WHOOPING CRANE (*Grus americana*) DEMOGRAPHY AND ENVIRONMENTAL FACTORS IN A POPULATION GROWTH SIMULATION MODEL

A Dissertation

by

KARINE GIL DE WEIR

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2006

Major Subject: Wildlife and Fisheries Sciences

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Approved by:
Chair of Committee, William E. Grant
Committee Members, R. Douglas Slack
Kirk Winemiller
Richard Woodward
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ABSTRACT

Whooping Crane (*Grus americana*) Demography and Environmental Factors in a
Population Growth Simulation Model. (May 2006)

Karine Gil de Weir, Licenciate in Biology, Universidad Simón Bolivar;
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Chair of Advisory Committee: Dr. William E. Grant

The Whooping Crane (*Grus americana*) is among North America's most charismatic species. Between 1938 and 2004, the population that migrates between Aransas National Wildlife Refuge (ANWR) and Wood Buffalo National Park (WBNP), grew from 18 to 217 individuals. The recovery plan objective for this endangered species is to downlist the population in 2035, but this requires interpretive assessment of population responses to environmental factors over the long term. I analyzed 27 years of banding data, 37 years of nest monitoring data, and 20 years of winter reports to estimate age-specific mortality and fecundity rates. The resulting life table yielded an intrinsic rate of increase (r) of 0.14/y, a net reproductive rate (Ro) of 6.4/y, and a mean length of a generation (G) of 13y.

Path analysis of environmental factors, demographic variables (natality and mortality), and the finite rate of population increase (lambda) showed that annual mortality, temperatures from the ANWR, WBNP and at a migration stop-over in

Nebraska, and pond water depth were good predictors of lambda variability. However, other environmental factors were significantly correlated: at ANWR, October- March temperature (extreme minimum and maximum), December temperature (mean and extreme minimum), November-January precipitation, and September-March freshwater inflow; at WBNP, March-September precipitation, March-May temperature, and temperatures during the September - October fall migration. The Pacific Decadal Oscillation (PDO) affected lambda indirectly through environmental factors in Nebraska and ANWR.

I graphically analyzed relevant data trends from 1967 to 2004 to identify the relation between phases of PDO and environmental and demographic variables. During PDO cold phases, a synchronization of “extreme” environmental values was observed from the different regions; during warm phases extreme environmental values were scattered. Most periods of Whooping Crane population decline happened during cold phases.

I developed a compartment model to represent Whooping Crane population dynamics utilizing the new data on survivorship and fecundity from banded birds. The model was capable of simulating historical population trends with adjustments in brood success and egg mortality. The model will allow future studies to test population responses to various environmental scenarios at the WBNP, during fall and spring migrations, and at the ANWR.

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation to my advisor, Dr. Bill Grant, who not only provided me with a significantly rich source of ideas and guidance, but was also a permanent support during the whole research process. His lectures and comments both motivated and inspired my interest on the systems ecology approach used in this research.

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I want to extend special gratitude to Drs. Neal Wilkins, Bill Grant, R. Douglas Slack and Stephen Davis who strongly supported me during my studies at Texas A&M University through two projects: The Rio Grande Basin (first semester), and the San Antonio Guadalupe Estuarine System (SAGES) from 2003 to 2005.

I am also deeply grateful to The Beijer International Institute of Ecological Economics, The Royal Swedish Academy of Sciences, and to Dr. Karl-Göran Mäler for support during the last period of my dissertation.

I would like to dedicate this dissertation to my infinite source of motivation during the time that I have spent studying, my husband Enrique, my son Hector Enrique, my daughter Karen Cristina, my parents Hugo and Cata, my family and friends.

Thanks GOD, they made this possible.

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CHAPTER I

INTRODUCTION

LITERATURE REVIEW

The only free-living, non-experimental population of Whooping Cranes (*Grus americana*) winters from October through March at the Aransas National Wildlife Refuge (ANWR) and adjacent areas along the Gulf of Mexico in Texas. The population breeds and spends the summer (late April through mid-September) at Wood Buffalo National Park (WBNP) and adjacent areas in northwestern Canada. During fall (late September) and spring migration (early to mid-April), the population (ANWR-WBNP) uses areas in southern Saskatchewan, the central portion of the Platte River in Nebraska, and the Quivira NWR in Kansas as stopover sites (Lewis 1995 and Chavez-Ramirez personal communication) (Fig. 1). Both the United States Fish and Wildlife Service (USFWS) and the Canadian Wildlife Service (CWS) list the Whooping Crane as an endangered species (CWS and USFWS 2003). The main objective of the CWS-USFWS recovery team is to reclassify the threatened status (downlist) of the Whooping Crane and the ultimate goal is to recover the population and remove the Whooping Crane from the list of threatened and endangered species (delist). The objective of the CWS-USFWS recovery plan is to establish and maintain wild self-sustaining populations of Whooping Cranes that are genetically stable and resilient to stochastic environmental events. The ANWR-WBNP is not the only wild population; there are two others, the

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This dissertation follows the style of Ecology.

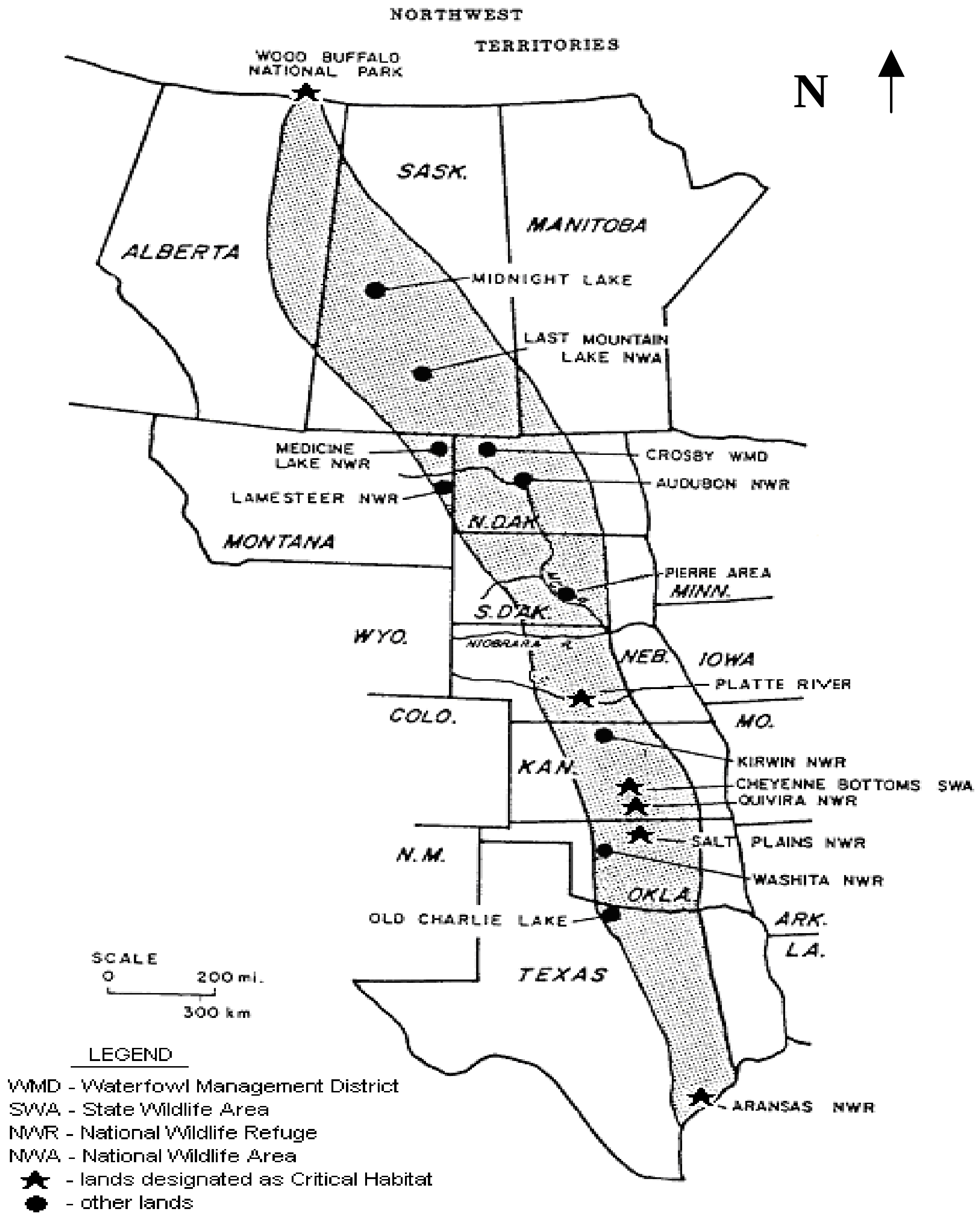

Fig. 1. Map indicating breeding grounds at WBNP in Canada; migration route, with stopover in Nebraska (NE) U.S, and wintering grounds at ANWR in Texas U.S, of the only free-living population of Whooping Crane (Kuyt 1992).

Florida non-migratory and the Eastern migratory populations (87 and 36 individuals for year 2003-04, respectively), but they are experimental. If the experimental and ANWR-WBNP populations cannot become self-sustaining for a decade, then the recovery plan goal is to insure that the only wild non-experimental population be sustaining and remain above 1,000 individuals (i.e. 250 reproductive pairs) for downlisting to occur (CWS and USFWS 2003). If growth of the Whooping Crane population continues at the same rate, this number of individuals will be reached in 2035 (Mirande et al. 1997). However, delisting criteria are not yet available, because the status and biology of the species dictate that considerable time is needed to reach down-listing goals (CWS and USFWS 2005).

The population grew from 18 individuals in 1938 (Binkley and Miller 1988) to 217 individuals in 2004 (Stehn 2004). Although information on Whooping Crane life history and ecology has been available since 1926 (Table 1), more information for the recovery plan for this small population is required. Essential data are needed on conservation biology; population dynamics and population responses to future threats, such as impacts due to stochastic and catastrophic events. In addition, effective Whooping Crane population size over the long term should be determined, to maintain genetic viability (CWS and USWFS 2003, 2005).

Over more than three decades, several researchers have studied Whooping Cranes on their wintering and breeding grounds, but with little emphasis on migration routes or stopovers (Table 1). Information on breeding ecology at the breeding grounds included age of first reproduction, nest site fidelity, clutch size, hatching success, sex ratio,

Table 1. Summary of literature on Whooping Crane life history, ecology, and population trends.

Topic	Source
General information	Bent 1926, Allen 1952, Erickson 1976, Erickson and Derrickson 1981, Lewis 1995.
Breeding ground habitat conditions, dynamics at the nesting grounds, clutch size, hatching success, and juvenile survival	Novakowski 1966, Miller 1973, Kuyt 1981a, 1981b, 1993, Kuyt and Goosen 1987, Lewis et al. 1988, Kuyt and Barry 1992, Johns 1997, Johns et al. 2003, Timoney 1999, Bergerson et al. 2001.
Population age structure and population trends	Miller et al. 1974, Binkley and Miller 1980, 1983, 1988, Boyce and Miller 1985, Nedelman et al. 1987, Link et al. 2003.
Migration	Drewien and Bizeau 1981, Howe 1985, Lingle 1985, Kuyt 1992, Chávez-Ramirez 2004.
Wintering ground habitat conditions, territories, dynamics of juveniles, sub-adults, and adults at wintering grounds	Blankinship 1976, Labuda and Butts 1979, Bishop and Blankinship 1981, Bishop 1984, Bishop et al. 1985, Stehn 1992, 1997, Stehn and Johnson 1985.
Diet and foraging ecology	Shields and Benham 1969, Hunt and Slack 1987, 1989, Chávez-Ramirez 1996, Chávez-Ramirez et al. 1996, Nelson et al. 1996, 1997.
Demography, population projections, population fluctuations, PVA models, and recovery plan	Mirande et al. 1993, 1997, Brook et al. 1999, 2000, Tischendorf 2004, CWS and USFWS 2003, 2005.

fledgling mortality, juvenile survival, breeding range and breeding habitat (See Table 1). Studies at the wintering ground described activity pattern, flock size, dynamics of subadult flocks, adult-young relationships, movement, behavior, territoriality, distribution of winter territories, mortality, winter habitat, habitat use, correlation with fire-treated uplands habitat, food (diet, consumption, nutritional value), foraging behavior and energetic ecology (see Table 1). Studies on migration routes, or stopovers, were carried out on the movement of juveniles, habitat use and the conditions of the migratory habitat in the Great Plains of North America (See Table 1).

Species and populations respond to environmental factors and climate changes through changes in physiology, abundance, and distribution. Environmental factors can vary markedly from year to year, and, within any given year, they can be favorable during one part of the annual cycle and unfavorable during another (Hughes 2000).

The migratory Whooping Crane may respond to environmental factors from different regions. Environmental factors at the breeding grounds include low temperatures, heavy precipitation, flooding, drought, food scarcity, predators, and fire (Erickson and Derrickson 1981, Kuyt and Barry 1992, Lewis 1995, and Johns 1997). Environmental factors at the wintering grounds include low temperatures, heavy precipitation, salinity, food scarcity, hurricanes and drought (Blankinship 1976, Erickson and Derrickson 1981). Environmental factors along migration routes include low temperatures, snow, hailstorms, and food scarcity (Drewien and Bizeau 1978, Lingle 1985). Although many environmental abiotic elements have been described in numerous publications, studies are lacking at the different grounds and long-term responses of Whooping Cranes to these factors are still unknown.

Among other studies developed on the Whooping Crane population, projections have been made recently as a part of population viability analyses (PVA) (Mirande et al. 1997, Brook et al. 1999, 2000, Tischendorf 2004). These projections were based primarily on demographic analyses published before 1989 (Miller et al. 1974, Binkley and Miller 1980, 1983, 1988, Boyce 1987, Boyce and Miller 1985, Kuyt and Goosen 1987, Nedelman et al. 1987) (Table 1) and on unpublished data (Brian Johns CWS and Tom Stehn ANWR). However, they did not include data from marked individuals (program carried out from 1977 to 1988).

Management decisions concerning endangered species, including Whooping Cranes, are being made in part based on the predictions of PVA packages. Brook et al. (1999) and Reed (2004) said there was no way to determine which PVA package used for Whooping Cranes was most accurate, so these researchers recommended modeling with more than one package to provide perspectives. They also suggested development of other models as PVAs in order to answer questions about the different regions and population responses to specific environmental conditions (e.g. temperature changes) at the different grounds. Commonly used PVA packages have lacked flexibility for evaluating specific environmental effects during different phases of the annual cycle (Brook et al. 1999).

Based on the benefits of the systems approach compared to other methods of problem solving (Grant et al. 1997), one of the possibilities for providing an approach to finding new answers and solutions for the Whooping Crane population is to use a systems analysis and simulation model of the ecology of this species. This is another tool for addressing several questions regarding population dynamics and the relationship between environmental factors and demographic parameters, such as natality and mortality rates.

OBJECTIVES

First, study the demography of the only free, non-experimental Whooping Crane population at ANWR, WBNP, and during fall and spring migrations. Update Whooping Crane demographic statistics with the valuable information obtained from 27 years of banding data, 37 years of nest monitoring data and 20 years of winter reports. Develop a life table for the ANWR-WBNP Whooping Crane population and compare population dynamics during the past 20 years with previous demographic studies, based on data obtained before the 1980´s.

Second, relate environmental factors of the different regions to the demographic statistics (natality and mortality) of the Whooping Crane population. Analyze the effect of each environmental factor at the breeding grounds (WBNP), during migration with Nebraska (NE) as the main stopover, and at the wintering grounds (ANWR), and the effects on fecundity and mortality at different life stages of the cranes. Identify the environmental factors on each ground that, from 1967 to 2004, could be important in causing variations in the Whooping Crane population.

Third, build a simulation model of Whooping Crane population growth to test hypotheses about the effects from 1938 to 2004 of the environmental factors at the different grounds on population demography. Develop a model with a structure capable of simulating general historical trends with data on survivorship and fecundity based on records of cranes banded from 1977 to 2004. Make the model capable of projecting population growth over the next 10 years by responding to various environmental scenarios at the breeding grounds, during fall and spring migrations, and at the wintering grounds.

Demographic parameters, life table, and deterministic and stochastic population projections for this project are investigated in Chapter II. Analysis of historical records of environmental factors (abiotic) at the different grounds, and an analysis of historical demography (fecundity and mortality of eggs, chicks, fledglings, juveniles, and adults) at the different grounds are presented in Chapter III. A model simulation of the dynamic population of the Whooping Crane, capable of mimicking historic trends and responding to different scenarios at the different grounds is presented in Chapter IV. The study concludes with a summary and brief analysis of the implications of the empirical results in Chapter V.

CHAPTER II

WHOOPING CRANE DEMOGRAPHY

INTRODUCTION

The only free-living, non-experimental population of Whooping Crane (*Grus americana*) spends winters (October through March) at the Aransas National Wildlife Refuge (ANWR) and adjacent areas along the Gulf of Mexico, in Texas. The population breeds and spends the summer (late April through mid-September) at Wood Buffalo National Park (WBNP) and adjacent areas, in northwestern Canada. During fall (late September) and spring (early to mid-April) migration, the population uses areas in southern Saskatchewan, the central portion of the Platte River in Nebraska, and the Quivira NWR in Kansas as stop-over sites (Lewis 1995, Chavez Ramirez personal communication) (Figs. 1 and 2).

Both the United States Fish and Wildlife Service (USFWS) and the Canadian Wildlife Service (CWS) list the Whooping Crane as an endangered species (CWS and USFWS 2003). The ANWR-WBNP population is not the only wild one; there are 2 experimental wild populations (the non-migratory “Florida” population, and the migratory “Florida–Wisconsin” or “Eastern” population). If the 2 latter populations cannot become self-sustaining, then the recovery plan goal for year 2035 is that the only wild non-experimental population be sustaining and remain above 1,000 individuals (i.e. 250 reproductive pairs) for down-listing to occur (CWS and USFWS 2003, Mirande et al. 1997).

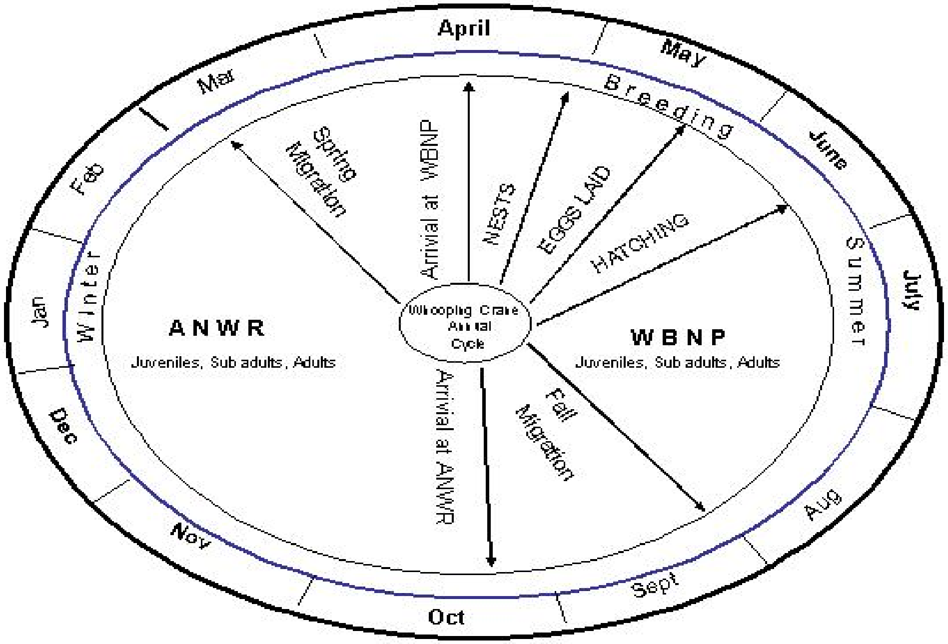

Fig. 2. Calendar representing the annual cycle of Whooping Cranes. Breeding occurs at WBNP in Canada, and the population winters at the ANWR in Texas (Fig. 1). Arrows indicate periods of peak activity.

A wealth of information is available on the charismatic Whooping Crane's life history and ecology (Table 1). The population has grown from 18 individuals in 1938 (Binkley and Miller 1988) to 217 individuals in 2004 (Stehn 2004). Whooping Cranes have experienced several periods of temporary decline throughout their history (Nedelman et al. 1987). Two periods of population increase were analyzed in the past, the first period was from 1938 to 1956 (Miller et al. 1974), and the second from 1957 to 1987 (Binkley and Miller 1988) (Fig. 3).

Several Whooping Crane population projections have been made recently, as part of population viability analyses (PVA) (Mirande et al. 1997, Brook et al. 1999, 2000, Tischerndorf 2004), but these projections have been based primarily on demographic analyses published before 1989 (Miller et al. 1974, Binkley and Miller 1980, 1983, 1988, Boyce and Miller 1985, Nedelman et al. 1987, Boyce 1987, Kuyt and Goosen 1987).

In this chapter, I present analysis of demographic data on the ANWR-WBNP population of Whooping Cranes; I compare the new demographic statistics obtained to those previously reported. I project deterministic population numbers to the year 2035, using both new and previous estimates of population growth rate, and then I project stochastic population numbers for 2035.

METHODS

Data base description

Data from WBNP was provided by the Canadian Wildlife Service (CWS) (Lea Craig-Moore and Brian Johns, CWS unpublished data). These data had been collected from aerial surveys each May and June, from 1967 to 2004. Each survey consisted of approximately 25 hours of observations over the approximately 927 km^2 of WBNP and adjacent areas.

Data included estimates of (1) number of nests (1968 through 2004), with each nest identified by nesting area and whether or not it belonged to a banded breeding pair; (2) number of eggs laid in each nest (1967 through 2004); (3) number of eggs collected (by CWS) from each nest (1967 through 1996, except 1970, 1972, and 1973); (4) number of eggs hatched from each nest (1967 through 2004); and, (5) number of chicks fledged from each nest (1967 through 2004).

From 1977 through 1988, during late July or the first half of August, the CWS leg-banded 67 (33 female and 34 male) breeding-ground juveniles (about 60 - 65 days of age). The sex of marked birds was determined by behavioral observations, chromosomal analysis, and vocalizations (Johns et al. 2003). Nesting success of banded Whooping Cranes has been determined annually, and age at death has been recorded (Lea Craig-Moore and Brian Johns, CWS unpublished data).

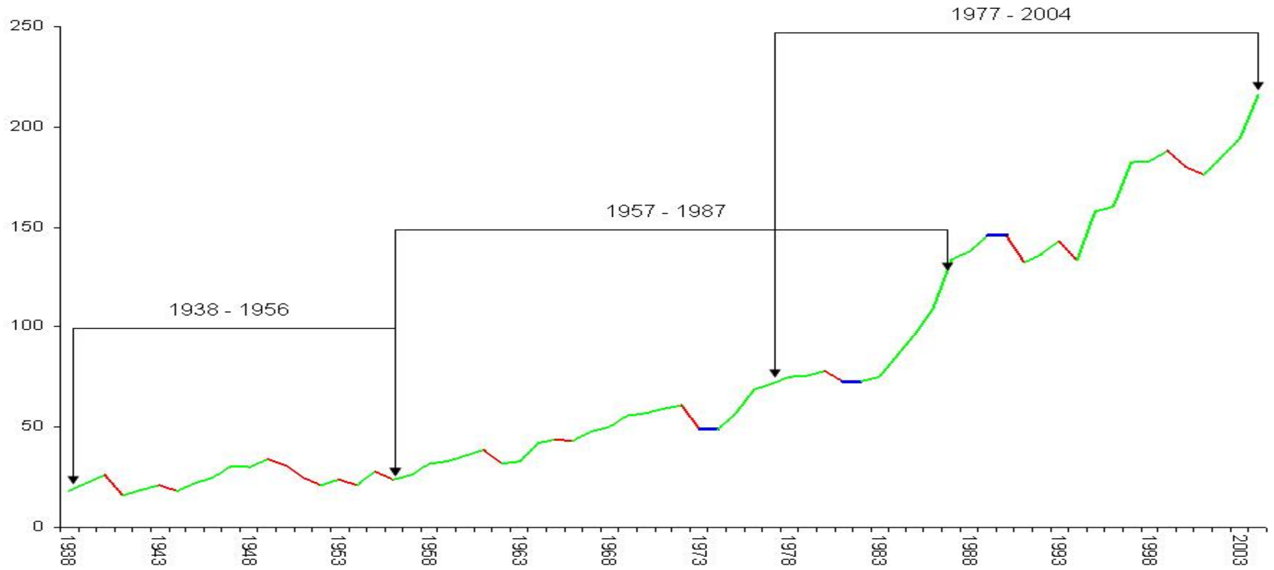

Fig. 3. Number of Whooping Cranes (n), in the only free-living, non experimental population from 1938 to 2004. The figure shows 3 general growth phases :1st, from 1938 to 1956, described by Miller et al. (1974); 2nd, from 1957 to 1987 (Binkley and Miller 1988); and, 3rd, this study, from 1977 to 2004. Specific periods of population change are indicated by colors: green, growth; red, decline; and, blue, stability.

Data from ANWR was provided by the USFWS (Tom Stehn, winter reports 1986 - 2004). These data included censuses of juveniles, sub-adults, and adults conducted weekly by aerial or ground surveys (mid-October through April) from 1977 to 2004, and incidental observations provided in annual winter reports. Aerial surveys were conducted along the approximately 56-km long extent of coastal salt marsh, adjacent uplands of ANWR, and surrounding area. Each survey consisted of a single, approximately 7-h, flight. Mortality was recorded primarily as the disappearance of one territorial adult, or its juvenile.

Data analysis

I estimated age-specific survivorship (l_x, see Appendix A for definitions of demographic parameters, Table A1*)* from 67 banded birds using the Kaplan-Meier method of survival analysis (K-M method; Kaplan and Meier 1958, Pollock et al. 1989, Kleinbaum and Klein 2005). I represented the number of individuals at age 0 in each cohort, as the number of eggs laid in the nests in which banded individuals hatched; thus, estimates of l_0 accounted for egg, chick, and juvenile mortality. The K-M method adjusts l_x estimates to account for marked individuals whose fate is unknown. In this case, banded individuals who still were alive, were "censored" from the age classes which they had not yet had enough time to reach (for example, individuals from the 1988 cohort that were still alive in 2004, at age 16, were censored from age classes >16; individuals from the 1987 cohort that were still alive in 2004, at age 17, were censored from age classes >17, etc.). I also calculated l_x for each of the 12 cohorts individually ($l_x = n_x / n_o$) using the K-M method.

I estimated age-specific fecundity (b_x) from 33 banded females; values of b_x for $x > 19$ were estimated by extrapolating the linear regression of b_x on x for $14 \leq x \leq 19$ ($b_x = 1.46 - 0.03 * x$, $r^2 = 0.96$), since each of these older age classes was represented by only 1 or 2 females. I also calculated b_x for each of the 9 cohorts with banded females individually (no females were banded in 1978, 1981, and 1983).

Based on the estimates of l_x and b_x, I calculated age-specific reproductive values (V_x) and the stable age-class distribution (C_x), as well as the net reproductive rate (Ro), the mean generation time (G), the intrinsic rate for increase (r), and the finite rate of increase (λ) of the population. I also calculated C_x, Ro, G, r, and λ based on the life table presented by Binkley and Miller (1988), and Ro, G, r, and λ based individually on data from the 9 cohorts with banded females.

Finally, I projected deterministic and stochastic population numbers to the year 2035. Deterministic projections were obtained via the equation $N_{t+1} = \lambda N_t$, with estimates of λ from this and previous studies. Stochastic projections were developed using the same equation, but values of lambda were substituted randomly in the equation using STELLA® V7. This program allowed use of annual lambdas with the following criteria: type of period (down, no change and up); duration of periods (no change = 1 year, down = 1 or 2 years, up = 2, 3, 5, 6, and 7 years); frequency of each period [0.16 (2 years), 0.33 (3 years), 0.5 (5 years) and 0.83 (6 years)]. Values of lambda for each type of period, obtained from historical records, were: down = 0.92 to 0.99, no change = 1, and up = 1.001 to 1.05 (Binkley and Miller 1988, Mirande et al. 1997). Lambda = 1.08 is the maximum value recorded from one year to another from history, and 1.14 was the value from the new life table. In the model selected for each period of up, down, and stability, a value of lambda as observed throughout the history followed the criteria described above, and projected a new total population number, for every year.

RESULTS

Estimates of survivorship rates *(lx)* (Table 2) and comparison with l_x previously reported (Fig. 4) showed that values obtained in this study were lower than those reported by Binkley and Miller (1988) for ages $(x) \leq 16$, and higher for ages $(x) > 16$. The curve of survivorship, obtained from 12 cohorts of banded individuals monitored during 27 years of study, illustrated that rates from ages 1 to 15 decreased gradually, and after age 16, rates remained more stable until age 27.

My study also showed the survivorship rate of the Whooping Crane population for individuals at age 0 (l_0), from eggs to juvenile. Survivorship rates from individual cohorts, showed a noticeable variation in l_x among the 12 banded cohorts (Appendix A: Table A2, Fig. A1).

Estimates of fecundity rate (b_x) were age-specific for female ages from 3 to 27 years (Table 2, see Appendix A: Table A1 for definition). The highest value $b_x = 1$ was obtained at age 14. A comparison of these results with the constant values from previous estimations is plotted in Fig. 5. Results showed higher fecundity rates for this Whooping Crane population, than those previously reported (Binkley and Miller 1988, Brook et al. 1999, Tischendorf 2004).

Table 2. Age-specific survivorship (l_x), fecundity (b_x), reproductive value (V_x), the stable age-class distribution (C_x), for the Whooping Crane population estimated in this study. Estimates of net reproductive rate (*Ro*), the mean length of a generation (*G*), the intrinsic capacity for increase (*r*), and the finite rate of increase (λ) of the population also are presented.

x (Years)	l_x	b_x	V_x	C_x
0	1	0	6.42	0.2498
1	0.5276	0	12.16	0.1148
2	0.5276	0	12.16	0.1
3	0.5276	0.055588	12.16	0.0871
4	0.5276	0.356176	12.11	0.0759
5	0.5276	0.572941	11.75	0.0661
6	0.4882	0.793548	12.08	0.0533
7	0.4724	0.904	11.67	0.0449
8	0.4567	0.948276	11.13	0.0378
9	0.4331	0.958889	10.74	0.0313
10	0.4016	0.942308	10.55	0.0253
11	0.3937	0.923077	9.8	0.0216
12	0.3543	0.956522	9.86	0.0169
13	0.3307	0.936364	9.54	0.0137
14	0.2992	1	9.51	0.0108
15	0.2598	0.969231	9.8	0.0082
16	0.2598	0.94	8.83	0.0071
17	0.2598	0.881667	7.89	0.0062
18	0.2512	0.885714	7.25	0.0052
19	0.2512	0.833333	6.36	0.0046
20	0.2512	0.86	5.53	0.004
21	0.2512	0.83	4.67	0.0035
22	0.2512	0.8	3.84	0.003
23	0.2512	0.77	3.04	0.0026
24	0.2512	0.74	2.27	0.0023
25	0.1884	0.71	2.04	0.0015
26	0.1884	0.68	1.33	0.0013
27	0.1884	0.65	0.65	0.0011

$Ro = 6.4$, $G = 13$, $r = 0.138$, $\lambda = 1.14$

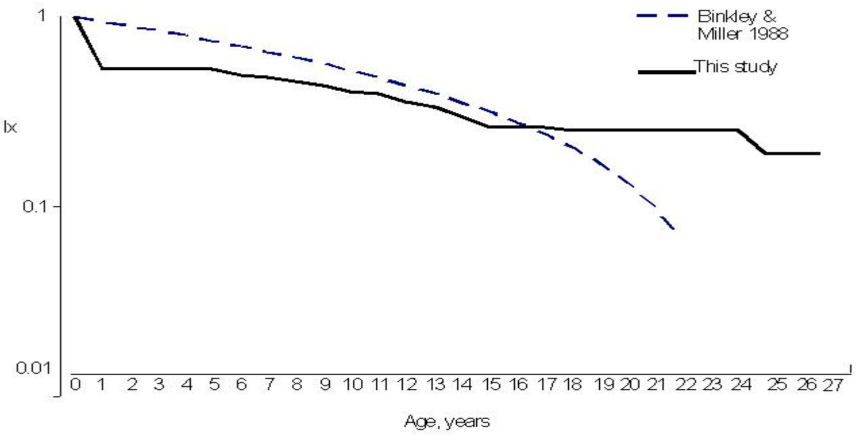

Fig. 4. Age-specific survivorship (l_x) for Whooping Cranes. Curves estimated in this study and by Binkley and Miller (1988).

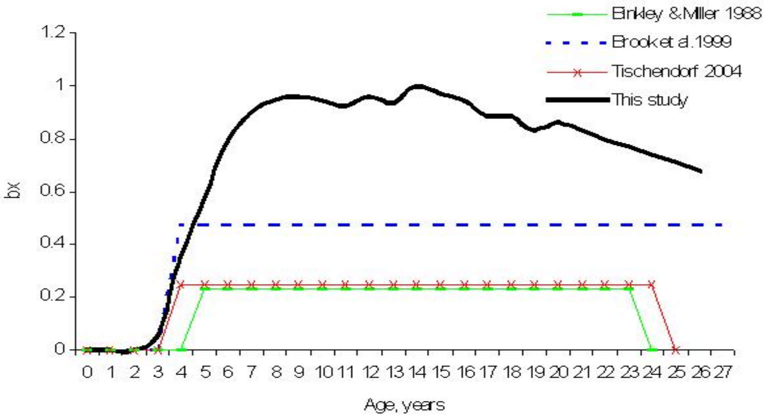

Fig. 5. Comparison of age-specific fecundity (b_x) for Whooping Cranes. Curves estimated in this study and those reported by Brook et al. (1999), Binkley and Miller (1988), and Tischendorf (2004).

The ages at first reproduction among banded females were 3, 4, 5, 6 and 7 years, and the proportions of females estimated to have nested, produced eggs and hatchlings at these ages were 6.06%, 36.4%, 24.2%, 21.2% and 12.1% respectively. The oldest age at reproduction was 27 years (Appendix A: Table A3). Values of b_x varied noticeably among the 9 cohorts represented by banded females (Appendix A: Table A4).

Estimates of reproductive value (V_x) (Table 2) showed the age-specific contribution to the future ANWR-WBNP Whooping Crane population made by females from ages 3 to age 27. The maximum value was 12 individuals between ages 3 and 6, and decreased thereafter to less than 1 individual at age 27 (Fig. 6).

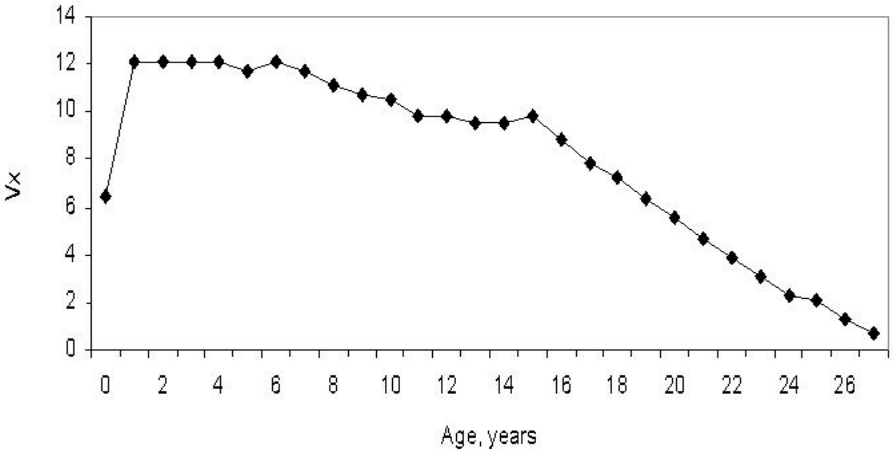

Fig. 6. Age-specific reproductive values (V_x) for Whooping Cranes estimated in this study.

Estimates of the proportion of the Whooping Crane population distributed in each age class (C_x) (Table 2) showed a highest proportion of individuals at age 0, which represents numbers of eggs. The stable age-class distribution for Whooping Cranes estimated in this study compared with C_x obtained by Kuyt and Goosen (1985), Binkley and Miller (1988), and Link et al. (2003) indicated differing proportions of individuals distributed in the various age classes. From this study, the proportion of Whooping Crane (C_x) individuals and the eggs needed to be produced yearly at WBNP were 25% for age 0, 49% from ages 1 to 6, in aggregate, and 26% for all ages ≥ 7 in aggregate (Fig. 7, Appendix A: Table A5).

The estimated value of r (0.138) (Table 2) was much higher than the value reported by either Miller et al. (1974) ($r = 0.020$) for the period from 1938 to 1956, or by Binkley and Miller (1988) ($r = 0.043$) for the period from 1957 to 1987 (Appendix A: Table A6).

In my study, values of r estimated from each of the 9 cohorts, individually, ranged from –0.173 to 0.200 with a mean (± 1 SD) of 0.099 (± 0.100), and values for *Ro*, *G*, and λ also differed among cohorts (Appendix A: Table A7).

