricane-related contamination events in non-protected areas of wintering grounds), and increased mortality due to human-related threats (i.e., 15% increase in migration mortality; 10% increase in mortality in wintering areas outside of Aransas National Wildlife Refuge).

Higher threat impacts: Similar to range-wide threats but with 2m sea level rise and 22.5% increase in migration mortality. An additional high threat scenario considered a 30% increase in migration mortality and 50% increase in mortality in non-protected wintering grounds.

In all scenarios the AWBP population reaches Criterion 1 immediately in year 1, with a mean population size of 470, and no risk of falling below 160 cranes in the future (over the projected 100 years). In Year 1 the mean number of adults is 328 and mean number of pairs is 156.

Meeting Criterion 1 for EMP

The Eastern migratory population is a reintroduced population established from captive-reared released cranes beginning in 2001. Despite continued annual releases for almost two decades, the population has struggled in recent years with no growth since 2009. Survival of released cranes is good and approximates that of cranes in the wild AWB population. Reproduction has been poor, with low survival from egg to fledging, and is insufficient at this point for the population to be self-sustaining. Nest abandonment is an issue, possibly related to black flies present especially in the Necedah National Wildlife Refuge area.

Ultimately, the future of this reintroduced population is dependent upon improved reproductive rates and continued good survival. The paucity of surviving wild-hatched offspring means that there have been few breeding pairs that contain a wild-hatched mate and no breeding pairs of two wild-hatched cranes. The substantial uncertainty regarding the reproductive success of wild-hatched cranes in this population makes it difficult to estimate the likelihood of the EMP meeting down-listing criteria. Additional uncertainty is whether reproductive rates of captive-reared released cranes will remain poor or will improve over time.

Additional releases may help bolster population size to reduce the impact of stochastic processes, but this can be a double-edged sword as it also may extend the time to population growth if captive-reared cranes continue to reproduce poorly. Management that promotes better reproduction in all cranes, both captive-reared and wild-hatched birds, would encourage population viability, as would efforts to minimize sub-adult and adult mortality in this population.

Scenarios explored in this PVA for the EMP incorporate a range of demographic rates and management actions, including scenarios with and without additional releases. Table 19 outlines the attributes of those scenarios that are projected to result in down-listing within 100 years. All scenarios assume:

1) Pairs of wild-hatched cranes will demonstrate reproductive rates similar to the wild AWBP cranes;
2) Pairs of captive-reared released cranes will continue to show poor reproductive success (unless otherwise noted);
3) Pairs with one wild-hatched mate and one captive-reared released mate will show significantly improved reproductive success over historical rates for captive-reared pairs; and
4) Sub-adult and adult crane mortality will be similar to the wild AWBP (no more than 10% increase of the AWBP mortality rate).

Better reproductive success is a key factor for progress toward down-listing. Significantly improved reproductive success in released cranes (e.g., higher success with age or experience, reduced impact of black flies or other environmental conditions) would shorten time to down-listing, increase its likelihood, and promote population growth. Management actions that improve reproductive success in released cranes can have significant benefits and, if effective, can lead to down-listing even without future releases. If reproduction in pairs of released cranes remains low, then significantly improved reproduction by mixed-origin pairs (e.g., ~24% survival from egg to six months) is key to population viability and is a common feature to most scenarios in Table 19.

Most scenarios in Table 19 suggest that, on average, the population will meet Criterion 1 approximately 10 years after releases end, given that other conditions are met immediately in year 1. However, there is significant variability in the confidence of this estimate, Table 19 provides the year at which there is ≥90% probability that down-listing population size will be met and maintained into the future. In some cases this target may be met almost immediately, although the 10-year sustainability criterion cannot be met until at least 10 years post-releases. This situation can be achieved either with significant improvement in reproductive of pairs of released cranes, or with the release of 50-100 additional cranes over the next 5-10 years and improved reproduction of released cranes when paired with a wild-hatched mate. The release of 10 cranes for 10 years is most robust across adult mortality rates. While both strategies for 50 total releases perform well, releasing 10 cranes for 5 years has a higher probability of meeting the criteria (~95%) than releasing 5 cranes for 10 years (~90%).

Headstarting scenarios did not perform as well as releases of captive-origin juveniles in this PVA. This conclusion is dependent upon several assumptions that may or may not be valid. Headstarted and released juveniles were assumed to have the same demographic rates once released into the EMP. Data available for this model suggests that when the first clutch is removed from an EMP breeding pair, the pair may not re-nest one-third of the time, and those that do re-nest demonstrate a reduced fledging rate; thus, these pairs may have a higher fledge rate if left undisturbed. If 'forced re-nesting' pairs are more likely to re-nest and fledge a wild-hatched chick than the data available at the time of model development, then headstarting scenarios may be more beneficial than indicated by model results.

The scenarios explored in this PVA suggest that continued releases may be insufficient for establishing a viable population unless the reproductive success of mixed-origin pairs is at least 11% (twice the value modeled for released pairs). If good mixed-pair reproductive success can be achieved, and if mortality of other age classes does not increase, then the EMP may be able to achieve down-listing via Criterion 1.

In summary, PVA results suggest that the following conditions will lead to achieving down-listing criteria ~10 years after releases cease with 90% confidence:

1. Release of 50-100 additional cranes over the next 5-10 years;
2. Mixed-origin pairs have at significantly improved reproductive success than released cranes to date (i.e., ~24% survival to six months, which is midway between the rates for the AWBP and for EMP released birds);
3. Wild-hatched cranes have good reproductive success, similar to AWBP rates (~42% survival); and
4. Adult and sub-adult survival remains good (not > 1.05% of AWBP rates).

The actual time approximation to the EMP meeting Criterion 1 will be dependent upon the reproductive rates of mixed-origin pairs and the release schedule.

Table 19. Demographic characteristics and required management actions to meet down-listing Criteria 1 and 1A for the EMP. Numbers in red indicate scenarios that lead to >90% chance of meeting down-listing target ~10% after releases cease. *Success rates given for egg-to-six month survival of one chick; **Includes 10 years of sustainability (positive growth).

Adult mortality	Repro of wild pairs	Repro of released cranes	Future releases of juveniles	Management actions	**Mean yrs to:		Yrs to ≤10% risk	
					N=100	N=120	N=100	N=120
SCENARIOS WITH: Adult mortality ≤ 10% increase over AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; no future releases. Minimum year for 10-year sustainability = 11.								
1x/1.05x/ 1.1x AWBP rates	AWBP rates	24% success w/ wild mate*	None	-Threat reduction to prevent higher mortality -Management actions that promote reproduction of wild-hatched cranes	14	14	34/43/97	41/49/--
		Success w/ all mates* 16.5%		-Threat reduction to prevent higher mortality -Management actions that promote reproduction of wild and released cranes	14	14	68/69/--	80/89/--
		22%			14	14	38/42/--	46/54/--
		27.5%			13	13	1/1/49	34/41/86
SCENARIOS WITH: Adult mortality ≤ 10% increase over AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; additional 25-50 releases over 5-10 years. Minimum year for 10-year sustainability = 16 or 21.								
1x/1.05x/ 1.1x AWBP rates	AWBP rates	24% success w/ wild mate*	25 total *5/yr x 5 yrs*	-Threat reduction to prevent higher mortality -Management actions that promote reproduction of wild-hatched cranes -Release of 25-50 cranes over 5-10 years	16	16	1/30/60	34/37/77
			50 total *10/yr x5yrs*		16	16	1/1/35	1/1/56
			5/yr x10yrs		21	21	1/1/44	5/6/64
SCENARIOS WITH: Adult mortality ≤ 10% increase over AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; additional 100 releases over 10 years. Minimum year for 10-year sustainability = 21.								
1x/1.05x/ 1.1x AWBP rates	AWBP rates	24% success w/ wild mate*	100 total *10/yr x 10 yrs*	-Threat reduction to prevent higher mortality -Management actions that promote reproduction of wild-hatched cranes -Release of 100 cranes over 10 years	21	21	1/1/3	1/1/3
		11% success w/ wild mate*			22	22	49/53/--	64/67/--
SCENARIOS WITH: Adult mortality ≤ 5% increase over AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; release 35-70 headstarted juveniles over 5 yrs (~ 5-10 pairs/yr). Minimum year for 10-year sustainability = 16.								
1x/1.05x/ 1.1x AWBP rates	AWBP rates	24% success w/ wild mate*	35 HS total *7/yr x 5yrs*	-Threat reduction to prevent higher mortality -Management actions that promote reproduction of wild-hatched cranes -Release of 35-70 cranes over 5 years	16	16	45/47	58/58/--
			70 HS total *14/yr x 5yrs*		16	16	41/50	64/68/--

Meeting Criterion 1 for LNMP

The Louisiana non-migratory population is a newly established reintroduced population based on annual releases of captive-reared juvenile cranes, beginning in 2011. The steady growth in this population is due to releases and not reproduction in the wild. The first released cranes recently reached breeding age, with the first chicks hatched in 2016. Nesting attempts by young pairs have been strong, but were accompanied by a high rate of nest failure due to infertility, embryo death and other causes in the first few years. Reproductive success improved in 2018.

Like the EMP, the future of this reintroduced population is dependent upon improved reproductive rates and good adult survival. Given the young age and short history of this population, there are not sufficient data to estimate either reproduction or survival with any certainty. As a non-migratory population, the LNMP may face different challenges than the AWBP and EMP migratory populations, but it is difficult to know exactly how this might affect demographic rates. Management actions that promotes good reproduction and survival of all age classes will help this population to become established.

