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Whooping crane demographic responses to winter drought focus conservation strategies



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ABSTRACT

Focusing conservation strategies requires identifying the demographic parameters and environmental conditions affecting the growth of animal populations most. Therefore, we examined relationships between population demographics and winter drought (1950–2011) for endangered whooping cranes (*Grus americana*) wintering in Texas, USA. We modeled winter loss and its contribution to annual mortality as functions of winter drought, determined recruitment needed to maintain population growth after drought, and identified which demographic parameters underpin this population's growth. Previous research assumed winter loss (i.e., birds missed in subsequent surveys) represented mortality. We show that loss includes temporary emigration to upland habitats, early migration, and incomplete detection. Despite this, we maintained this assumption to evaluate the relevance of winter mortality to population growth. We found that winter loss ($\hat{\beta} = -0.308$, SE = 0.042) and its contribution to annual mortality ($\hat{\beta} = -0.318$, SE = 0.047) increased with drought severity (Palmer hydrological drought index; PHDI). Given average recruitment (0.145, SD = 0.090), this population increases 1.2% (95% CI = -2.9% to 4.2%) after extreme drought (PHDI = -4). No recruitment must occur for 3 years with moderate to severe drought (PHDI < -2.5) to delay species' recovery ≈ 7 years. This scenario has not occurred since population monitoring began in 1938. Of the demographic parameters we examined, winter loss explained population growth least (14.4%; 95% CI = 3.6–35.8%), and it was partially compensatory. Breeding–migratory mortality explained 42.2% (95% CI = 19.1–61.5%) of population growth and recruitment 49.9% (95% CI = 20.6–75.2%). Our results focus conservation on breeding and migratory periods, and deemphasize winter mortality and drought. On the wintering grounds, conservation of whooping cranes should emphasize maintaining coastal, upland, and interior habitats for this population.

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1. Introduction

Understanding animal population demographics and their ecological drivers helps focus conservation and management strategies on the relevant life-history traits or environmental conditions that impact population growth most (e.g., [Caughley, 1994](#); [Mills, 2007](#); [Grande et al., 2009](#); [Schaub et al., 2012](#)). When such information is lacking, or inadequate, then biologists risk ineffective conservation actions in inappropriate places and periods. For the Aransas–Wood Buffalo whooping crane (*Grus americana*) population, long-term monitoring on its wintering grounds has provided a rich data source for modeling relationships between demographic parameters and the environment ([Lewis et al., 1992](#); [Link et al., 2003](#); [Stehn and Taylor, 2008](#); [Butler et al.,](#)

[2013](#); [Stehn and Haralson-Strobel, 2014](#)). Our objective was to use this information for steering conservation strategies for this endangered bird.

A current paradigm holds that winter mortality is an important component of whooping crane population dynamics. Further, it contends that whooping cranes wintering along the Texas coast of the Gulf of Mexico are highly territorial, so during adverse drought conditions, they run out of resources in their territories and perish ([Stehn and Johnson, 1987](#); [Stehn, 2009](#); [Pugesek et al., 2013](#); [Stehn and Haralson-Strobel, 2014](#)). Alternatively, whooping cranes may vacate coastal saltmarshes and seek resources in other habitats such as upland areas, interior regions, or elsewhere along the gulf coast, instead of dying from insufficient food and water in their territories during drought.

This distinction is important. If drought conditions directly increase mortality of whooping cranes on their winter territories, then it supports management actions (e.g., supplemental feeding) that may mitigate winter mortality (U.S. Fish and Wildlife Service

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[USFWS], unpublished), although unintended consequences may ensue (e.g. increased disease, poisoning, and predation; Baskin, 1993; Oberheu and Dabbert, 2001; Miller et al., 2003). However, if the assumed mortalities represent birds vacating their territories in search of resources elsewhere, then an appropriate management response would be to identify the alternative habitats in which whooping cranes select and conserve or restore those areas. Clearly, biologists must untangle how this population responds to winter drought to identify appropriate conservation and management strategies.

We address this issue by analyzing 61 years of demographic data for the Aransas–Wood Buffalo whooping crane population. This population overwinters on and around Aransas National Wildlife Refuge (NWR), Texas, USA, and breeds on and around Wood Buffalo National Park, Alberta and Northwest Territories, Canada (CWS and USFWS, 2007). Since 1950, the USFWS has conducted annual whooping crane surveys from fixed-wing aircraft in Texas (Stehn and Taylor, 2008). Some consider that these aerial surveys provided a technique for documenting mortality during the winter period (Lewis et al., 1992; Pugesek et al., 2008, 2013; Stehn and Taylor, 2008; Stehn and Haralson-Strobel, 2014). The technique relied on repeated, though unequal, survey effort during each winter, assumptions of whooping crane territorial fidelity, identification of individual birds with many lacking unique marks, and the interpretation of changes in the composition of whooping crane family groups (Pugesek et al., 2013; Stehn and Haralson-Strobel, 2014). Therefore, when observers failed to record the presence of individual birds in their territories on two consecutive surveys, they counted those missing birds as mortalities (Stehn and Haralson-Strobel, 2014). Reliance on such clues to count mortalities allows for many other possible explanations, such as temporary emigration from winter territories to upland or interior habitats, early departure to the breeding grounds, or incomplete detection of birds within a family group (Stehn, 1992; Strobel and Butler, 2014). The difficulty in making clear inference from these survey data is indicative of a poor technique, suggesting that the mortality data may represent a combination of mortality, early migration, temporary emigration, and incomplete detection. Thus, estimates previously interpreted as winter mortality are best described as “loss” from the coast during winter, instead of mortality alone.

By examining the extent that reported losses (Stehn and Haralson-Strobel, 2014) varied with survey effort and the use of upland habitats by whooping cranes, we illustrate that there are explanations other than mortality for the missing birds. An inverse relationship between winter loss and survey effort would suggest the technique produced results dependent upon methodological differences between years instead of generating a consistent index of winter mortality. Additionally, if the use of upland habitats by whooping cranes increased during years of higher loss, then some losses reported were likely due to temporary emigration, not death. Despite these potential sources of bias, we considered winter loss to consist entirely of deaths to evaluate the relevance of winter mortality on the dynamics of this population.

We modeled the effects of 7 climatic indices on whooping crane winter loss, the contribution of winter loss to annual mortality, and use of upland habitat. The climatic variables served as surrogates for habitat conditions (i.e., food availability, hyper-salinity, and drought) during the winter period. Identifying which climatic indices were most associated with winter loss enabled us to gauge and predict the amount of winter loss that could occur under a variety of drought scenarios. The relationship between climate and the contribution of winter loss to annual mortality revealed the influence of winter mortality on annual mortality during the worst drought conditions. Relating climatic factors to upland use demonstrated behavioral responses of this population to drought.

After establishing these relationships, we examined the impact of winter drought on whooping crane population growth. First, we identified the drought conditions, if any, that could result in population decline. Second, we determined the combination of drought on the wintering grounds (that indicated potential winter mortality) and the reduction in recruitment necessary to delay this species' recovery (by tying into modeling scenarios outlined in Butler et al. (2013)). We show that reductions in population growth and delays in population recovery are contingent upon extreme drought conditions on the wintering grounds and poor recruitment the following year, not simply drought alone. Third, we quantified the importance of recruitment, plus mortality during the breeding and migratory periods, winter mortality, and annual mortality to population growth. Their effects on population growth are unlikely to be equal (Mills, 2007). Determining which demographic parameter(s) this population's growth hinges upon focuses when and where management intervention might be most effective and warranted.

For over 6 decades, the whooping crane monitoring technique was trusted to produce information that it could not credibly provide (e.g., winter mortality). Unfortunately, this represents a common story in which poorly designed monitoring programs become institutionally ingrained and relied upon to inform conservation strategies (Anderson, 2001; Legg and Nagy, 2006; Nichols and Williams, 2006; Lindenmayer and Likens, 2009, 2010). Dependence on inadequately designed monitoring programs often results in poor inference and misplaced conservation actions. By evaluating and addressing the situation for whooping cranes, our results focus research and management of this population on the life-history traits, locations, and periods that matter most.

2. Methods

2.1. Study area and aerial surveys

Whooping cranes arrive on their wintering grounds on and around Aransas NWR beginning in October and depart by late April (Johnsgard, 1983). On the wintering grounds, the birds are distributed in coastal saltmarshes, tidal flats, and shallow bay edges with occasional use of upland areas (CWS and USFWS, 2007). Though the population has been surveyed since 1938, consistent aerial survey efforts did not begin until 1950 (Stehn and Taylor, 2008; Butler et al., 2013, 2014; Strobel and Butler, 2014). Since then, repeated aerial surveys of whooping cranes have been conducted each year during the winter period resulting in indices of abundance, winter mortality (i.e., loss), and the number of hatch-year (HY) birds (Lewis et al., 1992; Link et al., 2003; Stehn and Taylor, 2008; Stehn and Haralson-Strobel, 2014).