The instantaneous rate of increase of the Whooping Crane population was converted to the finite rate of increase, lambda, $\lambda = e^{0.138} = 1.148$. $\lambda = 1.04$ for Binkley and Miller (1988), and $\lambda = 1.05$ for Mirande et al. (1997).

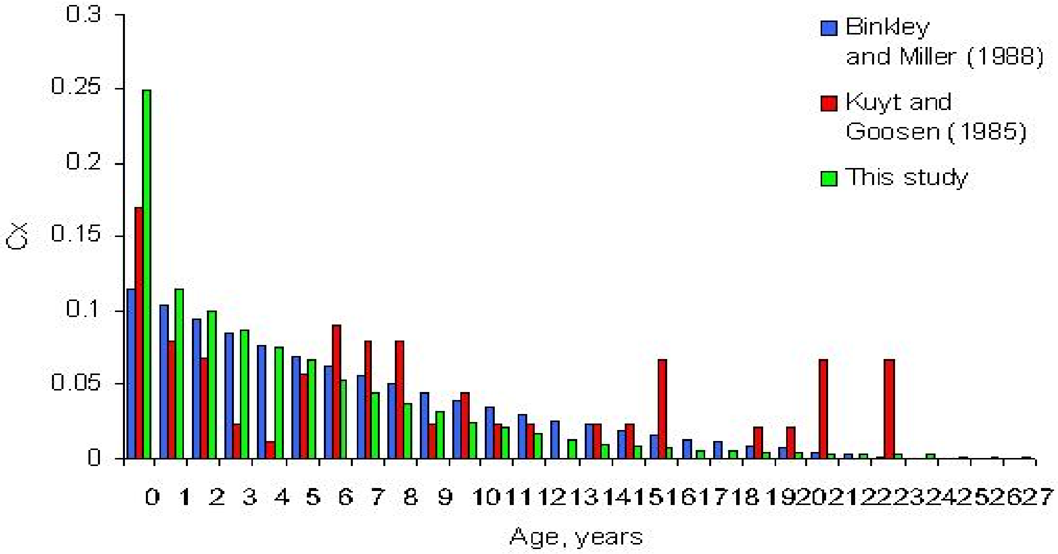

Fig. 7. Comparison of stable age-class distribution (C_x) for Whooping Cranes. Values estimated in this study, versus those reported by Binkley and Miller (1988), and by Kuyt and Gossen (1985).

Deterministic population projections to the year 2004, based on estimates of *r* = 0.02 from Miller et al. (1974) and *r* = 0.04 from Binkley and Miller (1988), reached values below the population observed in 2004 and, with *r* = 0.049 from Mirande et al. (1997), reached a value above the observed (Fig. 8). The set of deterministic population projections until 2035, developed with all values of *r* obtained in this study and from previous studies (but not presented in earlier papers) (Appendix A: Table A8), showed that some values are unreasonably high and others could lead to extinction. The range was from 1 (with value of *r* from cohort 1988) to 103,369 (with *r* from cohort 1982).

Analysis of the population growth curve from 1967 showed that phases of decrease occurred at approximately 6- and 7-year intervals. Phases of decline and stability occurred 5 times, for one or two consecutive years. Phases of population increase lasting 7, 5, 3, and 2 years occurred once, 6 year increases occurred twice, and peak-to-peak periods from 1961 – 2004 had 9.5 ± 1.29 (mean, SD) years of duration (Fig. 3) (Appendix A: Table A9).

Stochastic population projections with the model, using historical values of lambda (1.08), produced curves of growth with oscillations that had up, down, and stability phases, similar to those observed in past fluctuations. Also, the frequency of occurrence and duration in years of simulated oscillations were similar to those observed from 1967 to 2004 (Fig. 9).

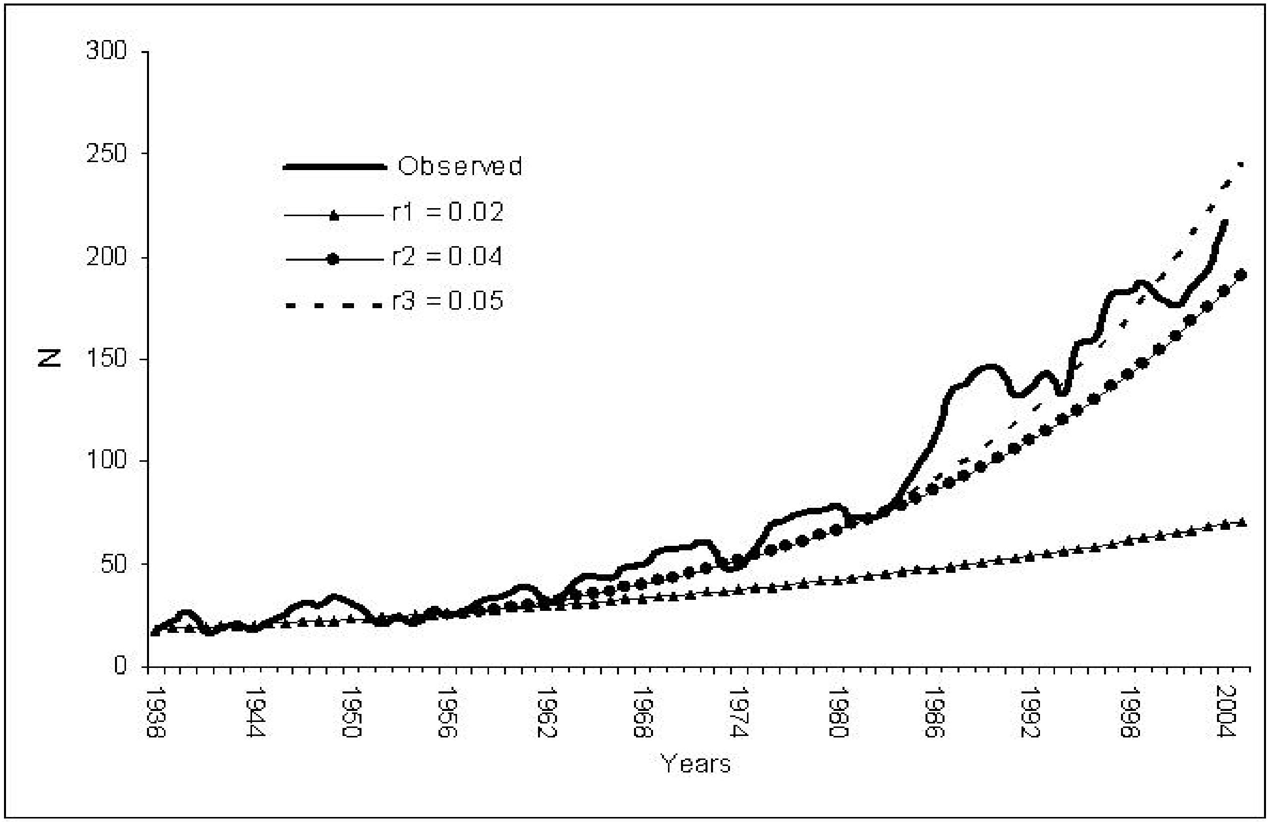

Fig. 8. Comparison of deterministic population projections for Whooping Cranes (N), from 1938 to 2004. Curves calculated with values of *r* = 0.02 from 1938 – 1956 (Miller et al. 1974), *r* = 0.04 from 1957 – 1987 (Binkley and Miller 1988), and *r* = 0.05 from 1983 – 2004 (Mirande et al. 1997); *r* represents the intrinsic capacity for increase of the population.

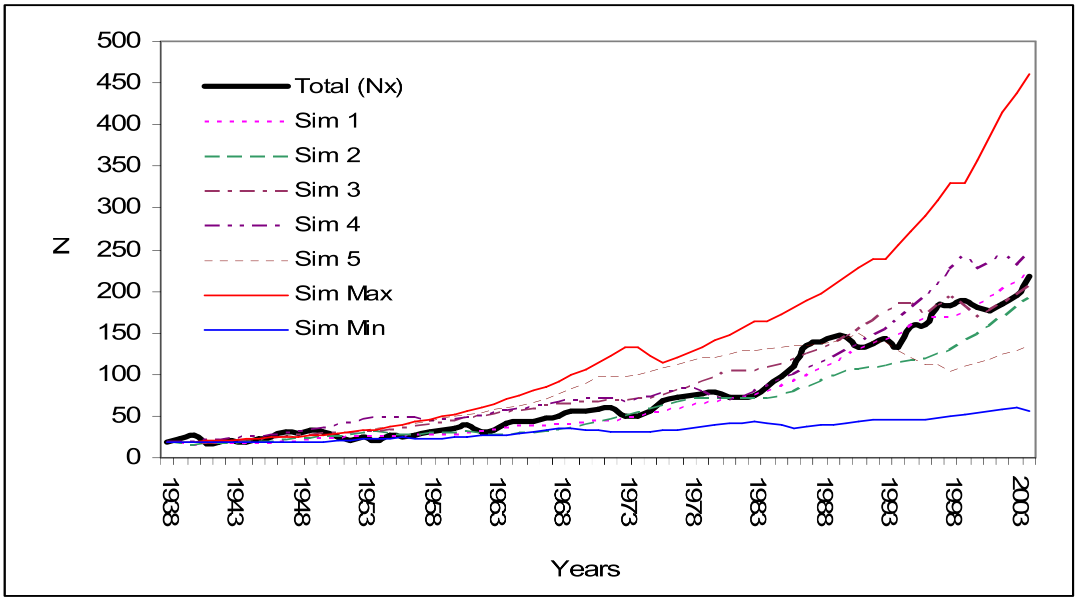

Fig. 9. Comparison of the number (N) of Whooping Cranes observed from 1938 to 2004 (thick black line) and stochastic projections (dashed lines λ ≤1.05, *r* = 0.05). Projections Sim 1 to Sim 5 represent 5 of 40 simulations similar to historical pattern. Sim Max and Sim Min (thin continue red and blue lines) represent simulations of number of Whooping Cranes, maximum and minimum, respectively.

Stochastic population projections for the year 2035, with values of λ≤1.05 (Appendix A: Table A9) for up phases, reached 1,000 individuals, with a probability of 2.5%. Simulations with lambdas for up-phase ≤1.08 (Appendix A: Table A9; maximum historical lambda observed) reached 1,000 individuals with a probability of 15%. Finally, projections for 2035 with lambdas ≤1.14 (value from the life table) reached 1,000 individuals, with a probability of 40% (Table 3).

Table 3. Number (N) of Whooping Cranes predicted for 2004 and 2035, with stochastic model that projects population growth with oscillations. Number of simulations N = 40, mean ± 1SD, N Maximum – Minimum, and probability to yield in 2035 $N \geq 1{,}000$ individuals (down-listing criterion). Lambdas used randomly in the model were: for periods of decline (0.957±0.018), stability (1), and for growth, a set of simulations changing lambda to: (a) 1.05 (Binkley and Miller 1988), (b) 1.08 (max λ, from historical period of growth 1982 - 1989) (Appendix A: Table A9), and (c) 1.14 (from the life table obtained in this study) (Appendix A: Table 8).

	Projections from 2004 to 2035		
Lambda (λ)	No. individuals Mean ± 1SD	Model Yield Min-Max (N)	Probability $N \geq 1{,}000$ (%)
1.05 (Binkley and Miller 1988)	749 ± 149	508 – 1004	2.5
1.08 (Max. Hist. 1982 – 1989)	736 ± 2,236	343 – 1,298	15
1.14 (New Life Table, this study)	1095 ± 854	239 – 4,112	40

DISCUSSION

The Whooping Crane life table (Table 2) summarized the observed mortality and fecundity schedules, and was used to estimate net population change, giving values of Ro, G, V_x, C_x and λ. The value of r obtained from the new life table was greater than the value estimated by Binkley and Miller (1988). This means that the Whooping Crane population may have a higher rate of intrinsic growth than previously reported, and its potential rate (0.14) allows faster increase and higher probability of continued existence, if other variables continue on the same trend. This value of *r* depends on species fertility, reproductive rate (*Ro*), longevity, and generation time (*G*) (Begon et al. 1996, Krebs 2001). The new Whooping Crane data yielded higher values for fecundity and survivorship, which determined values of *Ro* and *G*, in this study (Appendix A: Table A1).

Higher fertility in the Whooping Crane population was observed in the comparison between the age-specific fecundity curve from this study and constant values of fecundity rate used by Binkley and Miller (1988), Brook et al. 1999, and Tischendorf 2004 (Fig. 5). I found that some of the factors related to fertility that increased the value of *r* in this Whooping Crane population study were (1) fecundity was recorded from age 3, and a high proportion of females bred at age 4 (50% of the cohort in 1986 females bred at age 4); whereas, the age at first breeding used by Binkley and Miller (1980) in their model was 5 years, based on information from captive females (Erickson 1976). (2) I analyzed a larger volume of data from banded females, while age-specific data was not available in previous studies**.** (3) More reproductive events, with females breeding successfully up to 27 years old, were recorded. Note that previous studies grouped all individuals into pre-reproductive and reproductive age classes, and fecundity was taken as the same constant value for all reproductive ages.

In addition, the higher value of *r* may be explained by increased age-specific survival rate (Table 2, Fig.4). The increased survivorship tended to be, and remained, high; although, a drastic declination occurred for the first age. This survivorship, of only 52% at age 0, resulted from high mortality of eggs and chicks at WBNP, mortality of young during fall migration, and mortality of young at the wintering ground, according to banded birds. These results confirmed observations by Kuyt (1981a, 1981b), Kuyt and Goosen (1987), Lewis et al. (1988), and Bergerson et al. (2001) on fledged mortality. It is not possible to compare values of survivorship for the Whooping Crane population at age 0 with the rates from previous studies for the following reasons: (1) differences in definition of age class 0 to determine survivorship [Binkley and Miller (1980, 1988) defined age 0 based on young arrived at ANWR, while in this study age 0 is defined from eggs in WBNP] and (2) based on this criteria for l_o, this rate for age 0 is reported for the first time on this species and is very important information for population projections, management plans, and contribution for ecology, due to the lack of information on this age class in many species of animals and plants (Begon et al. 1996).

The rates of survivorship from age 1 to age 5 obtained in this study were below Binkley's and Miller's values, and remained stable during those years. This stable survivorship is probably due to the gregarious nature of the sub-adults group. Sub-adults consistently arrive, feed, rest, and depart together; in addition, flocking behavior by non-breeding sub-adults enables them to avoid predators and enhances likelihood of finding small salt marshes and prey (Bishop and Blankinship 1981). Analysis of the same group of values for survivorship showed a higher survivorship rate for older ages than those values from Binkley and Miller (1988), because, in this study, Whooping Cranes showed a longer life span and a gradual mortality until 27 years, from banded birds (Fig.4).

The differences observed between Binkley and Miller (1988) and this study's curves can be attributed to procedures used to determine survivorship. For example, Binkley and Miller (1980, 1988) survivorship rates were obtained from a least squares regression for a life span of 24 years; in contrast, I used Kaplan-Meier survival analysis for the 27 ages. Lastly, survivorship curves also may vary drastically due to environmental factors (Odum and Barret 2005). After 1980, environmental conditions have been found to be substantially different compared to the years studied by Binkley and Miller (1980, 1988), based on environmental records from Johns (1997) and Kuyt and Barry (1992).

Values obtained from the Whooping Crane life table (Table 2), Ro, V_x, G, and C_x, showed that these parameters were different from Binkley and Miller (1988) values. These values (Ro, V_x, G) were estimated with data from their life table for this study, with the exception of C_x which was estimated by them and published. The net reproductive rate (R_o), 6.4, in this study was higher than the 1.59 obtained with data from Binkley and Miller (1988), suggesting that the Whooping Crane population was replacing itself faster than expected by Binkley and Miller (1988). The mean generation time, $G = 13$, indicates that Whooping Crane population has a longer generation time, in comparison with value of G obtained from Binkley and Miller (1988), which was 10 years.

The results of this study found that the stable age-class distribution obtained (C_x) (Table 2), specifically, the proportion of individuals at age 0 (eggs), cannot be compared with age 0 from age-structures previously published (Binkley and Miller, 1983, 1988, Kuyt and Goosen 1985, Link et al. 2003) because the criteria for age 0 used was different from the criteria established in this research. The proportion of individuals from ages 1 to 3 was compared, and also is higher than previous studies, indicating a larger number of individual sub-adults and birds from age 4 to age 27. The proportion of individuals in each age class followed a subsequent decrease, which is different from the age composition presented by Kuyt and Goosen (1985), who obtained more individuals in medium and older ages classes (Fig 7). The difference observed between the three estimations of C_x could be explained by different reasons (Table 2, Fig. 7, see also Appendix A: Table A6). The stable-age distribution derived by Binkley and Miller (1983, 1988) was estimated with age-specific survivorship for 24 age classes and constant fecundity. Kuyt and Goosen (1985) used survivorship data from banded and non-banded birds. Link et al. (2003) used aggregate age-class data from 1940 to 2001 assuming that there was no age-specific variation in survival. I believe that the age structure of the Whooping Crane population has changed from 20 years ago, and the age structure from Kuyt and Goosen (1985) was probably more accurate. Changes occurred in the proportion of individuals as a result of increased survivorship of older ages classes and increased numbers of young produced. The actual age structure obtained with this study shows a stable age distribution, with a pyramidal shape in the distribution of individuals, which is characteristic of an expanding population (Begon et al. 1996).

Growth rate of the ANWR-WBNP Whooping Crane population, as reflected in the value of *r,* has changed several times, since 1938. Two distinct periods were identified, the first by Miller et al. (1974), the second by Binkley and Miller (1980); and, this study has identified the third period, from 1986 to 2004 (Fig. 3). The first period, with slow population growth, was described with few breeding adults, sub-adults, and young. Mirande et al. (1993) estimated only 3 to 4 breeding pairs in the 1940s, and 5 to 6 in the 1950s. In 1956, a marked imbalance of the age classes during this period was mentioned by Binkley and Miller (1980). The increment of the intrinsic rate of population growth observed from 1956 to 1984 produced a slow increase in number of adult individuals, from 38 to 51 in 1967-1972, and to 110 in 1986. Miller et al. (1974) reported that the Whooping Crane population was in the initial phase of exponential increase, and the second period observed represented an early stage in a logistic growth curve. Further, exponential increase of the population was explained by Binkley and Miller (1988) as the result of a stabilizing death rate, and that the population had suffered no major environmental catastrophes since the annual census began in 1938. During the last and current period (from 1986 to 2004), the population has continued with an exponential increase, as a consequence of increased birth rate, stable death rate, extended longevity, and better environmental conditions after the 1980s, with exception of years 1980, 1990, and 1991 (John 1993, Kuyt and Barry 1992, Lewis 1995).

Deterministic projections of Whooping Crane population growth until 2004, with earlier rates from Miller et al. (1974) and Binkley and Miller (1988), did not reach 2004 Whooping Crane numbers observed (Fig. 8) with a constant population growth assumption. It appears that a change in rate of increase occurred in the Whooping Crane population 20 to 30 years ago. This change was identified by observation on values of r for the previous two periods studied (mean and standard deviations) (Appendix A: Table

A5). The third value used for deterministic projection $r = 0.05$ approached more closely to the number of individuals observed in 2004. This included values of r (from 1983 to 2003) when the population experienced higher historical values of r and was also the value used by Mirande et al. (1997) for PVA projections (Appendix A: Table A5).

Population growth projections in this study included population fluctuations. Therefore, the observed fluctuations were used in the simulation population model to produce the stochasticity required to generate fluctuations in a simulated population growth. Whooping Crane population fluctuations observed in the curve of growth from 1961 to 2004 (Fig 3) suggested a periodicity of almost 10 years between peaks of growth (mean ± SD = 9.5 ±1.29) and analyses of fluctuations in Whooping Crane population done by Boyce (1987), Boyce and Miller (1985), and Nedelman et al. (1987), which responded to a decadal cycle. However, some correlations with decadal periodicity were weak, and although the evidence was consistent for adults, young seemed not to have experienced similar cycles. Based on this discrepancy, I found that a closer analysis on population fluctuations could better explain the variability observed through the period of record. The stochastic model developed for this objective, based on the duration of each phase (decline, stability, or increase) from 1967 to 2004 (Fig. 9), suggested that it is possible to mimic historical population fluctuations.

The stochastic model developed showed that rates of increase lower than 0.05 ($\lambda = 1.04$) do not yield 1,000 individuals for simulations until year 2035, as was reported by Mirande et al. (1997). The stochastic model indicated that only with historical values of lambda, $\lambda = 1.08$ (observed from 1982 to 1989, $r = 0.07$) is it possible to yield 1,000 individuals in 2035, with a 15% of probability; and, with lambda from the life table (λ = 1.14), the probability increased to 40% (Table 3).

These results were only compared with the value of 1,000 individuals for year 2035, which was obtained from the PVA by Mirande et al. (1997); however, these results could be compared with other stochastic projections from other population viability analyses that included stochastic variation in breeding structure (Brook et al. 1999), and be discussed as to levels of similarity or discrepancies.

I stochastically projected Whooping Crane population numbers into the future, as previous authors have done. My projections were like the PVA done by others (e.g., Boyce 1992), in that I assumed no catastrophes and no stochasticity in mate availability. The stochasticity that I used reflected a random selection of historical values of population growth rates. These values had magnitude, frequency, and duration representing the various phases in the historical record. Results suggested a 40% probability that Whooping Crane numbers will reach 1,000 individuals by 2035. Thus, the number of individuals required for down-listing could be reached if the population continues growing at a maximum rate of λ = 1.14, and experiences similar fluctuations as in the past; however, there exists a 60% possibility that this number will not be reached by 2035.

Natural habitats vary continually. They are never consistently favorable or consistently unfavorable conditions. When environmental conditions are favorable, numbers increase; when they are not favorable, numbers decrease or remain stable (Begon et al. 1996). The what, why, when, and where of the environmental factors, causing these ups and downs in the Whooping Crane population is the objective to be developed in the next chapter, Chapter III.

CONCLUSIONS

The only free-living, non-experimental Whooping Crane population demonstrated an age-specific survivorship rate different from that observed in previous studies. The curve of survivorship, obtained from a 27 year record from 12 cohorts of banded individuals, showed lower survivorship values for ages (x) ≤15 than those reported by Binkley and Miller (1988), and higher values for ages (x) ≥16. The survivorship curve illustrated that rates from ages 1 to 16 decreased gradually, and after age 17, rates remained more stable, until age 27.

This study also found that at age 0, from egg to juvenile, the rate of survivorship declined to 52%. This information is reported for the first time for the species, and was based on records of banded birds and identified nests.

Whooping Crane fecundity rates obtained in this study were age specific, and showed higher and different values than reported in previous studies. Fecundity rates increased exponentially from $b_x = 0.05$ at age 3 to $b_x = 0.9$ at age 7, and remained stable with little fluctuation ($0.90 \leq b_x \leq 0.95$) until age 14, when females reached the maximum ($b_x = 1$). Then fecundities declined gradually until age 27, with $b_x = 0.67$. These results contrasted with ($b_x = 0.47$) the highest value of fecundity previously reported (Brook et al. 1999), which was lower and constant for ages 4 to 23.

The demographic statistics obtained from the new life table of the Whooping Crane were: the net reproductive rate $Ro = 6.4$/y, the generation time $G = 13$y, the intrinsic instantaneous rate of population increase $r = 0.138$, and the finite annual rate of increase $\lambda = 1.148$. In general, all demographic statistics were higher than values estimated from previous studies (Ro=1.59, $G = 10$, $r = 0.04$, $\lambda = 1.04$) from Binkley and Miller (1988). The intrinsic rate of Whooping Crane population increase changed from 0.02 (Miller et al. 1974) for years from 1938 to 1956, to 0.04 (Binkley and Miller 1988) from 1957 to 1982, to finally reach 0.138 **(**from 1977 to 2004) in this study. This Whooping Crane population is increasing at a higher rate in more recent years, because of higher fecundity, higher survivorship, and more favorable environmental conditions in WBNP and ANWR, with the exception of the years 1980, 1990 and 1991.

The Whooping Crane age class distribution (C_x) obtained in this study yielded the proportion of number of individuals (as eggs) required to be produced at WBNP, to yield the observed number of individuals at age 0 at ANWR. These proportions were 25% for age 0, 49% for ages 1 to 6 and 26% for ages ≥7. This larger number of individuals at first ages produced a population with a pyramidal shape, which is suggestive of a population in recovery.

The stochastic model from this study projected by 2035 a Whooping Crane population of 1,000 individuals, with 40% probability; and, values of $r = 0.14$ were generated from the new life table. In contrast, projections with values below the maximum historical rate of 0.08, and from Binkley's and Miller's (1988) rate of 0.04, indicated a very low probability for the Whooping Crane population to be down-listed in 2035.

CHAPTER III

EFFECTS OF ENVIRONMENTAL FACTORS ON WHOOPING CRANE DEMOGRAPHY

INTRODUCTION

From October to March, the world's only natural population of Whooping Crane (*Grus americana*) winters at the Aransas National Wildlife Refuge (ANWR) and adjacent areas along the Texas Gulf Coast. From late April through mid September, the population inhabits marshes, bogs and shallow lakes at Wood Buffalo National Park (WBNP) and adjacent areas in northwestern Canada and breeds there. From early to mid April until late September, during migration, the population uses areas in southern Saskatchewan, the central portion of the Platte River in Nebraska, and the Quivira NWR in Kansas as stopovers (Howe 1985, Kuyt and Barry 1992, Lewis 1995, Chávez-Ramírez personal communication) (Fig. 1) (Plate 1).

Although the Whooping Crane has returned from the brink of extinction, historical data have shown several periods of decline over the years. Lewis (1995) proposed that the single most important factor regulating Whooping Crane numbers is habitat quality, which is defined as suitable wetlands and food resources on the nesting grounds and good food resources on the wintering grounds. For all species, environmental relations are important in population distribution, abundance and success (Odum and Barret 2005). However, species and individuals respond in different ways to abiotic and biotic factors, such as temperature, light and other environmental variables. For example, climate changes affect species physiology, phenology, abundance and distribution (Hughes 2000). The identification of these environmental factors and Whooping Crane responses to them is the main objective in this chapter.

Plate 1. Whooping Crane habitats. Wetlands at WBNP breeding ground in Canada, at Platte River during spring and fall migrations in Nebraska, and at ANWR wintering ground in Texas. Photo credits: Brian Johns CWS, http://platteriver.unk.edu, and http://www.texmaps.com.aerials/09san-antonio-bay/slides/332896501.

Temperature is important as a controlling factor, and its variation is significant ecologically and influences bird populations through the control of food resources (Krebs 1994). For temperate birds, such as the Whooping Crane, temperature variability has a stimulating effect, including extreme levels, and has a direct influence on bird survival, especially on the young (Odum and Barret 2005). In addition, temperature has been identified as a factor that impacts adult survival, breeding success and the proportion of breeders (Jenouvrier et al. 2005). Also, temperature is especially important in the timing of water birds' migration, particularly in relation to arrival conditions at breeding or wintering sites (Weller 1999).

Water is a primary driver of resource dynamics in wetland ecosystems. Hydrology dictates the timing of seasonal plant growth and animal community dynamics (Weller 1999). Water in the form of precipitation, distributed over the year, is an extremely important factor for organisms, and may determine the timing of wetland water conditions (Krebs 1994). In addition, extreme temperature and weather events, such as hailstorms, may kill birds directly, by creating extremes beyond their limits of tolerance. Exceptionally cold winters, storms or the combination of a cold wet spring followed by a drought may cause starvation and mortality of young (Weller 1999).

Atmospheric processes operating at different spatial and temporal scales, and reflected in climate indices such as El Niño/Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO), are known to be associated with local climate in the Pacific Northwest (PNW). ENSO originates with anomalies in tropical sea-surface temperatures, but affects climate across western North America, especially winter conditions. El Niño conditions tend to produce warmer, drier winters; and, La Niña conditions typically produce cooler, wetter winters in the PNW (Hessl et al. 2004). Like ENSO, in North America, the PDO is a long-lived El Niño-like pattern of Pacific climate variability. The warm phase of PDO is correlated with El Niño-like North American temperature and precipitation anomalies; while cold phase of PDO is correlated with La Niña-like climate patterns (Latif and Barnett 1996, Zhang et al. 1997, Mantua et al. 1997, Mantua and Hare 2002). The PDO Index is defined as the leading principal component of North Pacific monthly sea surface temperature (SST) variability, and also is related to sea level pressure (SLP). The PDO may also influence summer rainfall and drought in the U.S. (Cayan 1996, Bitz and Battisti 1999) (Appendix B. Fig. B32).

During the PDO cold phase, cold and wet conditions in northwestern North America tend to coincide with anomalously warm and dry periods in the southeastern US and Mexico (Mantua and Hare 2002). During a PDO warm phase, the weather events are reversed (Hamlet and Letternmeier 1999, Nigam et al. 1999*)*. The geographic area used by the Whooping Crane population during its life cycle may be affected by PDO, due to the breeding locations in Canada (western North America, PNW) and wintering grounds in Texas (South U.S.). The species' fly-way lies between the two locations.

Mortality

The period of highest mortality for Whooping Cranes is during the first months of life (Lewis 1995). Chick mortality increases during late summer, when water levels in the breeding area decline steadily, suggesting a relationship between lower water levels and predation on young cranes (Kuyt 1981b). Other causes of mortality on the breeding ground at WBNP are predation from foxes and ravens, exposure, infection, unusually low temperatures or blizzards in late spring or early fall, as well as severe hailstorms, flooding, parent-borne disease, food scarcity and uncontrolled fire (Erikson 1976, Bergerson et al. 2001).

Migration-route mortality has been estimated to account for between 60% and 80% of the annual losses of fledged Whooping Cranes during fall migration (Lewis et al.

1988). In contrast, Kuyt and Goosen (1987) estimated fledgling survivorship at over 76% during this period, based on survivorship of chicks banded in Canada from 1977 to 1984. Subadult and adult mortality from April to November is three times greater than during winter (Lewis et al. 1988). However, Bergerson et al. (2001) described high survivorship during spring migration (March, April and May). Despite all efforts with radio-tracking during 1981-1984, Whooping Cranes mortality rates during fall and spring migrations have not been estimated (Howe 1985).

Lewis (1995), when studying mortality, found 51 dead Whooping Cranes on the wintering grounds between 1950 and 1990. The probable causes of death for wintering cranes were shooting, avian tuberculosis or a closely related disease, avian predation, traumatic injury (probably incurred during fall migration), and predation by coyotes and bobcats, which are the only large predators found on the refuge (Lewis 1995, Hunt et al. 1985).

Fecundity

Body "condition," as judged by bodyweight and fat storage, is a major requirement for migration and breeding in many bird species, especially those that fly long distances between stops (Weller 1999). When birds encounter either difficult environmental conditions or shortages of other requisites, population growth can be affected by fluctuations in reproduction (Pianka 1994).

Resource shortages during a critical period, such as the pre-migration stage, may affect survival during migration and reproduction during the upcoming breeding season. Reproductive success may depend on the accumulation of adequate energy reserves while on the wintering grounds (McLandress and Raveling 1981, Joyner et al. 1984). More directly, a limited availability of resources, or the time in which to procure them, during any portion of winter, may directly affect winter survival and overall fitness (Chávez-Ramirez 1996). The definition of breeding success considered by Chávez-Ramirez (1996) is based on breeding pairs that arrive at ANWR with chicks. However, breeding success has also been defined in terms of the number of eggs laid and fertility (Nelson et al. 1996), or measured by the number of pairs found to be nesting (Miller et al. 1974). Under some conditions of food availability, Whooping Cranes on the ANWR may have difficulty meeting maintenance requirements and building their energy reserves needed for spring migration (Krapu et al. 1985, Chávez-Ramirez 1996).

The sources of energy and lipid required for Whooping Cranes come from a diet consisting largely of blue crabs (*Callinectes sapidus*), stout razor clams (*Tagelus plebeius*), wolfberries (*Lycium carolinianim*), and acorns (*Quercus virginianus*), and each of them has a marked difference in nutrient composition (Nelson et al. 1996). Blue crabs constituted 42.9% of the total mean volume of winter food consumed (Hunt and Slack 1989), and made up a mean of 88% of the species' percent daily energy uptake during winters 1992-93 and 1993-94, according to Chávez-Ramirez (1996). Food restriction or species distribution within estuarine environments are often affected by temperature and salinity, as estuaries are exposed to large diurnal, seasonal and yearly fluctuations in salinity, temperature and dissolved oxygen (Leffer 1972). Harsh winter conditions are a potentially important source of blue crabs stock loss (Rome et al. 2005).

The influence of both temperature and salinity on blue crab growth, respiration and mortality is well documented by laboratory and field studies from Chesapeake Bay. Low-temperature tolerance decreases in lower salinity waters; thus, the physiological stress of low salinity and extreme low temperature may have a synergistic effect in lowering blue crabs tolerance to winter conditions (Guerin and Stickle 1992, Rome et al. 2005). Rome et al. (2005) also observed that the highest mortality rates in blue crabs were found in the lowest temperature and salinity conditions in both field and laboratory, and that life stage was an important predictor in over-wintering mortality. Finally, studies on the abundance of blue crabs, relating to density and distribution relative to environmental factors, have been done recently by Jensen and Miller (2005} and Hamlin (2005), demonstrating that a significant decline in winter abundance and concurrent changes in distribution in the field appear to be related to inter-annual differences in freshwater flow and density-dependent habitat selection.

The relationship between Whooping Crane demography and environmental factors; including wetland suitability, water depth and net-evaporation, wet or dry conditions (precipitation), temperature (maximum, minimum and average), salinity or freshwater inflows, food resources in the breeding and wintering grounds and stopovers; are important factors regulating Whooping Crane numbers.

The data set described in the present chapter represents the first attempt to 1) measure simultaneously all environmental factors from the breeding and wintering grounds and the main stopover of the migratory Whooping Crane, including PDO global climatic effect and 2) integrate all demographic components of the different life-stages of the Whooping Crane. It is also the first attempt to use path analysis to interpret this type of data set for Whooping Cranes.

In this study, I analyze the role of environmental factors in the life cycle of the Whooping Crane population from 1967 to 2004. I also determine the relationship of each important environmental factor identified, with the fecundity and mortality for specific life stages of the Whooping Crane. The goals of this chapter are to address the following questions: (1) What are the environmental factors at ANWR, NE (during spring and fall migrations) and at WBNP that regulate the Whooping Crane population? (2) Can I explain the variability of mortality and fecundity based on the specific effect of each environmental factor? (3) Do environmental factors at ANWR affect the pre-migratory and pre-breeding conditions of the Whooping Crane with regard to reproductive success and, if so, how? (4). Through the history of Whooping Crane population growth, what environmental factors produced fluctuations in the population and how do they do so? (5) What demographic factors were responsible for Whooping Crane population declines during each period?

Answers to these questions will help improve the understanding of environment - bird population interactions and facilitate incorporating biological processes in a Whooping Crane demographic model.

METHODS

This study was developed with historical information on the Whooping Crane population and the environmental factors that potentially affect different stages in its life cycle (Fig.10). I assumed no density-dependent factors were regulating this population

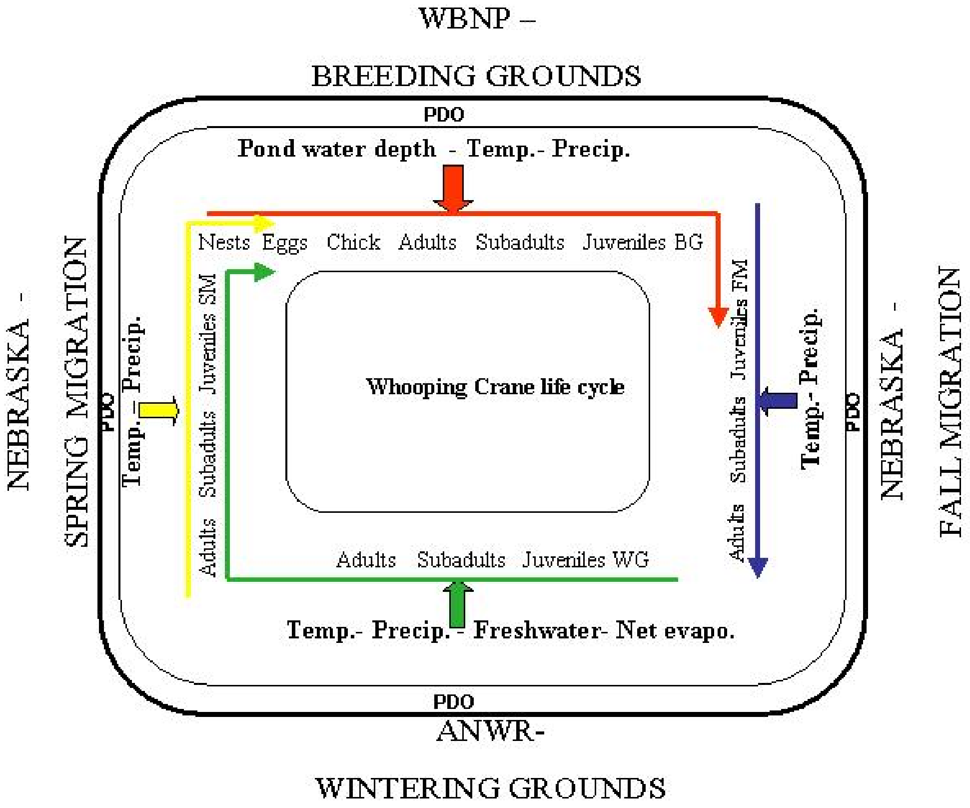

Fig. 10. Whooping Crane population life cycle and environmental factors associated. Arrows represent hypothetical effect of environmental factors and extension of the effect on the age groups of the population (nests, eggs, chicks, juvenile, subadults, and adults). Aransas National Wildlife Refuge (ANWR) - wintering grounds, Nebraska during Spring Migration (NE-SM), Wood Buffalo National Park (WBNP) - breeding grounds and Nebraska during Fall Migration (NE-FM).

because 1) the density of the population from 1938 to 2004 is low; 2) the number of territories in ANWR and adjacent areas has been increasing with the increment of breeders during the last 37 years (Stehn, winter reports 1985 – 2004) and, 3) suitable habitat in Canada is still available (only 12% is used) (Tischendorf 2004). The density-independent abiotic factors selected as main regulators in Whooping Crane biology were temperature and precipitation (Begon et al. 1996). I also chose three other factors related to population regulation, as associated with Whooping Crane mortality and fecundity: pond water depth in Canada (CWS), associated with chick mortality, net-evaporation (precipitation – evaporation); and, freshwater inflows to Aransas estuary, from Texas Water Development Board (TWDB).