If the LNMP demonstrates good survival like the AWBP but poor reproductive success similar to the EMP, then additional releases will be necessary to grow and secure this population. Scenarios explored in this PVA for the LNMP incorporate a range of demographic rates and management actions, including scenarios with juvenile releases, cross-fostering captive-laid eggs, and translocation of adults from the Florida non-migratory population. Table 20 outlines the attributes of those scenarios that are projected to result in the best and quickest chance of down-listing. All scenarios assume:

1) Pairs of wild-hatched cranes will demonstrate reproductive rates similar to the wild AWBP;
2) Pairs of captive-reared released cranes will show poor reproductive success similar to the EMP;
3) Pairs with one wild-hatched mate and one captive-reared release mate will show significantly improved reproductive success over EMP rates;
4) Mortality for released cranes through age 4 will be similar to past LNMP rates;
5) Adult mortality will be similar to the wild AWBP; and
6) Additional releases for at least 5 years.

The scenarios described in Table 20 suggest that, on average, the population will meet Criterion 1 approximately 10-13 years after releases end, given that other conditions are met immediately in year 1. There is less variability in the confidence of these estimates than in the scenarios for the EMP in Table 19 because *all LNMP scenarios assume good adult survival, good mixed-origin pair reproductive success, and future additional releases.* Table 20 provides the year at which there is $\geq$90% probability that down-listing population size will be met and maintained into the future. In some cases this target may be met in a few years, although the 10-year sustainability criterion cannot be met until at least 10 years post-releases. PVA results project that this can be achieved with the release of at least 100 additional cranes over the next 5-10 years. The best results are for scenarios with 150-200 releases over 10-15 years.

The translocation of cranes from the failing FNMP, especially in combination with continued juvenile releases, may also be beneficial; however, caution should be used to consider potential impacts not included in the PVA model, such as disease risk and behavioral consequences.

Cross-fostering scenarios (i.e., egg swapping) did not perform as well as expected in the model. This strategy required a complex model structure to specify cross-fostering for a specific number of pairs, and it is possible that the model was not constructed or parameterized correctly. Caution should be used in interpreting these results. If successful in practice, cross-fostering may provide another option for population reinforcement. This management strategy is just being tested for the LNMP, and it will be important to collect pertinent information and examine the results for potential impacts.

Table 20. Demographic characteristics and required management actions to meet down-listing Criteria 1 and 1A for the LNMP. Numbers in red indicate scenarios that lead to >90% chance of meeting down-listing target ~10% after releases cease. *Success rates given for egg-to-six month survival of one chick; **Includes 10 years of sustainability (positive growth).

Adult mortality	**Repro of wild pairs**	**Repro of released birds**	**Future releases of juveniles**	**Management actions**	****Mean yrs to:**		**Yrs to ≤10% risk**	
					N=100	**N=120**	**N=100**	**N=120**
SCENARIOS WITH: Adult mortality similar to AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; additional 50-120 releases over 5 years. Minimum year for 10-year sustainability = 16.								
AWBP rates	AWBP rates	24% success w/ wild mate*	50 total *10/yr x 5yrs*	-Threat reduction to prevent higher mortality -Management actions that promote reproduction of wild-hatched cranes -Release of 50-120 cranes over 5 years	17	17	48	59
			100 total *20/yr x 5yrs*		19	19	4	41
			120 total *30/yr x2yr; 20/yr x3yr*		19	19	3	24
SCENARIOS WITH: Adult mortality similar to AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; additional 100-200 releases over 10 years. Minimum year for 10-year sustainability = 21.								
AWBP rates	AWBP rates	24% success w/ wild mate*	100 total *10/yr x10yr*	-Threat reduction to prevent higher mortality -Management actions that promote reproduction of wild-hatched cranes -Release of 100-200 cranes over 10 years	22	22	10	43
			200 total *20/yr x10yr*		23	23	4	6
			150 total *10/yr x5yr; 20/yr x5yr*		23	23	8	9
			170 total *30/yr x2yr; 20/yr x3yr; 10/yr x5yr*		22	22	3	5
SCENARIOS WITH: Adult mortality similar to AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; additional 150 releases over 15 years. Minimum year for 10-year sustainability = 26.								
AWBP rates	AWBP rates	24% success w/ wild mate*	150 total *20/yr x5yr; 10/yr x5yr*	-Threat reduction as above -Management actions that promote reproduction of wild-hatched cranes -Release of 150 cranes over 15 years	27	27	4	6
SCENARIOS WITH: Adult mortality similar to AWBP; improved reproduction of released cranes; wild crane reproduction similar to AWBP; translocate all cranes from Florida FNMP; release 50-100 juveniles and crossfoster 15 nests over 5 yrs. Minimum year for 10-year sustainability = 16.								
AWBP rates	AWBP rates	24% success w/ wild mate*	50 total *10/yr x 5yrs*	-Threat reduction as above -Management actions that promote reproduction of wild-hatched cranes -Release of 50-100 cranes over 5 years -Crossfoster eggs to 3 pairs/yr for 5 yrs Translocation cranes from FNMP	16	16	22	43
			100 total *20/yr x 5yrs*		16	16	3	20

In summary, PVA results suggest that the following conditions will lead to achieving down-listing criteria ~10-13 years after releases cease with 90% confidence:

1. Release of 100-200 additional cranes over the next 5-15 years;
2. Mixed-origin pairs have at significantly improved reproductive success than released cranes to date in the EMP or LNMP (i.e., ~24% survival of egg to six months);
3. Wild-hatched cranes have good reproductive success, similar to AWBP rates (~42% survival); and
4. Adult and sub-adult survival similar to that for the AWBP (94.4% annual survival).

The actual time approximation to the LNMP meeting Criterion 1 will be dependent upon the reproductive rates of mixed-origin pairs and the release schedule.

Meeting Criterion 2 for SSP

Model projections for the SSP population indicate that, under projected future conditions and management, the SSP can maintain a genetically diverse and demographically self-sustaining captive population that can serve as a long-term insurance population against species extinction, thus meeting Criteria 2 for down-listing.

The SSP also is projected to be able to meet Criterion 2 if offspring are produced in excess of the demographic and genetic needs of the SSP and are provided for release to reinforce the reintroduced populations. Two recent challenges that face the SSP in providing juveniles for release are:

1. Priority needs for cranes for release in the past have translated into the SSP retaining fewer juveniles than needed to maintain a balance age structure (Boardman *et al*. 2017); and

2. Loss of the Patuxent breeding facility may result in reduced capacity for the SSP to manage breeding pairs and to provide parent-reared offspring.

Rearing and other management techniques that maximize the reproductive success of released cranes is a priority. If this means that parent rearing is a priority for the SSP, this may limit the number of juveniles available for release to a greater extent than in the past. Scenarios designed to simulate increased parent-reared chicks via higher proportion of single clutches estimate chick production at ~16 juveniles in 2020 and slowly increasing to and stabilizing around ~24 juveniles annually after 10 years. Actual juvenile production is not only stochastic but will be influenced by how quickly the SSP can rebuild its reproductive capacity both in terms of the number of breeding facilities and the number of breeding pairs. This also limits the potential for headstarting previously provided by Patuxent. Cross-fostering capabilities may or may not be less affected, depending upon the timing of captive and wild clutches. Alternate rearing methods (e.g., costume rearing) may allow for the production of additional juveniles beyond parent rearing capabilities.

Modeling suggests that the SSP can continue to retain fewer chicks than ideal to maintain the population at 165. Depending upon the shortfall this may lead to population decline for the SSP, but if a short-term practice, the population should be resilient both demographically and genetically to recover once full retention is implemented. Retaining 2-4 chicks each year may be a reasonable compromise and sufficient to maintain a population that meets both of its conservation roles as an insurance and source population. This means than the SSP might be able to provide ~10-15 parent-reared juveniles for release annually for the next few years, increasing to ~20 per year in about 7-8 years. These estimates are approximate and may be conservative, and additional offspring may be produced if other rearing methods are used.

Meeting Criteria 1 and 2 as a meta-population

This strategy, if successful, would provide multiple viable crane populations across the widest landscape and provide redundancy as protection against local catastrophic events. The AWBP already meets Criteria 1, and the SSP meets Criteria 2 as an insurance population. The two reintroduced populations are not currently self-sustaining, and will need better reproductive success and continued good survival to meet down-listing Criteria 1. *Future releases will improve the probability of down-listing but are not sufficient without good survival and reproductive success.* Management actions that promote these demographic rates are important components for population viability and eventual down-listing.

PVA results suggest that the optimal release strategy of those tested would be 5-10 releases per year for 5-10 years (50-100 total) to the EMP, and 10-20 releases per year for 5-15 years (100-200 total) to the LNMP. Ideally the SSP would retain 5-8 juveniles per year to maintain its population, but could withstand the retention of smaller holdbacks on a short-term basis. These total 20-35 juveniles needed per year, which is above the projected SSP production capacity given model inputs. Alternative scenarios with fewer releases can also lead to similar results for meeting Criteria 1 and may be feasible, requiring 15-20 juveniles per year. A sample allocation is given in Table 21, assuming that priority for limited releases is given to the LNMP and that holdbacks for the SSP are limited (when necessary) for the next few years. Modeling based on available data suggests that most if not all of the released cranes may be parent reared. Headstarting eggs from the EMP may provide additional juveniles for release if some captive-reared chicks (either of SSP and/or EMP origin) are costume reared rather than parent reared.