The survey has been primarily conducted from a fixed-wing aircraft with transects spaced approximately 250–800 m apart and flown parallel to the coast (Stehn and Taylor, 2008; Butler et al., 2014). Transect spacing was varied according to flight conditions by the observer in an attempt to detect all whooping cranes (Stehn and Taylor, 2008; Butler et al., 2014; Strobel and Butler, 2014). Prior to revision of the survey technique in winter 2011–2012, the surveyed area was not recorded for each year and likely fluctuated from year to year (Butler et al., 2014). Though the survey did not result in a true census of the population, many have treated these data as a census (Boyce and Miller, 1985; Boyce, 1986; Dinsmore and Johnson, 2005; CWS and USFWS, 2007; Stehn and Taylor, 2008).

Estimates of winter abundance and the number of HY birds were compiled from multiple sources (Table 1; Boyce, 1986; Link et al., 2003; CWS and USFWS, 2007; Butler et al., 2013). Estimates of the number of whooping cranes lost during the winter period

Table 1
Whooping crane aerial survey data from the wintering grounds on and around Aransas National Wildlife Refuge, Texas, USA.

Winter	N ^a	HY ^b	AHY ^c	WL ^d	Upland/Total ^e	Surveys ^f	PHDI ^g	Winter	N ^a	HY ^b	AHY ^c	WL ^d	Upland/Total ^e	Surveys ^f	PHDI ^g
1950–1951	31	5	26	1	9/53	8	-3.024	1981–1982	73	2	71	0	7/268	9	2.794
1951–1952	25	5	20	2	8/67	10	-3.674	1982–1983	73	6	67	2	16/422	16	-0.229
1952–1953	21	2	19	0	7/61	10	-2.134	1983–1984	75	7	68	0	8/486	17	0.680
1953–1954	24	3	21	0	5/74	10	-2.131	1984–1985	86	15	71	2	4/416	14	0.434
1954–1955	21	0	21	0	4/60	8	-4.779	1985–1986	97	16	81	1	6/476	17	0.677
1955–1956	28	8	20	1	5/30	4	-4.730	1986–1987	110	21	89	1	12/397	12	2.057
1956–1957	24	2	22	0	7/146	19	-5.176	1987–1988	134	25	109	3	3/212	6	1.597
1957–1958	26	4	22	0	2/34	4	3.557	1988–1989	138	19	119	6	33/438	11	-2.853
1958–1959	32	9	23	0	7/49	5	2.290	1989–1990	146	20	126	4	15/203	6	-3.037
1959–1960	33	2	31	0	4/129	11	1.907	1990–1991	146	13	133	11	24/404	10	-1.577
1960–1961	36	6	30	0	8/109	13	3.853	1991–1992	132	8	124	1	50/626	14	4.097
1961–1962	39	5	34	1	9/149	13	0.154	1992–1993	136	15	121	0	33/466	10	3.687
1962–1963	32	0	32	4	12/269	21	-2.864	1993–1994	143	16	127	7	17/332	8	0.339
1963–1964	33	7	26	1	18/211	17	-3.647	1994–1995	133	8	125	0	21/592	13	1.741
1964–1965	42	10	32	0	47/262	20	-1.774	1995–1996	158	28	130	1	24/407	10	-0.851
1965–1966	44	8	36	0	20/181	14	1.104	1996–1997	160	16	144	0	28/693	15	-1.819
1966–1967	43	5	38	0	27/185	19	-1.956	1997–1998	182	30	152	1	30/606	12	3.219
1967–1968	48	9	39	1	31/207	17	3.276	1998–1999	183	18	165	0	22/688	11	3.256
1968–1969	50	6	44	0	17/171	12	3.753	1999–2000	188	17	171	1	32/648	13	-2.343
1969–1970	56	8	48	0	16/190	13	1.697	2000–2001	180	9	171	6	48/700	14	0.521
1970–1971	57	6	51	1	23/285	15	-1.403	2001–2002	176	15	161	2	15/842	14	1.160
1971–1972	59	5	54	1	12/379	17	1.300	2002–2003	185	16	169	1	16/796	13	3.754
1972–1973	51	5	46	1	14/375	19	2.051	2003–2004	194	25	169	1	45/882	13	0.350
1973–1974	49	2	47	1	7/297	14	4.066	2004–2005	217	34	183	2	43/822	12	3.271
1974–1975	49	2	47	0	11/332	16	2.356	2005–2006	220	30	190	6	61/756	11	-3.356
1975–1976	57	8	49	0	10/366	17	0.333	2006–2007	237	45	192	0	30/301	5	-1.563
1976–1977	69	12	57	0	19/468	19	4.494	2007–2008	266	39	227	0	26/435	8	2.821
1977–1978	72	10	62	1	15/419	15	-0.999	2008–2009	270	38	232	23	125/568	8	-4.294
1978–1979	75	7	68	1	12/412	15	1.377	2009–2010	264	22	242	1	102/528	8	0.957
1979–1980	76	6	70	0	8/505	17	2.090	2010–2011	283	45	238	4	33/354	5	0.404
1980–1981	78	6	72	1	16/452	17	-1.229								

^a Winter abundance estimates were available in [Butler et al. \(2013\)](#). Winter abundance during 1949–1950 was 34 birds.

^b The number of hatch-year (HY) whooping cranes in the winter population ([Link et al., 2003](#); [CWS and USFWS, 2007](#); [Stehn, 2009, 2010, 2011](#)).

^c The number of after-hatch-year (AHY) whooping cranes in the winter population (abundance – no. of hatch-year birds; [Link et al., 2003](#); [CWS and USFWS, 2007](#)).

^d The number of whooping cranes lost (i.e., early migration, temporary emigration, and/or mortality) during the winter period were available in [Stehn and Haralson-Strobel \(2014\)](#).

^e Whooping crane locations observed during aerial surveys between December 1st and March 31st were digitized and classified as upland or wetland based on National Wetland Inventory data ([USFWS, 2008](#)). Total is the total number of locations.

^f Number of aerial surveys conducted between December 1st and March 31st.

^g The Palmer hydrological drought index (PHDI) indicates long-term moisture supply; PHDI values of 0.0 to -0.5 represent normal moisture, -0.5 to -1.0 indicate incipient drought, -1.0 to -2.0 indicate mild drought, -2.0 to -3.0 represent moderate drought, -3.0 to -4.0 indicate severe drought, and values <-4.0 indicate extreme drought ([NCDC, 2007](#)).

(i.e., potential winter mortality) were obtained from [Stehn and Haralson-Strobel \(2014; Table 1\)](#). Their method assumed an ability to identify unmarked birds that was contingent upon whooping cranes having fidelity to their wintering ground territories and family groups ([Stehn and Haralson-Strobel, 2014](#)). Therefore, they used repeated aerial surveys and considered whooping cranes missed on two or more flights and not relocated on later flights as mortalities ([Stehn and Haralson-Strobel, 2014](#)).

The winter surveys provided many observations of coarse habitat use by whooping cranes (i.e., locations of observations; [Stehn and Taylor, 2008](#)). During the aerial surveys, observers hand mapped whooping crane locations on paper copies of 1:46,080 digital orthophotograph quarter quadrangles (DOQQ; [Stehn and Taylor, 2008](#)). As part of a larger data archiving effort, we digitized the hand mapped locations of whooping cranes into a geodatabase. Though information about specific habitat types does not exist back to 1950, we delineated whooping crane locations into two coarse classifications: upland or wetland (based on National Wetland Inventory data; [USFWS, 2008](#)).

2.2. Demographics

We estimated annual whooping crane mortality (\hat{m}_t) as $(\hat{N}_t - \hat{A}_{t+1})/\hat{N}_t$, where \hat{N}_t was the total abundance during winter t and \hat{A}_{t+1} was the number of after-hatch-year (AHY) birds in the population during winter $t + 1$. Annual mortality estimates only

apply to birds >6 months of age (i.e., time of arrival on the wintering grounds through the beginning of the next winter). To index recruitment of HY birds into the winter population, we estimated the ratio (\hat{R}_t) of HY:AHY birds on the wintering grounds as $(\hat{N}_t - \hat{A}_t)/\hat{A}_t$. We calculated winter loss (\hat{w}_t) as the proportion of whooping cranes that died or disappeared from the survey area based on the possible winter mortalities reported in [Stehn and Haralson-Strobel \(2014; Table 1\)](#). We assumed all winter losses were deaths and then estimated the proportion (\hat{p}_t) of annual mortality that was due to winter loss as \hat{w}_t/\hat{m}_t (i.e., contribution of winter loss to annual mortality). We estimated apparent mortality during the breeding and migratory periods (breeding–migratory mortality; \hat{b}_t) as $\hat{m}_t - \hat{w}_t$. Presently, no data are available to separate mortalities on the breeding grounds from those that occur during migration. We reported summary statistics for the demographic rates as geometric means and calculated variance using the delta method ([Skalski et al., 2005:301](#); see Section 2.4 for additional details).