I obtained historical information on temperature, precipitation and pond water depth on the summer ground (WBNP in Canada) from the Canadian Meteorological Service. The temperature and precipitation data from Nebraska (NE), where the peak of observations during fall and spring migrations occur, were ascertained from the National Oceanic and Atmospheric Administration (NOAA).

The data referring to the precipitation and temperature at the wintering ground at ANWR in Texas, were obtained from National Oceanic and Atmospheric Administration (NOAA) and National Climatic Data Center for Texas. The freshwater inflow and net evaporation from Guadalupe Estuary were gathered from TWDB, USGS. The Pacific Decadal Oscillation (PDO} index was obtained from the Joint Institute for the Study of the Atmosphere and Ocean (JISAO). I identified these variables as independent variables, with possible effect on Whooping Crane demography. Their description, units, date and source are in Table 4, and their associations with the grounds and life cycle are shown in Fig. 10.

I used changes in the population of the Whooping Crane at the level of 1) brood failure, 2) clutch size reduction, 3) egg mortality during periods of egg collection and no collection, 4) chick mortality, 5) juvenile fall migration mortality, 6) April - November mortality, 7) juvenile winter mortality, 8) adults and subadult winter mortality, 9) total winter mortality, 10) annual mortality and 11) lambda (finite rate of population growth) as dependent variables to represent variability in Whooping Crane demography. These dependent variables are described, and units, date and source are in Table 5. Their association with the grounds and environmental factors are illustrated in Fig. 10.

I organized all data on each independent and dependent variable in a data base, in order to 1) obtain descriptive statistics, 2) develop regression analysis with multiple variables, 3) develop path analysis, 4) describe annual pattern distribution, and 5) identify historical peak values from each variable for ecological analysis.

Statistical analysis

I used simple linear regression (SPSS 11.0 for window) to examine the strength of the association between dependent variables and independent variables, to explore relationships among variables and to identify candidate variables for inclusion in the path analysis.

I used linear regressions of the formula $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \epsilon$, to relate environmental conditions to mortalities, and fecundity (breeding failure or clutch size reduction), where Y represented the dependent variables, for example mortality of a

Table 4. Database of environmental factors in the summer and winter ranges and flyway of the only-free Whooping Crane population.

Location	Independent Variables	Description	Units	Date	Source
Breeding ground, (BG), (WBNP) -. CANADA	Precipitation (ppt BG)	Total mean monthly precipitation: March to September, March, March-May, June, June-July, Jun – Aug.	mm	January to December, 1941 to 2001	Station Fort Smith - Canadian Meteorological Service
	Temperature (temp BG)	Mean monthly temperature. March to September, March, March-May, June, June-July, Jun – Aug	°C	January to December 1942 to 2004	Station Fort Smith, NT- Canadian Meteorological Service
	Ponds water depth (pwd BG)	Mean water depth at 1m from distance to nest	cm	May 1974 to 1996	Canadian Wildlife Service, J. Brian Unpublished
Fall (FM) migration / Spring migration (SM) Nebraska (NE)	Precipitation (ppt FM) (ppt SM)	Total mean monthly precipitation: August – October, October (FM), February-April (SM)	Inches	January to December 1938 – 2003	NOAA (233660) Nebraska Platte River Station (USMS). http://cdo.ncdc.noaa.gov/cdo/
	Temperature (temp FM) (temp SM)	Monthly mean min temp. September, October (FM), March, April (SM)	°F converted to ºC	January to December, 1938 – 2003	NOAA (233660) Nebraska Platte River Station (USMS) http://cdo.ncdc.noaa.gov/cdo/
Winter ground, (WG), (ANWR)	Precipitation (ppt WG)	Total mean monthly precipitation: April-March, September - March, October	Inches	January to December 1942 to 2004	NOAA 410302 Aransas Refuge. http://cdo.ncdc.noaa.gov/cdo/
	Temperature (temp WG)	Monthly mean temperature (M): Jan-Dec, Apr-Mar, Sep-Mar, Oct-Mar, Nov, Dec, Jan, Nov–Jan. Monthly mean min. temp. (MIN): Jan-Dec, Oct-Mar, Nov, Dec, Jan. Monthly mean max. temp (MAX): Jan-Dec, Oct-Mar. Extreme min. temp. month (EMIN): Jan-Dec, Oct-Mar, Nov, Dec, Jan, Feb, Mar. Extreme max. temp. month (EMAX).: Jan- Dec, Oct-Mar.	°F converted to ºC	January to December 1942 to 2004	NOAA 410302 Aransas Refuge. http://cdo.ncdc.noaa.gov/cdo/
	Fresh water Inflows (fw WG)	Total mean monthly water inflow: Jan-Dec, April-March, Sep-March.	Sum of acft/mo	January to December 1941 – 1999. 2000 to 2001	Historical flow Guadalupe Estuary TWDB Website. Gaged flow (Victoria + Goliad) USGS website
	Net Evaporation, or water balance (nevap WG)	Net balance between: Precipitation – Evaporation.: April-March, Sep-March	Sum of acft/mo	January to December 1941 – 1999. 2000 to 2001	Historical Evaporation Guadalupe Estuary TWDB website. Gaged flow (Victoria + Goliad) USGS website

Table 4. Continued.

Location	Independent Variables	Description	Units	Date	Source
	Pacific Decadal Oscillation Index (PDO)	Average monthly index: Jan - Dec . Patterns of North Pacific SST and SLP anomalies (ocean temperature anomalies in the northeast and tropical Pacific ocean).	PDO index	1938 to 2004	Joint Institute for Study of the Atmosphere and Ocean (JISAO). http:// jisao.washington.edu/pdo. PDO.

Table 5. Database for Whooping Crane demographic variables. Mortalities brood failure and clutch size reduction. Dependent variables.

Location	Variable	Description	Units	Date	Source
Breeding ground , (BG), (WBNP) .- CANADA	Brood failure	Percentage of potential breeders and breeders failing to breed = No. pairs (potential breeders and breeders) at ANWR / No. nests at WBNP	%	From 1985 to 2004	ANWR winter reports and CWS fidelity data -base.
	Clutch size reduction	Percentage of nests with a clutch size lower than 2 eggs= (No. nests with 2 eggs)/ No. nests 1 egg.	%	From 1967 to 1996	CWS, database egg records during egg management
	Egg mortality during collection = (egg mort-c)	Percentage of eggs left after collection, that did not hatch in June (no chick hatched)	%	From 1967 to 1996 except years 1970, 1972, 1973.	CWS, database egg records
	Egg mortality during no collection = (egg mort.-nc)	Percentage of eggs laid that did not produce chick in June	%	During 1970, 1972, 1973 and from 1997 to 2004	CWS, database egg records.
	Chick mortality	Percentage of chicks dead = chicks in June /chick in August	%	From 1967 to 2003, except 1969, 1975, 1990 and 1994.	CWS database yearly production.
Fall migration (FM) , Nebraska (NE)	Juvenile mortality = (juv mort FM).	Percentage of young dead FM = (chick August = young August) / young in ANWR	%	From 1967 to 2003, except 1969, 1975, 1990 and 1994.	CWS, database yearly production and ANWR winter reports
	April – November mortality. = (Apri-Nov. mort.)	Percentage of individuals reported dead from April to November (Subadults and Adults)	%	From 1985 to 2004	ANWR winter reports.
Winter ground (WG) ANWR	Juvenile mortality = (juv mort WG.)	Percentage of individuals < 1 year old reported dead at ANWR	%	From 1985 to 2004	ANWR winter reports.
	Adult and Subadult mortality = (Adu + Subadul WG)	Percentage of individuals > 1 year old reported dead at ANWR	%	From 1985 to 2004	ANWR winter reports.
	Total winter mortality	Percentage of total individuals reported dead at ANWR (Sum of young and subadult+ adult mortality)	%	From 1985 to 2004	ANWR winter reports.

Table 5. Continued.

Location	Variable	Description	Units	Date	Source
North America (US)	Total annual mortality	Percentage of individuals disappeared annually = No. subadults and adults recorded in November year t+1 / No. individuals (young , subadult and adults) recorded at ANWR in November year t $N(t+1)= Nt + N(t+1) – M(t+1)$ $M(t+1) = Nt – (A+ SA(t+1))$	%	From 1938 to 2004	ANWR winter reports. Nt = peak of individuals (Adults (A) + Subadults (SA) +Juveniles) year t Estimation of Annual mortality is reported for first time in this research. Appendix B. Table B1.
	Lambda (λ)	Annual population growth rate. Value of r was calculated from total population size from ANWR winter reports. Finite rate of increase = $\lambda = e^{r}$	N.A	From 1938 to 2004	ANWR winter reports.

given age-group (eggs, juveniles, subadults, and adults) each year during a given phase of the annual cycle (on the breeding ground, during fall migration, on the wintering ground or during spring migration). X_1 represented independent variables (environmental factors) (X_1), for a year interval during that phase of the annual cycle**,** X_2 represented environmental factor 2 (X_2), and Є is the error term.

For example, egg mortality was related to environmental factors in WBNP, such as temperature, precipitation, and water depth at WBNP, and PDO index.

egg mort = f (temp BG, ppt BG, wd BG, PDO)

where *egg mort* is egg mortality (proportion of eggs that fail to hatch), temp BG is mean monthly temperature (C°) from March to September on the breeding ground, BG ppt is total mean monthly precipitation from March to September (mm), and wd BG is mean pond water depth (cm) measured at 1 m from the nest.

The same process was applied to all possible relationships of mortality, and the list of hypotheses to be tested is presented in Table 6, with equations from 1 to 9.

Fecundity represented by reproduction (brood failure) and clutch size (reduction), is determined by both proximate (factors pre breeding) and ultimate factors (factors during nesting) (Krebs 1994). Fecundity of the Whooping Crane population was associated with environmental factors at ANWR during spring migration (SM), at WBNP and to the global climatic factor PDO, (Table 6, Eq. 10 and Eq.11).

The last dependent variable analyzed was the annual population growth rate expressed as lambda (λ) = $N_{(t+1)}/N_{(t)}$,where N is population size of Whooping Cranes at ANWR, and *t* is year. This variable is an index that represents the change in the

Table 6. List of hypotheses between demographic and environmental variables. All variable abbreviations are in Table 4 and Table 5.

Equations	n
egg mort = f (temp BG, ppt BG, pwd BG, PDO)	(1)
egg mort. no collection = f (ppt BG (M-May), temp BG (M-May), ppt BG, Temp BG, pwd BG, PDO)	(2)
chick mortality = f (ppt BG (Jun-Aug), ppt BG (Jun), temp BG (Jun-Aug), temp BG (Jun), pwd BG, PDO)	(3)
juv mort FM = f (temp BG, ppt BG, temp FM (Oct), temp FM (Sep), ppt FM (Oct), ppt FM (Aug–Oct), PDO)	(4)
April - Nov. mort. = f (temp SM (Mar), temp SM (Apr), ppt SM (Feb-Apr), temp BG (Mar-Sep), ppt BG (Mar-Sep), temp FM (Oct), ppt FM (Oct), PDO)	(5)
adu + subadul mort WG = f (temp (M, MIN, MAX, EMIN, EMAX)WG, ppt WG (Apr-Mar), ppt WG (Sep– Mar), ppt WG (Oct), fw WG (Jan-Dec), fw WG (Apr-Mar), fw WG (Sep-Mar), nevap WG (Apr-Mar), nevap WG (Sep-Mar), PDO)	(6)
juv mort WG. = f (temp (M, MIN, MAX, EMIN, EMAX)WG, ppt WG (Apr-Mar), ppt WG (Sep– Mar), ppt WG (Oct), fw WG (Jan-Dec), fw WG (Apr-Mar), fw WG (Sep-Mar), nevap WG (Apr-Mar), nevap WG (Sep-Mar), PDO)	(7)
Total mortality WG = f (temp (M, MIN, MAX, EMIN, EMAX)WG, ppt WG (Apr-Mar), ppt WG (Sep– Mar), ppt WG (Oct), fw WG(Jan-Dec), fw WG (Apr-Mar), fw WG (Sep-Mar), nevap WG (Apr-Mar), nevap WG (Sep-Mar), PDO)	(8)
Total annual mortality = f (temp BG, ppt BG, temp FM, ppt FM, temp WG, ppt WG, ppt FM, temp FM, temp SM, ppt SM, fw WG, nevap WG, PDO).	(9)
brood failure = f (temp WG, ppt WG, fw WG, nevap. WG, temp SM, ppt SM, temp BG, ppt BG, pwd BG, PDO)	(10)
clutch size reduction = f (ppt WG, temp WG, fw WG, net evap. WG, temp SM, ppt SM, temp BG, ppt BG, pwd BG)	(11)
Lambda = f (PDO, temp WG, ppt WG, fw WG, net evap.WG, temp SM, ppt SM, temp. BG, ppt BG, pwd BG, temp. FM, ppt FM)	(12)

population, a general value that compiles mortalities occurring annually, and was related to all environmental factors along the life cycle, equation (Table 6, Eq. 12).

Also, the variable annual population growth (lambda) was analyzed with all demographic variables as independent variables (above dependent variables), in order to understand which of these demographic variables explained better the population variability observed (Table 6, Eq. 13).

Linear regressions were completed with SPSS ® 11 for Windows, using stepwise procedures, with a probability of F "entry" 0.05 and "removal" 0.10, and collinearity diagnostics [analysis of variance inflation factors (VIF) to obtain levels of co-variance]. Variables with high collinearity (VIF close to 10) in the regression models were removed from the models. However, collinear variables could still be biologically important for the Whooping Cranes. These variables were identified and correlated with path analysis. Once I had identified a causal model with the independent variables listed above, I confirmed that the model could not be further simplified, and that no other combination of independent variables provided better explanatory power than the chosen model, using the criterion of maximizing adjusted R^2 (Sokal and Rolhf 1998).

One of the main goals of this research was to determine the impact of environmental factors acting together on the age-specific demography of the Whooping Crane. I used a path analytical approach for this objective, because demography involves a series of sequential events and various factors in complicated interaction systems, and this method allowed me to identify causal relationships among the independent variables for these complicated causal schemes, estimated the strength and sign of directional relationships and allowed analysis of multicollinearity among explanatory variables (Sokal and Rolhf 1998).

Path analysis was performed with Statistics/Data Analysis STATA $^{\mathrm{tm}}$ V7 linked to http://www.ats.ucla.edu/stat/stata/ado/analysis/pathreg/hlp. I displayed standardized partial regression coefficients (i.e., standardized to maximum of 1.0, minimum of -1.0), together with their standard error $U = (1\text{-}R_Y{}^2)^{½,}$ that represented all the unknown sources of unexplained variation in the path diagram (Sokal and Rohlf 1998) (see Appendix B: Table B4, for an example of path analysis). Two indices were used to verify how data fitted the models: the minimum fit function, adjusted R^2 which tested for an exact fit to the data (the “best “ fit); and, the root mean square error of approximation (RMSEA) which tested for an adequate fit between model and data.

Ecological analysis

In addition, as a complement to the statistical analyses (regression and path), I analyzed the same database to review environmental factors relative to trends in the Whooping Crane population in an illustrative and descriptive table. Although the statistical analyses were based on correlations of values of dependent and independent variables, paired explicitly in time and space, I complemented this by graphically representing a temporal scale from 1967 to 2004, a geographical location (Canada, Texas and Nebraska), and the distribution frequency of data. This was done in order to detect patterns, synchronized or not, among the environmental factors and demographic variables along the history and, by accommodating the complexity of all data, to allow observed interactions hierarchically and at different levels.

First, because every organism has its range of environmental tolerance and optimal conditions under which its population increases, I assumed that any factor above or below ±1SD or ±2SD could affect specific life stages of the Whooping Crane life cycle. Based on this, I estimated the pattern of annual distribution of environmental factors (temperature, precipitation) at WBNP, NE, and temperature, precipitation, freshwater inflow and net-evaporation at wintering ground ANWR. Then, I established the mean or typical environmental values during the period of occurrence of the Whooping Cranes at the different regions, from the last 34 years of data from each environmental variable. Those values represented at least the "average-optimum" environmental conditions for the ANWR-WBNP Whooping Crane population because they arrival at each region coincided with these values every winter, summer and migration, when conditions at the different regions turned more stable before their arrival (Appendix B: Table B2, Figs. B1 to B8).

Then, each environmental and demographic variable was plotted (Appendix B: Figs. B9 to B32), and historical means and ranges (maximum and minimum) were represented on the figures. For the historical period of record, I categorized all values as high or low (close to ±1SD), and extremes values called "extreme" between +1SD and +2SD, or between -1SD and -2SD). Each of these extreme or peak values was presented in Appendix B: Tables B2 and B3, and then represented every year on a timetable.

Extreme values of each environmental and demographic factor at WBNP, NE and ANWR, and PDO phases were represented with filled squares (cells) on the timetable. They were located in an upper section (all demographic variables) and in a lower section (all environmental variables). Cells were filled with colors. Environmental factors were represented by dark blue (cold /wet) and light blue (cool weather), and red (hot /dry) and orange (warm weather). Demographic variables were represented with filled cells, colors yellow and green represented peak and high values respectively for mortalities, clutch size reduction and brood failure.

All these variables and values of lambda, were represented every year and analyzed based on ecological relationships along the history of Whooping Cranes. I related five phases of Whooping Crane population decline from 1967 to 2004 (Chapter II) with all extreme values of the dependent and independent variables. The five phases analyzed were periods when Whooping Crane population did not grow, and values of lambda were ≤1. Those periods were: period 1 from 1972 – 1974, period 2 from 1980 – 1982, period 3 from 1989 – 1991, period 4 from 1993 – 1994, and period 5 from1999 – 2001.

For example, on the timetable, it was possible to represent from 1972 to 1974 values of lambda, extreme or high mortality of egg, chick, young during fall migration and total annual mortality (by colors yellow and green), and also independent variables (peak of environmental factors) with colors red or blue, during the same phase of population decline. I represented from 1967 to 2004, the frequency of extreme environmental and demographic factors from different grounds that occurred during Whooping Crane population growth with fluctuations.

RESULTS

Regression analysis and path analysis between environmental and demographic variables showed multi-environmental factors (ultimate factors) correlated with demographic parameters (proximal factors) in the life cycle of the Whooping Crane that influenced the finite rate of population growth, lambda.

Regression analyses showed that from the large data-set of variables from different regions (Table 4), a combination of 18 environmental factors was useful in explaining 9 of the 10 dependent variables (demographic) affecting lambda variability. From this regression analyses only the demographic variable, total mortality in winter, was not significant. The variability in all mortalities together at ANWR--juvenile, subadult and adult mortality--was not explained by the variability in specific environmental factors; but, juvenile mortality and subadult-and-adult mortality, separately, had high adjusted R^2 with environmental factors (Table 7). Correlations between PDO and environmental factors showed that only two variables were significantly correlated (r): temperature in October during fall migration (-0.52) and mean extreme minimum temperature from October to March at ANWR (0.59); remaining variables showed weaker correlations: temperature extreme maximum from October to March at WG (-0.30), total precipitation from August to October in NE (0.24), temperature extreme minimum in January (0.18), freshwater inflow (-0.18), pond water level (-0.17), temperature mean in November (0.12), and all others (< ABS(0.10)).

Path analysis, developed with selected environmental factors from regression analysis and all demographic parameters, yielded path coefficients (standard

Table 7. Whooping Crane regressions between demographic variables (dependent): brood failure, clutch size reduction, lambda, and 8 mortalities, and environmental variables (independent).

Variables (Dependent)	Equation	P	Adjusted R^2
Brood failure	Y = 111.57 + (-0.46) x (PDO) + (-0.57) (pwd BG) + (-2.47) x (tempEMIN_OM WG)	0.007	0.56
Clutch size reduction	Y=47.02 +(5.46 x10^{-6}) x (fw WG) + (-0.68) x (pwd BG) + (-0.48) x (tempN WG) + (3.94 x 10^{-6}) x (neva AM WG)	0.006	0.45
Egg mortality during collection	Y = -26.53 + (0.21) x (ppt BG) + (-4.2) x (temp MM BG) + (-0.71) x (PDO).	0.001	0.48
Chick mortality	Y = 124.83 + (-3.70) x (pwd BG) + (-8.64x10^{-2}) x (ppt JA BG)	0.015	0.38
Juv mort fall migration	Y = -149.17 + (3.05) x (temp O FM) + (0.29) x (PDO)	0.012	0.21
April – November Mortality	Y =-70.17+(0.73) x (temp O FM)+(0.45) x (temp S.FM) + (0.035) x (ppt BG) + (-0.22) x (ppt FM AO)	0.0003	0.69
Juv mortality winter	Y = 67.73+ (-1.2) x (temp D WG) + (-1.5 x 10^{-6}) x (fw WG) + (1.01) x (ppt NJ WG)	0.0009	0.70
Adult and SA mortality	Y = -79.07 + (0.29) x (ppt NJ WG) + (1.0) x (temp EMAX_OM WG) + (-0.14) x (temp EMIN_J WG)	0.023	0.35
Total winter mortality	Y = 30 + (-0.48) x (temp.NJ WG) + (-1x10^{-5}) (neva SM WG)	0.09*	0.23
Total annual mortality	Y = 63.11 + (-0.59) x (temp O FM) + (-0.20) (temp MIN_N WG) + (-0.19) x (temp EMIN_D WG) + (0.75) x (temp MM BG) + (-0.31) x (pwd BG)	0.009	0.42

Note: Variables abbreviation. Pond water depth at breeding grounds (pwd BG), Pacific Decadal Oscillation Index (PDO), freshwater inflow at winter ground (fw WG), precipitation at breeding ground from March to September (ppt BG), temperature at breeding ground from March to September (temp BG), from March to May (temp MM BG), temperatures September and October in Nebraska during fall migration (temp O FM), (temp S FM), temperatures in ANWR: in December (temp D WG), mean from November to January (temp NJ WG), minimum November (temp MIN_N WG), extreme minimum December (temp EMIN_D WG), extreme minimum January (temp EMIN_J WG), extreme maximum October to March (temp EMAX_OM WG), total precipitation in ANWR : from November to January (ppt NJ WG), from September to March (ppt WG), net evaporation from September to March in ANWR (neva SM WG) *NS (No significance).

coefficients) with positive and negative signs, P>t, n (sample size), R^2 and sqrt(1-R^2) = U (the residual term). Factors with the strongest effect on demographic variables (path coefficient >0.5) were: temperature in December at ANWR, temperature extreme maximum during October to March at ANWR, temperature in October during fall migration, precipitation from March to September at WBNP, pond water depth at WBNP, freshwater inflows at ANWR, and temperature extreme minimum during October to March at ANWR (Fig. 11).

Path analysis identified two pathways to explain variability of lambda with demographic (proximal) factors that might influence Whooping Crane population growth at ANWR, WBNP and NE. The first causal model showed that proximal mechanisms included variation of annual mortality and brood failure, 5 significant environmental factors (ultimate factors) and PDO (Fig. 12A, Table 8A). This causal model was identified as the "aggregated model" because one highly significant variable explained practically all variability of lambda, and the terminal error was *U= 0.44*.

The second set of demographic variables (proximal) yielded a "fully resolved model". In this model, changes in the Whooping Crane population were explained by 6 proximal factors from three different regions but only 3 were significant (total mortalities at the wintering ground, mortality from April to November, and chick mortality) (Table 8B). However, clutch size reduction, brood failure, and juvenile fall migration mortality were demographic variables that also had minor roles in this model, but their path coefficients were not significant, and egg mortality was dropped from this path analysis. Fourteen ultimate factors were correlated with this set of demographic variables, and the terminal error was U= 0.62, but only 8 environmental variables were significant (p-value < 0.05) or marginally significant ($0.05 <$ p-value < 0.1) (Sokal and Rolhf 1998) (Fig. 12B) (Table 8B).

The main objectives of my path analysis were to investigate the magnitude and direction of each variable's effect, rather than the issue of significance of path coefficients, because a test of significance for multiple regression analysis would be inappropriate for some variables (Sokal and Rolhf 1998). However, I considered for discussion all variables with p-value < 0.05 as significant, and some variables with levels of significance that indicated moderate to suggestive, but inconclusive evidence, as marginally significant.

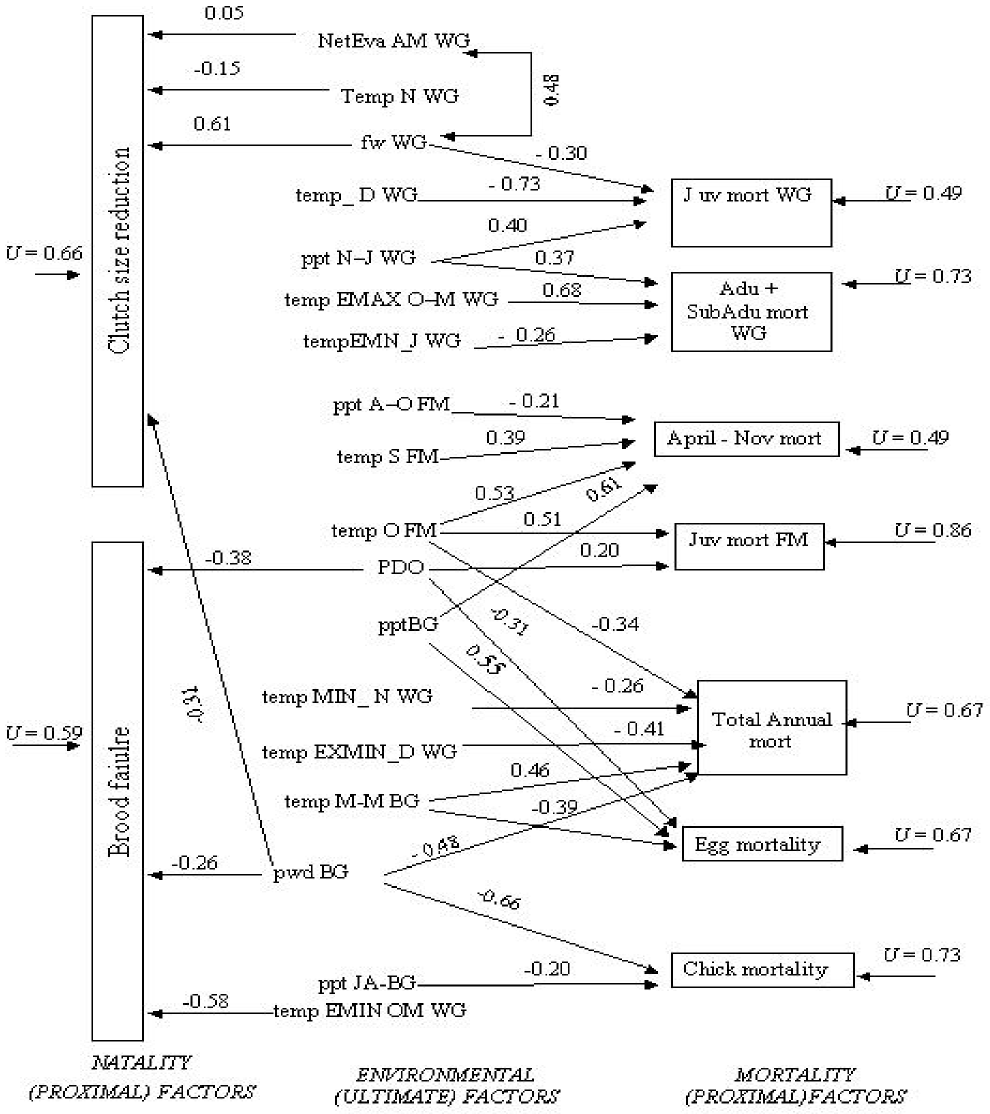

Fig. 11. Path diagram between environmental (ultimate) factors: at wintering ground (WG), at breeding ground (BG), and during fall migration (FM); and demographic parameters of the Whooping Cranes: natality and mortalities (proximal factors). Arrows represent the direct effect, and numbers beside arrows show path coefficients (with + or-) for direction. Double-headed arrows indicate the correlation between two variables. Values of *U* (residual terms: the proportion of unexplained variance). For abbreviations see Table 4. See Appendix B, Table B4 example of path analysis estimation.

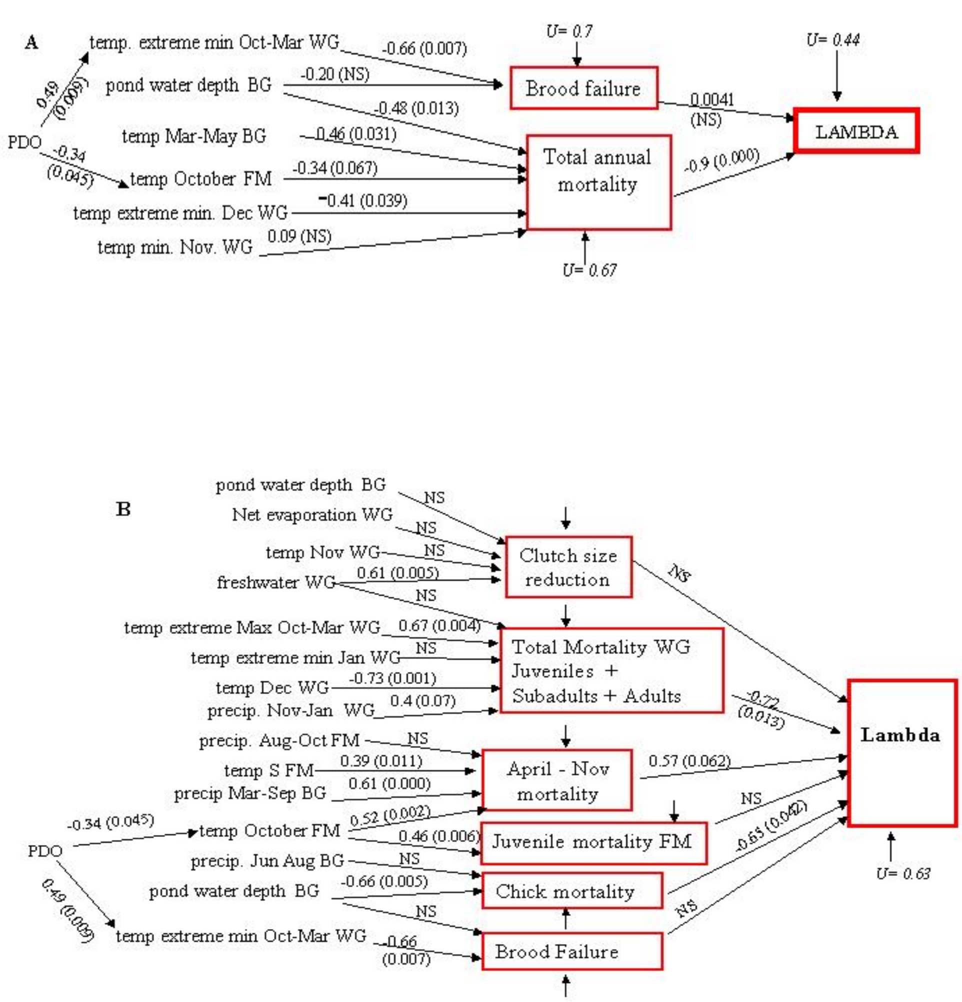

Fig. 12. Two causal models of the Whooping Crane population growth variability identified by path analysis. Path diagrams depicted pathways between proximal factors (demographic), and ultimate factors (environmental), and lambda. (A) The aggregated model with two proximal variables annual mortality, and brood failure at WBNP, and. (B) the fully model with all demographic parameters (except egg mortality). Arrows represent the direct effect of one variable upon another. Path coefficient values (standardized partial regression coefficients with sign and SE in parentheses) are presented above the arrows and values of *U* (residual terms) represented by short arrows (See Table 4 for explanation of environmental factors abbreviations).

Table 8A. Path Analysis. Whooping Crane population growth "aggregated" model.

Explanatory variables of lambda Proximal Factors	Coefficient	P>t	n	R^2	Sqrt(1-R^2)
Annual Mortality	-0.90	0.000	19	0.85	0.44
Brood failure	0.004	NS*			

Table 8B. Path Analysis. Whooping Crane population growth "fully resolved" model.

Explanatory variables of lambda Proximal Factors	Coefficient	P>t	N	R^2	Sqrt(1-R^2)
April-November mortality	0.57	0.062^{+}	17	0.60	0.62
Juvenile fall migration mortality	-0.47	0.132*			
Chick mortality	-0.65	0.042			
Total mortality winter ground	-0.72	0.013			
Clutch size reduction	-0.35	0.285*			
Brood failure	0.28	0.285*			

* NS (No Significance), $^{+}$ MS (Marginal Significance, 0.05<p-value<0.1)

Annual mortality alone was a good predictor of lambda but, with brood failure variable included, the value of the proportion of unexplained variance reached the lower value (0.44) (Table 8a). Variability of annual mortality was explained by 5 factors from WBNP, NE during fall migration and from ANWR (R^2 = 0.42, $F_{5,19} = 4.35$, $P = 0.009$, $\alpha = 0.05$, $U = 0.67$) (Table 7, Fig. 11). Path analysis indicated that 4 of the factors were significant: temperature extreme minimum in December at ANWR, temperature in October in NE, temperature mean from March to May at WBNP, and pond water depth in the breeding ground (Fig. 12A). Also, pond water depth at WBNP and extreme minimum temperatures all winter affected variability of brood failure ($F_{3,14} = 6.84$, $P = 0.007$, $\alpha = 0.05$) (Table 7). PDO also explained variability of temperature October in NE, and extreme minimum temperature all winter. PDO affected indirectly lambda via effect on mortality during fall migration and via brood failure due to effect on temperature extreme in the wintering ground. This path analysis showed that hot and dry conditions at WBNP reduced the number of adults and sub-adults summering, cold temperatures during fall migration and extreme cold at ANWR increased annual mortality of individuals, and PDO's cold phase increased annual mortality due to its association to temperature in October during migration, and positive correlation to temperature extreme minimum during wintering. The second model obtained from path analysis was "fully resolved". In this causal model, proximal mechanisms included variation of total mortality at wintering ground (represented by the sum of all individuals dead at ANWR), April-November mortality (represented by mortality of subadult and adults during spring, at WBNP, and during fall migration), and chick mortality, as significant variables. Although mortality of juveniles during fall migration, brood failure and clutch size reduction yielded a good fit, and the best model was with U = 0.62 their path coefficients were not significant, (Table 8B, Fig. 12B).

Total mortality on the wintering ground (sum of mortalities of subadult, adult, and young at ANWR) was correlated with environmental factors but was not statistically significant (P = 0.09) (Table 7); however, independent analysis of the two variables, juvenile mortality and subadult-and-adult mortality at ANWR, showed statistically significant responses to different factors. Juveniles winter mortality variation was explained by atmospheric and aquatic environmental factors $R^2 = 0.70$ ($F_{3,11} = 11.74$, $P = 0.0009$, $\alpha = 0.05$, $U = 0.49$) (Table 7). A strong and negatively correlated effect was produced by December mean temperature (-0.73), and freshwater inflow (-0.30), and total precipitation from November to January was positively correlated (0.40) (Fig. 11

and 12B). Adult and subadult mortality was explained by extreme maximum temperature from October to March, extreme minimum temperature during January and precipitation from November to January (0.68,-0.26, 0.37, respectively), $R^2 = 0.352$, $F_{3,15} = 4.26$, $P = 0.023$, $U = 0.73$ (Table 7, Fig. 11 and Fig. 12B). Path coefficients indicated that too cold temperature, wet conditions, and too hot and low freshwater inflow increased mortality at AWNR.