Table 21. Example of possible minimum allotments of juveniles to the LNMP, EMP and SSP over the next 10 years.

	2019	**2020**	**2021**	**2022**	**2023**	**2024**	**2025**	**2026**	**2027**	**2028**	**Total**
LNMP	10	10	10	10	10	10	10	10	10	10	100
EMP	0	5	5	5	5	5	10	10	10	10	65
SSP	2	2	2	4	4	5	2	2	3	4	30
Total	12	17	17	19	19	20	22	22	23	24	195

PVA results suggest that the following actions would lead to down-listing based on Criteria 1 in about 20-22 years:

1. Management actions to minimize sub-adult and adult mortality in all wild populations, and in particular in the reintroduced populations, to historical levels for the AWBP;
2. Management actions to promote improved reproductive success in all cranes in the reintroduced populations, including rearing and releases strategies for captive-reared cranes, exploration of cross-fostering as a method of population reinforcement with wild-hatched cranes, and management of environmental factors that promote better reproductive success for all cranes regardless of origin and rearing history;
3. Consideration of the benefits and risks of translocating cranes from Florida (FNMP) to the LNMP, with translocation conducted if deemed appropriate; and
4. Additional releases to the two reintroduced populations for the next 10-15 years, with a minimum of 10 releases to the LNMP and 5 releases to the EMP annually.

These actions are provided as a guide. Actual results are stochastic and will be dependent upon the extent to which actions 1-4 above can be achieved.

Down-listing Under Alternative Criteria 1A and 2

If only one reintroduced population can be established, then down-listing is possible by meeting Objective 1 under Alternative Criterion 1A (and Objective 2 under Criterion 2, as described above). This would require the establishment of two self-sustaining wild crane populations, comprised of the original wild population in Aransas-Wood Buffalo National Park and one reintroduced population, as well as a genetically and demographically viable captive population as a source for cranes for release and insurance against species extinction. Specific numerical criteria are:

Criterion 1A:
AWBP: Maintain a population of 400 cranes (100 productive pairs).
EMP or LNMP: Maintain a population above 120 cranes (30 productive pairs)
Both populations must be self-sustaining for a decade at the designated levels before down-listing could occur.

Criterion 2: Maintain 153 whooping cranes in captivity (21 productive pairs). Genetic analysis suggests that 90% of the genetic material of the species can be sustained for 100 years at this population size.

Meeting Criterion Alternative 1A for AWBP

In all scenarios outlined in Criteria 1 above, the AWBP population reaches Alternative Criterion 1A immediately in year 1, with a mean population size of 470 and no risk of falling below 400 cranes in the future (over the projected 100 years). In Year 1 the mean number of adults is 328 and mean number of pairs is 156.

Meeting Criterion Alternative 1A for EMP

Conditions that promote the ability of the EMP to meet Criterion Alternative 1A (a sustainable population of at least 120 cranes) is similar in most ways to the conditions needed to meet Criterion 1 (a sustainable population of at least 100 cranes) – see section on Criterion 1 above. Ultimately the growth and sustainability of this population is dependent upon improved reproductive rates and continued good survival. Releases over the next decade also promote down-listing especially for this higher population size.

Scenarios listed in Table 19 give similar estimates for mean year at which the population target is reached and the population is sustainable, whether the target is 100 or 120 cranes. Generally speaking, this is approximately 10 years after releases cease provided that adult survival remains good and mixed-origin pair have substantially better reproductive success that pairs of released cranes. However, variation in population growth and therefore size leads to greater uncertainty that the larger target of $N \geq 120$ will be met and sustained; thus, while the mean time to sustainable target size is the same, the years to $\leq$ 10% risk are greater under Alternative Criterion 1A.

A few scenarios stand out as substantially different between Criteria 1 and 1A. Increasing the reproductive success of pairs of released cranes in the absence of additional releases is less likely to maintain 120 vs 100 cranes under the conditions modeled. Releases of only 25 additional cranes perform worse under Alternative Criterion 1A, and the release of 50 additional cranes is less robust across increased adult mortality. As with Criterion 1, the release of 10 cranes per year for 5 years performs better than 5 cranes per year for 10 years, and the release of 10 cranes per year for 10 years (100 releases in total) is most robust across adult mortality rates tested.

In summary, PVA results suggest that the following conditions will lead to achieving down-listing Criteria 1A in ~10 years after releases cease with 90% confidence:

1. Release of 10 additional cranes per year over the next 5-10 years;
2. Mixed-origin pairs have at significantly improved reproductive success than released cranes to date (i.e., ~24%, which is midway between AWBP and EMP released birds);
3. Wild-hatched cranes have good reproductive success, similar to AWBP rates (~42% survival); and
4. Adult and sub-adult survival remains good (not >1.05% of AWBP rates).

The actual time approximation to the EMP meeting Alternative Criterion 1A will be dependent upon the reproductive rates of mixed-origin pairs and the release schedule.

Meeting Criterion Alternative 1A for LNMP

Conditions that promote the ability of the LNMP to meet Criterion Alternative 1A (a sustainable population of at least 120 cranes) is similar in most ways to the conditions needed to meet Criterion 1 (a sustainable population of at least 100 cranes) – see section on Criterion 1 above. Ultimately the growth and sustainability of this population is dependent upon good reproductive rates and adult survival. Additional releases over the next decade or longer likely will be required to achieve down-listing especially for this higher population size.

Scenarios listed in Table 20 give similar estimates for mean year at which the population target is reached and the population is sustainable, whether the target is 100 or 120 cranes. Generally speaking, this is approximately 10 years after releases cease provided that adult survival is good and that reproductive success improves. In most scenarios the year at which there is $\leq$10% risk of down-listing criteria not being permanently met is also similar for Criteria 1 and 1A. There are some scenarios, however, in there is greater uncertainty that the larger target of N$\geq$120 will be met and sustained quickly, resulting in substantially longer time to $\leq$ 10% risk for Alternative Criterion 1A.

The release of ~100 cranes over 5-10 years is less effective in leading to down-listing under Alternative Criterion 1A than Criterion 1. Increasing the total releases to 150 over 10 years is effective under Alternative Criterion 1A, provided that other conditions are met. A limited number of scenarios were developed to explore various schedules for 150 releases but suggest that a minimum of 10 releases per year in the first several years is valuable. A smaller number of releases can also lead to down-listing in about the same time period of ~20 years if combined with translocation of cranes from Florida (provided there are no negative impacts of translocation not considered in the model).

In summary, PVA results suggest that the following conditions will lead to achieving down-listing under Criteria 1A in ~10-15 years after releases cease with 90% confidence:

1. Release of 150-200 additional cranes over the next 10-15 years; this total may be reduced to ~100 if cranes are translocated from Florida with no negative impacts;
2. Mixed-origin pairs have at significantly improved reproductive success (~24% survival) compared to pairs of released cranes in the EMP;
3. Wild-hatched cranes have good reproductive success, similar to AWBP rates (~42% survival); and
4. Adult survival is good, similar to AWBP rates (94.4% annually).

The actual time approximation to the LNMP meeting Alternative Criterion 1A will be dependent upon the reproductive rates of mixed-origin pairs, adult mortality and the release schedule.

Meeting Criterion 2 for SSP

Model projections for the SSP population indicate that, under projected future conditions and management, the SSP can maintain a genetically diverse and demographically self-sustaining captive population that can serve as a long-term insurance population against species extinction, thus meeting Criteria 2 for down-listing. The SSP also is projected to be able to meet Criterion 2 while providing excess juveniles for release to reinforce a reintroduced population.

As described above under Criterion 1, the SSP might be able to provide ~10-15 juveniles for release annually for the next few years, increasing to ~20 per year in about 7-8 years. These estimates are approximate and may be conservative. It may be possible to produce additional offspring depending upon rearing method; however, it is important to use rearing, release and other management strategies that promote successful survival and reproduction in the wild.

Meeting Criteria Alternative 1A and 2 as a meta-population

This strategy, if success, would provide a secondary viable crane population that extends the geographic distribution of the species and provides redundancy as protection against local catastrophic events. The AWBP already meets Criteria 1, and the SSP meets Criteria 2 as an insurance population. Neither of the two reintroduced populations are currently self-sustaining, and both of them will need better reproductive success and good adult survival to meet down-listing Alternative Criterion 1A. *Future releases will improve the probability of down-listing but are not sufficient without good survival and reproductive success.* Management actions that promote these demographic rates are important components for population viability and eventual down-listing.

PVA results suggest that the optimal release strategy of those tested would be 10 releases per year for 5-10 years (50-100 total) to the EMP, and 10-20 releases per year for 10-15 years (150-200 total) to the LNMP. Ideally the SSP would retain 5-8 juveniles per year to maintain its population, but could withstand the retention of smaller holdbacks on a short-term basis. These total 25-35 juveniles needed per year if all populations were to receive these allotments, which is above the projected SSP production capacity at least for the next 5-8 years given model inputs. Headstarting eggs from the EMP may provide additional juveniles for release if some captive-reared chicks (either of SSP and/or EMP origin) are costume reared rather than parent reared.