2.3. Modeling winter loss and upland use

We modeled winter loss (i.e., proportion of whooping cranes that died or disappeared from the survey area; \hat{w}_t), contribution of winter loss to annual mortality (i.e., number of birds lost in winter/number of annual mortalities; \hat{p}_t), and upland habitat use (i.e., number of upland observations/total number of observations

during the aerial surveys) as functions of predictor covariates using binomial generalized linear modeling (event/trials syntax of PROC LOGISTIC in SAS; Zuur et al., 2009; SAS Institute, 2010). Since whooping cranes missed on two or more flights and not relocated on later flights were considered mortalities (Stehn and Haralson-Strobel, 2014), we suspected more birds were considered dead during winters with fewer surveys than in winters with more surveys. Therefore, we used the number of aerial surveys conducted between December 1st and March 31st as a covariate when modeling winter loss and the contribution of winter loss to annual mortality. We also expected the proportion of upland use to be related to winter loss and its contribution to annual mortality, since emigration from saltmarsh territories could cause individuals to be missed during consecutive surveys. Likely this caused Stehn and Haralson-Strobel (2014) to identify those individuals as dead, when birds actually vacated the survey area. Therefore, we used the proportion of upland use as a covariate when modeling winter loss and the contribution of winter loss to annual mortality.

We included covariates to describe climatic conditions (i.e., drought) for each winter (Table 2). We also examined linear time trends to evaluate if winter loss, contribution of winter loss to annual mortality, and upland use increased or decreased through time. We obtained monthly values for the Palmer drought indices for Texas Climatological Division 7 (Palmer, 1965; National Climatic Data Center [NCDC], 2007; Jacobi et al., 2013). For each of the Palmer indices, we averaged the months of October through April of each year. We obtained monthly freshwater balance (i.e., balance = inflow – evaporation + precipitation) for the Guadalupe and Mission-Aransas estuaries (Texas Parks and Wildlife Department [TPWD], 1998; TPWD, 2010). For each of these estuaries, we summed the months of October through April of each year and scaled estimates to 1 million acre-feet (Table 2). Since the Aransas–Wood Buffalo whooping crane population overwinters along both estuaries, we also combined freshwater balance for both estuaries. Freshwater balance data was unavailable after 2009 (Texas Water Development Board; Table 2). Therefore, we only used data from winter 1950–1951 to winter 2008–2009 to maintain a consistent dataset across models (see Burnham and Anderson, 2002:80–81).

Before assembling the model set, we examined the associations among our covariates using Pearson's correlation coefficient (Zar, 1999). Because the climatic covariates were highly correlated with each other (see results, Section 3.3), we fit univariate models to avoid potential problems with multicollinearity (Zar, 1999). We also examined a quadratic effect for each climatic covariate. To evaluate evidence for each model, we used AIC_c (Anderson and Burnham, 2002; Burnham and Anderson, 2002). We considered models plausible if ΔAIC_c was ≤2 (Burnham and Anderson, 2002; Arnold, 2010). We evaluated the goodness of fit of the best model(s) using the Hosmer–Lemeshow test (SAS Institute, 2010; Hosmer and Lemeshow, 2000).

Salinity in the saltmarshes around Aransas NWR was influenced by bay salinity in Guadalupe Estuary (Wozniak et al., 2012). The

bay salinity levels have been measured since 2004 (GBRA Station #1; Division of Nearshore Research, 2013). We estimated average salinity during October through April of each winter (winter 2004–2005 through winter 2010–2011); salinity data limited to 7 years. We used Pearson's correlation coefficient (Zar, 1999) to examine the association of bay salinity to winter loss, upland use, and the contribution of winter loss to annual mortality.

2.4. Population growth, recruitment and winter drought

We estimated the finite rate of change for this whooping crane population ($\hat{\lambda}_t$) as \hat{N}_{t+1}/\hat{N}_t (Skalski et al., 2005) where \hat{N}_{t+1} was equivalent to $\hat{N}_t(1 - \hat{m}_t)(1 + \hat{R}_{t+1})$ and $\hat{m}_t = \hat{w}_t + \hat{b}_t$. These relationships allowed us to decompose population growth into its constituent components. We estimated the geometric mean of the finite rate of change ($\hat{\lambda}$) as

$$\hat{\lambda} = e^{\left(\frac{\sum \ln(\hat{N}_{t+1}/\hat{N}_t)}{n}\right)}$$

which is equivalent to

$$\hat{\lambda} = (1 - \hat{m})(1 + \hat{R}),$$

where \hat{m} and \hat{R} are geometric means estimated as

$$\hat{m} = 1 - e^{\left(\frac{\sum \ln(1 - \hat{m}_t)}{n}\right)}$$

and

$$\hat{R} = e^{\left(\frac{\sum \ln(1 + \hat{R}_t)}{n}\right)} - 1,$$

where n is the number of years. Below we report population growth as a percentage which is estimated as $(\hat{\lambda} - 1) \cdot 100\%$.

Winter loss (\hat{w}) and the contribution of winter loss to annual mortality (\hat{p}) were related to long-term moisture supply (Palmer hydrological drought index [PHDI]; see modeling results in Section 3.3) where

$$\hat{w} = \text{logit}(\hat{\alpha}_w + \hat{\beta}_w \text{PHDI})$$

and

$$\hat{p} = \text{logit}(\hat{\alpha}_p + \hat{\beta}_p \text{PHDI}).$$

For each predictive model, $\hat{\alpha}$ and $\hat{\beta}$ were the intercept and slope, respectively. We estimated $\hat{\lambda}$ as a function of PHDI by substituting annual mortality (\hat{m}) with \hat{w}/\hat{p} and used predictive models for \hat{w} and \hat{p} ,

$$\hat{\lambda} = \left(1 - \frac{\text{logit}(\hat{\alpha}_w + \hat{\beta}_w \text{PHDI})}{\text{logit}(\hat{\alpha}_p + \hat{\beta}_p \text{PHDI})}\right)(1 + \hat{R}). \quad (1)$$

This equation allowed us to estimate the magnitude of winter drought that would result in negative population growth given

Table 2

Climatic indices used in the analysis of winter loss, contribution of winter loss to annual mortality and upland habitat use for the Aransas–Wood Buffalo whooping crane population.

Index	Data source ^a
Palmer drought severity index (PDSI)	www1.ncdc.noaa.gov/pub/data/cirs/
Palmer hydrological drought index (PHDI)	www1.ncdc.noaa.gov/pub/data/cirs/
Modified Palmer drought severity index (PMDI)	www1.ncdc.noaa.gov/pub/data/cirs/
Palmer "Z" index (ZNDX)	www1.ncdc.noaa.gov/pub/data/cirs/
Guadalupe Estuary freshwater balance (GEFB)	midgewater.twdb.texas.gov/bays_estuaries/hydrology/summary/guadalupesum.txt
Mission-Aransas Estuary freshwater balance (MAEFB)	midgewater.twdb.texas.gov/bays_estuaries/hydrology/summary/missionsum.txt
Combined Estuary freshwater balance (CoEFB)	Combined data from Guadalupe and Mission-Aransas estuaries

^a All freshwater balance data were downloaded on 21 June 2012 and all Palmer drought indices were downloaded on 30 September 2013 (formula for Palmer indices was modified in April 2013; Jacobi et al., 2013).

average recruitment (i.e., we solved for $\hat{\lambda}$). We also determined the amount of recruitment that would continue average population growth (i.e., $\hat{\lambda} = 1.035$) or result in no population growth (i.e., $\lambda = 1.0$) for various drought conditions on the wintering grounds (i.e., we solved for \hat{R} given specific values of PHDI). To characterize the uncertainty in our predictions of $\hat{\lambda}$ and \hat{R} for various PHDI values, we used a bootstrap procedure with 10,000 replicates (R Development Core Team, 2012).

2.5. Components of population growth

We examined the importance of winter loss (\hat{w}), annual mortality (\hat{m}), breeding–migratory mortality (\hat{b}), and recruitment (\hat{R}) to population growth ($\hat{\lambda}$). Our approach used linear regression between $\hat{\lambda}$ and each demographic parameter (Zar, 1999; R Development Core Team, 2012). The contribution of a demographic parameter to population growth was indicated by the coefficient of determination (\hat{R}^2). We used a bootstrap procedure with 10,000 replicates to characterize the uncertainty in our estimates of \hat{R}^2 (R Development Core Team, 2012).