Mortality of Whooping Cranes from April to November had a good model fit ($R^2 = 0.685$, $F_{4,14} = 10.82$, $P = 0.0003$, $\alpha = 0.05$, $U = 0.49$) (Table 7, Fig.11, Fig. 12B). Only ultimate factors at WBNP and in Nebraska during fall migration had an effect on this mortality, because no environmental factor from NE affected spring migration in April (Table 7). The strength of the relationships obtained by path coefficients indicated that a high level of precipitation at WBNP (0.61) and hot temperatures in October (0.53) and September (0.39) were the main causes of mortalities from April to November, and also affected fall migration temperatures by a positive correlation with PDO (Fig. 12B).

The third significant proximal factor included for explanation of lambda oscillations in the fully resolved model was chick mortality variability, which was explained by the ultimate factors precipitation from June to August, and values of ponds water depth from May to June at WBNP ($R^2 = 0.375$, $F_{2,14} = 5.8$, $P = 0.015$, $U = 0.73$) (Table 7). Negative and strong correlation with pond water depth (-0.66) showed that chick mortality increased highly when ponds at WBNP were shallow (Fig. 11, Fig. 12B)

Other proximal factors correlated in the model of lambda were variability in clutch size reduction, explained mainly by freshwater inflow, but also by pond water depth in May, mean temperature in November at ANWR, and net evaporation at ANWR ($R^2 = 0.45$, $F_{4,17} = 5.32$, $P = 0.006$, $\alpha = 0.05$) (Table 7, Fig. 11). Brood failure, which also was included in this model, was explained above with the first model (aggregated); and juvenile mortality during fall migration was explained by two ultimate factors: temperature in October and positive correlated PDO index ($R^2 = 0.21$, $F_{2,30} = 5.152$, $P = 0.012$, $U = 0.86$) (Table 7, Fig. 12B). But, these last three demographic variables were not significant in the path analysis.

The last proximal factor, egg mortality, was not correlated with lambda variability. This variable was not included in the path analysis, because data for egg mortality did not fit with the same number of years as the rest of the variables thus, the program dropped this variable. However, path analysis between ultimate and proximal factors showed that 48% ($F_{3,19} = 7.67$, $P = 0.001$, $\alpha = 0.05$, $U = 0.67$) of its variation was explained mainly by strongly and positively correlated total precipitation all summer at WBNP (0.55), and by temperature from March to May (-0.39), and both low and negatively correlated PDO index (-0.31) (Table 7, Fig. 11).

Results of the ecological analysis from the annual pattern distribution of environmental factors helped me to understand the relationship between environmental factors and Whooping Crane demography throughout the period of record. Table 9 depicts physical factors that may have contributed to population declines from 1967 to 2004. The average and standard deviation (mean ± 1 SD), peaks (extreme maximum and minimum), range of each environmental factor that occurred when Whooping

Cranes were present at WBNP, NE during spring and fall migration, and at ANWR were identified and plotted (Appendix B: Table B2, Table B3, and Figs. B9 to B20).

Extreme conditions of environmental factors at WBNP, NE and ANWR, and PDO phases were identified and presented with cells color-filled in the lower section of Table 9. This timetable shows all extreme environmental factors distributed along the history and geographical regions. Also extreme values of demographic variables are represented by cells color filled in the upper portion of the same Table 9 (Appendix B: Figs. B21 to B31). This timetable shows demographic variables distributed along the history and geographical regions, and the association with values of lambda ($\lambda \leq 1$) through the years when the population declined or remained static.

The five periods from 1967 to 2004, identified with lambda ($\lambda \leq 1$) were: period 1 from 1972 to 1974, period 2 from 1980 to 1982, period 3 from 1989 to 1991, period 4 from 1993 to 1994, and period 5 from 1999 to 2001.

Table 9. Representation of Whooping Crane demographic and environmental variables with values extreme and high, from 1967 to 2004. (Data from Appendix B: Figs. B9 to B31). Legend: Years in gray (λ ≤1). Demographic variables: extreme >1SD (yellow), high >mean (green). Environmental variables: extreme >1SD dry /hot (red), high > mean (orange), extreme cold/wet (blue), PDO phases: cold (dark blue), warm (pink). Data that was available from 1985 (*). FM= Fall migration, WG = Wintering ground, BG = Breeding ground, GE = Guadalupe Estuary.

	Variables Demography	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
1	Lambda							0.8	1						0.9	1								1	0.9			0.9						1	1				
2	Brood Failure																								🟨	🟩			🟨							🟨	🟨		🟩
3	Clutch size reduction																									🟨			🟨										
4	Egg Mortality						🟩	🟨	🟨	🟨						🟩		🟩							🟩	🟨					🟨				🟨		🟩		
5	Chick Mortality								🟩					🟩	🟨	🟨										🟨	🟩	🟨						🟨	🟨	🟨	🟩		
6	Young mortality FM							🟨	🟨							🟨	🟩	🟨															🟨		🟩				
7	Mortality Apr - Nov*																						🟩			🟩					🟩		🟨		🟨			🟩	
8	Young Mortality WG*																			🟩	🟩			🟨						🟩					🟨	🟩	🟩	🟩	
9	Adu-Suba Mortality WG*																			🟩	🟨		🟨			🟨													
10	Total Mortality WG*																								🟨			🟨							🟨				
11	Total Annual Mortality						🟨								🟩							🟩			🟨		🟩					🟨		🟩	🟩				🟨
	Environment	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
1	Temperature WBNP	🟦	🔷				🔷	🟥	🟦				🔷	🟦			🟦		🟧										🟥				🟥	🟥		🟥	🟦		
2	Precipitation WBNP			🟧		🟥		🟦		🟦	🟧			🟥		🟧				🟥			🟦	🟥		🔷					🟦		🟧	🟦					
3	Water Depth WBNP								🟦	🟦	🔷				🟥	🟥									🟥	🟥				🟥		🟥	🟦	🔷					
4	Temperature NEFM			🟦	🟦	🟥		🟥	🟥	🟥	🟦											🟦	🟦														🟦	🟥	
5	Precipitation NEFM		🟦	🟦				🟦		🟥	🟧			🟦							🟦		🟥				🔷				🟥	🟦	🟥				🟦		
6	Temperature ANWR	🟦			🟥	🟥	🟦				🟦								🟦	🟥			🟦										🟥	🟥	🟦				
7	Precipitation ANWR				🟦	🟦	🟥		🟦	🟥	🟦			🟥	🟧		🟦			🟥	🟦	🟧	🟥		🟧	🟦	🟦					🔷					🟦	🟥	
8	Freshwater Inflows GE	🟦			🟥			🟦			🟦												🟥	🟥		🟦				🟥			🟦	🟥					
9	Net Evaporation GE	🟦	🟥		🟧	🟦				🟥			🔷		🟧					🟥	🔷	🟥	🟧			🟦	🟦				🔷	🟦							
10	PDO peaks (Cold / Warm)	🟦				🟦	🟦	🟦		🟦								🟥	🟧		🟧	🟥				🟦	🟧	🟥				🟥		🟦	🟦	🟦		🟥	
11	PDO Phases (Cold /Warm)	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟦	🟦	🟦	🟪	🟪	🟦	🟪	🟪	🟪	🟪	🟦	🟦	🟦	🟣	🟣	🟣

Period 1: had extreme conditions of low temperature, high precipitation, and high pond water depth at WBNP; high temperature and low precipitation at NE; high/low precipitation and high freshwater inflows at ANWR, extreme cold PDO index, recorded during 1972 - 1973 and 1973 - 1974, which coincided with extreme high total annual mortality, egg and young mortality during fall migration, and high chick mortality, (Table 9, Appendix B: Table B2, Table B3, Table 4). The combination of these factors during two consecutive years contributed to produce a population decline from 61 to 49 individuals ($\lambda = 0.8$ and $\lambda = 1$) from 1972 to 1974.

From 1975 to 1980, no extreme demographic variables occurred and few or isolated extreme of environmental factors were recorded, and the minority that did occur had small impact on demographic variables (Table 9). From 1975, until 1989, the PDO index changed from the cold/wet phase to the warm/hot phase.

Period 2: the second period of population decline from 1980 to 1982, was characterized by two consecutive years of low pond water depth, a year of low precipitation and warm phase of PDO in WBNP, and a year of drought in ANWR (Table 9, Appendix B: Table B3). These environmental conditions accompanied two consecutive highest values of chick mortality and young mortality during fall migration, in combination with high total annual mortality and high mortality of eggs (Table 9, Appendix B: Table B3, Table B4). These demographic changes produced values of lambda 0.904 and 1, in 1980 and 1981 respectively, when total population decreased from 78 to 73 Whooping Cranes.

From 1983 to 1988, few extreme environmental conditions occurred in WBNP, and not many in NE and ANWR. The only demographic variable affected was adult and sub-adult mortality at ANWR, but without negative consequences on the values of lambda.

Period 3, from 1989 to 1991, was characterized by an extreme drought at WBNP, low precipitation and low pond water depth, a very high value of freshwater inflow and precipitation in ANWR, and three years of consecutive cold PDO phase (Table 9, Appendix B: Table B3). These factors produced three consecutive years of brood failure, an extreme reduction of eggs laid in 1991, high egg mortality, a very high value of annual mortality, and high April – November mortality (Table 9, Appendix B: Table B4). These demographic variables caused a decline of the population from 146 cranes in 1989 to 132 in 1991, with lambdas 1 and 0.93 respectively.

Period 4 of population decline, from 1993 – 1994, was only one year long. A few environmental factors produced extreme values during this period. A PDO warm phase and high temperature occurred in WBNP in 1993, and there was a PDO cold phase in 1994, but they were not extreme. These factors coincided with a high annual mortality, an extreme values of brood failure, clutch size reduction, chick mortality, and high value of total mortality in ANWR. These demographic factors caused a reduction of the Whooping Crane population from 143 to 133 individuals (λ= 0.93) (Table 9, Appendix B: Table B3, Table 4).

Period 5, from 1999 – 2000 and 2000 – 2001, which was the last period of population decline until 2004, occurred during an extreme low freshwater inflow and extremes in high and cold temperature in ANWR, and two consecutive years of extreme values of PDO cold phase. These environmental factors produced high annual total mortality; high young, sub-adult and adult mortalities at ANWR; an extremes brood failure, egg mortality, and chick mortality; high young mortality during fall migration; and, an extreme value of April-November mortality. All these demographic variables produced lambda values of 0.957 and 0.977, and a reduction from 188 to 174 individuals (Table 9, Appendix B: Table B3, Table B4).

Another interesting result obtained from this ecological analysis, and not observed in the same way with statistical analysis, was an evident relationship between lambdas and PDO phases during the history from 1967 to 2004 of the Whooping Crane population. Four of the five periods of population stability or decline ($\lambda \leq 1$) coincided with PDO cold phases, and periods of population growth occurred during PDO warm phases (Table 9). Based on this information, a closer analysis between PDO and lambda was developed, and population growth represented by the coefficient of variation of the intrinsic rate of growth as another measure of lambda (CVr = 100* (r-mean r)/mean r)) was compared with the index of Pacific Decadal Oscillation (PDO index). PDO index versus Whooping Crane population growth with 1 year lag (CVr t+1) is represented in Fig. 13. Whooping Cranes (line) and PDO index (columns) overlapped from 1977 to 2004. Also a linear regression between Whooping Cranes population rates CVr (t+1) and PDO showed that 12% of the variability of Whooping Cranes population rates of growth was explained by the PDO effect produced one year before (Fig. 14).

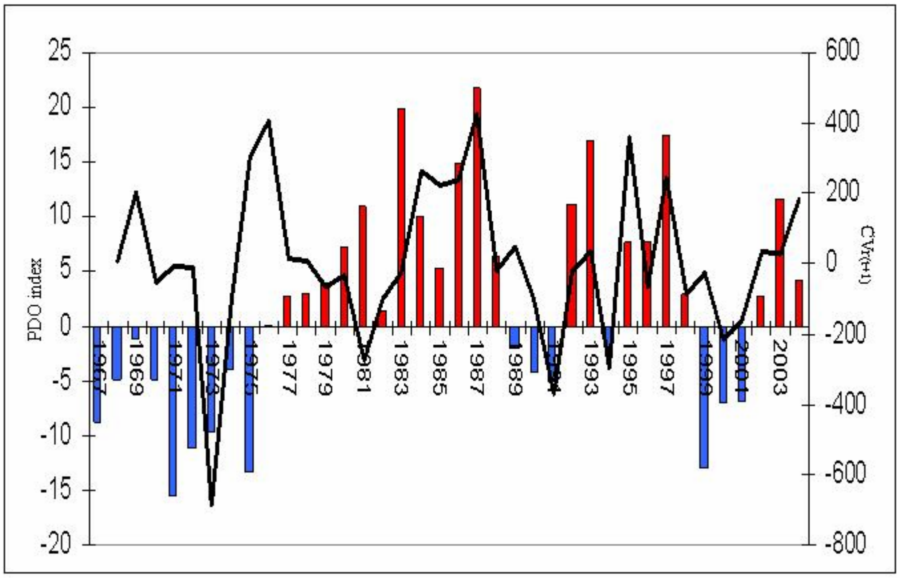

Fig. 13. Relation between Whooping Crane population and PDO. Population was represented by coefficient of variation of r (rate of intrinsic growth) with one year of lag time (line), and the Pacific Decadal Oscillation (PDO index) (columns red = warm phase, blue = cold phase).

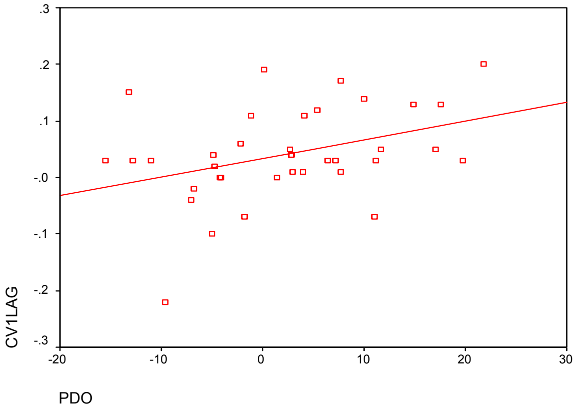

Fig. 14. The relationship between Whooping Crane population growth (CVr) 1 year lag, and PDO index. Regression showed $R^2 = 0.12$ ($F_{1,35} = 5.8$, $P = 0.021$, $\alpha = 0.05$). Fit is shown with solid line.

DISCUSSION

From 1938 to 2004, the ANWR-WBNP Whooping Crane population experienced 12 periods of decline in total, and seven of them occurred before 1960 (through 22 years). Nedelman et al. (1987) documented from the mid-1950′s to 1987 at least three periods of temporary decline (Fig. 3). In this study I investigated the factors identified from 1967 to 2004 (last 37 years) that might be the proximal (demographic) causes of Whooping Cranes number reduction during this period, and the ultimate causes (environmental factors) that produced changes in natality and mortality rates of the Whooping Crane.

The variability of the finite rate of increase of the Whooping Crane, lambda, investigated with the first path analysis, showed that environmental factors from the three regions and the PDO had significant effect on Whooping Crane mortality of subadult and adults that disappeared annually (Fig. 12A, Table 8A). Functions of temperature at the three regions was the main environmental factor set that caused demographic changes at the level of total annual mortality; also, PDO and pond water level at WBNP had effects on brood failure affecting lambda via fecundity reduction and also dry ponds increased mortality on the breeding ground. Results from this analysis implicated causes that certainly could affect directly or indirectly subadults and adults, including breeding pairs; but, these results cannot be considered to explain, with the same confidence, causes that affected the population at the breeding grounds (eggs, chicks and juveniles during fall migration). This is because annual mortality is based only on individuals counted at ANWR every winter. Extreme minimum temperatures at

ANWR affected Whooping Cranes directly, because juvenile birds and weak subadult and adults are very sensitive to cold and wet conditions, and weather beyond their limit of tolerance can have a drastic effect (Weller 1999). Indirectly, mean extreme minimum temperature during winter has a strong link to mortality of Whooping Cranes (Fig. 11) and to breeders that fail to breed. Water temperature decreases with extreme minimum air temperature, and this could affect aquatic prey distribution and abundance. Leffer (1972) and Rome et al. (2005) observed that the highest mortality rate for blue crabs occurs in the lowest temperature and salinity conditions in both field and laboratory, and these factors were important predictors in over-wintering blue crab mortality.

Studies on blue crabs in ANWR for 1993 - 1994, indicated that blue crabs numbers, the principal winter food of cranes, were very low throughout most of the winter (Chavez-Ramirez 1996, Stehn winter report), and data from NOAA reported for the same years, extremes of low temperature (Table 4). During this period, the cranes exhibited a net energy loss and many were most likely in poor physical condition prior to the breeding season (Chavez-Ramirez 1996). Logically, if the cranes do not replenish their energy reserves, by consumption of blue crabs and other foods at ANWR, to compensate for reduction of energy reserves used during the fall migration, "body condition" declines, reproductive output is reduced (McLandress and Ravelling 1981, Joyner et al. 1984, Goldstein 1990, Gauthier et al. 2003), and mortality increases.

The other factor identified as significant for total annual mortality and affecting lambda, was pond water depth at the breeding ground. Mortality of juveniles and adults was increased during drought years by low levels of water in the ponds, because this produced a condition of reduced food (invertebrates) and increased predation (Kuyt and Barry 1992, Johns 1997).

The second, “fully resolved” model obtained with path analysis, described other environmental factors that had effects on demographic variables, and these demographic variables form part of the total annual mortality. These environmental factors that increased total mortality at the wintering ground and were not identified with the total annual mortality variability were extreme maximum temperature from October to March, temperature in December, and total precipitation from November to January. Extreme weather conditions, too-high temperatures, or hailstorms increase the mortality of young, sub-adults and adults in wetlands (Weller 1999), and also have negative indirect impacts because extremes of temperature affect water resources, food distribution and the availability of aquatic organisms (Krebs 1994, Rome et al. 2005).

This second model also identified that high levels of total precipitation from March to September at WBNP and high temperature in September during fall migration explained variability of April - November mortality, which is a demographic variable included in the total annual mortality, too. High precipitation at WBNP, and too-wet and cold years are unfavorable conditions for Whooping Cranes; high success rates were associated with average and warm years (Novakoswki 1966, Jonh 1997) (Plate 2). High temperatures in Nebraska during October increased mortality indirectly, because higher temperatures increased evaporation and dried the habitat, thus degrading feeding and roosting sites (Chávez – Ramirez 2004). For Whooping Cranes, stopover areas could be just as important as staging areas.

Plate 2. Nesting ground and pond water depth conditions at WBNP, during a dry and wet year. Photo credits: Brian Johns, CWS.

If Whooping Cranes were unable to find a suitable area for roosting for just a single night, they might be vulnerable to predation or accidents that would potentially increase their mortality. Cranes could increase the chances of a collision with power lines or fences when are looking for suitable roost sites, flying at low elevation (Chávez – Ramirez 2004), and arrive to ANWR with injuries occurred during fall migration (Lewis 1995). Cold weather resulted in highly significant increases in mortality of Whooping Cranes during migration. Studies with radiotelemetry (Drewien and Bizeu 1985) reported that Whooping Cranes only started migration when environmental conditions, temperature, wind direction, and barometric pressure were in specific favorable ranges. During cold weather and windy conditions the movements of juveniles was delayed. Extreme declines in temperature is associated with bad weather, storms, and directly and indirectly affect Whooping Cranes--directly, because temperatures too low can produce hypothermia and presumably affect body condition for migration, and indirectly because in stormy weather it is difficult for birds to find altitudes with the best wind conditions for their flight, and may become disoriented or even grounded (Weller 1999). Both extremes of temperature in October during fall migration seemed detrimental for Whooping Cranes.

Another environmental factor with significant impact on demography, at the level of clutch size, was freshwater inflow. Path analysis showed that the same factor had effects in two directions. Freshwater inflow low levels on the wintering ground increased total mortality in winter ground, and high levels in the wintering ground significantly reduced clutch size on the breeding ground. The relationship between freshwater inflow and clutch size reduction is not direct or linear; instead, it is a relationship based on availability of food resources, linked to freshwater or salinity as drivers of distribution and abundance of blue crabs. These environmental conditions (biotic and abiotic) affect the ability of Whooping Cranes to obtain fat reserves for reproduction and other activities. Such complex, indirect relationships presumably accounted for failure to resolve a significant path coefficient of clutch size and brood failure in path analysis.

Studies on the abundance of blue crabs, relating density and distribution, demonstrated significant declines in winter abundance and concurrent changes in distribution in the field due to inter-annual differences in freshwater flow (Jensen and Miller 2005}, and some bird species, such as many waterfowl, depend on fat deposits upon arrival at the breeding grounds as their primary energy source for reproduction. The larger their fat deposits and availability of high-protein food for laying females, the more able they are to reproduce (Reed 2004). Given the nutritional value of the blue crabs in terms of lipids and proteins (Nelson et al. 1996), if the main food of Whooping Cranes was not available during the year, reproductive nutrient reserves were limited. The high cost of egg laying could account for the clutch size reduction observed, probably because energetic reserves were below a threshold (Walsberg 1983, Alisauskas et al. 1990, Ankey et al. 1991, Alisauskas and Ankney 1992).

Egg mortality was a demographic variable not included in the path analysis due to methodological reasons, but it was strongly and positively correlated to precipitation, low temperature during incubation at WBNP and cool PDO phase (Fig. 11, Table 7). These conditions, accompanying wet and cold summers, are characteristic of periods of low Whooping Crane productivity. This is consistent with the observations of Novakowski (1966). He found that, in general, weather records indicated that average conditions (low precipitation particularly) on the Whooping Crane nesting ground were most likely to produce good hatches.

PDO index, warm/dry and wet/cold phases showed a pattern of synchrony with the Whooping Crane population fluctuation. During cold phase (blue) several environmental extreme factors were happening simultaneously in the different geographical areas and population did not increase or declined. During warm phase (pink), few environmental factor extremes occurred at the same time, and the population did not decrease (Table 9, Fig. 13). Two periods of population decline did not coincide with PDO cold phase; they were years 1981 and 1993. During the summer of 1981, a fire on WBNP occurred during a warm PDO phase, and, in 1993, a very extreme value during warm phase was recorded. Positive phases or warm phase of PDO are associated to regional fire events more than negative phases (Hessl et al. 2004). PDO is associated with decadal scale patterns in precipitation and impacts on salmon production (Mantua et al. 1997), with productivity in high elevation forests and possibly with large fire occurrences (Hessl et al. 2004); however, no association with wildlife or aquatic birds had been studied recently (Mantua and Hare 2002, Nathan Mantua personal communication), but this kind of relationship has been established with the long-term climatic factor in the North Atlantic Oscillations (NAO).

In Scandinavian countries, it has been found that NAO affect the population dynamics of several marine vertebrates. NAO contribute to the synchronization of population fluctuations of Great Cormorants (*Phalacrocorax carbo*) over large areas (Engen et al. 2005) and also affect adult survival in five species of North Atlantic seabirds (Sanvick et al. 2005). Engen et al. (2005) found that large population growth rates were associated with positive values of NAO, and these conditions were mild winters. In a similar way, the analysis of Whooping Crane population growth rates developed with data from 37 years showed that long periods of years of PDO cold phase were unfavorable for cranes, and long periods of warm phase were favorable. Warm phase was associated with positive values of the PDO index. Also, the NAO index alone accounted for about 10% of the variance of Great Cormorant population (Engen et al. 2005). In this study, the PDO index alone accounted for about 12% of the variation of the Whooping Crane population growth with a one-year lag.

Correlations with NAO suggested that meteorological parameters affect seabird mortality only indirectly, possibly through the food chain, because most NAO effects are lagged (Sandvik 2005). The PDO index had a good model fit, with a one-year lag, on Whooping Crane population growth, which indicated that anomalies in PDO index extended in effect to North American breeding grounds and migration route of the Whooping Cranes, and had effects on life stages of the population reflected one year later. Thus, the PDO index may affect the local climate on the North Pacific/North American sector and on the rest of the North American region used by Whooping Cranes, as was reported the effect of PDO and climate forecasting for North America by Mantua and Hare (2002), Hessl et al. 2004, and showed in a Appendix B: Fig B. 24.

Although these demographic data were not analyzed with other characteristics of the PDO, such as the marked effect from 20 to 30 years (Mantua and Hare 2002), I think that information on the Whooping Cranes population available from 1938 and the relationship found with this research, will open new lines for investigation on the effect of PDO and the relationship with other climatic factors as the ENSO, and other migratory species.

CONCLUSIONS

In summary, results from statistical and ecological analysis were combined and represented in a Whooping Crane population growth curve from 1967 to 2004. Five periods of decline were characterized by 9 demographic factors related to 18 environmental conditions from 10 environmental factors, which were the main causes of demographic responses. Several components occurred in synchrony on the Whooping Crane population during each period and were identified and represented during the historical period of record (Fig. 15).

Whooping Crane demography (natality and mortality) was affected throughout the life cycle (except during spring migration) by environmental factors from the three different regions: western Canada, and the states of Nebraska and Texas, in the United States. The best predictor of lambda variability for Whooping Crane was the demographic variable total annual mortality. Total annual mortality was negatively correlated with temperature in October during fall migration in NE, pond water depth at the breeding ground and temperature extremes in December at the wintering ground, and positively correlated to mean temperature from March to May at WBNP. The PDO was negative correlated with temperature October during fall migration. PDO affected lambda indirectly due to effects of temperature in October.

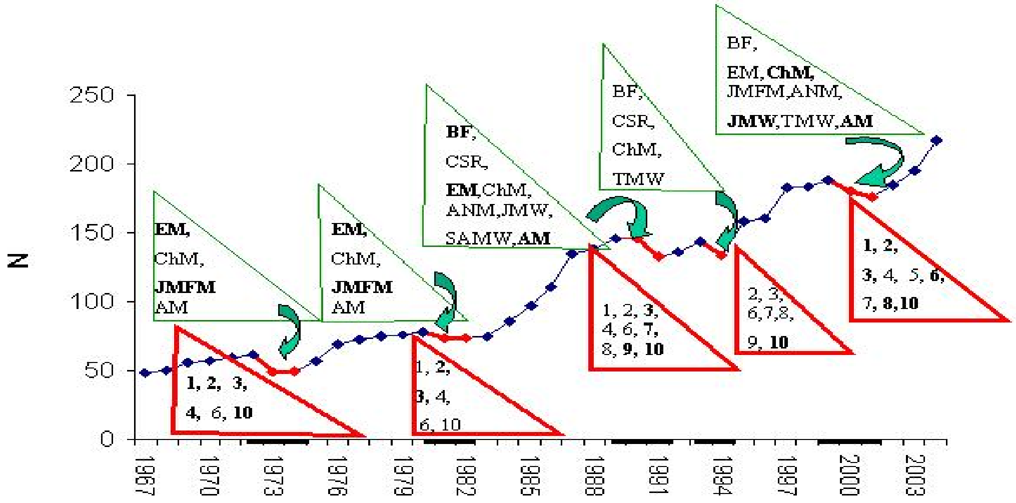

Fig. 15. Whooping Crane population growth and five periods of population decline. Demographic and environmental factors producing $\lambda \leq 1$. Demographic variables: BF = Brood failure, CSR = Clutch size reduction, EM = Egg mortality, ChM = Chick mortality, JMFM= Juvenile mortality fall migration, ANM= April – November mortality, JMW = Juvenile mortality winter, SAM= Subadult + Adult winter mortality, TMW= Total winter mortality, AM = Total Annual mortality. Environmental variables at: BG= Breeding ground, FM= Fall migration, WG = Wintering ground, 1 = Temperature BG, 2 = Precipitation BG, 3 = Pond water depth BG, 4 = Temperature FM, 5 = Precipitation FM, 6 = Temperature WG, 7 = Precipitation WG, 8 = Freshwater inflows WG, 9 = Net evaporation WG, 10 = PDO index peaks cold or warm. Letters for demographic variables in bold represent peaks of variables that occurred in consecutive years. Numbers for environmental variables represent strongest path coefficients and numbers in bold represent peaks observed (See Fig. 11, Fig. 12).

The variation in total annual mortality was not the only pathway by which population growth was related to environmental factors. A second causal model showed that other correlations with environmental factors were significantly associated with mortalities in the various regions. These mortalities formed part of the annual total mortality, but this “fully resolved” model implicated other factors for specific ages and regions--total mortality on the wintering ground, mortality of individuals from April to November (spring migration, breeding ground and fall migration) and, chick mortality at WBNP. These three demographic variables were correlated to other environmental factors that had a significant effect on their variability, but were not identified with the total annual mortality. Thus mortality at ANWR tended to increase with high temperature maxima from October to March, high total precipitation from November to January and low temperature in December. Mortality from April to November increased due to high temperatures in Nebraska during fall migration in September and October, and elevated total precipitation all summer (March to September) at WBNP. Chick mortality was explained by low pond water level at WBNP.

Both extreme low and high temperatures had an effect on Whooping Crane demography in ANWR, at NE; and at WBNP. Low and high freshwater inflow had an effect on juvenile mortality and clutch size reduction, respectively. Most of the environmental factors identified had a direct effect on Whooping Cranes individuals and indirect effects due to effects on the habitat (drought or availability of food resources) that increased mortality and reduced natality rates. Environmental factors from the wintering ground affected pre-migratory and pre-breeding conditions and subsequently reproduction, and lambda.

PDO had an effect on lambda indirectly, through temperature in October affecting mortality during fall migration and through extreme minimum from October to March in ANWR affecting brood failure. Although PDO showed weak correlations with other important environmental factors for the Whooping Crane population, probably these correlations could be significant or stronger if variables are combined or analyzed differently, or there may exist a synergistic effect among them on Whooping Crane ecology. With few exceptions, most periods of Whooping Crane population decline happened during PDO cold phases, and the population increased during PDO warm phases. PDO index had a one-year lag effect on population growth. During PDO cold phase there was observed a synchronization of extreme values from environmental factors from different regions; whereas, during warm phases extreme values of environmental factors were scattered.

CHAPTER IV

A WHOOPING CRANE POPULATION SIMULATION MODEL

INTRODUCTION

The Whooping Crane (*Grus americana*) winters at Aransas National Wildlife Refuge (ANWR) along the Gulf of Mexico in Texas, breeds and spends the summer in Wood Buffalo National Park (WBNP) in northwestern Canada, and uses the central Platte River in Nebraska as a major stopover during the fall migration of its annual cycle (Lewis 1995) (Fig. 1).

The goal of the U.S Whooping Crane Recovery Plan is to down-list the species from “endangered” to “threatened” by the year 2035 (CWS and TPWS 2003). The maintenance of 1,000 individuals for at least 10 years will be possible if the population growth rate of Whooping Crane is ≥ 0.05/y, twinning is allowed and mortality rate continues to decrease (CWS and TPWS 2003, Mirande et al. 1997). In order to improve measures for the management of the Whooping Crane population, it is crucial to develop or increase the ability to relate area-specific environmental factors to natality and mortality rates, and to distinguish environmental effects in different areas (Weller 1999). For example, understanding the effect of climate (temperature and precipitation) helps to understand the interplay between climate and other agents of change in population dynamics (Shaver et al. 2000), and also to measure the impact of these environmental factors on wildlife populations in national parks and conservation areas (Wang et al. 2002).

Currently the Whooping Crane population “ANWR-WBNP” is 217 individuals, but how will the dynamics of the population play out by 2035, given expected variation in environmental factors over the population’s geographic range, and the direct or indirect effects of those factors on the life cycle of the Whooping Crane?

Whooping Crane population trends have been projected within the context of population viability analysis (PVA), using commercially available simulation packages. There have been 6 PVAs for Whooping Cranes, all done using the same population database (the ANWR-WBNP population), but with different inclusive years of data. Mirande et al. (1997) used VORTEX, a Monte Carlo simulation of the effect of deterministic forces as well as demographic, environmental (catastrophes: diseases, hurricanes) and genetic stochastic events on wildlife population, and 57 years of data until 1995. Brook et al. (1999) used PVA several commonly applied packages (GAPPS®, INMAT®, RAMAS® age, RAMAS® metapop, RAMAS® Stage and VORTEX®) and compared the output of the different modeling packages. Although results of the PVA’s were expected to be similar, different results were found (Brook et al. 1999). Then, Brook et al. (2000) and Tischendorf (2004) also used RAMAS® GIS and these recent studies projected continued population growth, with decreasing probabilities of extinction (<1% chance in the next 100 years), but recognized, based on ecological principles, that growth rate eventually must decline as the population approaches carrying capacity.

Brook et al. (1999) and Reed (2004) considered that there was no way to determine which PVA package was most accurate, so these researchers recommended modeling with more than one package to provide perspectives. They also suggested the development of other models using the PVA concept to ask questions about breeding grounds, migration stopover sites and the wintering grounds. Previous PVAs did not address important questions on population responses to specific environmental conditions (i.e. temperature changes) on different grounds. Commonly used PVA packages have lacked the flexibility to evaluate specific environmental effects during different phases of the annual cycle (Brook et al. 1999).

Several studies have investigated the effects of environmental variability on specific demographic parameters, such as population size, breeding performance, or survival, on top-predator populations (Croxal et al. 2002, Wang et al. 2002), trying to understand how such vital rates and their variations, affect population dynamics and how environmental factors affect the vital rates. Studies on modeling relationships between aquatic birds and environment are few, time series are short, and quantitative knowledge of the dynamics of interactions between predators, their prey, and the environment remains very limited (Jenouvrier et al. 2005).

Although the system in which the Whooping Crane exists is complex, it is possible to partially understand it by simplified re-analysis of available information. The model of the Whooping Crane developed here was built in the simplest way that I could conceive, to account for the effects environmental factors on the population dynamics of the Whooping Crane. This model was built in parts, to connect relationships with information from the Whooping Crane population available from 1938 to 2004 (Table

1). I used a compartment model that provides the structure able to represent the different ages of the Whooping Crane, and grounds along their life cycle.

The following questions guided this research in the context of the general objective, which was to analyze population responses to environmental conditions on the breeding grounds, during migrations, and on the wintering grounds:

1. Is the structure of this model capable of simulating general historical trends with the same data used by previous models?

2. Is the structure of this model capable of utilizing new data on survivorship and fecundity obtained from banded birds during the last 27 years? This question was motivated by the desire of enabling future studies to project population responses to various environmental scenarios on the breeding grounds, during fall and spring migrations, and on the wintering grounds over the next 10 years.

METHODS

I formulated the model as a compartment model based on difference equations ($\Delta t = 1$ day) and programmed the model using STELLA® 7 (High Performance Systems, Inc.) (Fig.16). The model maintained the identity of daily cohorts of individuals from eggs (for 30 days) (Kuyt 1981b), chicks (for 10 days) (Kuyt 1981b), juveniles at WBNP (123 days), juveniles in fall migration (35 days), juveniles on wintering ground (155 days), and juveniles during spring migration (22 days) .

I assumed that all eggs were laid on day-of-year 134 (May 15, which was near the end of the egg laying season) (CWS unpublished data, Lewis 1995), and that all

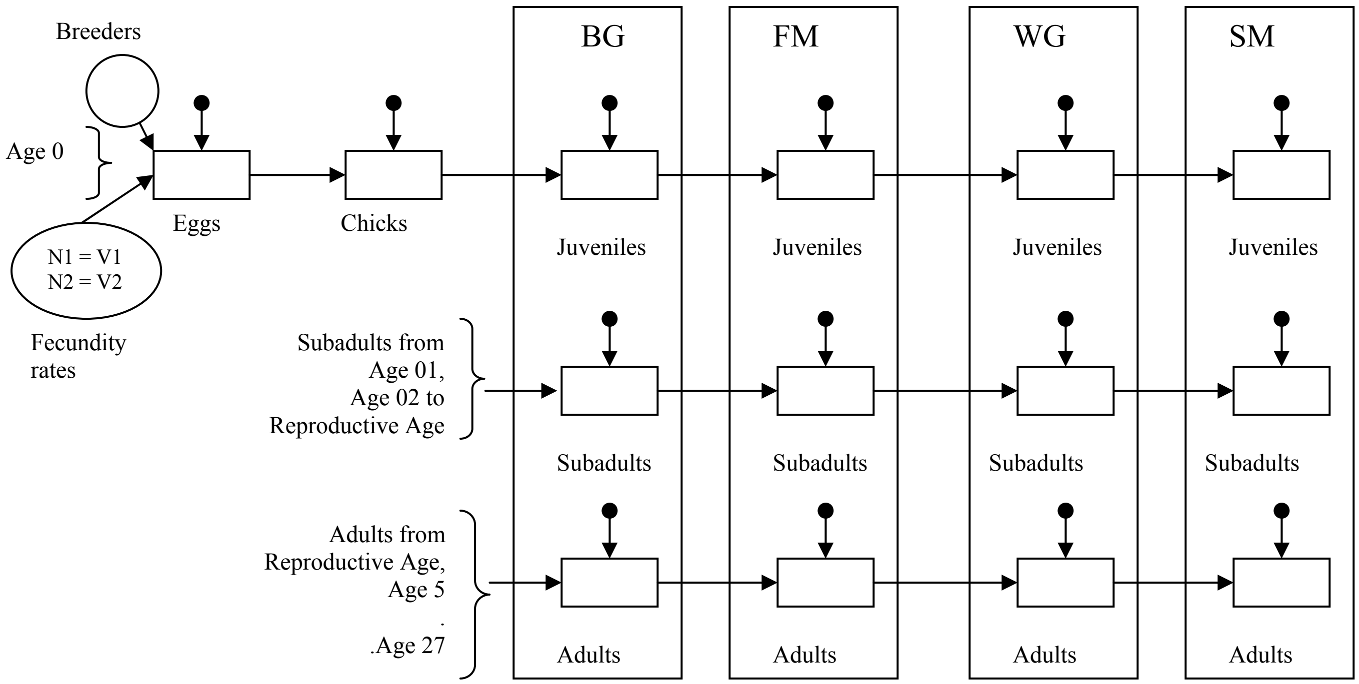

Fig. 16. General structure of the Whooping Crane population model representing daily cohorts of individuals. Eggs, chicks, juveniles, subadults and adults on the breeding grounds (BG), juveniles, sub-adults, and adults during fall migration (FM), on the wintering grounds (WG), and during spring migration (SM), and (↓) age specific mortality rates are represented. Models version 1and 2 used the same structure.

individuals were on the breeding grounds in Canada from day-of-year 106 (April 16) to day-of-year 258 (September 15), in fall migration for 35 days, on the wintering grounds in Texas from day-of-year 294 (October 21) to day-of-year 83 (March 24), and in spring migration for 22 days (Stehn 2003, Chavez-Ramirez 2004) (Fig.2).