One strategy would be to 'put all of the eggs in one basket', so to speak, and to devote all releases to one population to bolster its likelihood of meeting Alternative Criterion 1A. It is difficult to judge which of the two reintroduced populations stands the better chance of down-listing. The LNMP population is about one-half the size of the EMP and will need more supplementation than the EMP to promote conditions for down-listing. The EMP is larger and more established; however, the continued poor reproductive success of this population presents a potential obstacle for down-listing. Improved reproductive success at least for mixed-origin pairs and wild-hatched pairs is essential for either reintroduced population to be viable. It is unknown whether this is more likely in one reintroduced population or the other. Likewise, good adult survival is essential. The EMP historically has demonstrated good survival but may be vulnerable to increased threats during migration. The LNMP is newly established, and so estimation of future adult mortality is difficult, and this population could potentially be more vulnerable to seasonal storms or other threats. If one population were to receive all available releases for 10 years, either would be projected to meet Criterion 1A in ~10-13 years after releases cease, provided other conditions are met for good survival and reproduction.

An alternative strategy would be to implement additional management actions to improve EMP and LNMP viability, to split allocation of available juveniles similar to that proposed for Criterion 1, and to re-evaluate in a few years based on trends in demographic rates for each reintroduced population.

Examples of such potential actions include the translocation of cranes from Florida to the LNMP (provided there are no negative impacts not included in the model); experimental cross-fostering of soon-to-hatch eggs to the LNMP; increased effort to parent-rear chicks to be released; use of other rearing methods to increase annual juvenile production; exploration of release sites for the EMP that may experience better reproductive success; manipulation of timing of incubation and brooding in the EMP to promote better success; and management of environmental conditions for the EMP to improve overall reproductive success. While these scenarios were not explicitly modeled, PVA results in Tables 1 and 2 suggest that successful implementation of combined actions may allow either or both reintroduced populations to meet Alternative Criterion 1A in about 20-22 years. Since conditions for down-listing depend upon future demographic rates more heavily than releases, this strategy could provide options for future decisions if only one of the reintroduced populations are able to achieve adequate reproduction and survival.

In summary, PVA results suggest that the following conditions will lead to down-listing based on Alternative Criteria 1A in about 20-22 years:

1. Management actions to minimize sub-adult and adult mortality in all wild populations, and in particular in the reintroduced populations, to historical levels for the AWBP;
2. Management actions to promote improved reproductive success in all cranes in the reintroduced population(s), including rearing and releases strategies for captive-reared cranes, exploration of cross-fostering as a method of population reinforcement with wild-hatched cranes, and management of environmental factors that promote better reproductive success for all cranes regardless of origin and rearing history;
3. Additional releases to one or both of the reintroduced populations for the next 10-15 years, as suggested by the following options:
    a. LNMP priority: All available releases allotted to the LNMP up to 20 per year for 10-15 years (total of 200 releases), with any additional juveniles either released into the EMP or retained in the SSP; *or*
    b. EMP priority: All available releases allotted to the EMP up to 10 per year for 10 years (total of 100), with any additional juveniles either released into the LNMP or retained in the SSP; or
    c. LNMP/EMP: First 10 releases allotted to the LNMP and next 5 releases to the EMP; 2-4 juveniles retained in the SSP as available; any additional juveniles allotted to the EMP; in combination with the translocation of FNMP cranes to the LNMP provided that risks are evaluated and mitigated; also in combination with other management actions that promote reproductive success in the reintroduced populations.

These actions are provided as a guideline. Actual results are stochastic and will be dependent upon the extent to which actions 1-3 above can be achieved.

Down-listing Under Alternative Criteria 1B and 2

If the establishment of additional wild self-sustaining populations through reintroduction is not successful, then down-listing can occur by meeting Objective 1 under Alterative Criterion 1B (and also Objective 2 under Criterion 2, as described above). This would require the significant expansion of the original wild population in Aransas-Wood Buffalo National Park to buffer this single population against stochastic risks such as catastrophes or genetic drift. A genetically and demographically viable captive population as insurance against species extinction also is required. Specific numerical criteria are:

Criterion 1B:
AWBP: Maintain a self-sustaining population of 1000 cranes (250 productive pairs).

Criterion 2: Maintain 153 whooping cranes in captivity (21 productive pairs). Genetic analysis suggests that 90% of the genetic material of the species can be sustained for 100 years at this population size.

Meeting Criterion Alternative 1B for AWBP

The AWB population is projected to be a demographically sustainable and growing population under past and estimated future conditions with no risk of extinction over 100 years. Capacity in the breeding and wintering grounds is expected to remain well above 1000 individuals with 2m sea level rise and is not anticipated to be a factor in recovery unless major land use changes occur in these areas.

Under historical (low threat) conditions, the AWBP is projected to reach 1000 cranes, on average, in about 21 years, provided no severe population-wide catastrophe occurs. At year 22 the population has <10% risk of falling below 1000; at that point, mean population size is 1163 (SD=131), with a mean of 672 adults age 4+ (SD=57) and 299 pairs.

Under the best estimate of future range-wide threats, the AWBP is projected to meet the criterion of 1000 cranes, on average, in about 33 years, provided no severe population-wide catastrophe occurs. At year 54 the population has <10% risk of falling below 1000; at that point, mean population size is 1262 (SD=190), with a mean of 877 adults age 4+ (SD=114) and 410 pairs. The relatively large timespan between these two timelines is due to the cyclic nature of the population, which leads to oscillations in population size aligned with the solar cycle.

Management actions that increase fledging rates by 5% of the current rate lead to an average of 23 years to reach 1000 cranes, with the population having <10% of falling below 1000 by year 33.

Under higher levels of migration mortality (1.225x historical rates), the AWBP is projected to reach 1000 cranes, on average, in about 54 years, provided no severe population-wide catastrophe occurs. However, the population does not reach <10% risk of falling below 1000 within 100 years due to oscillations in population size with the solar cycle and slow population growth. Similarly, the population does not reach <10% risk with higher threat levels.

Management actions may be able to mitigate the effects of increased future threats and reduce the time to down-listing under these conditions. For example, actions that lead to a 15% increase in past fledging rates would offset the effects of estimated range-wide threats. A similar result is projected for the annual release of 12 headstarted (or captive-conceived) juveniles for 20 years, assuming that released cranes have post-release survival rates similar to wild cranes and demonstrate at least 50% of the reproductive success of wild cranes (Table 22).

Table 22. Threat conditions and required management actions to meet down-listing Criterion Alternative 1B for AWBP. All scenarios assume no severe population-wide catastrophe occurs prior to down-listing.

Level of threats	Mitigation	Mean years to N=1000	Years to <10% risk of <1000	Mean N at $T_{<10\%}$	Ne Estimate from PVA
Historical levels	Threat reduction to match historical levels	21	22	1163	889
Estimated future range-wide increases (climate change, human-related mortality)	Threat reduction to contain increased threats to levels modeled	33	54	1262	474
Estimated future range-wide increases (climate change, human-related mortality)	Threat reduction to contain threats to levels modeled, *PLUS* 5% increase in fledging rates	23	33	1222	621
Estimated future range-wide increases (climate change, human-related mortality)	Threat reduction to contain threats to levels modeled, *PLUS* 15% increase in fledging rates	21	22	1165	785
Estimated future range-wide increases (climate change, human-related mortality)	Threat reduction to contain threats to level modeled, *PLUS* headstarting 12 juveniles annually for 20 years (survival=wild rates; reproduction=50% wild rates)	20	22	1233	869
Higher mortality rates (30% increase during migration; 50% increase in non-protected lands)	Threat reduction to contain threats to levels modeled, *PLUS* 20% increase in fledging rates	22	32	1280	639

Meeting Criterion 2 for SSP

Model projections for the SSP population indicate that, under projected future conditions and management, the SSP can maintain a genetically diverse and demographically self-sustaining captive population that can serve as a long-term insurance population against species extinction, thus meeting Criteria 2 for down-listing. The SSP also can meet Criterion 2 if it provides 12 juveniles annually for 20 years to reinforce the AWBP, either through headstarting or by producing juveniles of captive origin.

Meeting Criteria Alternative 1B and 2 as a meta-population

The best estimates of future conditions and management for the AWBP and SSP populations suggest that down-listing criteria can be met within 54 years with 90% probability, with an average time of 33 years to reach AWBP down-listing size. Mitigation efforts to improve recruitment to offset future threats can reduce the time to down-listing to that projected based on historical conditions, which is 21 -22 years. This leads to an estimated down-listing time of ~2039, but is dependent upon actual future threats, management actions, and cyclicity in population numbers. This estimate is similar to that given in the 2007 international recovery plan of projected down-listing around the year 2035.

Demographic and genetic resiliency

These down-listing estimations assume that no multi-year severe catastrophes befall the AWBP. This is of consideration given the maintenance of a single wild population under this scenario. Model results suggest that, at 1000+ individuals, the AWBP has the capability to recover from a single substantial decline if impacts are temporary, due primarily to the long reproductive lifespan of this species and assuming that growth remains positive. Sustained ‘catastrophic’ conditions that result in several consecutive years of poor reproduction and/or poor survival potentially could reduce the population’s ability to recover, leading to lower viability and increased extinction risk.