3. Results

3.1. Abundance surveys and demographics

During the winters of 1950–1951 through 2010–2011, 4–21 aerial surveys (mean = 12.52, $n = 61$, SD = 4.288) were conducted between December 1st and March 31st of each winter (Table 1). Over the past 61 years, the whooping crane population grew from 31 individuals in winter 1950–1951 to 283 individuals by winter 2010–2011 (Table 1). The proportion of whooping crane observations in upland areas (i.e., upland use) ranged from 0.010 to 0.220 (mean = 0.068, $n = 61$, SD = 0.049). Recruitment of HY birds (\hat{R} ; ratio of HY:AHY) into the winter population ranged from 0 to 0.4 (geometric mean = 0.145, $n = 61$, SD = 0.090) and during 68.9% of years, recruitment was ≥ 0.1 . Annual whooping crane mortality (\hat{m}) ranged from 0 to 0.355 (geometric mean = 0.094, $n = 60$, SD = 0.060; not available for winter 2010–2011) and in 68.3% of years, annual mortality was < 0.1 . On average, the proportion of whooping cranes lost each winter (\hat{w}) was 0.016 (range = 0.0–0.125, $n = 61$, SD = 0.025) and rarely ($< 10\%$ of winters) exceeded 0.04.

By assuming that winter loss consisted entirely of mortalities, winter loss describes the maximum amount of winter mortality possible. Given this assumption, winter loss accounted for 17.3% (\hat{w}/\hat{m} ; bootstrap 95% CI = 10.9–25.8%) of annual mortality. If mortality were constant over the annual cycle, then winter mortality (December–March) would account for $\approx 33\%$ of annual mortality. Instead, during 78.9% of years, winter loss accounted for $< 33\%$ of annual mortality. Because loss over the 4-month winter period (i.e., December–March) was lower than expected (assuming constant survival rate throughout the annual cycle), most mortality occurred during other parts of the annual cycle (i.e., migration and breeding periods). We found that breeding–migratory mortality ranged from 0 to 0.323 (geometric mean = 0.077, $n = 60$, SD = 0.054; not available for winter 2010–2011), which equates to 82.7% (\hat{b}/\hat{m} ; bootstrap 95% CI = 74.2–89.1%) of annual mortality, on average.

3.2. Identifying biases in winter loss

We found no linear time trend in winter loss (odds ratio = 1.007, $\hat{\beta} = 0.007$, SE = 0.007, Wald statistic [W] = 0.952, $P = 0.329$). However, the number of aerial surveys conducted during a winter

was inversely associated with winter loss (odds ratio = 0.932, $\hat{\beta} = -0.071$, SE = 0.028, $W = 6.595$, $P = 0.010$) as was the contribution of winter loss to annual mortality (odds ratio = 0.945, $\hat{\beta} = -0.057$, SE = 0.031, $W = 3.384$, $P = 0.066$). For each additional aerial survey conducted, the observers reported 6.8% (95% CI = 1.7–11.8%) fewer winter losses and winter loss attributed 5.5% (95% CI = -0.4 to 11.0%) less to annual mortality. Therefore, during a year in which 5 surveys were conducted, expected winter loss would be 2.7% (95% CI = 1.9–3.9%) and would account for 26.0% (95% CI = 18.6–35.1%) of annual mortality, on average. However, during a year in which 15 surveys were conducted, expected winter loss would be reduced to 1.3% (95% CI = 1.0–1.8%) and its contribution to annual mortality would be reduced to 16.6% (95% CI = 12.7–21.6%). This indicates that the counts of winter mortalities reported by Stehn and Haralson-Strobel (2014) were confounded by survey effort.

Winter loss increased with upland use (odds ratio [1% change in upland use] = 1.106, $\hat{\beta} = 10.100$, SE = 1.482, $W = 46.464$, $P < 0.001$). Each 1% increase in upland use increased winter loss by 10.6% (95% CI = 7.5–13.9%). Hence, during a year with 5% upland use, our model predicts a winter loss of 1.3% (95% CI = 1.0–1.7%) but were upland use to increase to 10%, winter loss would increase to 2.2% (95% CI = 1.8–2.6%). The contribution of winter loss to annual mortality also increased with upland use (odds ratio [1% change in upland use] = 1.117, $\hat{\beta} = 11.059$, SE = 1.981, $W = 31.1632$, $P < 0.001$). Hence, winter loss attributed 11.7% (95% CI = 7.4–16.1%) more to annual mortality for each 1% increase in upland use. Therefore, during a year with 5% upland use, our model predicts winter loss would contribute 15.3% (95% CI = 12.2–19.0%) to annual mortality, but were upland use to increase to 10%, winter loss would contribute 23.9% (95% CI = 19.9–28.4%). This indicates the counts of winter mortalities reported by Stehn and Haralson-Strobel (2014) were confounded by upland habitat use.

3.3. Models of winter loss and upland use

All the climatic covariates were correlated with each other ($r > 0.60$, $n = 59$, $P < 0.05$; Table 3), though they were not correlated with time or the number of surveys conducted per winter (Table 3). We examined 18 models to predict winter loss and 2 were competitive (Table 4). The most competitive model included the Palmer hydrological drought index (PHDI), an indicator of long-term moisture supply (NCDC, 2007). Thus, our best model indicated declines in winter loss as long-term moisture supply increased (Fig. 1; Table 4; odds ratio = 0.735, $\hat{\beta} = -0.308$, SE = 0.042, $W = 52.430$, $P < 0.001$). This model fit the data ($\chi^2 = 13.763$, df = 8, $P = 0.088$). In the worst drought conditions (i.e., PHDI = -4), the model predicts 4.8% (95% CI = 3.6–6.2%) of the winter population would be lost (Fig. 1). During normal conditions (i.e., PHDI = 0), the model predicts 1.4% (95% CI = 1.1–1.8%) winter loss, and during the wettest conditions (i.e., PHDI = 4), 0.4% (95% CI = 0.3–0.7%) of the population would be lost (Fig. 1). The second most competitive model associated winter loss with the modified Palmer drought severity index (PMDI). This model exhibited a similar relationship as PHDI (Table 4; odds ratio = 0.722, $\hat{\beta} = -0.326$, SE = 0.045, $W = 52.128$, $P < 0.001$; $\chi^2 = 14.819$, df = 8, $P = 0.063$).

We examined 18 models to predict the contribution of winter loss to annual mortality and 1 model was competitive (Table 5). As with winter loss, the contribution of winter loss to annual mortality increased with decreasing long-term moisture supply (as measured by PHDI; Fig. 2; Table 5; odds ratio = 0.728, $\hat{\beta} = -0.318$, SE = 0.047, $W = 44.897$, $P < 0.001$). The Hosmer–Lemeshow test indicated adequate model fit ($\chi^2 = 13.090$, df = 8, $P = 0.109$). This model predicts that during extreme drought (i.e., PHDI = -4), winter loss contributes up to 42.5% (95%

Table 3

Matrix of Pearson's correlation coefficients (*r*) and *p*-values (*P*) for climatic indices used in the analysis of whooping crane winter loss (*n* = 59), Texas coast of the Gulf of Mexico, USA, 1950–2009.

Covariates ^a	Time	Surveys ^b	GEFB	MAEFB	CoEFB	PDSI	PHDI	PMDI	ZNDX
Time	–	–0.102	0.209	0.256	0.227	0.154	0.209	0.183	0.153
Surveys	0.443	–	0.081	–0.008	0.064	0.151	0.075	0.108	0.101
GEFB	0.111	0.544	–	0.810	0.992	0.761	0.720	0.757	0.822
MAEFB	0.051	0.954	<0.001	–	0.879	0.651	0.634	0.672	0.747
CoEFB	0.084	0.631	<0.001	<0.001	–	0.762	0.725	0.764	0.833
PDSI	0.245	0.254	<0.001	<0.001	<0.001	–	0.929	0.967	0.851
PHDI	0.112	0.571	<0.001	<0.001	<0.001	<0.001	–	0.985	0.739
PMDI	0.165	0.416	<0.001	<0.001	<0.001	<0.001	<0.001	–	0.807
ZNDX	0.249	0.448	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	–

^a Acronym definitions are provided in Table 2. Pearson's correlation coefficients (*r*) are provided in the top-right portion of the table and *p*-values (*P*) are provided in the bottom-left portion of the table.

^b Number of surveys conducted between December 1st and March 31st during a winter.

Table 4

Candidate binomial regression models of whooping crane winter loss (*w*) on the wintering grounds on and around Aransas National Wildlife Refuge, Texas, USA, 1950–2009.