1. I developed a deterministic age-structured (daily cohorts) population dynamics model, assuming constant age-specific mortality rates and a constant value for natality rate from Binkley and Miller (1988). Their mortality rates vary from age 0 (young at Aransas) to age 23, with constant values over time for each age class. Age specific natality rates vary only with two values, for non reproductive ages (age 0 to age 4 = 0) and for reproductive ages (age ≥ 5 = 0.229), and these rates were constant over time for each age class. I tested the ability of the model to simulate the general historical trend (exponential growth) from 1938 to 2004. This model was identified as Whooping Crane model version 1 (V1).

2. I modified the model from objective 1 (V1) such that mortality rates for age 0 were from eggs at WBNP and not from young at Aransas, as Binkley and Miller (1988) estimated. Also, age specific mortality rates were to age 27 and not until age 23. Mortality rates for age 0 were calculated separately for each group (egg, chick, juveniles fall migration, and juveniles at ANWR) and fecundity rates from age 0 to age 27 were age-specific. Fecundity rates were calculated from banded females (See Chapter II). I tested the ability of this model to simulate the general historical trend from 1938 to 2003, expecting improved goodness-of-fit. This model was identified as Whooping Crane model version 2 (V2).

The development of the two objectives mentioned above, or the two versions of the model to simulate the dynamics of the Whooping Crane population, required the following complete methodology for each version.

For version 1, I calculated daily age-specific mortality rates from Age 0 to Age 23 years based on the annual mortality rates presented by Binkley and Miller (1988) (Appendix C: Table C1). These rates were used on each age at the different grounds (Fig.16). These mortalities were identified as MR_AGE_X_ where X = age 0 to age 23 years. I used their estimates of per capita natality rates (b_x) (NR_BG) 0 and 0.229 for $X<4$ and $X\geq5$ respectively (Binkley and Miller 1988).

Population size in 1938 was 18 individuals, and I assumed that individuals in the initial population were distributed according to the stable age-class distribution. I suspected that I would need to make minor adjustments to the age-specific fecundity rates by Binkley and Miller (1988) before the model would be capable of simulating the general historical trend in the Whooping Crane population. Since there was evidence that age at first reproduction (AGE_FIRST_REP) for some individuals could be 3 and 4, instead of 5 years (Brian Johns, pers. comm.). I first adjusted this parameter to allow reproduction by at least a proportion of 34% (AGE_X_PROP) of 4-year-old (Appendix C: Table C2).

I recalibrated this model (V1) such that the simulated population increased exponentially from 18 individuals (the observed population in 1938; Binkley and Miller 1988) and I tested the hypothesis that this compartment model structure with values from the literature was capable of simulating the general population trend during 65 years.

For version 2, I modified the structure of model V1 by changing age-specific mortality rates from Binkley and Miller (1988) for new values obtained from the new life table (Appendix C: Table C1); these rates were identified in the model as new mortality rates (NMR AGE X). Fecundity rates from V1 were changed to age-specific fecundity rates obtained from 33 banded females (Appendix A: Table A3), and identified in the model as N2 (Fig. 16). For the corresponding age-specific mortality I used on the same structure of the model V1, the new daily mortality rates from age 0 (eggs) until Age 27, (Appendix C, Table C1). These annual age-specific mortality rates from Table 2 (Chapter II) I converted to daily rates. I recalibrated the model such that the simulated population initiated from 18 individuals.

I suspected that I would need to make other adjustments to the number of eggs laid before the model would be capable of simulating the general historical trend in the Whooping Crane population. This was because there is evidence that, on average, 47 % of females are successful in producing broods (Brook et al. 1999), and because from 1967 to 1996, with exception of 1970, 1972, 1973, a program of egg removal was conducted (Brian Johns, personal communication). I tested the hypothesis that the model is capable of simulating the general historical population trend and mortalities on different grounds, contrasting simulations with historical data from total population growth, number of breeders, number of adults and subadults, juveniles, and mortalities at different grounds.

RESULTS

Version 1, the Whooping Crane population growth curve simulated with data from Binkley and Miller (1988), produced an exponential curve similar to the historical growth observed, but projected a total population number below the observed from 1938 to 2004, and a total of 169 individuals vs.198 observed in 2003. After changing the age of first reproduction to 4 years old and a proportion of 34% breeders (4 years old), the curve was more similar to the observed and a good fit was obtained until 1985, when 88 individuals were simulated versus 87 observed. From 1985 to 2004 the simulated population continued increasing exponentially, however below the observed oscillatory trend. During year 1994 the number simulated vs. observed was very close (131 vs. 133) just when historical growth had a period of decline. In general, the simulated population showed a good fit during 45 years, but during the last 20 years, from 1984 to 2004, the simulated population never reached higher numbers as were observed through the last two periods of population fluctuations when higher numbers occurred (Fig. 17). The model was evaluated with the age-class distribution. The number of simulated juveniles, subadults, adults, and breeders was very similar to the age structure observed until 1980´s (Tom Stehn, USFWS, unpublished data) and the CWS (Brian Johns, CWS, unpublished data) (Appendix C: Fig. C4). Results from this version (V1) on number of eggs produced by breeders, chick and juveniles at WBNP, and juveniles during fall migration, and mortality during age 0, cannot be compared because Binkley and Miller (1980, 1988) did not estimate fecundity and mortality from censused eggs, chicks and juveniles at WBNP or during migration. The values used as “fecundity rates”

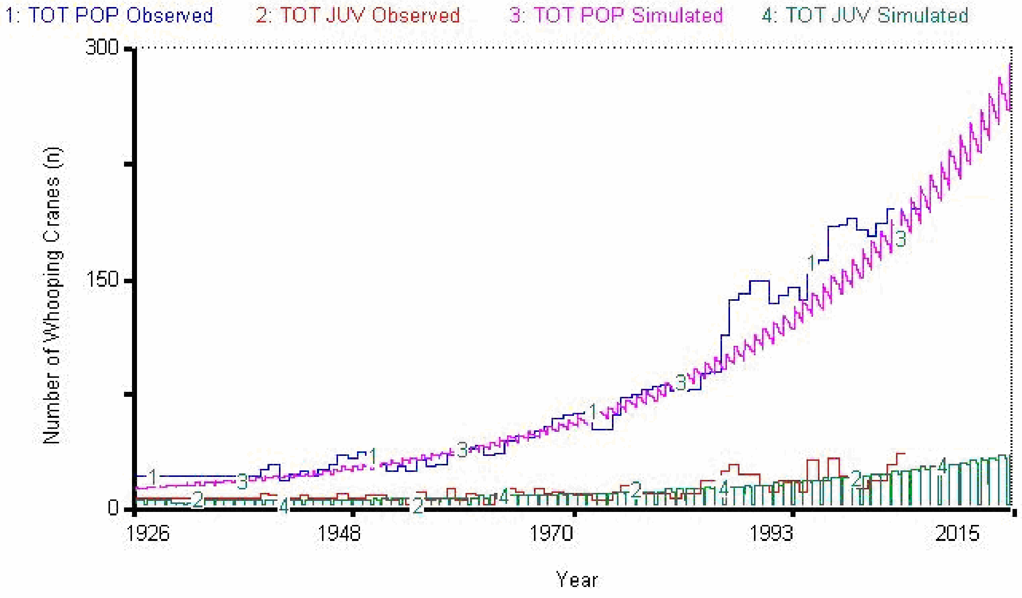

Fig. 17. Comparison of Whooping Crane population growth curves. Model version 1. Values of population observed vs. population simulated. TOT POP = Total population, and TOT JUV = Total number of juveniles. Version 1 used age-specific mortality rates and age-specific fecundity rates from Binkley and Miller (1988) and an adjustment of 34% of individuals breeding at 4 years old. These curves showed a good fit based on level of overlapping from 1938 to 1980¨s. Population is projected until year 2015.

estimated by Binkley and Miller (1988) included fecundity rate, brood success, and mortalities of eggs, chicks, juveniles at WBNP and juveniles during fall migration

A second evaluation of the model was done with the simulated cumulative mortality (AM) and mortalities recorded at the different grounds (Stehn, winter reports, USFWS, and Brian Johns, unpublished data base). Simulated mortality was low in comparison with observed mortality, represented by number of individuals dead on the breeding ground (BG) and during fall migration (FM) (Appendix C: Fig. C2).

This model (version 1) simulated for year 2015, a total population of 289 Whooping Cranes and 33 juveniles (Fig. 17). I accepted the hypothesis that this compartment model was capable of simulating the general historical population trend with data from Binkley and Miller (1988) but with adjustment on age at first reproduction and proportion of breeders or brood success. This model structure included the different grounds, 27 age classes, subdivision of age 0 and age-specific mortality, as no other model did before. This model allowed a test of changes in age at first reproduction, and proportion of breeders at different ages (age 3, age 4, age 5, age 6 and ages>7). This model simulated total population, total adults, total subadults, total breeders, total juveniles, accumulative mortality of each age class, and the age structure.

Version 2, the population simulated with age-specific mortality and fecundity from the life table, promptly produced an exponential pattern of growth, which was different from that observed historically, even starting from 18 individuals in 1938 (Fig. 18). Adjustments were made, first on the number of breeders based on the findings (Brook et al. 1999) that the average of females producing broods successfully was 47 %, and which produced a similar curve as observed only when 40% of the breeders brood (Fig. 19).

The second adjustment was on the number of eggs laid, based upon the fact that during 29 years eggs were removed (Brian Johns, personal communication), to simulate an increase in egg-mortality. This also produced a better fit to the historical data. Then, combining 47% of brood success (Brook et al. 1999) and egg mortality increased by a factor of 5 produced similar total numbers of individuals during the last 30 years (49 individuals observed vs. 43 simulated in 1974, and 188 vs. 189 in 1999), and the population was projected to reach 615 individuals by the year 2015 (Fig. 20). The evaluation of the age structure with this version, fitted well for chicks, juveniles at breeding grounds and breeders (Appendix C: Fig. C3, Fig. C4, and Fig. C5). In general, breeders, juveniles, and total population showed a better fit for the last 25 years than version 1, and also observed and simulated mortalities at the breeding ground showed a good fit (Appendix C, Fig.C9).

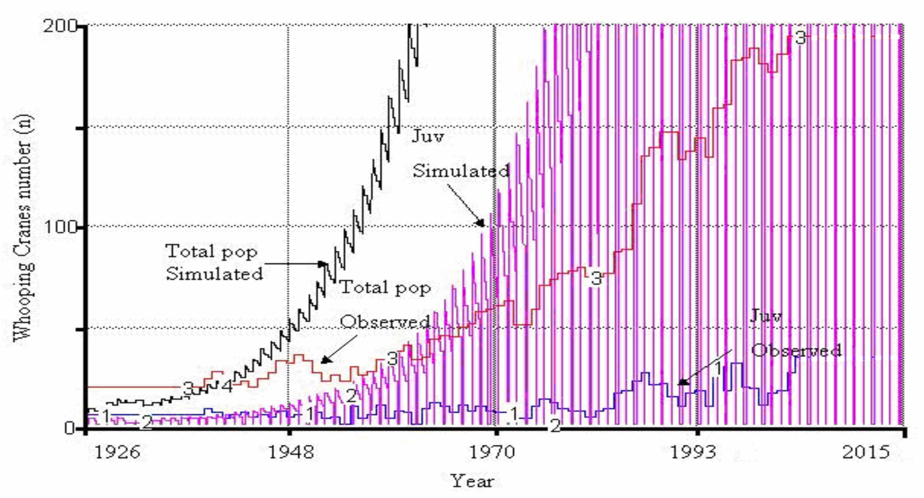

Fig. 18. Comparison of Whooping Crane population growth curves, version 2. Values observed vs. simulated of the total population, and total number of juveniles are indicated with arrows. This model included age-specific fecundity and mortality rates from the new life table (Table 2, Appendix C: Table C1), and individuals breeding at 3 years old, and 27 age classes.

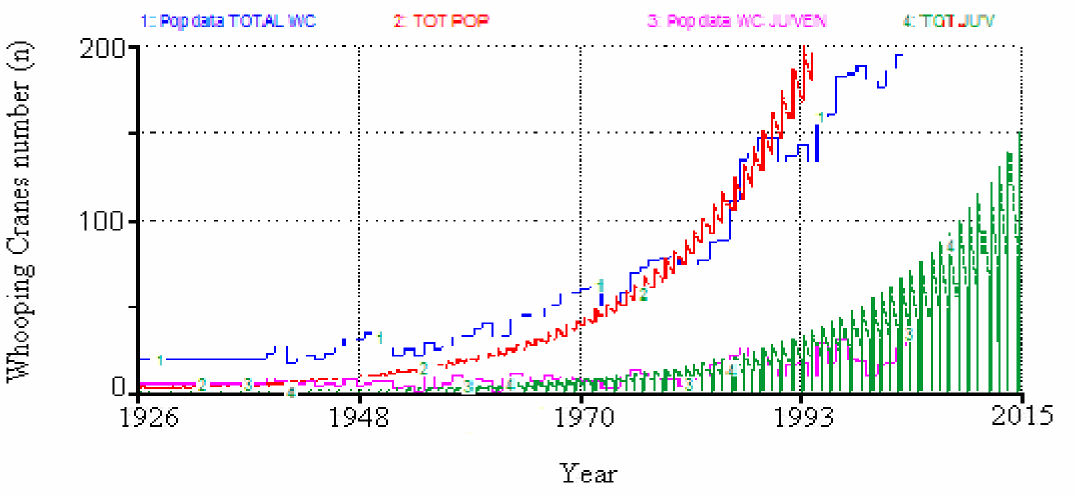

Fig. 19. Comparison Whooping Crane population growth, version 2 and adjustment of 40% of brood success. This model included age-specific fecundity and mortality rates from the new life table

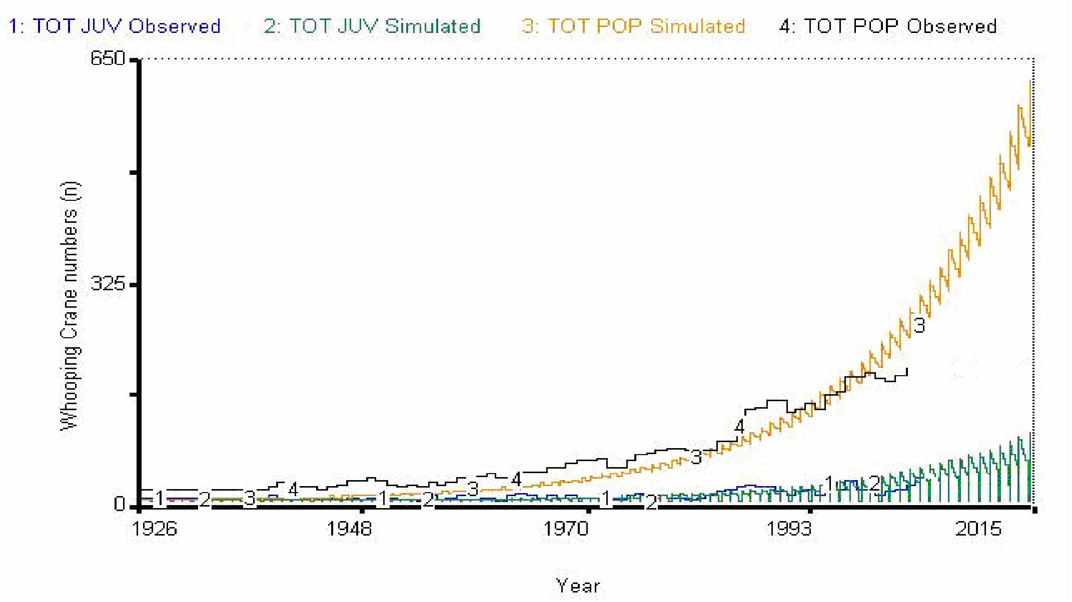

Fig. 20. Comparison of Whooping Crane population growth curves, model version 2 and adjustment of 47% of brood success and egg mortality increased by a factor of 5. Model included age-specific fecundity and mortality rates from the new life table. The total and juvenile population was projected until year 2015.

. This version of the model allowed evaluating of the different numbers of individuals and mortalities on stages at age 0, which was not possible with version 1.

This model of Whooping Cranes population (V2) simulated for year 2015, a total population of 615 individuals, including 96 juveniles and 331 breeders (Fig.20). I accepted the hypothesis that the model, with age-specific fecundity rates for females from age of first reproduction 3 years to age 27, obtained from banded females, new mortalities rates from the new life table (Appendix C: Table C1) and with 27 age classes at the different grounds, was capable of simulating an improved general historical population trend during the last 20 years with adjustments at level of brood success and increased mortality of eggs.

DISCUSSION

Version 1 of the Whooping Crane population dynamics simulation, with data from Binkley and Miller (1988) and information from the same population used by Mirande et al. (1997) and Brook et al. (1999) in their computer simulations, showed that Whooping Cranes exhibited exponential population growth, as they found in their projections. However, values used for rates of fecundity (*bx)* constants, and age-specific mortality rates for Whooping Cranes did not project the actual population growth observed, as it was below the numbers observed. Causes for this difference probably were as follows: 1) The value b_x = 0.229 was too low in comparison with values obtained from the life table. 2) The number of individuals for age 0 simulated with fecundity rates from Binkley and Miller (1988) was below the number required for the population to increase at the rate observed. 3) Values of b_x used for the simulation incorporated the mortality that occurred from egg to first-winter young in Aransas (Binkley and Miller 1980); thus, this value not only included fecundity and brood success, but also it included egg mortality and mortalities of chick and juvenile during fall migration, which produced a simulated value lower than the real (Appendix C: Fig. C2). 4) Fecundity rates were estimated for females ≥5 years old, not including breeders 3 and 4 years old that were reproductive but with a different rate and proportion. 5) Mortality rates were applied only until age 23 when currently 27 years is the oldest age for banded birds; these mortalities cannot be compared with mortality used by PVA packages because they used other age-specific classification with fewer age classes. 6) Mortality rates could change and increase from the 1980´s (Boyce and Miller 1985), because the population experienced two long periods of fluctuations to highest number of individuals after those years. 7) Age of first reproduction produced a very important change in the rate of increase and consequent dynamics of the model; Grant et al. (1997) found age at first reproduction to be a particularly sensitive parameter in population dynamic models.

The model simulated number of individuals for all age classes, but it was not able to compare simulated age class 0 (eggs, chicks, juveniles at breeding grounds and during fall migration) because these numbers do not exist independent of mortality in Binkley and Miller publication (1988).

There were differences between projections for the Whooping Crane population from the PVA model based on historical data (Binkley and Miller 1988) and from this model (V1) with deterministic age-specific mortality rates and two age-specific fecundity rates. Other models developed with other packages, with the same updated data (Mirande et al. 1997, Brook et al. 1999), using demographic and environmental stochasticity also yielded different outputs.

This study showed that building a new model with a new structure, a compartment model, made it possible to identify factors that were difficult to analyze separately with previous models, such as age specific mortalities at subdivided age 0 at WBNP, age specific fecundity rates from age 3 to age 27, number of eggs laid, number and proportion of breeders, ages of first reproduction, and it was also possible to analyze cumulative mortalities from different ages at the different grounds, among other benefits that PVA s were not capable to generate.

Version 2, model simulations with age-specific fecundity and mortality rates and age of reproduction starting from 3 years old, produced rapid exponential population growth because the factor of age at first reproduction younger than 5 or 4 increased the population quickly, which is a response produced in many populations with earlier reproduction (Begon et al. 1996). The applied adjustments, to only 47% of successful breeders (Brook et al. 1999) and a 5-time increased egg mortality, from removal of eggs and other unknown causes, showed how population dynamics of the Whooping Crane involved a balance and interaction between natality rate (brood success) and mortality at age 0 (Begon et al. 1996). The curve had a good fit for the last 20 years with only these adjustments. The first adjustment, from historical information, showed that not all potential breeders that arrived to WBNP were reproductive (Lewis 1995) or that other factors contributed to decrease the number of breeders laying eggs, such as the amount of energetic reserves from too-poor conditions on the wintering grounds (McLandress and Raveling 1981, Joyner et al. 1984, Pianka 1994, Chavez-Ramirez 1996), and habitat quality for nesting (Lewis 1995). An example of these conditions happened in 1994 when from 46 potential nesting pairs in WBNP only 28 nested (Lewis 1995).

The second adjustment simulated mortality of eggs increased 5 times, for example due to egg removal, only one egg hatched, the egg left did not hatch, predation, flooding of nest or droughts, or inclement weather. The last adjustment showed that high mortality (of this magnitude) probably could happen on eggs and produced the number of individuals observed along the history. This magnitude (5 times) however, could be represented by different factors distributed on different stages of age 0. Not only could it be that egg mortality increases 5 times, it could be chick mortality doubles, or that juvenile mortality doubles at the breeding ground, and during fall migration or some other combination, but all at the breeding ground. During 1939 to 1964, when there was no human interference in the form of egg removal, of 210 chicks that hatched only 85 (40.5%) survived to fledging and most losses of chicks occurred in the first 2 wk to 30 d of age (Kuyt 1981b, Lewis 1995). This effect was confirmed by comparing the number of chicks and juveniles at BG and FM observed and simulated along the last 25 years. Lewis (1995) and Kuyt (1981b) mentioned that the highest Whooping Crane mortality was registered at WBNP, and with this experiment I simulated the level of mortality occurring at the breeding ground and during fall migration on age 0 that produced numbers observed.

This version (V2) of the model also could accommodate the possibility that some factor(s) at the breeding ground affected only a certain proportion of Whooping Crane breeders. Identification of these factors (environmental or other possible documented events) is key to understanding the population dynamics of the Whooping Cranes so that future trends in the population can be projected with greater confidence.

CONCLUSIONS

My study produced an age-structured population dynamics model for the Whooping Crane capable of simulating the fate of daily cohorts of individuals as they developed from eggs to adults and as they passed through their annual cycle on the breeding grounds, during fall migration, on the wintering grounds, and during spring migration.

Model version 1 simulated the general historical population trend with data from Binkley and Miller (1988), but showed that fecundity rates and age mortality for age 0 cannot explain the number of individuals, eggs, chicks and juveniles produced by Whooping Cranes in WBNP throughout their history. For management purposes, information on egg production based on a real age-specific fecundity, brood success, and mortalities occurred on age 0 before arrival to ANWR is fundamental. Proportion of breeders, number of individuals for age classes, and a distinction of subadults and adults are also very important information for the recovery plan of the Whooping Crane population. Model version 1 simulated this information.

Model version 2, with age-specific fecundity rates and new mortality rates from the new life table, showed that Whooping Cranes have a high potential to increase exponentially, but factors associated with brood success, egg mortality and subsequent mortality to arrival at ANWR for the first winter, had an important effect on population regulation. This version was capable of simulating an improved general historical population trend with adjustments of only two factors: brood failure and egg mortality. Brood failure and egg mortality were measured at WBNP, but brood failure was linked to ANWR through environmental factors from ANWR (Chapter III). For management objectives, conditions of breeders that depend on environmental factors at the wintering grounds, and conditions for breeders that depend on the factors at the breeding grounds, have a great impact on the population. Factors that increased egg mortality or reduced the number of eggs or chicks, had an impact that also affected Whooping Crane numbers in the model simulation, yielding a curve similar to the historical trend.

Two Whooping Crane population projections from these two versions of the demographic model predicted total number of population and total number of juveniles for year 2015. The first version predicted a total population of 289 individuals and 33 juveniles based on data from Binkley and Miller (1988) and previous studies. The second version of the demographic model predicted 615 individuals and 96 juveniles, based on data from banded individuals, but only with adjustments on brood success, and on mortality at the breeding ground.

Since mortalities occurred through all the life cycle in the different regions, the last version V2 will allow for continued future studies to project population responses, to various environmental scenarios on the breeding grounds, during fall and spring migrations, and on the wintering grounds. Future modification of this version, will produce a third version, in which fecundity and age-specific mortality rates will be functions of environmental conditions on the different grounds. This future version is expected to improve the capability of the model to simulate observed population fluctuations about the general historical trend. Results from Chapter III will be a significant contribution for this phase of the model.

CHAPTER V

CONCLUSIONS

I performed an analysis of banding data for the Whooping Crane population ANWR-WBNP from 1977 to 1988, and I estimated all demographic parameters for this population with the development of a life table.

The Whooping Crane age-specific survivorship rate obtained from 12 cohorts, declined to 52% at age 0; continued decreasing gradually until age 15, at which $l_x = 0.25$; remained stable from age 16 until age 24; and, finally declined at age 27. The age-specific fecundity rates obtained from 33 banded females, increased exponentially from $b_x = 0.05$ at age 3 to $b_x = 0.9$ at age 7, but remained stable ($0.90 \leq b_x \leq 0.95$) from age 8 until age 14, when females reached the maximum rate ($b_x = 1$). After age 14, fecundities declined gradually until age 27 with $b_x = 0.67$. The age-specific survivorship and fecundity rates obtained from 12 cohorts of banded individuals, from records through 27 years, contrasted with survivorship and fecundity rate values reported in previous studies Binkley and Miller (1988) and Brook et al. (1999).

The demographic statistics obtained from the new Whooping Crane life table were as follows: the net reproductive rate $Ro = 6.4$/y the generation time $G = 13$y, the intrinsic instantaneous rate of population increase $r = 0.138$/y, the finite rate of annual population increase $\lambda = 1.148$, and the reproductive value V_x , and the stable age-class distribution C_x for age 0 to age 27. In general, all demographic statistics were higher than values estimated from Binkley and Miller's (1988) previous study (Ro =1.59, G = 10, $r = 0.04$, $\lambda = 1.04$).

The stochastic model from this study with values for $r \leq 0.14$, from the new life table, predicted for 2035 a Whooping Crane population of 1,000 individuals with a 40% probability of occurrence. Projections with values of r below 0.08, and Binkley and Miller's (1988) rate 0.04 indicated a lower probability for the Whooping Crane population to be down-listed in 2035.

The Whooping Crane population finite rate of annual increase (lambda) varied statistically with demographic variables (natality and mortality) that were affected throughout the life cycle, except during spring migration, by environmental factors from the three different regions: Canada and the states of Nebraska and Texas, in the United States. The best single predictor of lambda variability was the total annual mortality, which was affected by pond water depth and temperature from March to May at WBNP, extreme minimum temperatures in December at ANWR, temperature during fall migration, and the Pacific Decadal Oscillation (PDO) index. The variation in total annual mortality was not the only pathway to relate environmental factors with lambda variability. Demographic variables (mortalities at the three regions and natality) had significant correlations with other 9 environmental factors, which were not identified by the first path model. Some of these environmental factors had correlations with the global climatic factor PDO with different levels of significance. Environmental factors with more significant effects on demography included at WBNP, pond water depth, temperature from March to May and total precipitation from March to September.

During fall migration at NE, temperature in September and October; and at ANWR, temperatures in December (mean and extreme minimum), temperature (extreme maximum) from October to March, and total precipitation from November to January. Both extreme cold/hot temperatures had an effect on Whooping Crane demography in ANWR, at NE and at WBNP. Most of the environmental factors identified had a direct effect on Whooping Cranes individuals and indirect effect due to effect of habitat (drought or availability of food resources) that increased mortality and reduced natality rates (Fig. 21). Environmental factors at the winter ground affected pre-migratory and pre-breeding conditions, and, in consequence, natality. Natality was affected by freshwater inflow and extreme minimum temperature from October to March at ANWR. They were positively and significantly correlated to clutch size reduction and brood failure, respectively.

PDO had a significant effect on lambda indirectly through temperature in October affecting fall migration and annual mortality and, through extreme minimum temperatures from October to March in ANWR, affecting brood failure. With few exceptions, most periods of Whooping Crane population decline happened during PDO cold phases, and the population tended to increase during PDO warm phases. PDO index's effect on population growth lagged by one year. During PDO cold phase a synchronization of extreme values in the environmental factors were observed for the different regions; whereas, during warm phases extremes were scattered.

This study produced an age-structured population dynamics model for the Whooping Crane capable of simulating the fate of daily cohorts of individuals as they developed from eggs to adults and as they passed through their annual cycle on the breeding grounds, during fall migration, on the wintering grounds, and during spring migration.

The first version of the model to simulate Whooping Crane demography, based on data from Binkley and Miller (1988), simulated the general historical population trend observed, after adjustments on age of first reproduction 4-year-old and proportion of breeders. This model simulated total number of population, adults, sub-adults, juveniles, and individuals from subdivided age 0, and mortalities of age 0 before arrival to ANWR, and accumulated mortality for all ages in the different grounds. This version of the model projected for year 2015 a total population of 289 individuals and 33 juveniles.

A second version of the Whooping Crane demographic model, with age-specific fecundity rates and new mortality rates from the new life table, showed that Whooping Cranes have a high potential to increase exponentially, but factors associated with brood success and egg mortality and mortality on age 0 before arrival at ANWR, had an important effect on population regulation. This version was capable of simulating an improved general historical population trend for the last 20 years, with adjustments of two factors: brood failure and egg mortality. The structure of this model was capable of utilizing new data on survivorship and fecundity obtained from banded birds during last 27 years and predicted 615 individuals and 96 juveniles, but only with adjustments at the breeding ground.

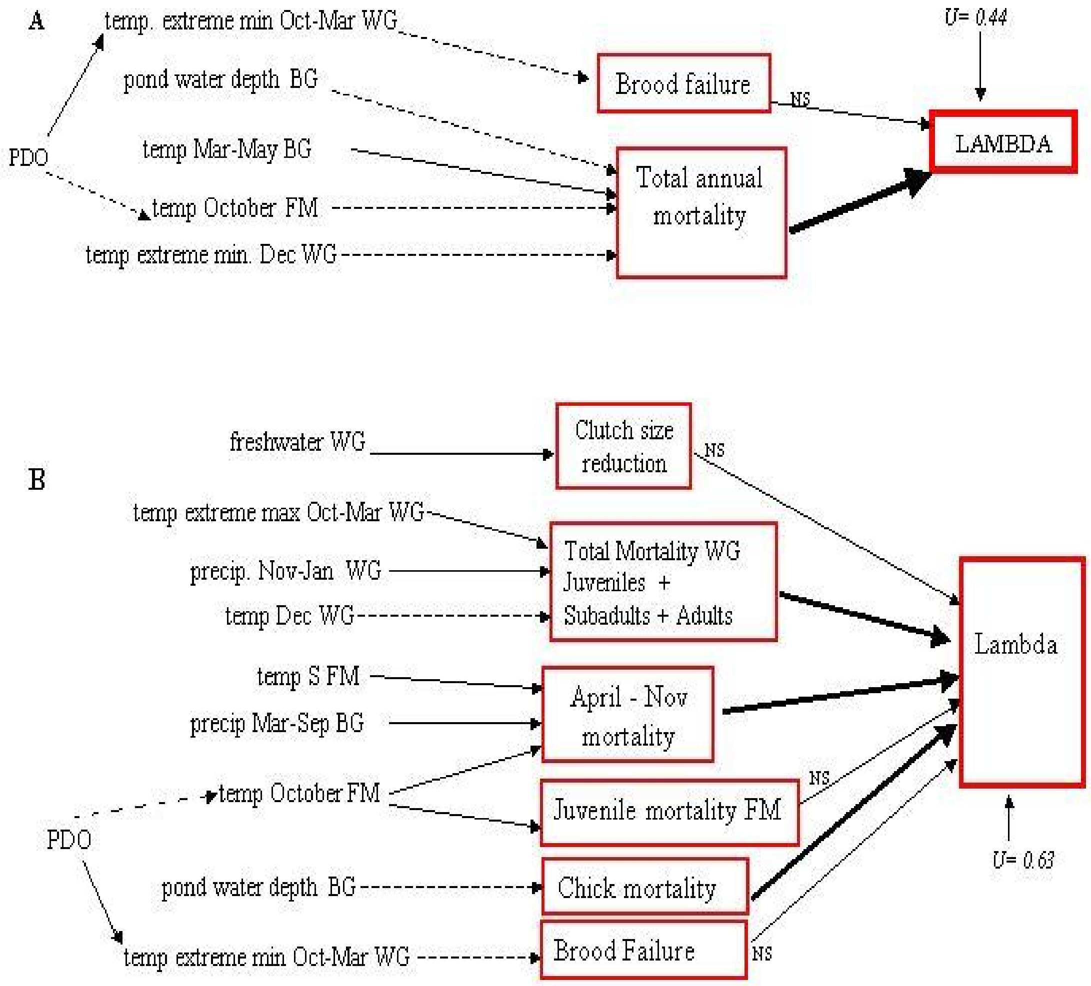

Fig. 21. Two causal models for variability of lambda of Whooping Crane population with demographic and significant environmental factors. A) The aggregated model with only two proximal variables annual mortality, measured at ANWR, and brood failure, and B) the fully resolved model, with all demographic parameters (except egg mortality) included in the path analysis. Path coefficients sign (continued lines = positive, and dashed lines = negative). Thick and thin lines indicate strong and weak or no significant (NS) correlation, respectively. U is the variation unexplained by the causal structure, (BG = Breeding ground, FM = Fall migration, WG = Wintering ground).

The last version of the model will allow continue future studies to project population responses, to various environmental scenarios on the breeding grounds, during fall/spring migrations, and on the wintering grounds over the next 30 years. Since mortalities occurs through all the life cycle in the different regions, future modifications of this model, with age-specific fecundity and mortality rates in function of environmental conditions in the different grounds, will improve the capability of the model to simulate observed population fluctuations about the general historical trend.

RECOMMENDATIONS

I suggest using the new life table of the ANWR-WBNP Whooping Crane population obtained in this study, for future demographic analysis and for adjusting the recovery plan.

Further attention must be paid to responses by lower trophic levels representing the Whooping Cranes food web, and to historical population variation of these organisms associated with variation in environmental factors on a regional and global (North America) scale. More historical analysis is needed on other abiotic factors (tides, water temperature and turbidity, wind, salinity, and ENSO among others) that could be responding to the same physical forces and climatic changes that directly affect the Whooping Crane population. Additional analysis on these relationships could contribute to identification of other important environmental factors on Whooping Crane demography.

I suggest continued improvement of the demographic model developed with the new data from Whooping Crane life table (Chapter II), and testing of the first group of environmental factors (temperature extreme minimum in December, and extreme temperature from October to March at ANWR, temperature October in NE, pond water depth and temperature from March to May at WBNP, and PDO) that were significantly associated with lambda variability (Chapter III). As a last recommendation, after completion of this model for adequate simulation of observed population fluctuations in response to abiotic environmental factors, there must come the inclusion of biotic factors for a future integrated model.