Population size and breeding structure impacts the rate of loss of genetic variation in populations through genetic drift (random loss of alleles). Small populations, or those with proportionately few individuals contributing to reproduction, lose genetic variation more quickly. Effective population size (Ne) is a measure that estimates how the population is behaving compared to an ‘idealized’ population that meets certain assumptions (e.g., random mating, equal family sizes, discrete generations). PVA results suggest that under the best estimation of future range-wide conditions, the mean effective population size for AWBP is estimated at Ne=474 based on the rate of genetic loss observed in the model over 100 years. This value approaches the recommendation by Franklin and Frankham (1998) for Ne of 500-1000 to maintain evolutionary potential in a population. These PVA projections, however, result in a much higher Ne/N ratio than is typically estimated for wild populations (Ne/N = 0.1) and should be viewed cautiously, as they are based on neutral genetic variation and are not subject to all genetic processes.

Summary

PVA results for whooping crane populations were used to assess the likelihood and associated potential timelines for whooping cranes to be down-listed under Criteria 1, 1A or 1B under Objective 1 and Criterion 2 under Objective 2 of the 2007 International Recovery Plan (CWS & USFWS 2007). Down-listing under Criteria 1 or 1A, consisting of the large wild Aransas-Wood Buffalo population and 1-2 reintroduced populations (Eastern migratory and/or Louisiana non-migratory population) would provide expanded geographic spread and multi-population redundancy against local threats. Additional releases to the reintroduced populations would be required to meet current down-listing criteria, as well as management actions to ensure good survival and significant improvement in reproductive rates in these populations. Recent reduction in the capacity of the captive SSP population as a source population for releases constrains its ability to provide the optimal number of cranes for release but is projected to be able to provide a valuable level of releases. The ability for either reintroduced population to reproduce sufficiently to become self-sustaining is uncertain, thus restricting the ability to down-list under Criterion 1 or 1A. Alternatively, down-listing can occur with a sufficiently large single wild AWB population and a demographically and genetically viable captive insurance population. PVA projections suggest that the AWBP will meet the down-listing target size of 1000 cranes, on average, in ~33 years, with 90% confidence within 54 years provided that threats do not increase above estimated levels. Management actions to improve fledging rates and/or population reinforcement (e.g., headstarting) may shorten time to down-listing for the AWBP under Alternative Criterion 1B. Scenarios that lead to down-listing in ~20-22 years were identified under all three sets of down-listing criteria.

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Appendix I. PVA Contributors

This PVA project and report was developed in consultation with the Whooping Crane International Recovery Team and numerous crane biologists and managers listed below who participated through workshops and/or electronic discussions in 2015-2018.

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Appendix II. Model development and inputs

Model Development Timeline

Discussion of model parameters and structure took place through a series of conference calls and emails from July 2015 to September 2018 with many of the wildlife managers and content experts for population data for the various whooping crane populations. These calls focused on model structure, input values and data resources. Numerous reports and publications, as well as data tables in some cases, were provided along with the 2015-2017 studbook databases for the captive population (i.e., a historical database that includes sex, pedigree, and life event information for individual birds).

A preliminary meta-population model was presented and discussed at the PVA development workshop on 1-3 December 2015 in Calgary, with many of the conference call participants attending the PVA workshop (Miller *et al*. 2016). Preliminary discussions of alternative management model scenarios also were initiated at this workshop by population-specific working groups.

Subsequent conference calls and electronic exchanges from June to October 2016 facilitated continued refinement of the baseline model reviewed at the second PVA workshop on 29 November - 1 December 2016 in Calgary. A draft list of alternative management scenarios and needed inputs was developed in working group and plenary discussions (Miller *et al*. 2017).

Continued conference call and electronic discussions through September 2018 further revised the baseline model to match historical and current conditions, as well as the addition of projected environmental conditions and human-related threats under current management actions. Final revisions to the AWBP model were made in April 2018, resulting in the final baseline models presented in this report in Section 2. This included the addition of demographic cyclicity and the exploration of multiple climate change-related impacts and potential additional mortality risks:

a. Cyclicity in juvenile mortality due to environmental conditions;
b. Inclusion of all habitat (protected and non-protected areas) in carrying capacity calculations;
c. Climate change effects (i.e., changes in K, changing survival rates, increased frequency of major hurricanes);
d. Density-related mortality as cranes expand into non-protected habitat with higher risk of mortality; and
e. Increased mortality risk during migration (due to wind farms, agro-conversion, Athabasca Oil Sands development, etc.).

The list of alternative management options was also refined and parameterized during these discussions.

PVA results were presented at the Whooping Crane PVA Review meeting in Calgary in December 2018 and to the Whooping Crane Eastern Partnership (WCEP) (electronically) in March 2019. Final revisions were completed in July 2019.

General Model Description

VORTEX Description

A stochastic, individual-based population model was developed for the whooping crane using the *VORTEX* 10.2.15 (Lacy and Pollak 2017) software program. *VORTEX* is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild or captive small populations. *VORTEX* models population dynamics as discrete sequential events that occur according to defined probabilities. The program begins by either creating individuals to form the starting population or importing individuals from a studbook database and then stepping through life cycle events (e.g., births, deaths, dispersal, catastrophic events), typically on an annual basis. Events such as breeding success, clutch size, sex at birth, and survival are determined based upon designated probabilities that incorporate both demographic stochasticity and annual environmental variation. Consequently, each run (iteration) of the model gives a different result. By running the model hundreds of times, it is possible to examine the mean and range of probable outcomes.

Relevant characteristics or options available in the *VORTEX 10* modeling software and used in this baseline model include:

- Individual age-based model incorporating both sexes and pedigree relationships
- Demographic stochasticity and environmental variation
- Cyclical or random events, including catastrophes
- Population-specific demographic rates and management
- Individual-specific demographic rates based on characteristic (e.g., age, sex, rearing type)
- Use of studbook data to establish the initial population
- Population management (e.g., genetic management, harvest, reinforcement, translocation)
- Changing future conditions (e.g., declining carrying capacity over time)

Demographic stochasticity is an inherent, emerging property of the model. During each time step each individual has a probabilistic chance for each relevant life event, most notably mortality and reproduction. For each event for each individual, a random number is generated between 0 and 1 and compared to the mean value for the corresponding rate, which determines the fate of the individual relative to that event. The overall rate observed for the population is a compilation of these individual rates and approaches the mean rate as population size increases, while small populations are likely to vary from the mean rate due solely to chance.

Environmental variation (EV) represents the year-to-year fluctuation in demographic rates (mortality and reproduction) due to different environmental conditions. This source of variation is incorporated into *VORTEX* by specifying EV, which is treated as one standard deviation (SD) for a binomial distribution around the mean value for that rate. Each year *VORTEX* selects a point along this distribution to represent that year (e.g., 1.2 SD below the mean); this is used as the mean rate for that year and is the value to which generated random numbers for individuals are compared. EV for reproduction (% females breeding) was estimated from partitioning observed (total) variance in AWB nesting data into that expected due to demographic stochasticity based on population size and with the remainder attributed to EV. This resulted in COV = 10%, which was also applied to mortality rates and matched that used by Tischendorf 2004. No EV was specified for first-year mortality, as this was accounted by cyclic rates. EV for reproduction and mortality were partially correlated in the model (0.5) for free-ranging populations to account for most EV occurring in the summer breeding grounds, while EV=0 for the captive population managed under controlled environmental conditions.

The model operates on a one-year time step, with most events (e.g., breeding) occurring once per year. Two mortality events occur in the model each year so that summer vs winter events can be altered separately in the model. Generally speaking, the model begins each 'year' in spring just prior to breeding, simulates breeding and summer mortality through fall migratory, and then imposes additional mortality during the second half of the year (winter and spring migration). Model scenarios were run for 100 years with 500 or 1000 iterations, as noted. Extinction was defined as only one sex remaining.

Population Structure

Population viability analyses (PVAs) were conducted for four distinct whooping crane populations using a stochastic, individual-based population model developed in the *VORTEX* 10.2.15 (Lacy and Pollak 2017) software program. Individual PVAs were conducted for the following populations:

1) Aransas-Wood Buffalo wild migratory population (AWBP)
2) Eastern migratory population (EMP)
3) Louisiana non-migratory population (LNMP)
4) Captive population (SSP)

Each of these populations has its own demographic rates, initial population structure, and management options. Each population is treated as a panmictic population isolated from each other in the absence of human-mediated transfers (e.g., translocation, reintroduction, headstarting. Models were used to project population status under best estimated future conditions, conduct sensitivity testing, and examine viability under alternative management scenarios for each of these whooping crane populations. These results were combined to evaluate the potential for these four populations collectively to meet down-listing criteria and contribute to recovery of this species.

Model Inputs and Validation

Model development focused initially on the wild AWBP and the captive population, as these represent very different population demographic rates and management strategies and have the most data available to inform the model. Population-specific data were used for the other wild populations (EMP and LNMP) for initial population, carrying capacity and demographic rates to the extent possible, using the AWBP model structure. Additional information on these populations was discussed and provided at the two PVA workshops as well as via post-workshop communications and model development.

Key resources for demographic rates included Gil-Weir *et al.* 2012, Moore *et al*. 2012, Butler *et al*. 2014, Servanty *et al*. 2014, Wilson *et al*. 2016, whooping crane SPARKS studbook databases (Jones 2015; Peregoy 2016, 2017), Whooping Crane Eastern Partnership (WCEP) annual reports and others, as well as expert opinion on conference calls and at the PVA workshops (see *Literature Cited* in PVA report).