Models ^a	–2LL	<i>K</i>	AIC _c	ΔAIC _c	Weight	Intercept		Covariate		Covariate ²	
						$\hat{\alpha}$	SE	$\hat{\beta}$	SE	$\hat{\beta}$	SE
PHDI	190.916	2	195.130	0.000	0.438	–4.229	0.120	–0.308	0.042		
PMDI	192.497	2	196.711	1.581	0.199	–4.263	0.123	–0.326	0.045		
PHDI ²	190.760	3	197.197	2.066	0.156	–4.268	0.157	–0.297	0.049	0.007	0.017
PMDI ²	191.735	3	198.172	3.041	0.096	–4.339	0.152	–0.296	0.054	0.016	0.018
MAEFB ²	191.900	3	198.337	3.207	0.088	–4.001	0.117	–4.296	0.653	2.776	0.841
PDSI ²	195.834	3	202.270	7.140	0.012	–4.460	0.154	–0.251	0.051	0.036	0.017
PDSI	199.791	2	204.005	8.875	0.005	–4.290	0.125	–0.316	0.047		
MAEFB	199.879	2	204.094	8.964	0.005	–3.859	0.102	–3.181	0.550		
CoEFB ²	206.428	3	212.864	17.734	0.000	–3.189	0.149	–1.056	0.202	0.119	0.035
UPLAND	211.657	2	215.872	20.742	0.000	–4.828	0.174	10.100	1.482		
CoEFB	214.631	2	218.846	23.715	0.000	–3.398	0.141	–0.567	0.117		
GEFB ²	214.930	3	221.366	26.236	0.000	–3.091	0.184	–1.221	0.270	0.161	0.055
ZNDX	220.600	2	224.814	29.684	0.000	–4.159	0.112	–0.465	0.089		
GEFB	221.511	2	225.725	30.595	0.000	–3.391	0.155	–0.603	0.138		
ZNDX ²	220.327	3	226.763	31.633	0.000	–4.209	0.149	–0.441	0.097	0.039	0.073
Surveys ^b	242.990	2	247.204	52.074	0.000	–3.233	0.320	–0.071	0.028		
Constant	249.612	1	251.682	56.552	0.000	–4.046	0.101				
Time trend	248.629	2	252.844	57.714	0.000	–4.342	0.324	0.007	0.007		

^a Acronym definitions are provided in Table 2. Estuary freshwater balances were scaled to 1,000,000 acre-feet. For each model, we give $-2 \times \log$ -likelihood (–2LL), no. of parameters (*K*), second-order Akaike's Information Criterion (AIC_c), difference in AIC_c compared to lowest AIC_c of the model set (ΔAIC_c), and AIC_c weight (weight).

^b Number of surveys conducted during a winter between December 1st and March 31st.

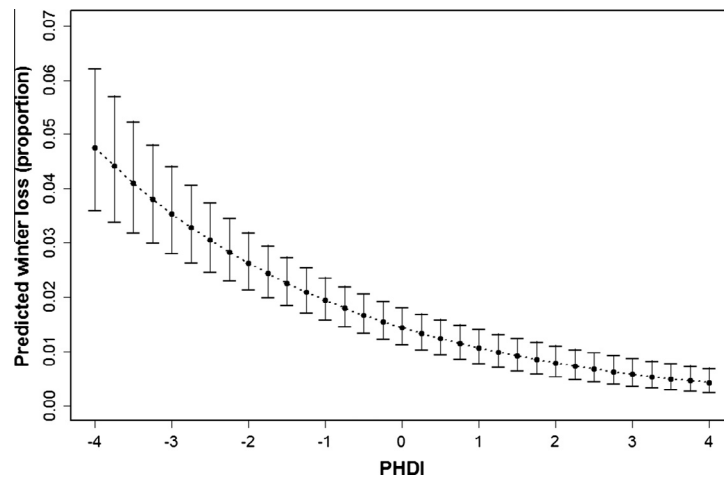


Fig. 1. Predicted proportion and 95% CIs of the whooping crane population that die or disappear during winter (winter loss; *w*). The Palmer hydrological drought index (PHDI) indicates long-term moisture supply; PHDI values of 0.0 to –0.5 represent normal moisture, –0.5 to –1.0 indicate incipient drought, –1.0 to –2.0 indicate mild drought, –2.0 to –3.0 represent moderate drought, –3.0 to –4.0 indicate severe drought, and values <–4.0 indicate extreme drought (NCDC, 2007).

CI = 34.2–51.3%) of annual mortality. During normal (i.e., PHDI = 0) and wet conditions (i.e., PHDI = 4) winter loss contributes 17.2% (95% CI = 13.9–21.1%) and 5.5% (95% CI = 3.3–9.0%), respectively (Fig. 2).

We examined 17 models to predict upland habitat use and 1 was competitive (Table 6). It indicated a quadratic relationship between upland use and the Palmer drought severity index (PDSI; Fig. 3; Table 6) but it did not fit well ($\chi^2 = 38.355$, *df* = 8, *P* < 0.001).

Table 5Candidate binomial regression models of the contribution of whooping cranes winter loss to annual mortality (w/m), 1950–2009.

Models ^a	–2LL	K	AIC _c	ΔAIC _c	Weight	Intercept		Covariate		Covariate ²	
						$\hat{\alpha}$	SE	$\hat{\beta}$	SE	$\hat{\beta}$	SE
PHDI	185.789	2	190.003	0.000	0.621	–1.571	0.130	–0.318	0.047		
PHDI ²	185.769	3	192.206	2.203	0.206	–1.589	0.182	–0.315	0.052	0.003	0.020
PMDI	189.129	2	193.343	3.340	0.117	–1.612	0.132	–0.331	0.051		
PMDI ²	188.477	3	194.914	4.910	0.053	–1.701	0.173	–0.309	0.056	0.017	0.021
PDSI ²	195.551	3	201.988	11.984	0.002	–1.873	0.174	–0.247	0.053	0.044	0.020
MAEFB ²	197.681	3	204.118	14.114	0.001	–1.366	0.129	–3.843	0.736	2.305	0.926
PDSI	200.186	2	204.401	14.397	0.000	–1.644	0.134	–0.302	0.053		
MAEFB	202.711	2	206.926	16.922	0.000	–1.248	0.115	–2.735	0.558		
Upland	207.168	2	211.382	21.379	0.000	–2.264	0.202	11.059	1.981		
CoEFB ²	209.708	3	216.144	26.141	0.000	–0.708	0.172	–0.832	0.224	0.083	0.041
CoEFB	213.148	2	217.363	27.359	0.000	–0.874	0.152	–0.462	0.111		
GEFB ²	215.177	3	221.613	31.610	0.000	–0.646	0.211	–0.929	0.304	0.105	0.064
GEFB	217.527	2	221.742	31.738	0.000	–0.860	0.164	–0.498	0.130		
ZNDX	221.483	2	225.698	35.694	0.000	–1.514	0.121	–0.378	0.096		
ZNDX ²	221.483	3	227.920	37.916	0.000	–1.515	0.164	–0.377	0.103	<0.001	0.079
Surveys ^b	234.509	2	238.723	48.720	0.000	–0.764	0.360	–0.056	0.031		
Constant	237.970	1	240.040	50.037	0.000	–1.406	0.112				
Time trend	235.837	2	240.052	50.048	0.000	–1.835	0.325	0.010	0.007		

^a Acronym definitions are provided in Table 2. Estuary freshwater balances were scaled to 1,000,000 acre-feet. For each model, we give $-2 \times \log$ -likelihood (–2LL), no. of parameters (K), second-order Akaike's Information Criterion (AIC_c), difference in AIC_c to lowest AIC_c of the model set (ΔAIC_c), and AIC_c weight (weight).

^b Number of surveys conducted during a winter between December 1st and March 31st.

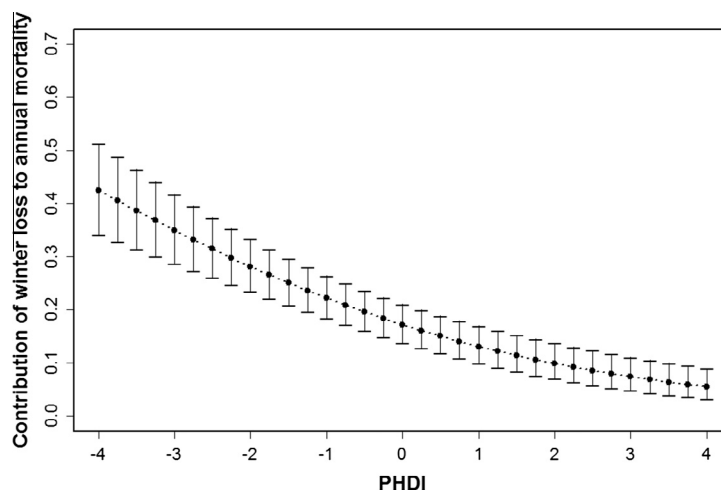


Fig. 2. Predicted contribution of winter loss to annual mortality (w/m) and 95% CIs. The Palmer hydrological drought index (PHDI) indicates long-term moisture supply; PHDI values of 0.0 to –0.5 represent normal moisture, –0.5 to –1.0 indicate incipient drought, –1.0 to –2.0 indicate mild drought, –2.0 to –3.0 represent moderate drought, –3.0 to –4.0 indicate severe drought, and values < –4.0 indicate extreme drought (NCDC, 2007).