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APPENDIX A

WHOOPING CRANE DEMOGRAPHY, FIGURES AND TABLES

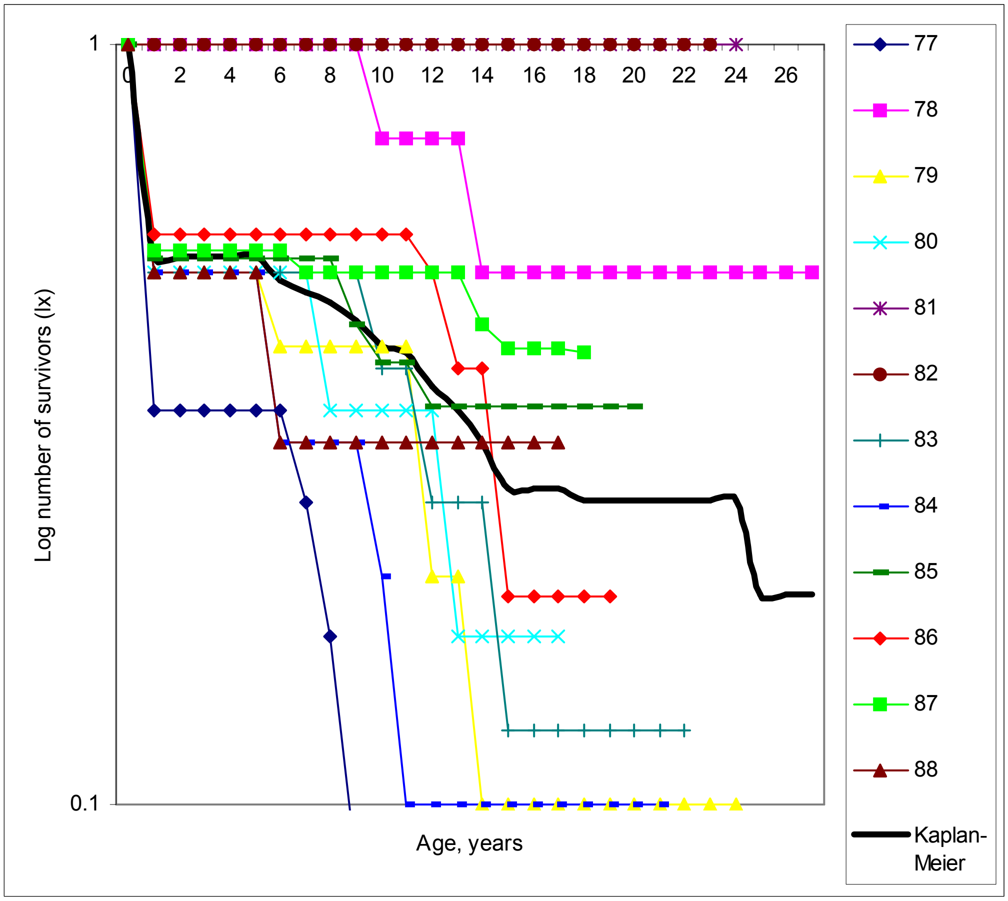


Fig. A1. Comparison of age-specific survivorship curves (l_x) for Whooping Cranes estimated with data from 12 cohorts from 1977 to 1988 and survivorship from each cohort of banded individuals. Each curve was estimated via Kaplan-Meier survival analysis.

Table A1. Definitions of symbols used in the text. Terminology and calculations follow Krebs (2001; except for e_x see Krebs 1978).

Symbol	Definition	Calculation
n_x	Number alive at age *x*	Data
l_x	Proportion surviving from start of life table to age *x*	$l_x = n_x / n_o$
d_x	Number dying during age interval *x* to *x + 1*	$d_x = l_x - l_{(x+1)}$
q_x	Per capita mortality rate during age interval *x* to *x + 1*	$q_x = d_x / n_x$
e_x	Expectation of life at age *x* (expected number of years from age *x* to death)	$e_x = T_x / n_x$ $T_x = \sum_{i=x}^{\infty} L_i \; ; L_i = (n_x + n_{x+1}) / 2$
b_x	Per capita fecundity rate for females aged *x* to *x + 1* (females / female-year)	Data
R_o	Net reproductive rate (multiplication rate of population per generation)	$R_o = \sum (l_x b_x)$
G	Generation time (length of time between birth of a female and mean birth date of her female offspring)	$G = \sum (l_x b_x x) / R_o$
r	Intrinsic (instantaneous) rate of population increase	$r = \log_e(R_o) / G$
λ	Finite rate of population increase (multiplication rate per year)	$\lambda = e^r$
C_x	Proportion of population in age category *x* to *x+1* with the population stable age-class distribution	$C_x = (\lambda^{-x} l_x) / (\sum_{i=0}^{\infty} \lambda^{-i} l_i)$
V_x	Reproductive value (contribution to future population made by a female aged *x; ω* is age of last reproduction)	$V_x = \sum_{t=x}^{\omega} (l_t b_t) / l_x$

Table A2. Age-specific survivorship ($l_x = n_x / n_o$; n_0 = number of eggs) and fecundity (b_x) of each of the 12 cohorts of Whooping Cranes born from 1977 to 1988, estimated based on data from banded individuals. (No females were banded in 1978, 1981, and 1983, b_x values for these cohorts were estimated based on data from all banded females). Estimates of the net reproductive rate (R_o), the generation time (G), the intrinsic capacity for increase (r), and the finite rate of increase (λ) based on data from each cohort also are presented.

	1977			1978		1979			1980			1981		1982		
Age	*nx*	*lx*	*bx*	*nx*	*lx*	*nx*	*lx*	*bx*	*nx*	*lx*	*bx*	*nx*	*lx*	*nx*	*lx*	*bx*
0	8	1	0	8	1	10	1	0	6	1	0	1	1	1	1	0
1	4	0.33	0	4	1	5	0.5	0	3	0.5	0	1	1	1	1	0
2	4	0.33	0	4	1	5	0.5	0	3	0.5	0	1	1	1	1	0
3	4	0.33	0.3	4	1	5	0.5	0	3	0.5	0	1	1	1	1	0
4	4	0.33	0.3	4	1	5	0.5	0	3	0.5	1	1	1	1	1	1
5	4	0.33	0.3	4	1	5	0.5	1	3	0.5	1	1	1	1	1	1
6	4	0.33	0.6	4	1	4	0.4	0.5	3	0.5	0	1	1	1	1	1
7	3	0.25	0.6	4	1	4	0.4	1	3	0.5	1	1	1	1	1	0
8	2	0.16	0.5	4	1	4	0.4	1	2	0.33	1	1	1	1	1	0
9	1	0.08	1	4	1	4	0.4	1	2	0.33	0	1	1	1	1	1
10	1	0.08	1	3	0.75	4	0.4	0.75	2	0.33	0	1	1	1	1	0
11	1	0.08	1	3	0.75	4	0.4	0	2	0.33	0	1	1	1	1	1
12	1	0.08	1	3	0.75	2	0.2	0	2	0.33	0	1	1	1	1	1
13	1	0.08	1	3	0.75	2	0.2	0	1	0.16	0	1	1	1	1	1
14	1	0.08	1	2	0.5	1	0.1	0	1	0.16	0	1	1	1	1	1
15	1	0.08	1	2	0.5	1	0.1	0	1	0.16	0	1	1	1	1	1
16	1	0.08	1	2	0.5	1	0.1	0	1	0.16	0	1	1	1	1	1
17	1	0.08	0	2	0.5	1	0.1	0	1	0.16	0	1	1	1	1	1
18	1	0.08	1	2	0.5	1	0.1	0	0	0	0	1	1	1	1	1
19	1	0.08	1	2	0.5	1	0.1	0	0	0	0	1	1	1	1	1
20	1	0.08	1	2	0.5	1	0.1	0	0	0	0	1	1	1	1	1
21	1	0.08	1	2	0.5	1	0.1	0	0	0	0	1	1	1	1	0.5
22	1	0.08	1	2	0.5	1	0.1	0	0	0	0	1	1	1	1	1
23	1	0.08	1	2	0.5	1	0.1	0	0	0	0	1	1			
24	1	0.08	1	2	0.5	1	0.1	0	0	0	0					
25	1	0.08	1	2	0.5	0	0	0								
26	1	0.08	1	2	0.5											
27	1	0.08	1													
λ		1.058		1.208			1.112			1.109		1.225			1.222	
r		0.057		0.189			0.106			0.103		0.203			0.200	
Ro		2.227		13.183			2.2			1.833		17.857			15.5	
G		13.98		13.630			7.409			5.814		14.169			13.645	

Table A2. Continued

	1983		1984			1985			1986			1987			1988		
Age	*nx*	*lx*	*nx*	*lx*	*bx*	*nx*	*lx*	*bx*	*nx*	*lx*	*bx*	*nx*	*lx*	*bx*	*nx*	*lx*	*bx*
0	8	1	10	1	0	21	1	0	16	1	0	28	1	0	10	1	0
1	4	0.5	5	0.5	0	11	0.52	0	9	0.56	0	15	0.53	0	5	0.5	0
2	4	0.5	5	0.5	0	11	0.52	0	9	0.56	0	15	0.53	0	5	0.5	0
3	4	0.5	5	0.5	0	11	0.52	0	9	0.56	0	15	0.53	0.11	5	0.5	0
4	4	0.5	5	0.5	0.6	11	0.52	0	9	0.56	0.43	15	0.53	0.33	5	0.5	1
5	4	0.5	5	0.5	0.75	11	0.52	0.3	9	0.56	0.63	15	0.53	0.61	5	0.5	0
6	4	0.5	3	0.3	1	11	0.52	0.8	9	0.56	0.75	15	0.53	1	3	0.3	0
7	4	0.5	3	0.3	1	11	0.52	1	9	0.56	1	14	0.5	0.88	3	0.3	0
8	4	0.5	3	0.3	1	11	0.52	1	9	0.56	1	14	0.5	1	3	0.3	0
9	4	0.5	3	0.3	1	9	0.42	1	9	0.56	0.94	14	0.5	0.93	3	0.3	0
10	3	0.37	2	0.2	1	8	0.38	1	9	0.56	1	14	0.5	1	3	0.3	0
11	3	0.37	1	0.1	0	8	0.38	1	9	0.56	1	14	0.5	1	3	0.3	0
12	2	0.25	1	0.1	0	7	0.33	1	8	0.5	1	14	0.5	1	3	0.3	0
13	2	0.25	1	0.1	0	7	0.33	0.9	6	0.37	1	14	0.5	1	3	0.3	0
14	2	0.25	1	0.1	0	7	0.33	1	6	0.37	1	12	0.42	1	3	0.3	0
15	1	0.12	1	0.1	0	7	0.33	0.9	3	0.18	1	11	0.39	1	3	0.3	0
16	1	0.12	1	0.1	0	7	0.33	1	3	0.18	0	11	0.39	0.88	3	0.3	0
17	1	0.12	1	0.1	0	7	0.33	0.9	3	0.18	1	11	0.39	0.83			
18	1	0.12	1	0.1	0	7	0.33	0.8	3	0.18	1						
19	1	0.12	1	0.1	0	7	0.33	0.75									
20	1	0.12	1	0.1	0												
21	1	0.12															
22		0.1															
23																	
24																	
25																	
26																	
27																	
λ	1.154		1.113			1.155			1.189			1.185			0.840		
r	0.143		0.107			0.144			0.173			0.170			- 0.173		
R_o	4.592		2.075			5.230			5.609			6.013			0.5		
G	10.605		6.783			11.482			9.944			10.516			4		

Table A3. Number of eggs laid at age class (years) by banded females in each of 12 cohorts of Whooping Cranes born (hatched) from 1977 to 1988 (no females were banded in 1978, 1981, and 1983), and the resulting age-specific fecundity estimates (b_x). X = No Nest, Gray = Death, ? = No nest found,* = Few data available.

Year born	Band $^+$	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13	Age 14	Age 15	Age 16	Age 17	Age 18	Age 19	Age 20	Age 21	Age 22	Age 23	Age 24	Age 25	Age 26	Age 27
1977	R-W	2	2	2	2																					
1977	R-G				2	2																				
1977	G-R					2	1	2*	2	2	2	2	2	2	2	X	2	2	2	2	2	2	2	2	?	2
	b b_x	**0.3**	**0.3**	**0.3**	**0.6**	**0.6**	**0.5**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
1979	BwB-r/w			2*	2	2	2	2	2	2	2	2														
1979	BwB-R			2	X	2	2	2	1																	
	b_x	**0**	**0**	**1**	**0.5**	**1**	**1**	**1**	**0.75**																	
1980	r/b-R		2	2	X	2	2	X																		
	b_x	**0**	**1**	**1**	**0**	**1**	**1**	**0**																		
1982	W-R		2	2	2	X	X	2	X	2	2	2	2	2	2	2	2	2	2	1	2					
	b_x	**0**	**1**	**1**	**1**	**0**	**0**	**1**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.5**	**1**					
1984	BWsp-BWsp		2																							
1984	W-B		2	2																						
1984	Y-Y			1	2	2	2	2	2																	
	b_x	**0**	**0.6**	**0.75**	**1**	**1**	**1**	**1**	**1**																	
1985	Y-R			2	2*	2	2	2*	2	2	2	2	2	2	2	2	2									
1985	BwB-GwG			1	2*	2	2	2*	2	2	2	2	2*	2	2	2	2	2								
1985	W-G				2	2	2	2	2	2*	2	2	2	2*	2	2	2	2								
1985	WbW-ByB				2	2*	2*	2*	2	2*	2*	1	2	1*	2	1	2	2								
1985	ByB-ByB					2	2*	2*	2	2*	2	2*	2	2	2	2	0	0								
	b_x	**0**	**0**	**0.3**	**0.8**	**1**	**1**	**1**	**1**	**1**	**1**	**0.9**	**1**	**0.9**	**1**	**0.9**	**0.8**	**0.75**								
1986	R-Y		1	2	2	2	2	2	2	2	2	2	2	2												
1986	Y/b-o		2	2*	2	2*	2	2	2	2	2	2	2	2												
1986	o-r/b		2	2	2	2	2	2	2	2	2	2	2	2												
1986	O/w-Bwsp		2	2	2	2	2	1	2	2	2															

Table A3. Continued

	Band	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13	Age 14	Age 15	Age 16	Age 17	Age 18	Age 19	Age 20	Age 21	Age 22	Age 23	Age 24	Age 25	Age 26	Age 27
1986	O/y-B			2	2	2	2	2	2	2	2	2														
1986	o-w				2	2	2*	2	2	2	2	2	2													
1986	R/b-o					2	2	2	2	2																
1986	B-o/y					2	2	2	2	2	2	2	2	2	X	2	2									
	***b*$_x$**	**0**	**0.43**	**0.63**	**0.75**	**1**	**1**	**0.94**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**1**	**1**									
1987	RwR-YbY		1	2	2	2*	2	2*	2	2	2	2	2	2	2	2										
1987	YbY-y/g		2	2	2	2	2	2	2	2	2	2	2	2	2	1										
1987	Y/g-Y		1	2	2	2*	2	2	2	2	2	2	2	2	2											
1987	YbY-RwR			1	2	2*	2	2	2	2	2	2	2	2	2	2										
1987	YbY-W			2	2	X	2	1	2	2	2	2	2													
1987	R-YbY				2	2	2	2	2	2	2	2	2	2	2	2										
1987	G-YbY				2	2	2	2	2	2	2	2	2	2	X	2										
1987	Y/b-YbY				2																					
1987	W-YbY	2	2	2	2	2*	2	2	2	2	2	2*	2	2	2	1										
	***b*$_x$**	**0.11**	**0.33**	**0.61**	**1**	**0.88**	**1**	**0.93**	**1**	**1**	**1**	**1**	**1**	**1**	**0.88**	**0.83**										
1988	RwR-BwB		2																							
	***b*$_x$**		**1**																							

Table A4. Age-specific fecundity estimates (b_x) for banded females in each of 12 cohorts of Whooping Cranes hatched from 1977 to 1988 (no females were banded in 1978, 1981, and 1983), and the corresponding weighted arithmetic mean values.

	b_x (1977)	b_x (1979)	b_x (1980)	b_x (1982)	b_x (1984)	b_x (1985)	b_x (1986)	b_x (1987)	b_x (1988)	b_x (mean)
Age 0	0	0	0	0	0	0	0	0	0	0
Age 1	0	0	0	0	0	0	0	0	0	0
Age 2	0	0	0	0	0	0	0	0	0	0
Age 3	0.3	0	0	0	0	0	0	0.11	0	0.055
Age 4	0.3	0	1	1	0.6	0	0.43	0.33	1	0.356
Age 5	0.3	1	1	1	0.75	0.3	0.63	0.61	0	0.572
Age 6	0.6	0.5	0	1	1	0.8	0.75	1	0	0.793
Age 7	0.6	1	1	0	1	1	1	0.88	0	0.904
Age 8	0.5	1	1	0	1	1	1	1	0	0.948
Age 9	1	1	0	1	1	1	0.94	0.93	0	0.958
Age 10	1	0.75	0	0	1	1	1	1	0	0.942
Age 11	1	0	0	1	0	1	1	1	0	0.923
Age 12	1	0	0	1	0	1	1	1	0	0.956
Age 13	1	0	0	1	0	0.9	1	1	0	0.936
Age 14	1	0	0	1	0	1	1	1	0	1
Age 15	1	0	0	1	0	0.9	1	1	0	0.969
Age 16	1	0	0	1	0	1	0	0.88	0	0.94
Age 17	0	0	0	1	0	0.9	1	0.83		0.881
Age 18	1	0	0	1	0	0.8	1			0.885
Age 19	1	0	0	1	0	0.75				0.833
Age 20	1	0	0	1	0					0.86
Age 21	1	0	0	0.5						0.83
Age 22	1	0	0	1						0.8
Age 23	1	0	0							0.77
Age 24	1	0	0							0.74
Age 25	1	0								0.71
Age 26	1									0.68
Age 27	1									0.111

Table A5. Age-class distribution of Whooping Cranes for the year 2001 estimated by Lynk et al. (2003) based on counts from 1938 to 2001, and from this study. Age 0 (include number of eggs as individuals)

Age	Proportion of individuals in age class	Proportion of individuals in age class, This study
0	(No estimated)	0.2498
1	0.08	0.1148
2	0.045	0.1
3	0.079	0.087
4	0.079	0.075
5	0.119	0.066
6	0.068	0.053
≥ 7	0.517	0.267

Table A6. Intrinsic capacity for increase *(r)* for the only free-living, non-experimental, population of Whooping Cranes calculated annually based on the number of individuals observed from 1938 to 2003. Mean (± 1 SD) values for each of the 3 general growth periods (1938 – 1956, 1957 – 1982, 1983 – 2003) also are presented.

Period 1938 - 1956		*Period 1957 - 1982*		*Period 1983 - 2003*	
Year	*r*	Year	*r*	Year	*r*
1938	0.2	1957	0.207	1983	0.136
1939	0.167	1958	0.037	1984	0.120
1940	-0.448	1959	0.087	1985	0.125
1941	0.171	1960	0.080	1986	0.197
1942	0.1	1961	-0.197	1987	0.029
1943	-0.154	1962	0.030	1988	0.056
1944	0.200	1963	0.241	1989	0
1945	0.127	1964	0.046	1990	-0.100
1946	0.215	1965	-0.022	1991	0.029
1947	-0.032	1966	0.11	1992	0.050
1948	0.125	1967	0.040	1993	-0.072
1949	-0.092	1968	0.113	1994	0.172
1950	-0.215	1969	0.017	1995	0.012
1951	-0.174	1970	0.034	1996	0.128
1952	0.133	1971	0.033	1997	0.005
1953	-0.133	1972	-0.219	1998	0.026
1954	0.287	1973	0	1999	-0.043
1955	-0.154	1974	0.151	2000	-0.022
1956	0.08	1975	0.191	2001	0.049
		1976	0.042	2002	0.047
		1977	0.040	2003	0.107
		1978	0.013		
		1979	0.025		
		1980	-0.066		
		1981	0		
		1982	0.027		
Mean	0.021	Mean	0.040	Mean	0.050
SD	±0.193	SD	±0.102	SD	±0.078

Table A7. Estimates of the net reproductive rate (*Ro*), the mean of a generation time(*G*), the intrinsic capacity for increase (*r*), and the finite rate of increase (λ) based on data from banded individuals in each of 9 cohorts of Whooping Cranes born from 1977 to 1988 (no females were banded in 1978, 1981, and 1983). Weighted (by number of individuals in each cohort) arithmetic mean (± 1 SD) values also are presented, as are the corresponding estimates made by Binkley and Miller (1988).

	1977	1979	1980	1982	1984	1985	1986	1987	1988	Mean	SD	Binkley & Miller
R_o	2.22	2.20	1.83	15.50	2.07	5.23	5.60	6.01	0.50	4.57	5.84	1.59
G	13.99	7.40	5.81	13.64	6.78	11.48	9.94	10.51	4.00	9.28	3.48	10.75
r	0.05	0.10	0.10	0.20	0.10	0.14	0.17	0.17	-0.17	0.09	0.10	0.04
λ	1.05	1.23	1.10	1.22	1.11	1.15	1.18	1.18	0.84	1.11	0.11	1.04

Table A8. Estimates of the intrinsic rate of increase (*r*) of the only free-living, non experimental, population of Whooping Cranes from this, and previous studies, indicating the years from which data were drawn to make the estimates. Estimates from this study were based on data from all banded individuals in 12 cohorts born from 1977 to 1988 (all cohorts), and based on data from each of the 9 cohorts individually. The weighted (by number of individuals in each cohort) arithmetic mean (± 1 SD) of *r* values from the 9 cohorts also is presented. Population projections to the year 2035 based on these *r* values were calculated in this study and were not presented in the earlier paper.

Years	*r*	Source	Estimated population in the year 2035 (calculated in this study)
1938-1956	0.020	Miller et al. (1974)	130
1957-1987	0.044	Binkley & Miller (1988)	641
	0.049	Mirande et al. 1997	1,022
1977-2004	0.138	This study (all cohorts)	15,194
1977-2004	0.057	This study (1977 cohort only)	1,276
1979-2003	0.106	This study (1979 cohort only)	5,773
1980-1997	0.104	This study (1980 cohort only)	5,346
1982-2004	0.201	This study (1982 cohort only)	103,369
1984-2004	0.107	This study (1984 cohort only)	5,989
1985-2004	0.144	This study (1985 cohort only)	18,308
1986-2004	0.173	This study (1986 cohort only)	44,767
1987-2004	0.171	This study (1987 cohort only)	41,105
1988-2004	-0.173	This study (1988 cohort only)	1
1977-2004	0.099 (± 0.10)	This study (9 cohorts *r*, mean ± 1 SD)	4,600

Table A9. Characterization of specific periods of growth, decline, and stability since 1966 of the only free-living population of Whooping Cranes, indicating duration of each period as well as the finite (λ) and instantaneous (*r*) rates of population change during the period.

Type of period	Calendar years	Duration (years)	λ	*r*
Growth	1966 - 1972	6	1.051	0.049
	1974 - 1980	6	1.068	0.066
	1982 - 1989	7	1.08	0.077
	1991 - 1993	2	1.027	0.026
	1994 - 1999	5	1.059	0.057
	2001 - 2004	3	1.052	0.051
	Mean (± 1 SD)	4.83 (± 1.94)	1.056 (± 0.018)	0.054 (± 0.017)
Decline	1972 - 1973	1	0.929	-0.073
	1980 - 1981	1	0.967	-0.033
	1990 - 1991	1	0.95	-0.05
	1993 - 1994	1	0.964	-0.036
	1999 - 2001	2	0.978	-0.022
	Mean (± 1 SD)	1.2 (± 0.44)	0.957 (± 0.018)	-0.042 (± 0.019)
Stability	1973 - 1974	1	1	0
	1981 - 1982	1	1	0
	1989 - 1990	1	1	0

APPENDIX B

HISTORICAL DATA: WHOOPING CRANE ANWR_WBNP POPULATION AND ENVIRONMENTAL FACTORS AT ARANSAS NATIONAL WILDLIFE REFUGE (ANWR), WOOD BUFFALO NATIONAL PARK (WBNP), AND NEBRASKA PLATTE RIVER STATION (NE), FIGURES AND TABLES.

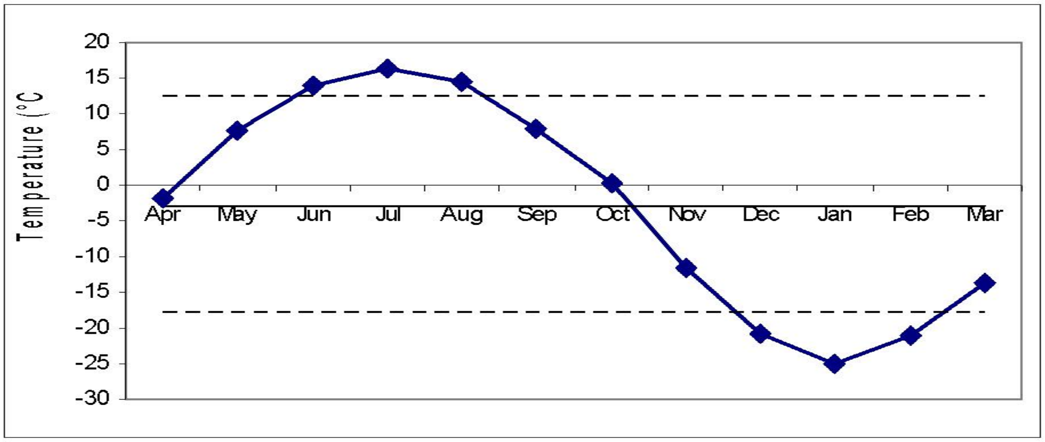


Fig. B1. Temperature at WBNP, monthly mean ºC, from 1947 to 2004, from Forth Smith, Canada. Mean (solid line), ±1SD (dashed lines).

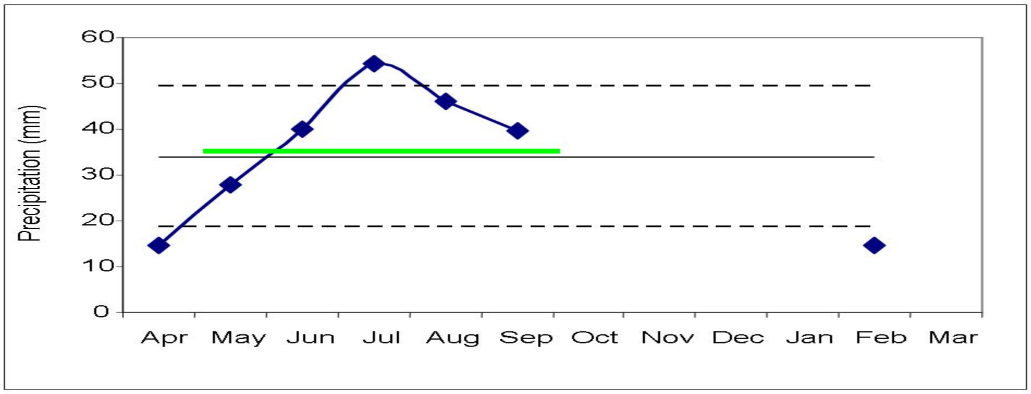


Fig. B2. Precipitation at WBNP, monthly average mm, from March to September 1938 to 2004 at Forth Smith, Canada.. Mean (solid line), ±1SD (dashed lines). Green line :Whooping Crane occurrences.

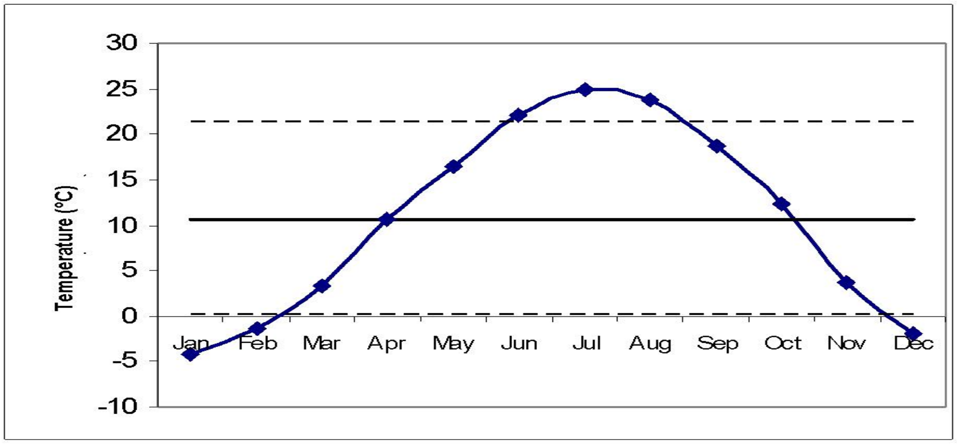


Fig. B3. Temperature in Nebraska (NE), º C degrees in average from 1967 to 2003 at NE, Platte River Station. Mean (solid line), ±1SD (dashed lines).

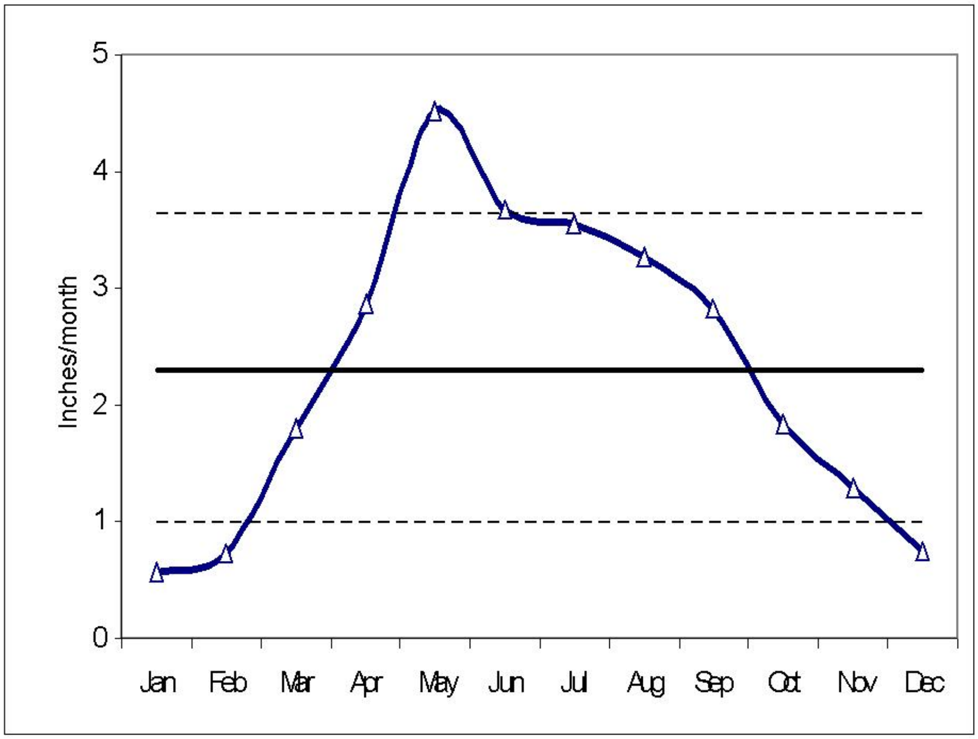


Fig. B4. Precipitation in Nebraska (NE), monthly inches average from 1967 to 2003 at NE, Platte River station. Mean (solid line), ±1SD (dashed lines).

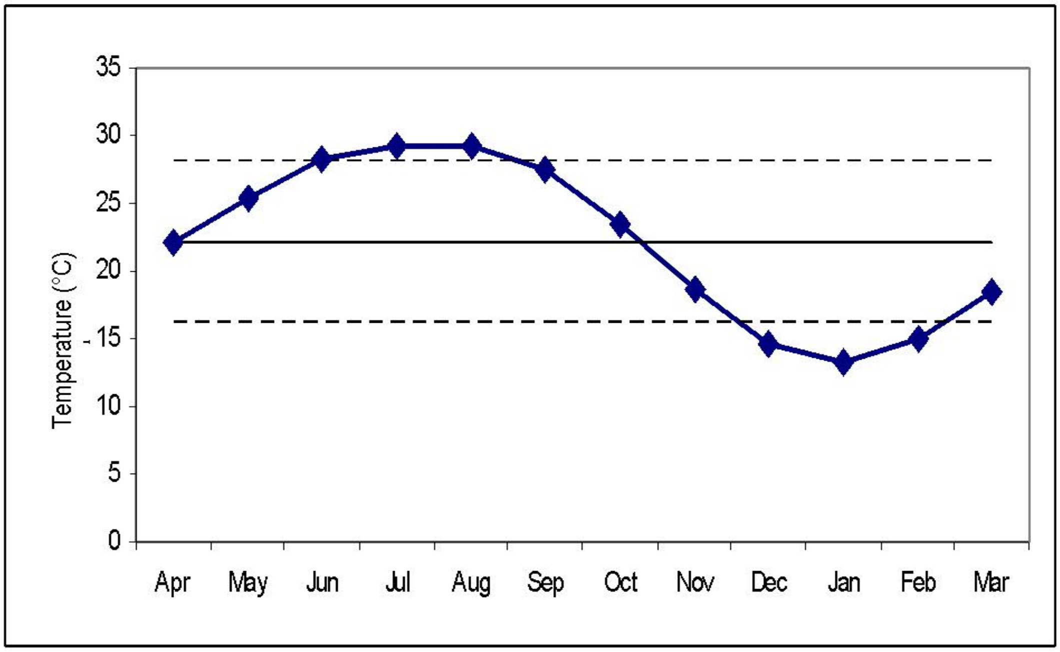


Fig. B5. Temperature in ANWR, monthly mean ºC, from 1940 to 2003. Mean (solid line), ±1SD (dashed lines).

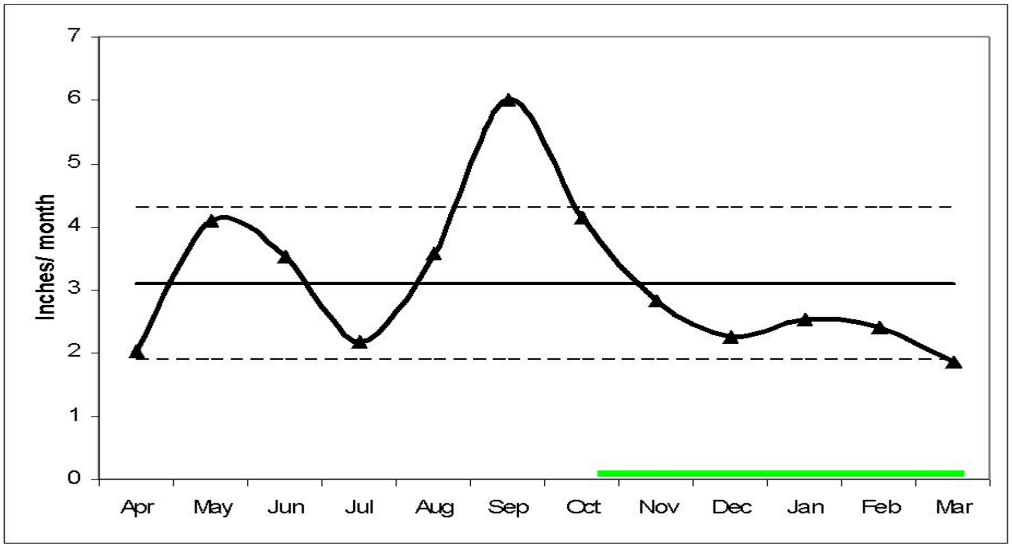


Fig. B6. Precipitation at ANWR, monthly average inches/month, from 1938 to 2004 Mean (solidline), ±1SD (dashed lines).

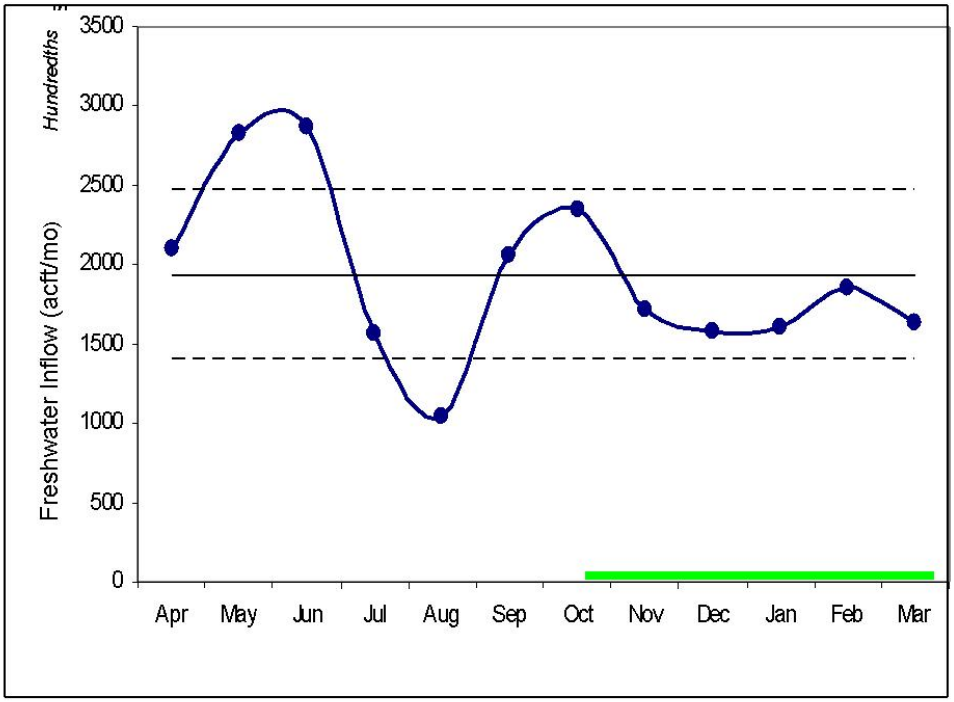


Fig. B7. Freshwater inflow in Guadalupe Estuary, sum of acft /month from 1938 to 2001. Mean (solid line), ±1SD (dashed lines).