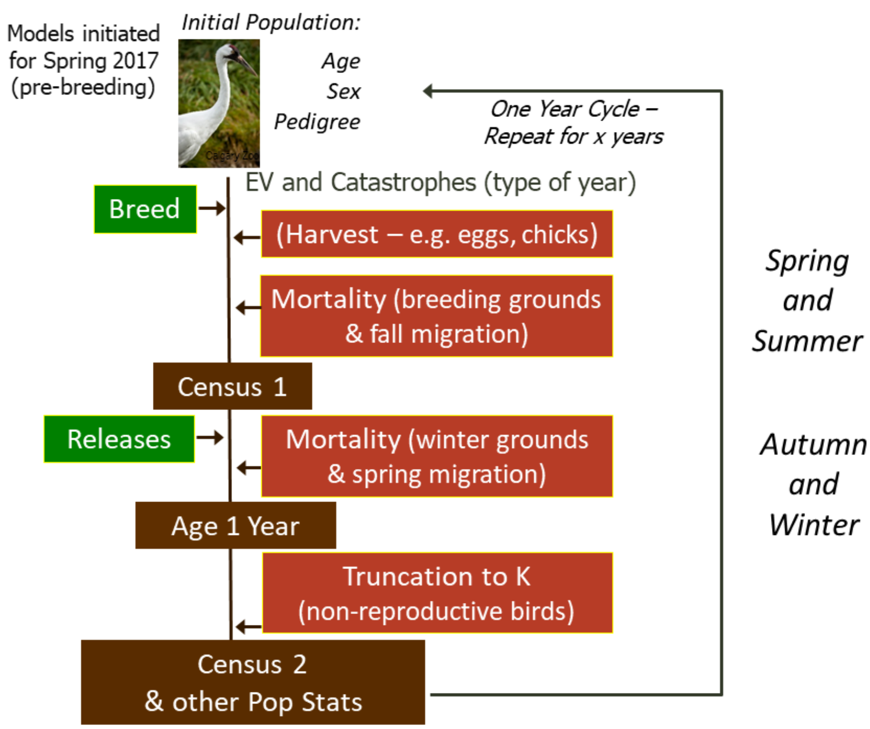

Fig. A1. Diagram of general model events, top to bottom, for each time step (year).

Model Assumptions

The following information summarizes the assumptions for the four whooping crane PVA models.

Assumptions (AWBP)

These scenarios assume that mortality rates during migration will not exceed 130% of estimated historical rates for the AWB migratory population, and that all birds are equally vulnerable to these threats regardless of age, sex or origin; that sub-adult and adult survival remains high in the breeding grounds and in the protected areas of the wintering grounds; that cranes preferentially use protected areas over non-protected areas; that changes in available wintering habitat do not exceed the projections for a 2m sea level rise; and that negative effects of rising atmospheric CO_2 levels do not exceed those modeled for 500ppm.

Assumptions (EMP)

Primary assumptions built into this PVA model include that wild-hatched EMP cranes will have similar reproductive rates as wild cranes in the AWBP (except when paired with a captive-reared mate) and similar sub-adult and adult survival as AWBP cranes; that historical demographic rates for released, captive-reared birds will continue into the future; and that the reproductive success of pairs does not improve with age, experience or population density. Furthermore, the model assumes no cyclicity in demographic rates and no impacts of climate change.

Assumptions (LNMP)

Assumptions for this PVA model are similar to those for the EMP, and include that wild-hatched LNMP cranes will have similar reproductive rates as wild cranes in the AWBP (except when paired with a captive-reared mate) and similar sub-adult and adult survival as AWBP cranes; that historical demographic rates for released, captive-reared birds up to age 4 will continue into the future, and that adult survival will approximate that of AWBP cranes; that captive-reared, released juvenile cranes will have similar reproductive rates as released cranes in the reintroduced EMP; and that the reproductive success of pairs does not improve with age, experience or population density. Furthermore, the model assumes no cyclicity in demographic rates and no impacts of climate change.

Assumptions (SSP)

This model assumes successful strong genetic management (including the use of AI to allow males to have two female 'mates', if needed); all adults are capable of reproduction; no genetically valuable breeding age adults are in non-breeding facilities; and no differences in the survival of chicks within a brood or between broods. The model assumes no cyclicity in demographic rates and no impacts of climate change. Survival and reproduction of captive-reared juveniles released into reintroduced wild populations is based on overall historical rates and are not differentiated based on rearing method.

Detailed information for selected inputs: Aransas-Wood Buffalo Population (AWBP)

This is the last original wild population of whooping cranes that remained prior to recent reintroductions. This population migrates internationally each year from its wintering grounds centered in the Aransas Wildlife Refuge, Texas, US to its breeding grounds in Wood Buffalo National Park in Alberta, Canada.

<u>Population</u>: An initial population of 414 birds was used based on results from the December 2016 survey (USFWS 2017), which estimated 431 cranes on the wintering grounds. The *VORTEX* model begins with the pre-breeding population, so mean winter and spring migration mortalities were applied to 2016 survey numbers to estimate the starting pre-breeding population in spring 2017 at 414 cranes (331 adults, 83 sub-adults age 1-3yrs). Running the model for one year projects 63 (SD=12.6) juveniles surviving through winter 2017-2018, slighter higher but similar to the 63 fledglings produced in 2017 (~6 are estimated to be lost due to winter mortality). An effort was made to initiate the model at the point in the solar cycle that best matches observed cycles in the field observations, recognizing that solar cycle length varies around an average of 11 years.

Carrying capacity: Revised estimates for the potential carrying capacity (K) of the whooping crane wintering grounds in the expanded Aransas National Wildlife Refuge (ANWR) area, including both protected and unprotected lands, were provided by K. Metzger (unpublished data, pers. comm.). Protected lands include all public protected areas, which extend beyond ANWR. Current K is estimated at 2550 cranes (774 in protected lands, 1776 in unprotected lands in the study region). Metzger also provided estimates of future K for scenarios with a sea level rise of 0.6m (K=3317), 1m (K=2505) and 2 m (K=2115) by the year 2100. The 1m rise scenario was recommended as a conservative estimate of sea level rise with low climate change impacts (see PVA report for more details). An approximation of the shape of the curve for K over time was developed using habitat types (especially regularly-flooded marsh) as a proxy, and assumed no further rise above 1m after 2100 (Fig. A2). This assumes that habitat utilization by cranes is similar to what has been observed in the past and that there are no behavioral or other density-dependent effects.

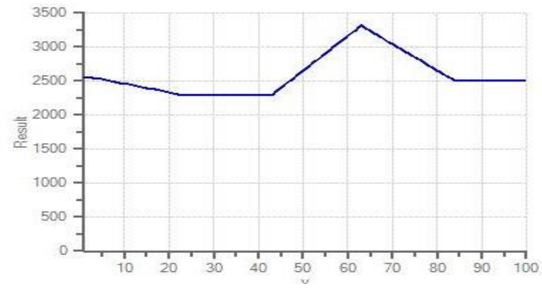

Fig. A2. Estimated K in wintering grounds for the AWBP representing 1m rise in sea level by 2100.

Reproduction: The mating system was modeled as long-term monogamous pairs, with reproduction (i.e., egg production) beginning as early as age 4. Female breeding rate (probability of producing a clutch that year) averaged 91.9% and is age specific, with essentially all females age 7-23 laying eggs (based on Gil-Weir *et al*. 2012 and Wilson *et al.* 2016) and rates declining slightly in older females (see Figure A3). Pairs can produce one clutch with one (4% of clutches) or two (96% of clutches) eggs (Gil-Weir *et al*. 2012).

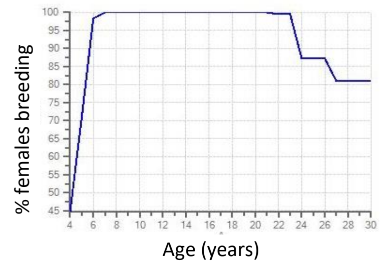

Fig. A3. AWBP model breeding rates.

Mortality: Mortality rates were based primarily on Wilson *et al*. 2016 with additional data from Gil-Weir *et al*. 2012 and raw data tables, and were implemented as two mortality events per year (summer vs winter mortality), with no sex-specific differences in mortality (Servanty *et al*. 2014). First-year mortality was divided into six-month mortality from egg to fledging to migration to wintering grounds (58.15% for first egg and 95% for second egg), with additional mortality (10%) applied to 6-month-olds for the remainder of the first year. Mortality rates used for other age classes were similarly applied to each six-month summer or winter period, resulting in the following annual mortality rates: 10.8% (1 and 2 year olds); 15% (3 year olds); and 5.6% (adults 4 years and older). Maximum lifespan was set at 30 years.

Cyclicity in Recruitment: Whooping crane demographic rates, primarily recruitment and population growth, fluctuate in a cyclic pattern, which has been reported to correlate with ~10-year cyclic patterns observed in boreal snowshoe hare-Canadian lynx and other boreal predator populations (Boyce *et al*. 2005; Wilson *et al*. 2016; Butler *et al*. 2017). Butler *et al*. 2017 also reported evidence of 11-year solar (sunspots) cycles affecting climatic conditions and demographic rates for whooping cranes. Weather on the breeding grounds and during autumn migration both likely influence juvenile mortality (directly or via increased predation risk) and therefore affect recruitment. While the proximate mechanism is uncertain, evidence suggests cyclicity in boreal species may be a product of complex interactions among food supply, predator abundance, hydrology and weather patterns influenced by the solar cycle (Butler *et al*. 2017). Cyclic recruitment data were provided by M. Butler and used to incorporate matching cyclicity (11-yr cycle) into first 6-month mortality in the AWBP *VORTEX* model.