In extreme drought conditions (i.e., PDSI = –4), the model predicts 13.3% (95% CI = 11.9–14.9%) upland use. During normal conditions (i.e., PDSI = 0) it predicts 4.1% (95% CI = 3.8–4.4%) upland use and during the wettest conditions (i.e., PDSI = 4) it predicts 6.3% (95% CI = 5.5–7.2%) upland use (Fig. 3).

Average bay salinity in Guadalupe Estuary during winter was associated with winter loss ($r = 0.758$, $n = 7$, $P = 0.048$), upland use ($r = 0.699$, $n = 7$, $P = 0.081$), and the contribution of winter loss to annual mortality ($r = 0.757$, $n = 6$, $P = 0.081$). Hence, a saltier estuary indicated more upland use and increased winter loss of whooping cranes.

3.4. Population growth, recruitment and winter drought

Population growth since winter 1950–1951 ranged from –19.4% to 33.3% (geometric mean = 3.5%, $n = 61$, $SD = 10.8$; variance calculated using the delta method in Skalski et al. (2005:301)). Given average recruitment into the winter population (geometric mean = 0.145, $SD = 0.090$), we predicted 1.2% (boot-

strap 95% CI = –2.9% to 4.2%) population growth during extreme winter drought (i.e., PHDI = –4) and 5.3% (bootstrap 95% CI = 1.6–8.8%) growth during the wettest conditions (i.e., PHDI = 4; Fig. 4). During 85.2% of years, recruitment has been >0.0725 (i.e., half the average). Were recruitment to decline to 0.0725, then we predicted –4.7% (bootstrap 95% CI = –7.4% to –2.4%) population decline during extreme drought (i.e., PHDI = –4) and –1.4% (bootstrap 95% CI = –4.4% to 1.1%) growth during the wettest conditions (i.e., PHDI = 4; Fig. 4). Understandably, population growth is always negative when there is no recruitment, provided some mortality occurs annually (Fig. 4).

Long-term moisture supply, as measured by PHDI, has little effect on population growth, especially when PHDI values exceed zero (Fig. 4). The minimal effect of PHDI on population growth stems from the relatively small contribution of winter loss to annual mortality and winter loss's lack of concordance with population growth (see Section 3.5).

We determined the recruitment rates that would result in zero population growth across a wide range of winter drought. This step

Table 6

Candidate binomial regression models of upland habitat use by whooping cranes on the wintering grounds on and around Aransas National Wildlife Refuge, Texas, USA, 1950–2009.

Models ^a	–2LL	K	AIC _c	ΔAIC _c	Weight	Intercept		Covariate		Covariate ²	
						$\hat{\alpha}$	SE	$\hat{\beta}$	SE	$\hat{\beta}$	SE
PDSI ²	634.324	3	640.760	0.000	0.861	–3.157	0.044	–0.104	0.011	0.054	0.005
PMDI ²	638.555	3	644.991	4.231	0.104	–3.104	0.044	–0.117	0.011	0.047	0.005
PHDI ²	640.726	3	647.162	6.402	0.035	–3.091	0.045	–0.120	0.011	0.041	0.004
MAEFB ²	686.168	3	692.604	51.844	0.000	–2.751	0.032	–2.331	0.187	1.973	0.190
ZNDX ²	711.817	3	718.253	77.493	0.000	–3.058	0.041	–0.190	0.023	0.150	0.016
PHDI	723.407	2	727.621	86.861	0.000	–2.803	0.030	–0.131	0.012		
CoEFB ²	729.348	3	735.785	95.025	0.000	–2.345	0.052	–0.566	0.053	0.078	0.008
PMDI	733.030	2	737.244	96.484	0.000	–2.815	0.030	–0.134	0.013		
GEFB ²	754.308	3	760.744	119.984	0.000	–2.311	0.061	–0.663	0.070	0.109	0.012
PDSI	762.308	2	766.522	125.762	0.000	–2.828	0.030	–0.118	0.013		
MAEFB	787.896	2	792.110	151.350	0.000	–2.721	0.033	–0.723	0.101		
ZNDX	789.483	2	793.697	152.937	0.000	–2.826	0.030	–0.190	0.025		
Surveys ^b	793.978	2	798.192	157.432	0.000	–2.027	0.114	–0.062	0.009		
CoEFB	816.934	2	821.148	180.388	0.000	–2.669	0.043	–0.105	0.021		
GEFB	825.013	2	829.228	188.468	0.000	–2.685	0.045	–0.107	0.025		
Constant	845.344	1	847.414	206.654	0.000	–2.840	0.030				
Time Trend	845.289	2	849.504	208.744	0.000	–2.821	0.086	<0.001	0.002		

^a Acronym definitions are provided in Table 2. Estuary freshwater balances were scaled to 1,000,000 acre-feet. For each model, we give $-2 \times \log$ -likelihood ($-2LL$), no. of parameters (K), second-order Akaike’s Information Criterion (AIC_c), difference in AIC_c compared to lowest AIC_c of the model set (ΔAIC_c), and AIC_c weight (w).

^b Number of surveys conducted during a winter between December 1st and March 31st.

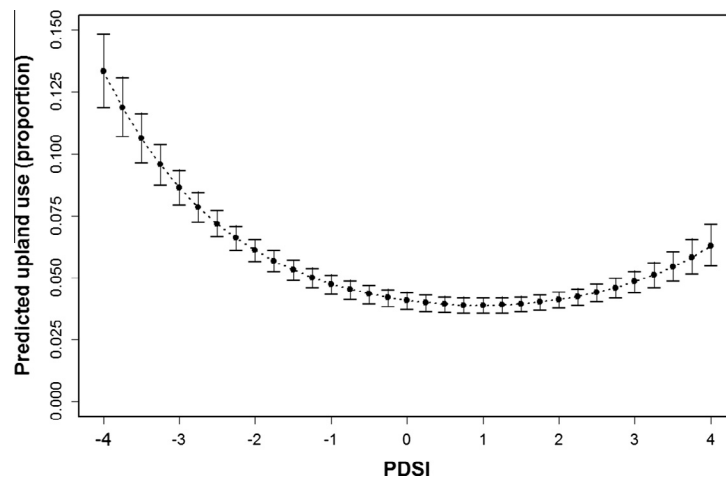


Fig. 3. Predicted proportion and 95% CIs of whooping crane use of upland areas during winter. The Palmer drought severity index (PDSI) indicates the severity of a wet or dry period; PDSI values of 0.0 to –0.5 represent normal moisture, –0.5 to –1.0 indicate incipient drought, –1.0 to –2.0 indicate mild drought, –2.0 to –3.0 represent moderate drought, and values –3.0 to –4.0 indicate severe drought, and values <–4.0 indicate extreme drought (NCDC, 2007).

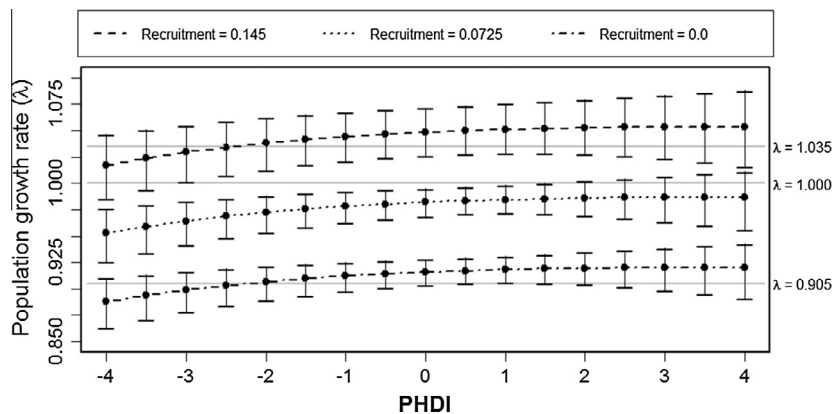


Fig. 4. Population growth rate λ and bootstrap 95% CIs given the relationships that winter loss and contribution of winter loss to annual mortality have with the Palmer hydrological drought index (PHDI). We examined this relationship for average recruitment of 0.145 (resampled dataset to incorporate uncertainty in mean recruitment). We also held recruitment constant at 0.0725 and 0.0 to assess how reductions in recruitment would impact population growth. $\lambda = 1.035$ is 3.5% population growth (geometric mean), $\lambda = 1.0$ is 0% growth, and $\lambda = 0.905$ is 9.5% decline.