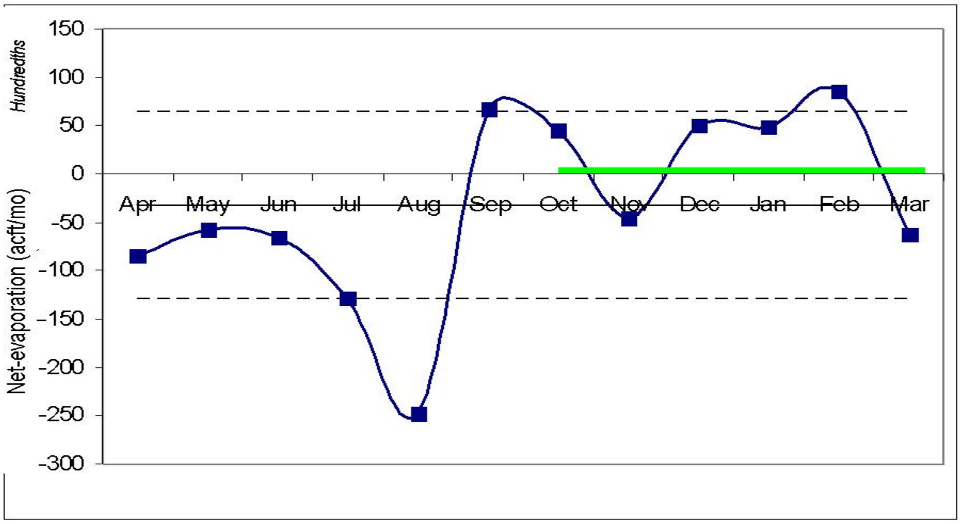


Fig. B8. Net-Evaporation in Guadalupe Estuary, sum of acft /month from 1941 to 1999. Mean (solid line), ±1SD (dashed lines).

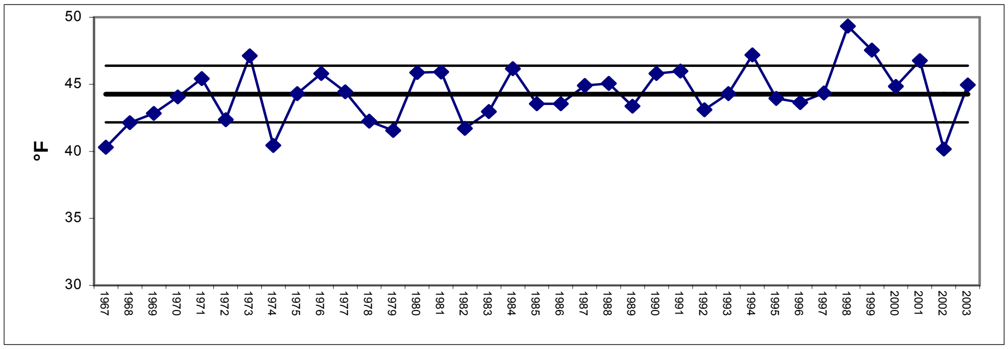


Fig. B9. Temperature, March – September WBNP, from 1967 - 2003, (ºF). Mean (thick line), ±1SD (thin lines).

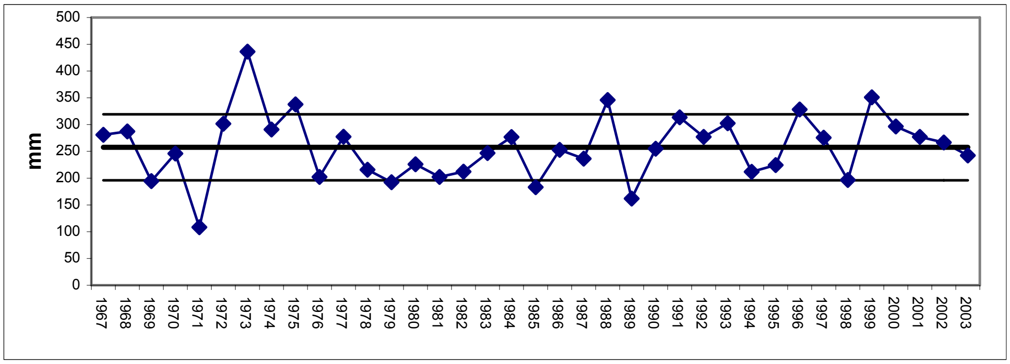


Fig. B10. Precipitation, March - September WBNP, 1967 – 2003, (mm). Mean (thick line), ±1SD (thin lines).

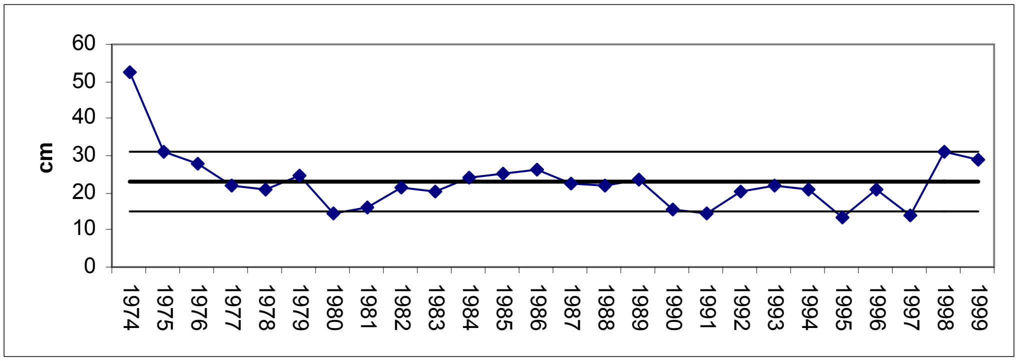


Fig. B11. Pond water depth, May WBNP, at 1m.of the nest, 1974 – 1999 (cm). Mean (thick line), ±1SD (thin lines).

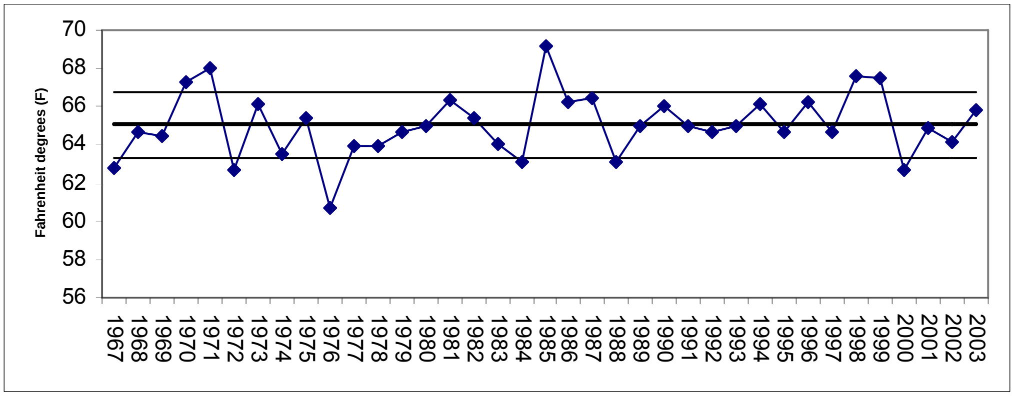


Fig. B12. Temperature, September – March, ANWR, 1967 – 2003, (ºF). Mean (thick line), ±1SD (thin lines).

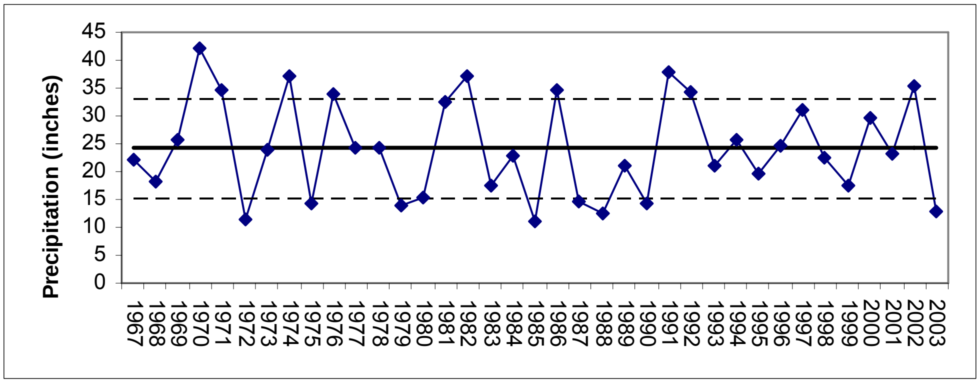


Fig. B13. Precipitation, September – March, ANWR, 1967 – 2003, (total inches). Mean (thick line), ±1SD (thin dashed lines).

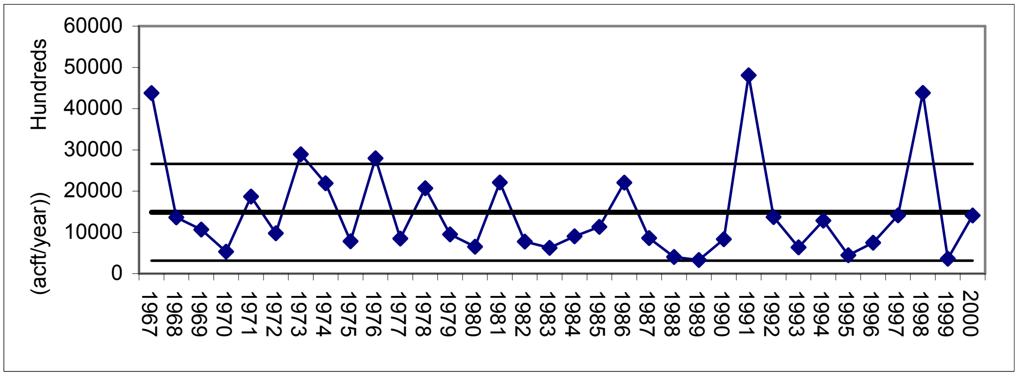


Fig. B14. Freshwater inflow, September – March, Guadalupe estuary, 1967 – 2000 (total acft/yr). Mean (thick line), ±1SD (thin lines).

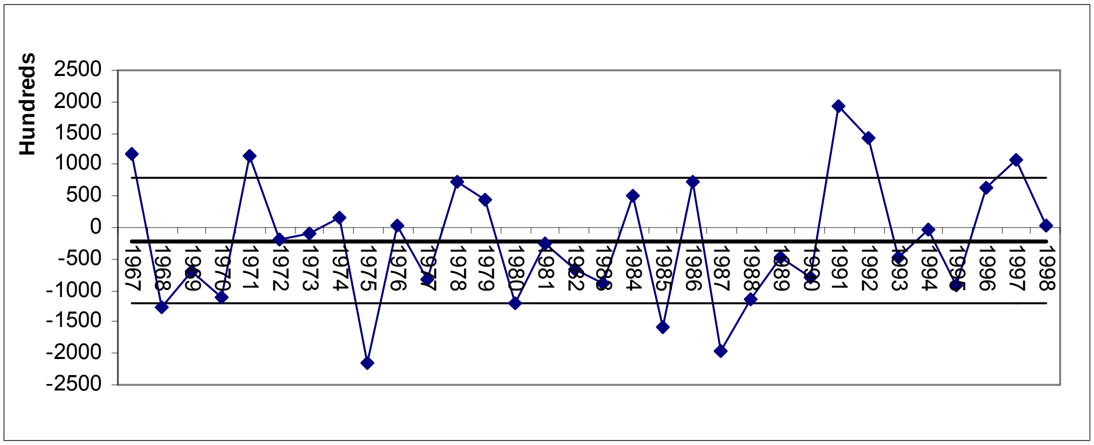


Fig. B15. Net- Evaporation, (Precipitation – Evaporation), September – March, Guadalupe estuary. From 1967 to 1998 (acft/yr). Mean (thick line), ±1SD (thin lines).

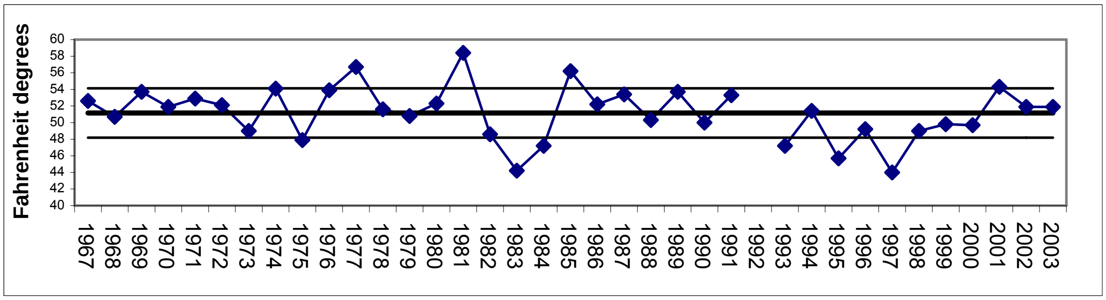


Fig. B16. Temperature spring migration, April, Nebraska (NE), from1967 to 2003 (ºF). Mean (thick line), ±1SD (thin lines).

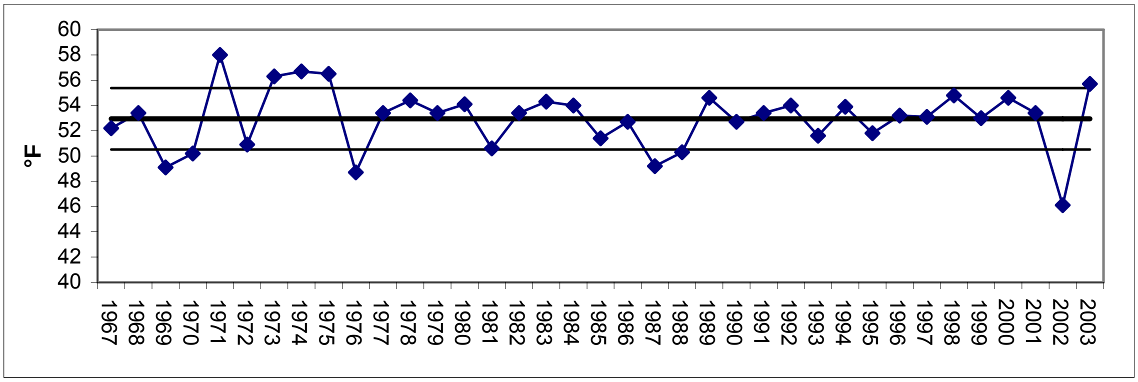


Fig. B17. Temperature fall migration, October, Nebraska (NE), from 1967 to 2003 (ºF). Mean (thick line), ±1SD (thin lines).

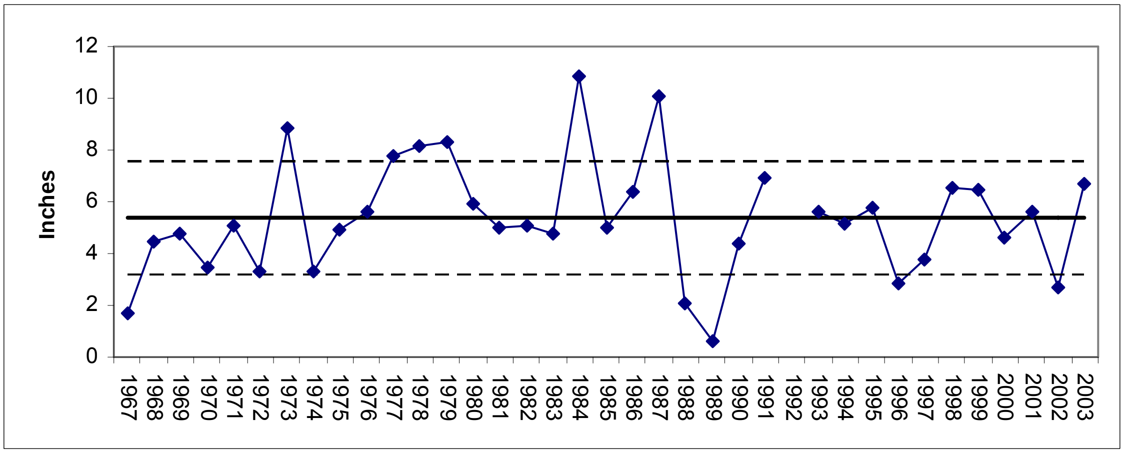


Fig. B18. Precipitation, February – March – and April (average), NE. From 1967 – 2003, (total inches). Mean (thick line), ±1SD (thin dashed lines).

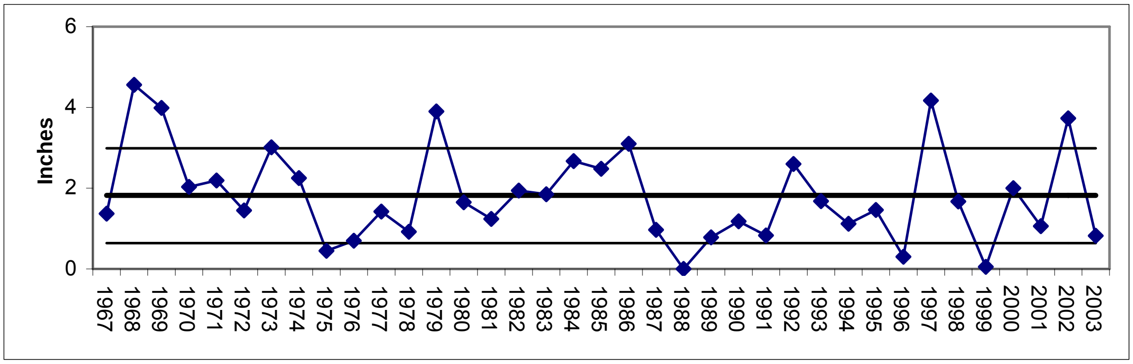


Fig. B19. Precipitation October, NE. From 1967 – 2003, (total inches). Mean (thick line), ±1SD (thin lines).

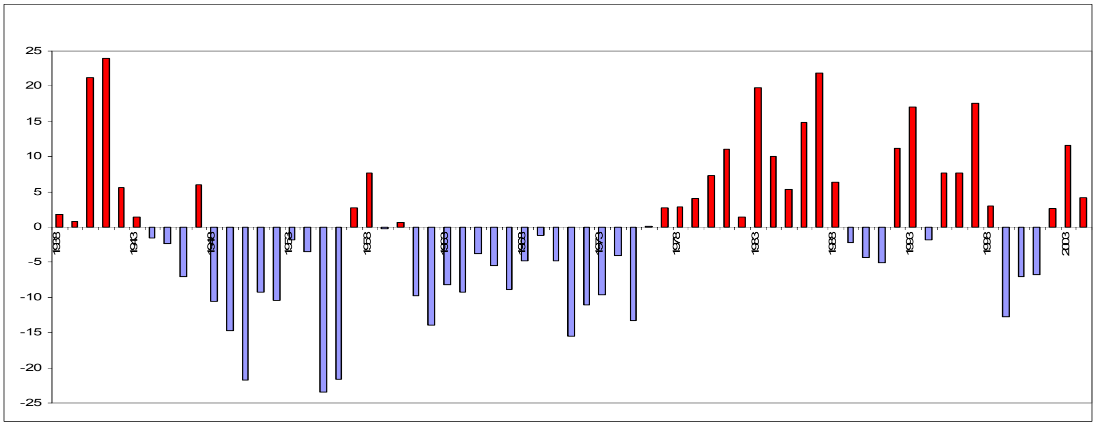


Fig. B20. PDO Index, from 1938 to 2004 (cool phase negative values, warm phase positive).

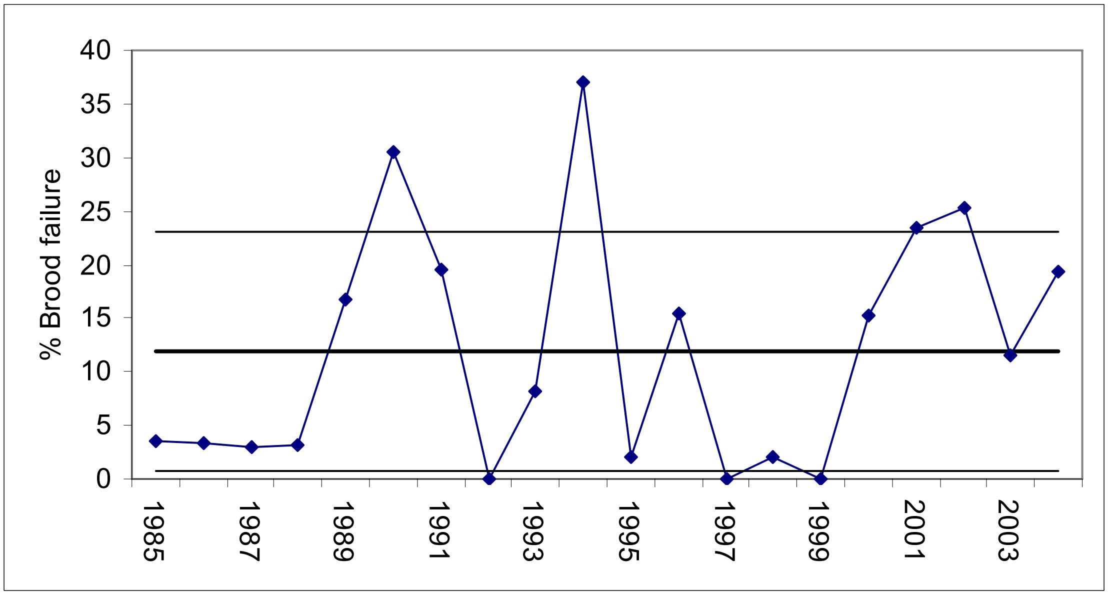


Fig. B21. Demographic dependent variable: brood failure from 1985 – 2004. Mean (thick line), ±1SD (thin lines).

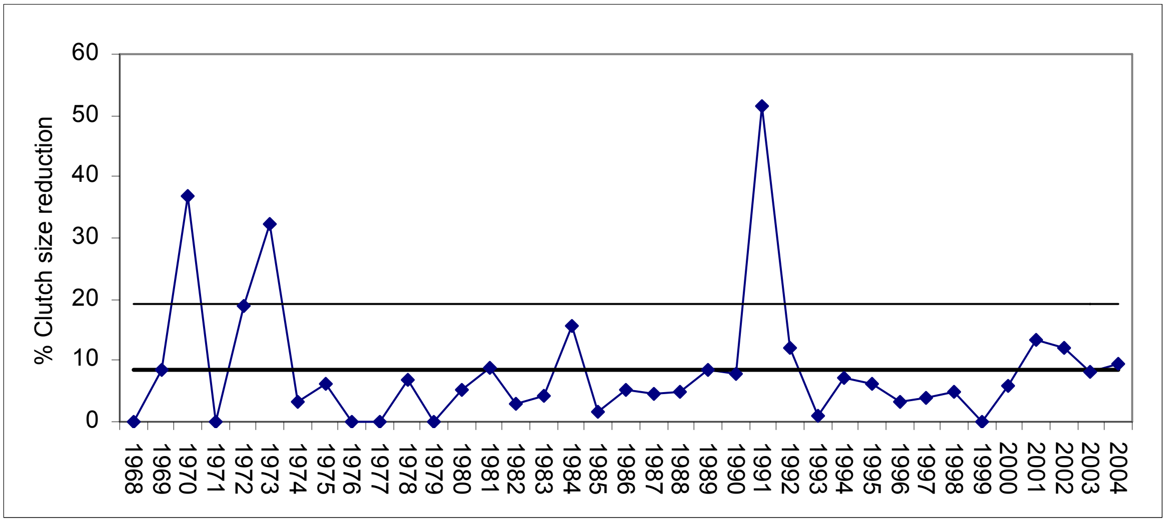


Fig. B22. Demographic dependent variable clutch size reduction Mean (thick line), ±1SD (thin lines).

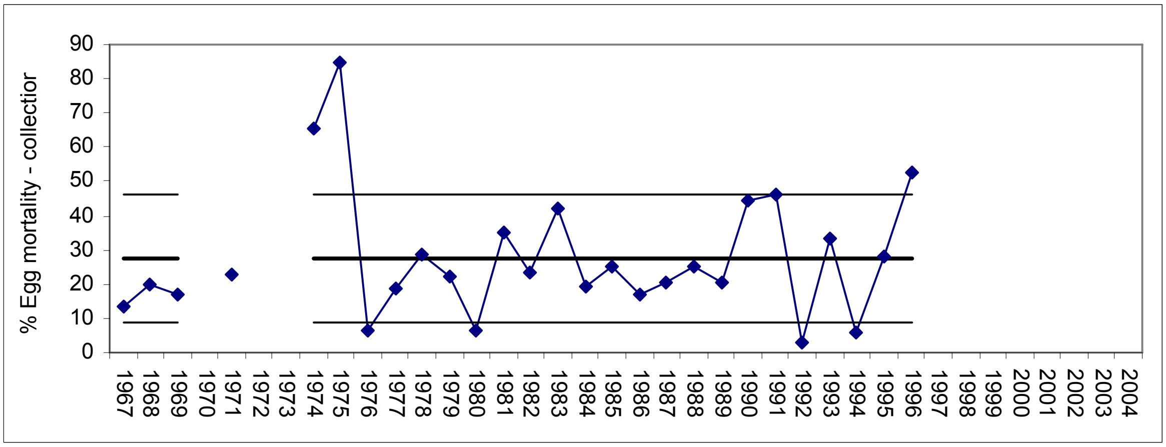


Fig. B23. Demographic dependent variable egg mortality (May 1967 – 1996, except 1970, 1972, 1973).

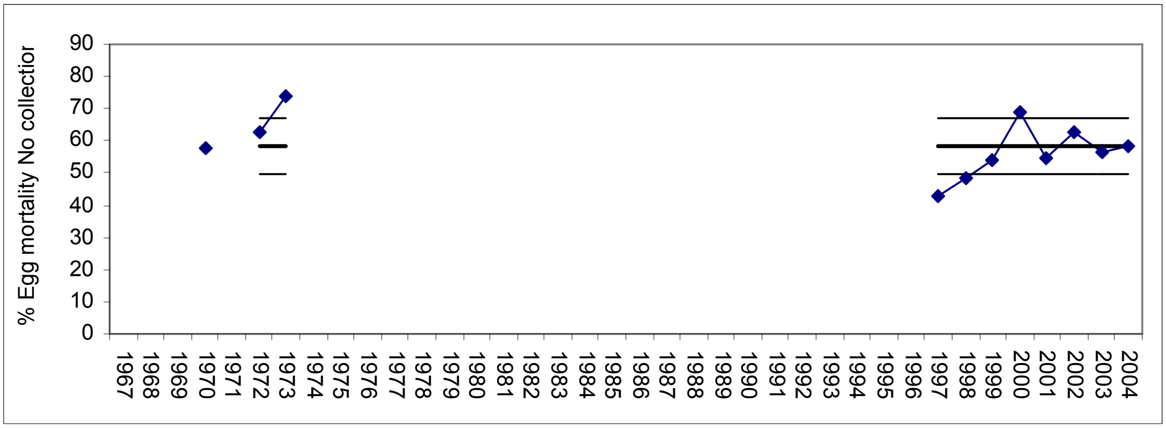


Fig. B24. Demographic dependent variable egg mortality during no collection (1970, 1972, 1973, 1997 – 2004).

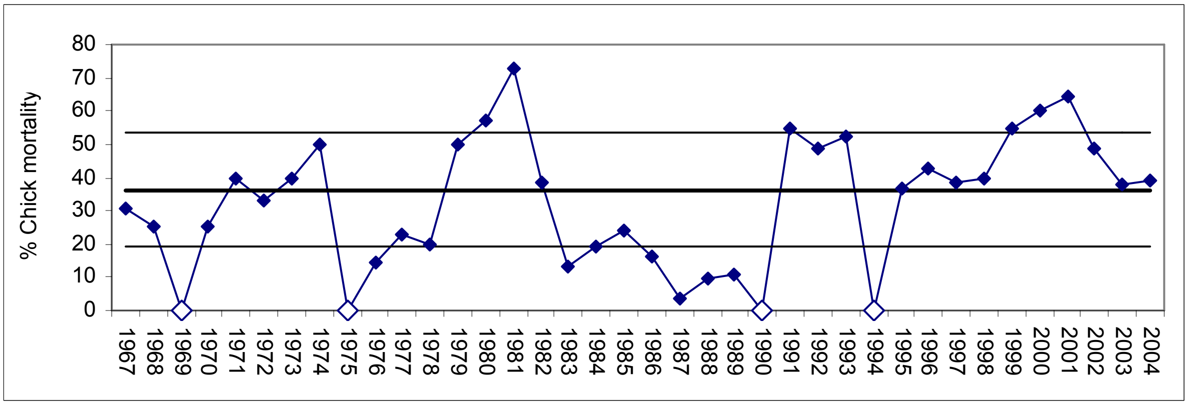


Fig. B25. Demographic dependent variable chick mortality. Mean (thick line), ±1SD (thin lines).

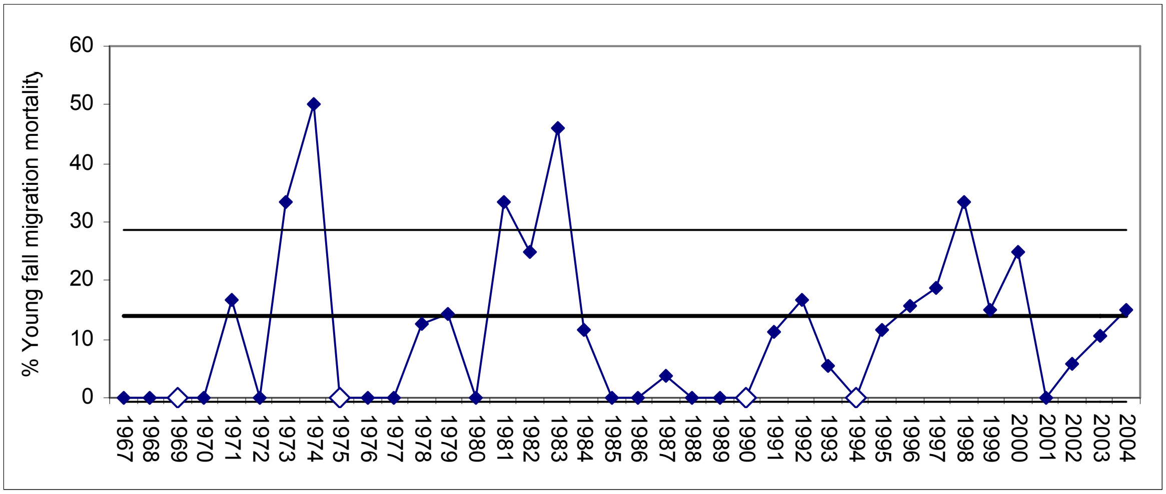


Fig. B26. Demographic dependent variable young fall migration mortality. Mean (thick line), ±1SD (thin lines).

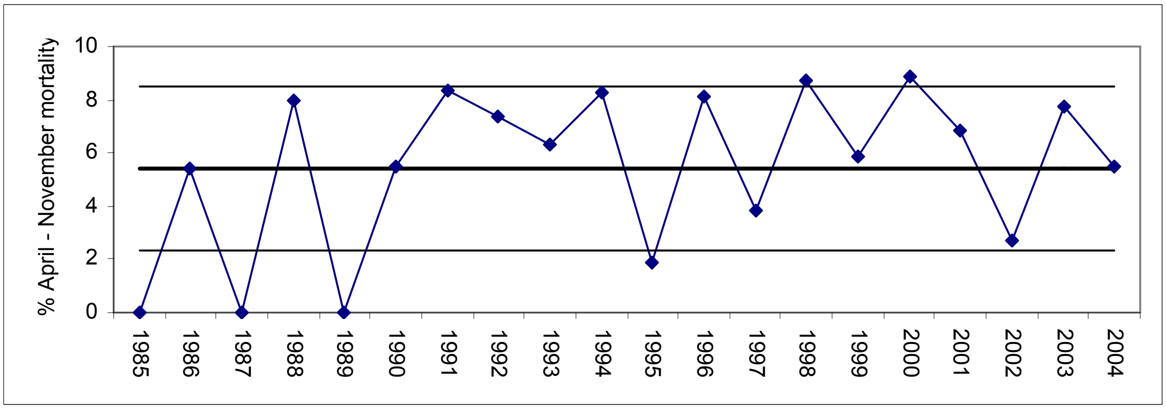


Fig. B27. Demographic dependent variable April-November mortality. Mean (thick line), ±1SD(thin lines).

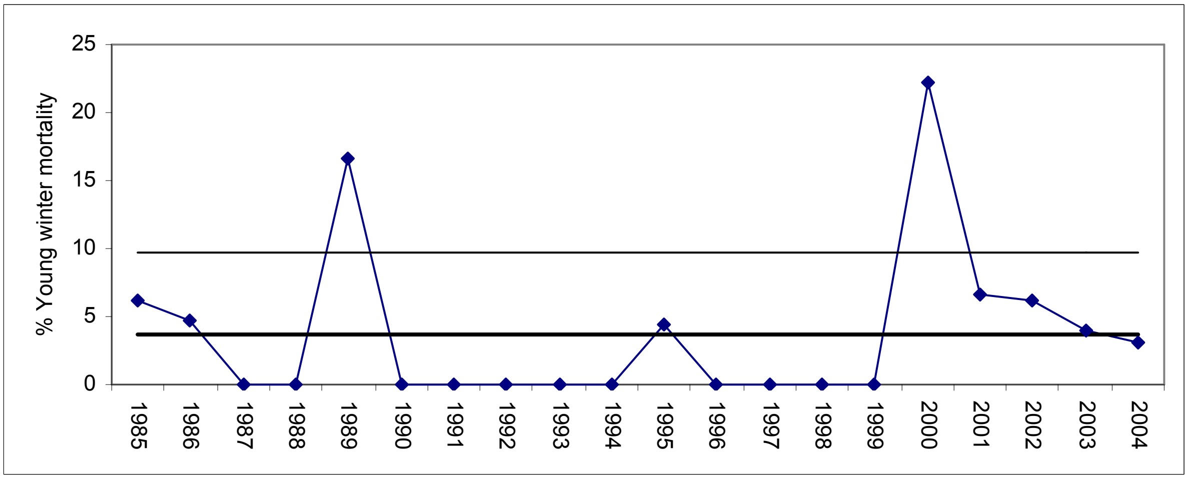


Fig. B28. Demographic dependent variable young winter mortality. Mean (thick line), ±1SD (thin lines).

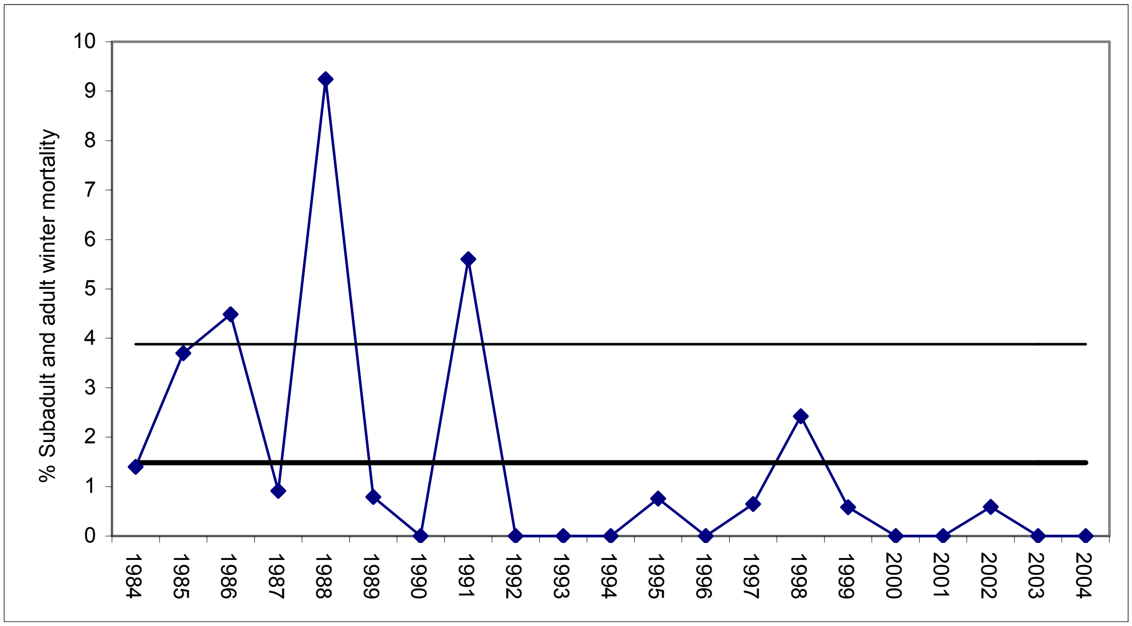


Fig. B29. Demographic dependent variable sub-adult and adult mortality. Mean (thick line), ±1SD(thin lines).