Environmental variation: Demographic stochasticity is an inherent property of the model, while EV, or environmental variation (annual fluctuation in demographic rates), must be explicitly added. EV for reproduction (% females breeding) was set at CV = 10% based on partitioning of EV from observed variance in AWB nesting data. EV for mortality was set at CV=10% for most mortality rates to match that used for breeding and by Tischendorf 2004. No EV was specified for first-year mortality, as this was accounted by cyclic rates. EV for reproduction and mortality were partially correlated in the model (0.5) to account for most EV occurring in the summer breeding grounds.

Catastrophes: Two catastrophic events were incorporated in the base model, based in part upon general trends in catastrophic declines observed in 88 species of wild vertebrates by Reed *et al*. (2003). Risk of a high mortality event in the wintering grounds was incorporated as a 0.5% risk (~ once every 200 years) of a 50% reduction in survival for all age classes over winter. The risk of a poor breeding season (90% reduction in fledgling production) was given a 5% risk of occurrence (~ once every 20 years) based upon a conservative estimate of similar historical population declines over the past 38 years.

Genetics: Initially a small genetic load (3 lethal equivalents, 1 as a lethal allele and 2 as non-lethal effects) was incorporated into the model and applied as lower juvenile survival in inbred individuals. This is lower than the genetic load suggested by O'Grady *et al.* 2006 of 12.29 lethal equivalents for wild vertebrate populations, as it is assumed that some of the initial genetic load may have been purged due to the historical bottleneck and population expansion experienced by this species. Birds in the initial population were modeled as unrelated, as observed demographic rates incorporate any inbreeding effects to date. The model tracked pedigree relatedness and applied inbreeding effects on any future additional inbreeding. Preliminary results indicated that the AWBP remained large enough such that this level of inbreeding depression did not affect model results (~1% inbreeding over 100 years). Final scenarios reported here for the AWBP were run without this genetic component to greatly reduce computing time.

Model Validation

Retrospective modeling of the AWBP was conducted by using the base model to project the trend of this population over the past 38 years (from 1977 to 2015). Overall the model appears to be a reasonable representation of the whooping crane AWBP (see PVA report for details).

Sensitivity Testing

Recognizing that there is some uncertainty around model input parameters, sensitivity testing (ST) was conducted by varying a single parameter at a time to assess the sensitivity of the model results to different variables. All ST scenarios were run for 100 years with 500 iterations with an initial population of 500 individuals at capacity (K=500) with no future reduction in K. Stochastic growth rate (r), calculated prior to truncation to K, was selected as the most appropriate measure of population viability and model results. While ST was conducted on the AWBP model inputs, the general pattern of sensitivity of model parameters to population performance may have some application to other whooping crane populations.

Reproduction and mortality: Historical data are most robust for demographic rates (age-specific reproduction and mortality). The following rates were varied with $\pm$ 10% and $\pm$ 20% of the mean: % females breeding; first-year survival; sub-adult survival (ages 1-3); and adult survival (age 4+). Figure A4 shows that growth rate is most sensitive to adult survival (varied from 75.5% to 100%), followed by sub-adult survival (68-100%) and juvenile survival (30-45%). Changes in breeding rate (i.e., egg production) have little effect in comparison over the range tested, possibly as the proportion of females breeding is high. Reproduction and first-year survival combine to affect recruitment, which is an issue of concern for reintroduced populations. Specifically, fledge rate (survival from egg to fledging) is the most variable vital rate among wild crane populations and is responsible for the greatest uncertainty regarding future demographic trends of reintroduced populations. Post-juvenile survival and nest/egg production are relatively similar among wild populations in comparison. Wilson *et al*. 2016 similarly noted that fledging rate had the greatest influence on annual growth rate ($\ln\lambda$), followed by breeding propensity (% females nesting), given the relatively low variation in adult survival. While adult survival typically drives growth in long-live species such as cranes, the concentration of demographic variation in survival from egg through the first and second years results in its greater observed effect (Wilson *et al*. 2016). Management actions that improve hatching and fledging rates and juvenile survival are likely to improve viability as long as sub-adult and adult survival remain relatively high. Future increases in adult (and to a lesser extent, sub-adult) mortality, however, could reduce population viability.

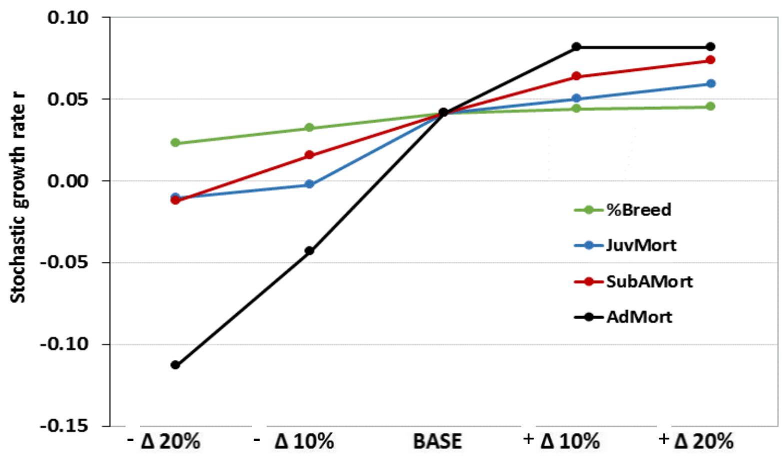

Fig. A4. Sensitivity testing for demographic rates (mean ±10%, ±20%) by stochastic growth rate.

<u>Additional input values</u>: Other model inputs relied more heavily on estimation and harbor greater uncertainty. These rates were explored through ST as follows: environmental variation (2x base value, base, ½ base value); lethal equivalents (2x base, base, none); maximum age (30 years as base value, 35 years); first age of reproduction (3 years, 4 years as base value); and catastrophes (2x annual base risk, base risk, none). The two catastrophes were also explored independently. Figure A5 shows that variation in these inputs over the range test result in relatively small impacts on growth rate.

EV, inbreeding sensitivity (LEs), and maximum age had little to no effect. Allowing three-year-old birds to breed (at the same rate of 36% as 4 year olds) slightly improved growth; breeding at lower rates would have less impact. Catastrophes do have some effect on growth rate, but populations of 500 grow well with no extinction risk even if the risk of both catastrophes is doubled. The effects of the two different catastrophes (egg loss on the summer breeding grounds vs severe mortality in the wintering grounds) are similar, with summer egg loss (which has a 10x greater risk than severe winter mortality) leading to a slightly more negative impact on population growth. These results suggest that model results are not particularly sensitive to the uncertainty in these parameters for populations of several 100 birds.

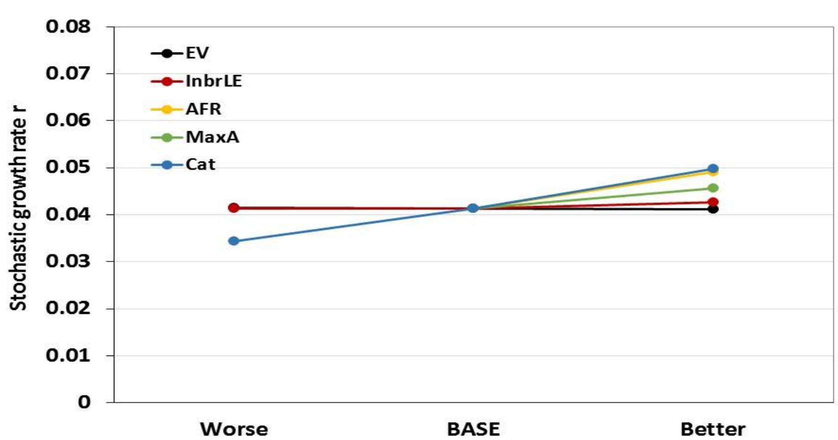

Fig. A5. Sensitivity testing for other variables (EV, LE, AFR, MaxAge, catastrophe rate) by stochastic growth rate.

Population size: Population size is known to impact population viability, as smaller populations are more vulnerable to stochastic processes such as demographic stochasticity, environmental variation, and genetic drift. The AWBP base model was run for populations with initial N = K for the following values: 50, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1000. Results show that populations of N=K=50 show slower growth (stoch r = 0.0248), reduced gene diversity (GD=0.8458), and 2.48% risk of extinction in 100 years. Once populations reach ~300 individuals, relative gains in growth rate with increased N begin to taper off, while gene diversity benefits taper at around N=700 (Fig. A6).

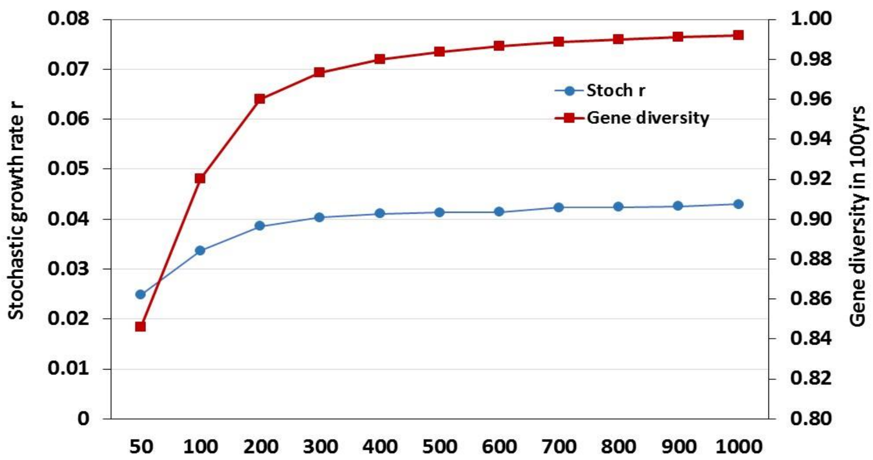

Fig. A6. Stochastic growth rate and gene diversity retained by population size.