enabled us to determine the thresholds in recruitment for each PHDI value (dotted line in Fig. 5A). Recruitment greater than these threshold values would result in positive population growth (light gray area in Fig. 5A), but recruitment below the thresholds would result in negative growth for that year (dark gray area in Fig. 5A). After normal or wet conditions (i.e., PHDI > 0) on the wintering grounds, recruitment ≥ 0.09 would result in positive population growth (Fig. 5A). However, recruitment must be >0.126 (bootstrap 95% CI = 0.099–0.159) to result in positive growth after extreme drought (i.e., PHDI ≤ -4) on the wintering grounds (Fig. 5A). To sustain average population growth (3.5%) after extreme drought (PHDI ≤ -4), we predicted recruitment would have to be 0.165 (bootstrap 95% CI = 0.137–0.199; Fig. 5B). However, recruitment of ≈ 0.13 would be sufficient to sustain average population growth after normal or wet conditions (i.e., PHDI ≥ 0) on the wintering grounds (Fig. 5B). In all drought conditions (PHDI of -4 to 4), average recruitment (geometric mean = 0.145, SD = 0.090) results in positive population growth (dashed line in Fig. 5A). Also, average

recruitment results in greater than average population growth ($\geq 3.5\%$) when PHDI > -2.5 (dashed line in Fig. 5B).

3.5. Components of population growth

We quantified the relative importance of winter loss, annual mortality, breeding–migratory mortality and recruitment to population growth, based on their fit with linear regression. Winter loss, assuming it were all mortality, explained 14.4% (bootstrap 95% CI = 3.6–35.8%) of population growth (λ ; Fig. 6). Mortality during the breeding and migratory periods explained 42.2% (bootstrap 95% CI = 19.1–61.5%) of population growth (Fig. 6). Annual mortality explained 52.4% (bootstrap 95% CI = 32.9–69.0%) of population growth, while recruitment into the winter population explained 49.9% (bootstrap 95% CI = 20.6–75.2%) of population growth (Fig. 6). On average, winter mortality had the least explanatory power, while the other demographic rates explained much more of the variation in population growth.

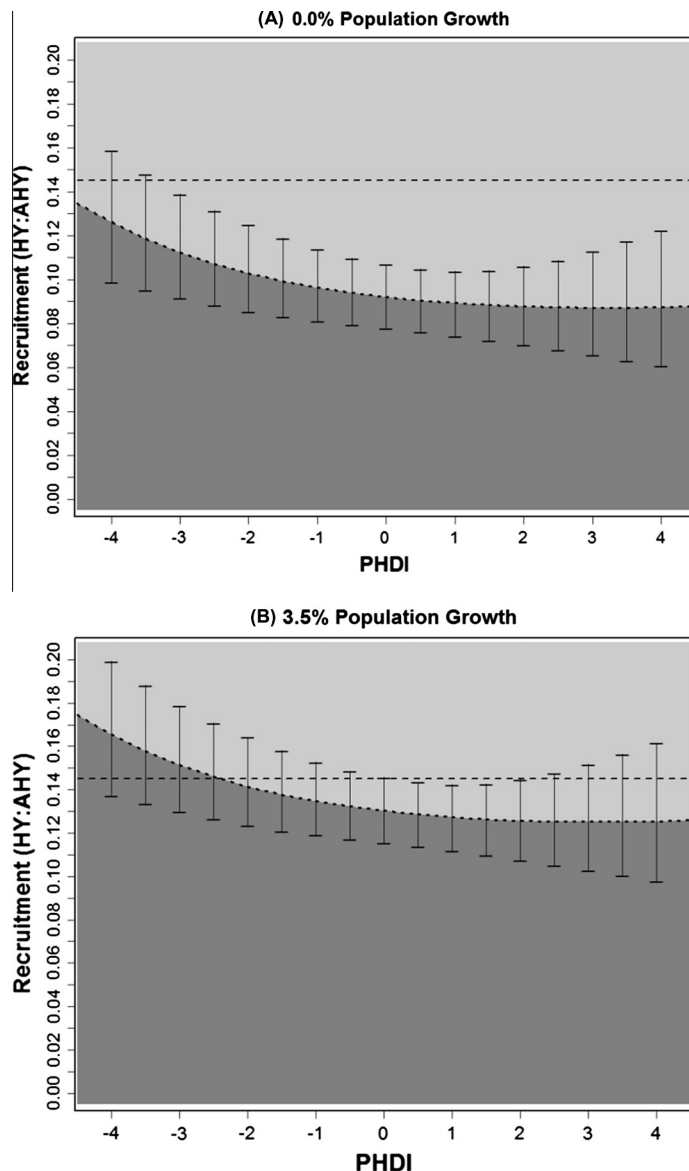


Fig. 5. Recruitment rate required to maintain 0% or 3.5% (average) population growth (dotted line and bootstrap 95% CIs) given the relationships between the Palmer hydrological drought index (PHDI) and winter loss and its contribution to annual mortality. The dashed line represents average recruitment (0.145). (A) Recruitment rates within the light gray region result in positive population growth while recruitment rates within the dark gray region result in negative population growth. (B) Recruitment rates within the light gray region result in above average population growth while recruitment rates within the dark gray region cause below average population growth.

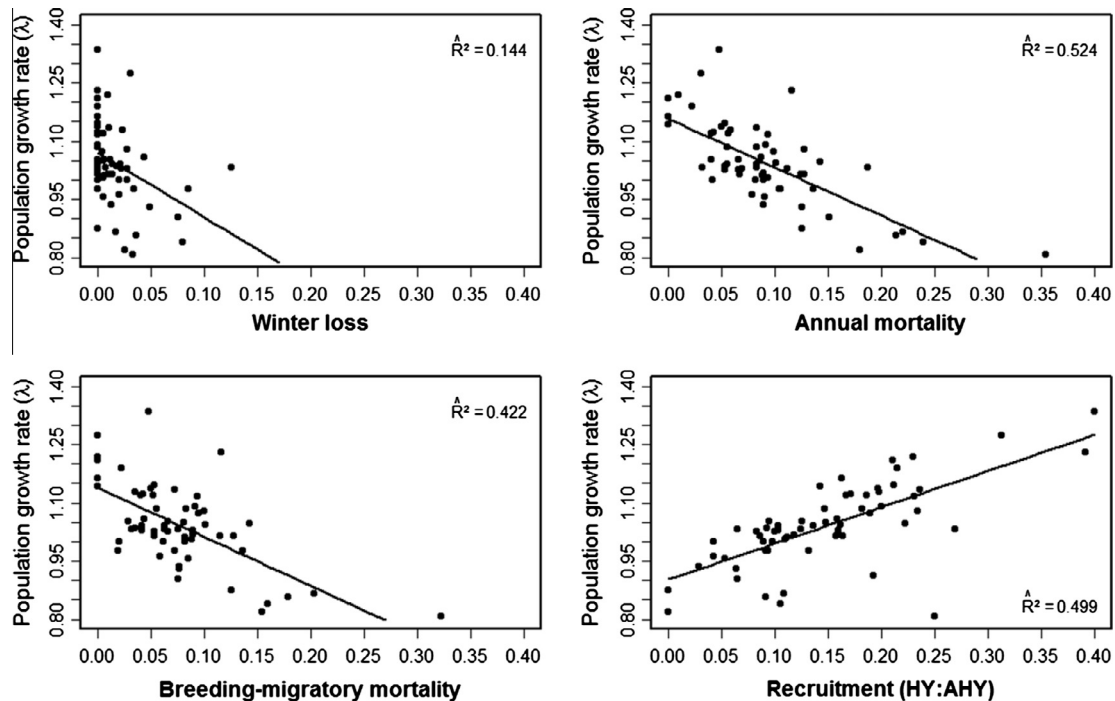


Fig. 6. An evaluation of the relative importance of winter loss (assumed winter mortality), combined mortality during the breeding and migratory periods (breeding-migratory mortality), annual mortality, and recruitment (ratio of hatch-year [HY] to after-hatch-year [AHY] birds) to population growth (λ) for the Aransas–Wood Buffalo whooping crane population. The \hat{R}^2 values describe the proportion of variation in λ explained by each demographic parameter.