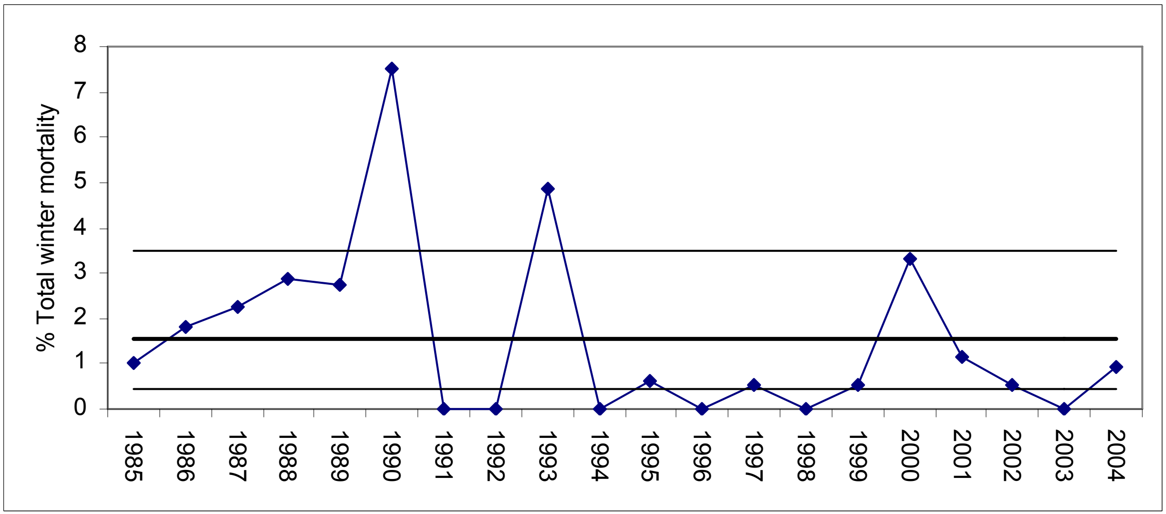


Fig. B30. Demographic dependent variable total winter mortality. Mean (thick line), ±1SD (thin lines).

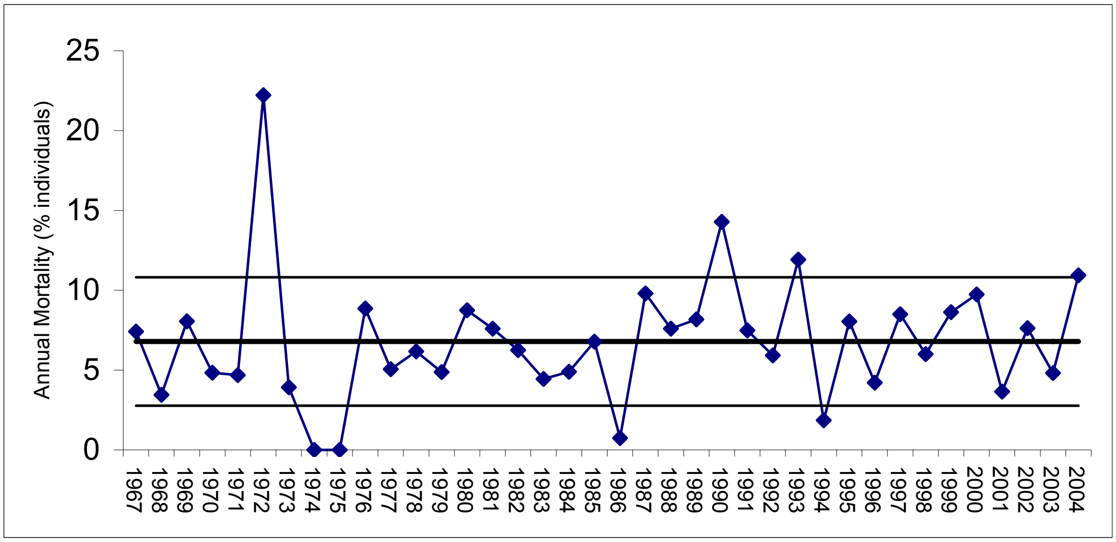


Fig. B31. Demographic dependent variable total annual mortality. Mean (thick line), ±1SD (thin lines).

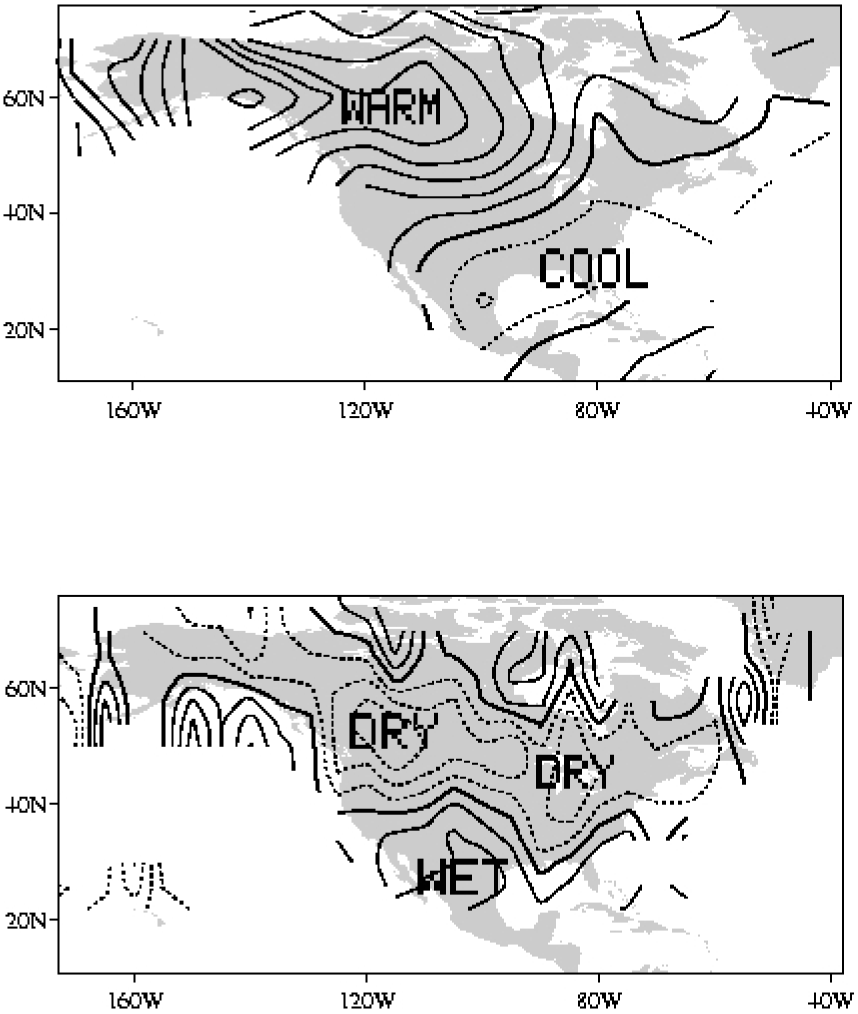
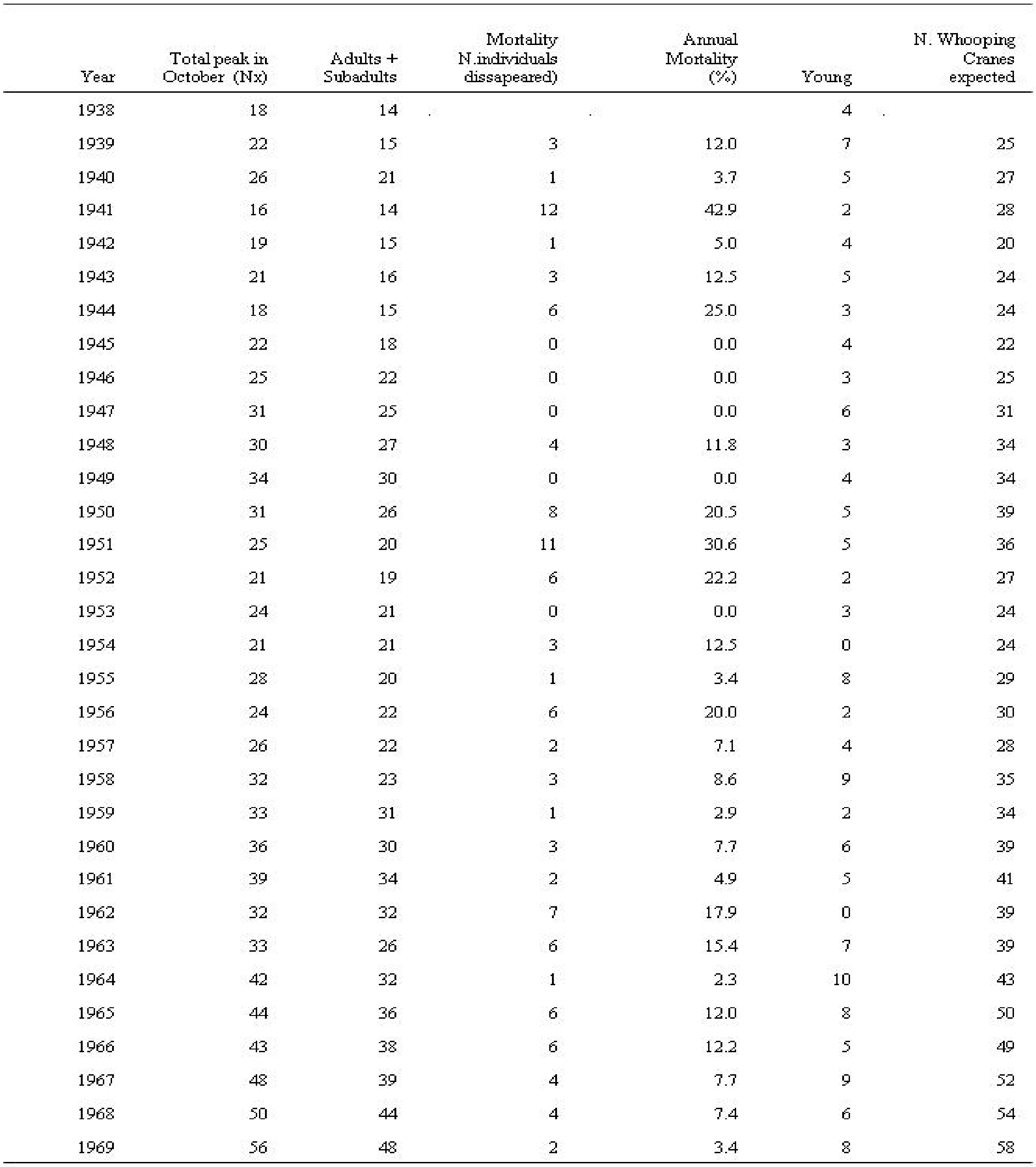


Fig. B32. PDO influence on North America climate. Top: Characteristic warm-phase PDO October-March air temperature anomalies, in degrees C, for period 1900 -.1998. Bottom: North American December – February precipitation. From Mantua web page (http:///www.atmos.washington.edu/~mantua/REPORTS/PDO/PDO_cs.htm).

Table B1. Annual mortality of Whooping Cranes, estimated from the peak of individuals counted every winter at ANWR, and the number of juvenile arrived every year. Annual mortality represented the number of individuals disappeared during winter, spring migration, and fall migration every year.



Year	Total peak in October (Nx)	Adults + Subadults	Mortality N.individuals dissapeared)	Annual Mortality (%)	Young	N. Whooping Cranes expected
1938	18	14			4	
1939	22	15	3	12.0	7	25
1940	26	21	1	3.7	5	27
1941	16	14	12	42.9	2	28
1942	19	15	1	5.0	4	20
1943	21	16	3	12.5	5	24
1944	18	15	6	25.0	3	24
1945	22	18	0	0.0	4	22
1946	25	22	0	0.0	3	25
1947	31	25	0	0.0	6	31
1948	30	27	4	11.8	3	34
1949	34	30	0	0.0	4	34
1950	31	26	8	20.5	5	39
1951	25	20	11	30.6	5	36
1952	21	19	6	22.2	2	27
1953	24	21	0	0.0	3	24
1954	21	21	3	12.5	0	24
1955	28	20	1	3.4	8	29
1956	24	22	6	20.0	2	30
1957	26	22	2	7.1	4	28
1958	32	23	3	8.6	9	35
1959	33	31	1	2.9	2	34
1960	36	30	3	7.7	6	39
1961	39	34	2	4.9	5	41
1962	32	32	7	17.9	0	39
1963	33	26	6	15.4	7	39
1964	42	32	1	2.3	10	43
1965	44	36	6	12.0	8	50
1966	43	38	6	12.2	5	49
1967	48	39	4	7.7	9	52
1968	50	44	4	7.4	6	54
1969	56	48	2	3.4	8	58

Table B1. Continued

Year	Total peak in October (Nx)	Adults + Subadult	Mortality (N.dissapeared)	Annual Mortality (%)	Young	N Whooping Cranes expected
1970	57	51	5	8.1	6	62
1971	59	54	3	4.8	5	62
1972	61	56	3	4.7	5	64
1973	49	47	14	22.2	2	63
1974	49	47	2	3.9	2	51
1975	57	49	0	0	8	57
1976	69	57	0	0	12	69
1977	72	62	7	8.9	10	79
1978	75	68	4	5.1	7	79
1979	76	70	5	6.2	6	81
1980	78	72	4	4.9	6	82
1981	73	71	7	8.8	2	80
1982	73	67	6	7.6	6	79
1983	75	68	5	6.3	7	80
1984	86	71	4	4.4	15	90
1985	97	81	5	4.9	16	102
1986	110	89	8	6.8	21	118
1987	134	109	1	0.7	25	135
1988	138	119	15	9.8	19	153
1989	146	126	12	7.6	20	158
1990	146	133	13	8.2	13	159
1991	132	124	22	14.3	8	154
1992	136	121	11	7.5	15	147
1993	143	127	9	5.9	16	152
1994	133	125	18	11.9	8	151
1995	158	130	3	1.9	28	161
1996	160	144	14	8	16	174
1997	182	152	8	4.2	30	190
1998	183	165	17	8.5	18	200
1999	188	171	12	6	17	200
2000	180	171	17	8.6	9	197
2001	176	161	19	9.7	15	195
2002	185	169	7	3.6	16	192
2003	194	169	16	7.6	25	210
2004	217	182	12	5.2	35	229

Table B2. Pattern of annual distribution of environmental factors, at WBNP, NE, and wintering ground ANWR. Annual mean ± 1SD, peak (mean ± 1SD), range during period of Whooping Cranes occurrence and curve description.

Variable	Mean ±SD	Extreme values	Range	Description
Temperature WBNP	2.78 ± 15.13°C (26.93 ± 27.51°F)	July, 16.42 ± 1.3°C (61.85 ± 34.29°F)	-2 to 16°C (26.93 to 61.8 °F)	Fig. B1.
Precipitation WBNP	33.8 ±15.35 mm	July, 54.4 ±30.2 mm	27.8 - 54.4 mm	Fig. B2.
Temperature NE	Spring 10.72 ± 7.19°C (51.31± 19.05°F) Fall 12.39°C, (54.31°F)	July 24.94°C (76.9°F)	Spring 0.13 -10.72 °C (38.13 - 54.31F) Fall 10.7 - 3.7-°C (54.31-38.51°F)	Fig. B3.
Precipitation NE	2.3 ± 1.90 inches.	May 4.52± 19.03 in.	Spring 1.8 to 2.86 inches. Fall 2.83 to 1.83 inches	Fig. B4.
Temperature ANWR	22.1 ± 5.9°C (71.24 ± 10.6°F)	July 29.23 °C (83.9 ± 1.3 °F)	23.52 – 13.25°C 73-76 – 55.41°F	Fig. B5.
Precipitation ANWR	3.11 ± 1.20 inches.	May (4.1 ± 3.69 in. Sept. (5.9 ± 5.2 in.)	4.13 –1.91 inches	Fig. B6.
Freshwater Inflows, WG	(193,226.6 ± 53,817.5 acft/mo).	June, (286,819 ± 376,544 acft/mo), October (234,960 ± 377,242 acft/mo)	234,960 – 139409 acft/mo	Fig. B7.
Net-Evaporation, WG	-21049,18 ± 99967 acft/mo.	August-24788, February 8542 acft./mo	-6270 – 8542 acft/mo.	Fig. B8.

Table B3. Whooping Crane (*Grus americana*) environmental independent variables. Values are means ± 1 SD, units, (n) = number of years. Years with extreme values ≥1SD; * ≥ ±2SD;** ≥ ±3SD, high ≈ 1SD, (+) > mean. D = Dry, H = Hot, W = Wet, C = Cool. Wood Buffalo National Park (WBNP), Nebraska, Platte River (NE), Aransas National Wildlife Refuge (ANWR), wintering ground (WG).

Independent Variables	Mean ± SD Unit (n),	Year: extreme – high (+) D = Dry or H = Hot	Year: extreme – high (+) W = Wet or C = Cold	Figure, Historical data plotted, mean, ±1SD
Temperature March – Sept. (WBNP)	6.81 ± 1.17 ºC (44.26 ± 2.10ºF) (36)	H: 1973, 1984, 1994, 1998*, 1999, 2001.	C: 1967, 1968, 1972, 1974, 1978, 1979, 1982, 2002	Fig. B9
Precipitation March – Sept. (WBNP)	257.7 ± 61.7 mm (36)	D: 1971*, 1979, 1985, 1989, 1969+, 1976+, 1981+, 1998+.	W: 1973*, 1975, 1988, 1996, 1999. 1991+	Fig. B10.
Pond water depth (WBNP)	22.99 ± 7.82 cm (25)	D: 1980, 1990, 1991, 1995, 1997, 1981+.	W: 1974**, 1975, 1998 1976+, 1999+.	Fig. B11.
Temperature Sept. – March. (ANWR)	18.36 ºC 65.05 ± 1.69 ºF (36)	H: 1970, 1971, 1985, 1998, 1999.	C: 1967, 1972, 1976*, 1984, 1988, 2000.	Fig. B12.
Precipitation Sept.- March (ANWR)	24.19 ± 8.81 inches (36)	D: 1972, 1975, 1979, 1985, 1988, 2003. 1980+, 1987+, 1990+.	W: 1970, 1971, 1974, 1976, 1982, 1986, 1991, 1992, 2002, 1981+, 1997+.	Fig. B13.
Freshwater Inflows Sept. – March (W G)	1485955 ± 1172958.2 total acft./y (34)	Low: 1970, 1988, 1989, 1995, 1999.	High: 1967*, 1973, 1976, 1991**, 1998*.	Fig. B14.

Table B3. Continued

Independent Variable	Mean ± SD Unit (n)	Year: extreme - high (+) D = Dry or H = Hot	Year: extreme– high (+) W = Wet or C = Cold	Fig.
Net-Evaporation Sept. – March (W G)	- 21049 ± 99967 acft./y. (31)	D: 1968, 1975, 1985, 1987, 1970+, 1980+, 1988+	W: 1967, 1971, 1991, 1992, 1997, 1978+, 1986+, 1996+.	Fig. B15.
Temperature April (NE)	10.64 ºC 51.16 ± 2.97 ºF (36)	H: 1977, 1981*, 1985, 2001.	C: 1975, 1983*, 1984, 1993, 1995, 1997*.	Fig. B16.
Temperature October (NE)	12.39 ºC 54.31 ± 3.32 ºF (36)	H: 1971, 1973, 1974, 1975, 2003.	C: 1969, 1970, 1976, 1987, 1988, 2002*.	Fig. B17.
Precipitation Mean Feb- Mar- Apr (NE)	5.5 ± 2.2 in. (36)	D: 1967, 1988, 1989*	W: 1973, 1977, 1978, 1979, 1984*, 1987*	Fig. B18
Precipitation October (NE)	1.87 ± 1.17 in. (36)	D: 1975, 1988, 1996, 1998. 1976+	W: 1968*, 1969, 1973, 1979, 1986, 1997*, 2002.	Fig. B19
PDO	Index (+ or -)(67)	Warm extreme values: 1983, 1987, 1993.	Cool extreme values:: 1967, 1971 – 1973, 1975, 1999, 2000, 2001	Fig. B20

Table B4. Whooping Crane (*Grus americana*) demographic variables. Percentage of failure, reduction and mortalities (%). Values are means ± 1 SD, (n) = number of years. Year: extreme values ≥1SD, * ≥ 2SD,** ≥ 3SD, high ≈ 1SD or (+) > mean.

Dependent variable	Mean ± SD % (n)	Years values: extreme	Years values: high	Fig., Hist. data mean, ± 1SD
Brood failure	11.95 ± 11.20 (19)	1990, 1994, 2001, 2002	1991, 2004	Fig. B21.
Clutch size reduction	7.1 ± 8. 84 (22)	1992, 1994*		Fig. B22.
Egg mortality after egg collection	27 ± 18.6 (29)	1974, 1975, 1991, 1996	1981, 1983, 1990	Fig. B23.
Egg mortality no egg collection	58.1 ± 8.6 (11)	1973, 2000	1972, 2002	Fig. B24.
Chick mortality	36.3 ± 17.2 (33)	1980, 1981, 1991, 1993, 1999, 2000, 2001	1974, 1979, 1992, 2002	Fig. B25.
Young mortality fall migration	13.97 ± 14.6 (33)	1973, 1974, 1981, 1983, 1998	1982, 2000	Fig. B26.
April – November mortality	5.45 ± 3.12 (19)	1998, 2000	1988, 1991, 1996, 2003	Fig. B27.
Young winter mortality	3.7 ± 6 (19)	1989, 2000	1985, 1986, 1995, 2001, 2002+, 2003+	Fig. B28.
Adult and subadult winter mortality	1.69 ± 2.47 (19)	1986, 1988, 1991	1998	Fig. B29.
Total winter mortality	1.5 ± 1.95 (19)	1990, 1993, 2000		Fig. B30.
Total annual mortality	12.93 ± 5.5 (37)	1972, 1990, 1991, 1997, 2000	1980+, 1992, 1993, 1998, 1999	Fig. B31.

APPENDIX C

WHOOPING CRANE SIMULATION MODEL, FIGURES AND TABLES.

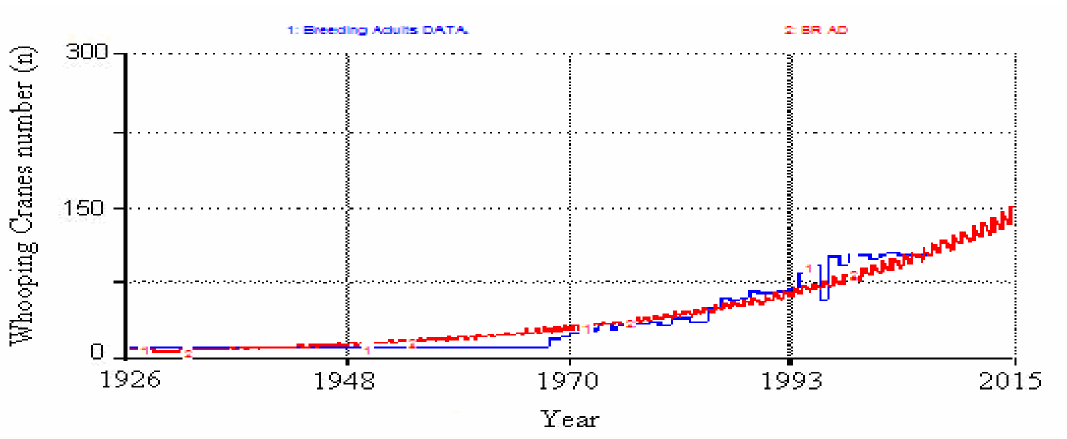


Fig. C1. Comparison between numbers of breeders simulated vs. breeders observed in the Whooping Crane population model, version 1. Breeding adults data overlapped the number of breeders simulated (BR AD).

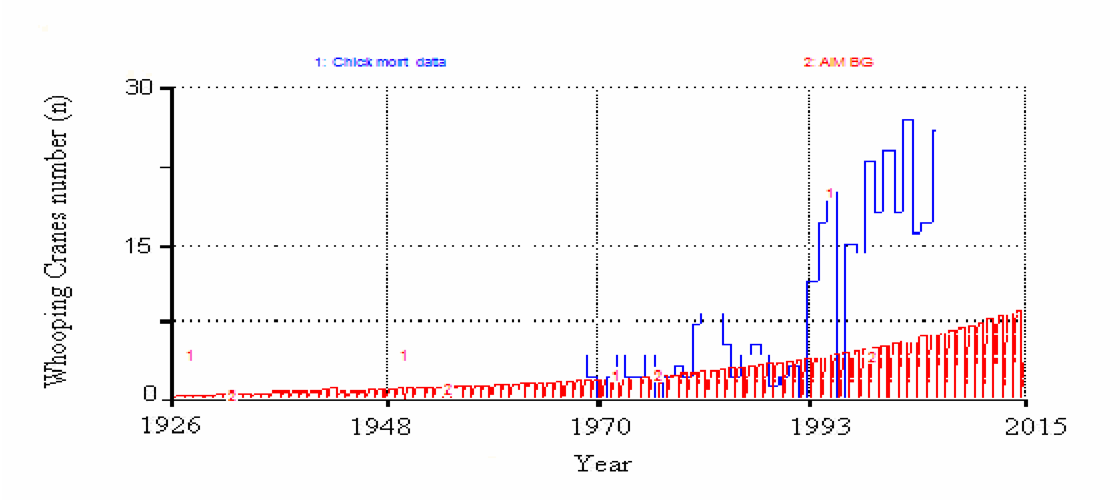


Fig. C2. Comparison of simulated vs. observed number of Whooping Cranes dead at the breeding ground (BG). . (Chick mort data was the number of chicks and juvenile dead at WBNP, from CWS reports) and AM BG is simulated accumulative mortality at breeding ground, the total number of individuals dead with the simulated rate of mortality.

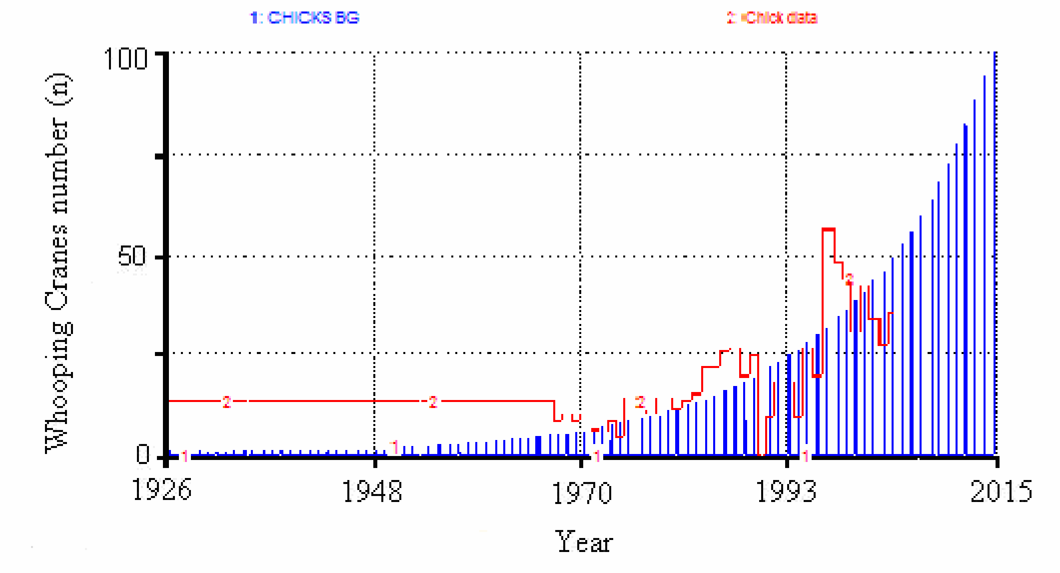


Fig. C3. Comparison of number of chicks simulated vs. observed in the Whooping Crane population model V2, after adjustments on number of breeders and egg mortality.

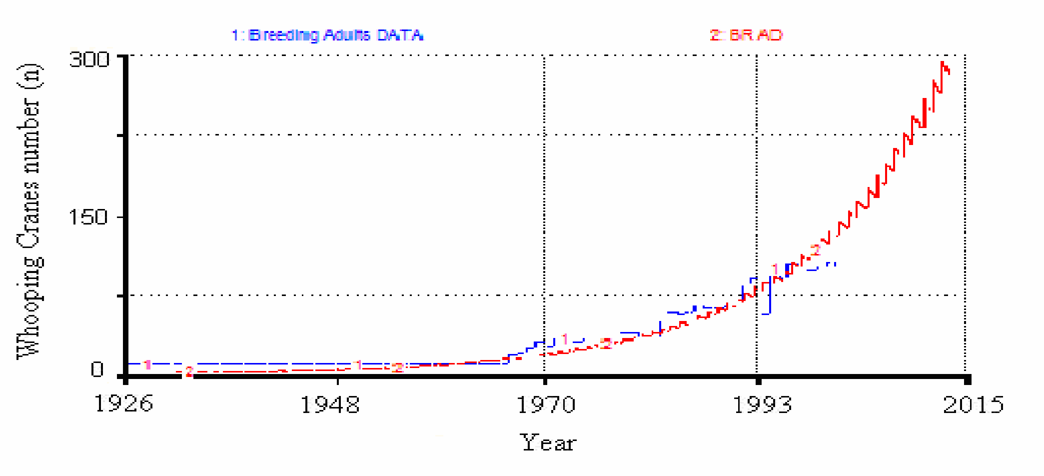


Fig. C4. Comparison between numbers of breeders simulated vs. breeders observed in the Whooping Crane population model, Version 2, after adjustments on number of breeders and mortality of eggs. Breeding adults observed overlapped the number of breeders simulated (BR AD). Number of breeders was projected until 2015.

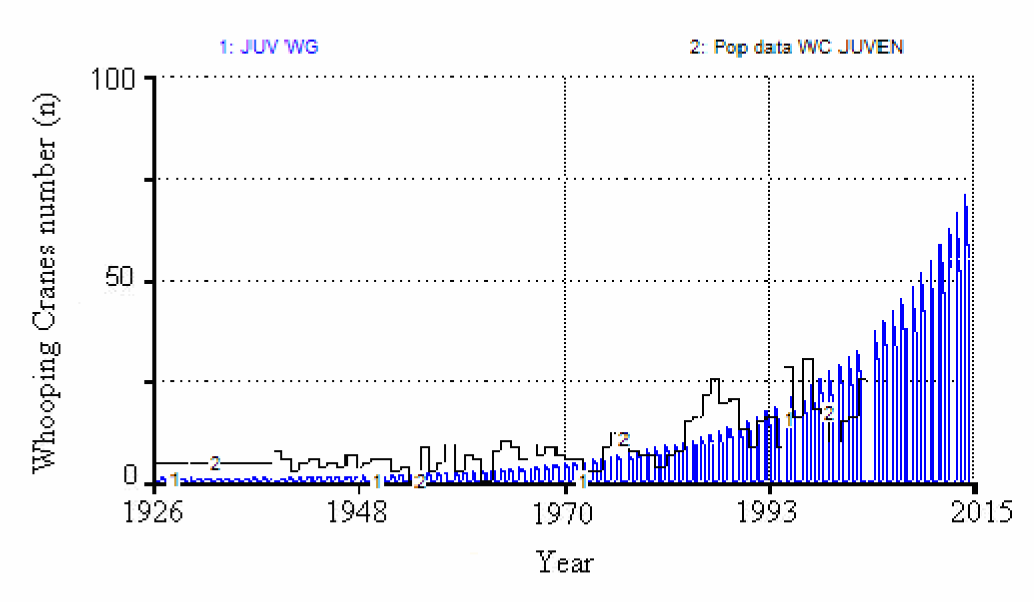


Fig. C5. Comparison number of juveniles simulated vs. observed in the Whooping Crane population model V2, after adjustments on number of breeders and mortality of eggs.

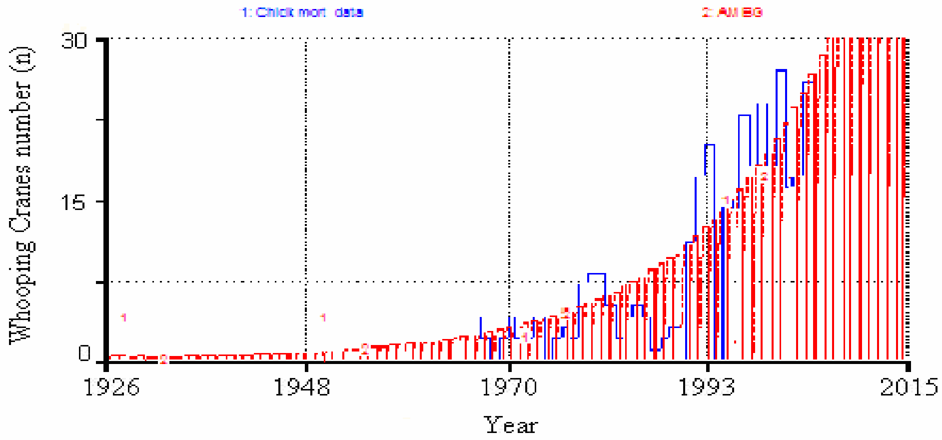


Fig. C6. Comparison on chick mortality (number of individuals dead) simulated vs. observed in the Whooping Crane population model V2 after adjustments on number of breeders and mortality of eggs.

Table C1. Age-specific mortality for model version 1 (V1) and version 2 (V2). Daily mortality rates for V1 (MR) were estimated from annual mortality rates from Binkley and Miller (1988). Daily mortality rates for V2 (NMR) were obtained from 12 cohorts of banded Whooping Cranes. From the new life table in Chapter II.

Age	Version 1 (q_x) MR	Version 2 (q_x) NMR
00	0.0003248 (*)	0.001755
01	0.0001500518	0
02	0.0001564250	0
03	0.0001628130	0
04	0.0001697987	0
05	0.0001776789	0.000213
06	0.0001867546	0.000089
07	0.0001964488	0.000095
08	0.0002070635	0.000145
09	0.0002197961	0.00021
10	0.0002343777	0.000055
11	0.0002508376	0.00029
12	0.0002704182	0.00019
13	0.0002941006	0.000275
14	0.0003207589	0.000387
15	0.0003563986	0.000
16	0.0003994691	0.000
17	0.0004554873	0.000092
18	0.0005335537	0
19	0.000646646	0
20	0.000823126	0
21	0.001146056	0
22	0.001933567	0
23	1	0
24	-----	0.00079
25	-----	0
26	-----	0
27	-----	1

(*)Age 0 from individuals at ANWR.

Table C2. Adjustments for Version 1 of the Whooping Crane population demographic model

Version 1	Equations
Age of first reproduction	AGE_FIRST_REP= 4
Breeders age 4	BR_4 = AGE_04_TOT*PR_BR_4
Proportion of breeders	BR_AD =PR_BR X (AGE_X_PROP) = AGE_X_TOT / TOT_POP.
Natality rate $x<4 = 0$, $x \geq 5 = 0.229$	NR_BG
Fecundity, number of eggs laid for version 1.	N1 = EGG LAID = BR_AD* NR_BG
Breeders adults from age 4 to age 6	BR_AD= BR_4 + BR_5 + BR_6 +
Breeders adults from age 7 and older	BR_7_PLUS = AGE 7 +…+AGE 23

VITA

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EDUCATION

- PhD. Wildlife and Fisheries Sciences. Texas A&M University, College Station, TX, USA. May 2006.
- M.Sc. Applied Ecology. La Universidad del Zulia, Maracaibo, Estado Zulia, Venezuela. October 2000.
- Licenciate in Biology. Universidad Simón Bolívar, Caracas, Venezuela. October 1984.

PROFESSIONAL EXPERIENCE

Dec. 2005 - Guest Researcher. The Royal Swedish Academy of Sciences, The Beijer Institute of Ecological Economics, Stockholm, Sweden.

Sep. 2002 - Nov. 2005. Research Assistant. Texas A&M University. WFSC. Research in systems model simulation: bird population dynamics, migration, energetic budget, reproductive ecology, and environmental effects.

Apr. 1997 - May 2002. Researcher. Universidad del Zulia, Systems Ecology Laboratory. Research in aquatic and terrestrial bird communities and biodiversity.

Jan. 1993 - Mar. 1997. Regional Manager, Laboratorios Rodeneza. Maracaibo, Venezuela.

Jan. 1989 - 2003. Director of Fundación Centro de Estudios Musicales FUNDACEM, Venezuela.

SELECTED PUBLICATIONS

Gil, Karine, C. Casler and E. H Weir. 2004. Biodiversidad en el Lago de Maracaibo, Campo Urdaneta Oeste. Biodiversity in Maracaibo Lake. West Urdaneta Camp. Universidad del Zulia – SHELL de Venezuela. S.A 2003. Maracaibo, Venezuela Ediciones Astro Data, S.A, 267 pp.

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Gil, Karine and Neal Wilkins.2003. Rio Grande/Rio Bravo Basin Endangered and Threatened Species: A Bibliography. Texas A&M Publication. CD and on line version, http://landinfo.tamu.edu/riogrande.

SKILLS AND TALENTS

Software: STELLA, STATA, SPSS, Arc. GIS, RAMAS, END NOTE, Microsoft Office.
Project manager, modeling workshop coordinator, and performing piano teacher 1983 –.
Languages: Spanish and English.