Impacts of Increasing Atmospheric CO_2

Butler *et al.* 2017 propose a reduction in recruitment with the expected rise in atmospheric CO_2 to 500ppm by 2050, mediated through climatic effects (see PVA report for details). Table A1 gives the values used in the model at 400ppm and 500ppm with a linear increase in values from 2017 to 2033 to give the best approximation to changes reported by Butler *et al*. 2017. Figure A7 shows the results in terms of cyclic stochastic growth over 100 years for the AWBP, with 5-6 years spent in negative growth at the valley of each cycle under 500ppm (similar to Butler *et al.* 2017). Mean growth rate declines over time but averages higher than that reported by Butler *et al*. 2017.

Table A1. Six-month (egg to December) mortality rates used in the AWBP model for the first and second egg under conditions of atmospheric CO_2 of 400ppm and 500ppm.

	Egg 1		Egg 2	
Solar cycle	400ppm	500ppm	400ppm	500ppm
Year 1	69.7	79.0	100.0	100.0
Year 2	67.3	78.3	100.0	100.0
Year 3	62.5	72.7	99.3	100.0
Year 4	56.7	66.1	93.6	100.0
Year 5	51.9	60.4	88.8	97.3
Year 6	49.5	57.7	86.4	94.5
Year 7	50.3	58.6	87.2	95.5
Year 8	54.1	61.3	91.0	98.2
Year 9	59.6	67.5	96.5	100.0
Year 10	65.1	73.8	100.0	100.0
Year 11	68.9	78.0	100.0	100.0
Mean	59.6	68.5	94.8	98.7

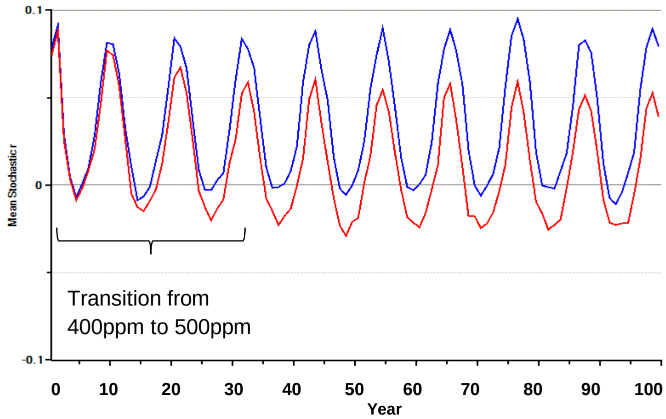

Fig. A7. Resulting cyclic growth rate resulting from constant atmospheric CO_2 at 400ppm (blue) and gradual increase to 500ppm conditions in 33 years (red).

Additional model structure and inputs for the Eastern migratory population (EMP), Louisiana non-migratory population (LNMP), and the captive Species Survival Plan (SSP) population can be found with their respective PVA report in Sections 3-5 of this report.

Table A2. Summary of base model inputs for each of the five Whooping Crane populations (see list of references 1-13 below the table).

Parameter	Aransas-Wood Buffalo (AWBP)	Eastern Migratory (EMP)	Louisiana Non-Migratory (LNMP)	Captive (SSP)
Initial population	N=414; equal sex ratio; stable age distribution (*based on (4) and Wilson model)*	N=104; plus 17 releases in 2017 *from 2017 SPARKS studbook (7)*	N=56; plus 23 releases in 2017 *from 2017 SPARKS studbook (7)*	N=160; *from 2017 SPARKS studbook (7)*
Reproduction				
First age of reproduction	4 years *(1)*			
Max. age of reproduction	30 years *(1)*			35 (male), 30 (female)
Maximum age	30 years *(1)*			40 years *(7)*
Mating system	Long-term monogamy (permanent pairs until mate dies)			Short-term polygyny (max. of 2 female mates per year)
% females reproducing	Based on female age, see Fig A3; 91.9% of paired females *(1,2)*	Based on reproductive experience *(5):* Proven: 95% (slightly less if old) Naïve: 50%	Based on reproductive experience *(5):* Proven: 95% (slightly less if old) Naïve: 50%	Based on reproductive experience and age *(7)*: Proven: 64% (43% if A>25) Naïve: 10% (0% if A>25) Limit on number of broods based on facility capacities
Male mates	Female can be paired with any unpaired male in the population	Female can be paired with any unpaired male in the population	Female can be paired with any unpaired male in the population	Sire (mate or sperm donor) selected based on prior mate, mean kinship value, and relatedness to female
Offspring production and survival				
Clutch number and size	One clutch/year	One clutch/year	One clutch/year	Up to 3 broods/yr *(7)* 55% produce one brood 36% produce two broods 9% produce three broods
Clutch size	1-2 eggs/clutch *(1)* 4% with one egg 96% with two eggs	1-2 eggs/clutch 4% with one egg 96% with two eggs	1-2 eggs/clutch *(1)* 4% with one egg 96% with two eggs	1-2 chicks/brood *(7)* 1st brood: 63% 2 chicks 2nd brood: 46% 2 chicks 3rd brood: 46% 2 chicks (A>25yrs: 13/0/0% 2 chicks)
Mortality: egg to winter grounds (first egg)	Cyclic; mean=59.6%, range=49.5-69.7% *(1,2,3,13)*	58.15% (wild-wild parents) 89% (mixed-origin parents) 94.5% (captive-reared parents)	58.15% (wild-wild parents) 89% (mixed-origin parents) 94.5% (captive-reared parents)	17.7% hatch to 4mo. *(7)*
Mortality: egg to winter grounds (second egg)	Cyclic; mean=94.8%, range=86.4-100% *(1,2,3,13)*	95% (wild-wild parents) 98% (mixed-origin parents) 99% (captive-reared parents)	95% (wild-wild parents) 98% (mixed-origin parents) 99% (captive-reared parents)	17.7% hatch to 4mo. *(7)*

Mortality rates				
Wintering grounds to end of first year	10% *(1,2,3)*	10.5% *(5)*	8.1% (wild reared) 11% (released juveniles)	6% from 4-12 mo. *(7)*
Sub-adults (annual)	10.8% for ages 1 & 2; 15% for age 3 *(2)*	11.34% for ages 1 & 2; 15.75% for age 3 *(2,5)*	10.8% for ages 1 & 2; 15% for age 3 *(2,5)* for wild-reared; 22% and 10.8% for releases	5% (females); 1% males *(12)*
Adults (annual)	5.6% *(2)*	5.88% 2,*(5)* (see Table 10)	5.6% 2,*(5)*; except for 12% (age 4 only) for released birds (see Table 12)	2.5% *(12)* 12% if female and age>27 12% if male and age>30
Environmental variation	$CV_{\%breeding}$=10% $CV_{mortality}$ = 10%	$CV_{\%breeding}$=8% $CV_{mortality}$ = 10%	$CV_{\%breeding}$=8% $CV_{mortality}$ = 10%	None, except for hatch to 4 mo. mortality: CV = 2.75%
Catastrophes				
Egg loss	5% risk 90% mortality of eggs	5% risk 90% mortality of eggs	5% risk 90% mortality of eggs	n/a
Winter mortality	0.5% risk 50% mortality on wintering grounds (all age classes)	0.5% risk 50% mortality on wintering grounds	0.5% risk 50% mortality on wintering grounds	n/a
Disease	n/a	n/a	n/a	2% risk; 95% survival (75% survival affecting 20% of SSP population (one center)
Adverse weather	n/a	n/a	n/a	Included as chick EV
Genetics				
Inbreeding impact	LE = 3 ; 34% lethal tested	LE = 3 ; 34% lethal	LE = 3 ; 34% lethal	LE = 3 ; 34% lethal
Initial relatedness	None	Pedigree from studbook *(7)*	Pedigree from studbook *(7)*	Pedigree from studbook *(7)*
Connectivity	None (isolated)	None (isolated)	None (isolated)	None (isolated)
Carrying capacity	K=2550 (winter) *(9*)* 774 (protected lands) 1776 (unprotected)	K=2000 (summer) ~1350 breeding adults ~ 675 pairs	K=3000 *(10*)*	K=165
K truncation method (removal of excess > K)	Only birds that have not yet reproduced	Only birds that have not yet reproduced	Only birds that have not yet reproduced	Excess offspring w/ MK > (population MK/3)
Loss of K due to climate change	Decrease in K to 2505 by 2100 with 1m sea level rise *(9*)*	Not incorporated	Not incorporated	Not incorporated

Data sources used in developing inputs:
1 = Gil-Weir *et al.* 2012
2 = Wilson *et al.* 2016
3 = Wilson (raw data tables)
4 = USFWS 2016
5 = Servanty *et al*. 2014
6 = Moore *et al*. 2012
7 = 2017 studbook data (Peregoy 2017)
8 = Converse, pers. comm.
9 = Metzger *et al.* 2014; *revised 2016
10 = Allen 1952
11 = International Crane Foundation data
12 = PMx data analysis project (2016)
13 = Butler *et al.* 2017