4. Discussion

Managing wildlife populations requires understanding how species' demographics respond to environmental conditions and the relative importance of demographic parameters to population growth (Rockwood, 2006; Mills, 2007). For the Aransas–Wood Buffalo whooping crane population, we related winter loss, the contribution of winter loss to annual mortality, and upland use with drought on the wintering grounds. We used these relationships to distinguish the drought conditions and recruitment rates needed to maintain population growth or, conversely, result in population decline. Though we found other demographic parameters were more important to whooping crane population growth than winter loss, this analysis enabled us to identify scenarios in which winter drought followed by poor recruitment could delay population recovery. Our investigation began by identifying biases in previous surveys to ensure that our analyses provided valuable information and sound interpretation.

4.1. Biases in winter mortality

From 1950 to 2011, the technique used for estimating the number of whooping cranes dying each winter was ad hoc and deficient (Pugesek et al., 2013; Stehn and Haralson-Strobel, 2014); biases are apparent due to flawed assumptions, inconsistent survey effort, incomplete detection, and whooping crane movements. The approach used to count winter losses assumed an ability to identify individual birds based on “normal” whooping crane behavior (i.e., group structure and territorial fidelity; Stehn and Haralson-Strobel, 2014). When an individual bird was not observed for two or more consecutive surveys, that individual was declared dead (Stehn and Haralson-Strobel, 2014). Hence, as the number of surveys in a given year increased, it provided more chances for individuals missed on a few surveys to be “rediscovered” on subsequent surveys. Imagine 5 consecutive surveys in which a whooping crane

was unobserved on the third and fourth survey occasions. Unless the fifth survey occurred, that whooping crane would have been considered dead. An inverse relationship between winter loss and survey frequency confirmed this deficiency. Each additional survey resulted in 6.8% (95% CI = 1.7–11.8%) fewer losses reported. Therefore, 4–5 additional surveys during a winter changes winter loss similarly to a unit change in PHDI (approximately 26.5%).

Previous work demonstrates that transect-based aerial surveys failed to detect 44.2% of whooping crane groups during a survey (Strobel and Butler, 2014). Evidence based on decoys suggested that, on average, group size was underestimated by 5.8% (Strobel and Butler, 2014). Hence, missed birds during the winter could represent incomplete detection, not death. Although the winter mortality estimates included information describing recovered carcasses, carcass recovery was an uncommon occurrence (mean = 0.82 carcasses/year, $n = 61$, SD = 1.008; 0.30 carcasses/year, $n = 61$, SD = 0.691; Stehn and Haralson-Strobel, 2014).

The aerial survey centered on saltmarsh and covered little upland habitat. Therefore, during drought, when whooping cranes spent less time in saltmarshes and more time in uplands (Fig. 3), the likelihood of missing whooping cranes during an aerial survey increased (Stehn, 2009). The area covered by the survey also fluctuated between years, as flights could shift to upland habitat when birds were observed there. These practices underestimated and inflated variability in the actual amount of upland habitat used between surveys, helping explain the poor fit for the model of upland use.

Regardless, the relationship between winter loss and upland use confirmed movement from saltmarshes, which caused additional bias in the reports of winter mortality. We found that a 1% increase in upland use resulted in 10.6% (95% CI = 7.5–13.9%) more losses and an 11.7% (95% CI = 7.4–16.1%) increase in the proportion of annual mortality attributable to winter loss. Hence, the missing birds could represent emigration from saltmarsh or early departure from the wintering grounds.

We cannot estimate the proportion of winter loss attributable to movement. Instead, we can only infer that some whooping

cranes, previously considered dead, were alive and emigrated from coastal saltmarsh to upland and interior habitats. Stehn (1992) reported that, occasionally, color-banded birds exhibited extra-territorial excursions (e.g., temporary emigration) and some pair-banded individuals overwintered apart. For these reasons, the mortality values reported in Stehn and Haralson-Strobel (2014; Table 1) do not represent winter mortality. Instead, these values represent a marginal index combining movement (i.e., temporary emigration, early migration, and/or increased searching activity by whooping cranes) with mortality. Despite this, we considered winter loss to consist entirely of deaths to evaluate the relevance of winter mortality on the dynamics of this population.

4.2. Winter mortality and drought

During extreme drought (PHDI = -4), upland use was most prevalent (13.3%; 95% CI = 11.9–14.9%), most winter loss occurred (4.8%; 95% CI = 3.6–6.2%), and winter loss contributed most to annual mortality (42.5%; 95% CI = 34.2–51.3%). The mechanisms behind these phenomena likely stem from a complex chain of events. Drought conditions result in increased salinity levels and reduced freshwater in the bays and saltmarshes (Longley, 1994), which have direct or indirect effects on the availability of resources (i.e., food and freshwater) and behavioral responses (i.e., movement) of whooping cranes (Chavez-Ramirez and Wehtje, 2012).

It has been reported that whooping cranes can tolerate brackish water up to 23 ppt (Chavez-Ramirez and Wehtje, 2012). When salinities in their saltmarsh habitat exceed that threshold, it has been suggested that whooping cranes must seek freshwater sources in upland areas requiring increased extra-territorial movement (Chavez-Ramirez and Slack, 1999; Chavez-Ramirez and Wehtje, 2012). We only found anecdotal evidence supporting this threshold (Stehn, 2011). Instead, our findings demonstrate a simple correlation of average winter bay salinity with winter loss and upland use, indicating a gradient of responses may occur rather than a strict threshold.

Whooping crane loss and upland use likely revolves around the response of food resources to drought conditions. Blue crabs (*Callinectes sapidus*), a primary food source of whooping cranes (Hunt and Slack, 1989; Nelson et al., 1996; Westwood and Chavez-Ramirez, 2005; Greer, 2010), may be directly influenced by drought through a physiological response to hyper-saline environments. Hyper-saline conditions along with other chemical and physical cues signal blue crab metamorphosis from a larval to post larval stage and ingress into estuaries (Forward et al., 2001). Disruption or changes to the timing of these cues can modify the availability of blue crabs to foraging whooping cranes. Additionally, inadequate freshwater inflows and little rainfall can reduce water levels, thereby limiting connectivity among ponds in the saltmarsh (Colón-Rivera et al., 2012). Loss of connectivity may limit the replenishment of blue crabs to isolated ponds (Colón-Rivera et al., 2012).

Pugesek et al. (2013) reports an association between the count of whooping crane winter mortalities (i.e., loss) and blue crab density (measured during March of each year). However, Pugesek et al.'s (2013) estimates of blue crab densities were unassociated with drought conditions (as measured by PHDI; $r = 0.476$, $n = 9$, $P = 0.195$) or freshwater balance in the Guadalupe Estuary ($r = 0.562$, $n = 9$, $P = 0.116$). Instead, their estimates of blue crab densities were associated with freshwater balance in the Mission-Aransas Estuary ($r = 0.725$, $n = 9$, $P = 0.027$). The location of the 2 transects they used to index blue crab density may have been more influenced by inflow into the Mission-Aransas Estuary more than the Guadalupe Estuary (the transects were located between these estuaries). Further, the 2 transects were close enough to each other that they probably should have been treated as one (i.e., they

were located on the “southwest and northeast sides of the Old Pump Canal”; Pugesek et al., 2008:13). Few samples with little spatial dispersion make inference to large-scale demographic processes such as winter mortality precarious.

Indirectly, drought may affect other food resources. Wolfberry (*Lycium carolinianum*) is a secondary food resource of whooping cranes (Hunt and Slack, 1989; Nelson et al., 1996; Westwood and Chavez-Ramirez, 2005), and low salinity levels correlate with higher fruit production (Wozniak et al., 2012). Wet years with high inflows also increase macrofaunal productivity in the Guadalupe Estuary (Montagna and Kalke, 1992). Thus, diminished inflows may reduce the amount and type of resources in the saltmarsh, causing whooping cranes to search farther for food and possibly freshwater. Hence, the increased use of upland habitats observed during drought.

4.3. Population growth, recruitment and winter drought

This whooping crane population has increased on average 3.5% per year (SD = 10.8; winter 1950–1951 through winter 2010–2011). To sustain such population growth after extreme drought conditions (i.e., PHDI < -4) on the wintering grounds, we found recruitment must be > 0.165 (bootstrap 95% CI = 0.137–0.199; Fig. 5B). Recruitment at these levels or greater has occurred 36.1% of the time (22 of 61 years). Given average recruitment into the winter population (geometric mean = 0.145, SD = 0.090), we estimate population growth to be 1.2% (bootstrap 95% CI = -2.9% to 4.2%) after extreme drought conditions (Fig. 4). Negative population growth would only occur after extreme drought conditions (PHDI ≤ -4) on the wintering grounds and below normal recruitment (i.e., < 0.126 ; bootstrap 95% CI = 0.099–0.159) the following year (Fig. 5A). Circumstances where PHDI was ≤ -4 and recruitment was ≤ 0.126 the following winter have only occurred twice; after the winters of 1955–1956 and 2008–2009.

After normal conditions on the wintering grounds (PHDI = 0), we estimate negative population growth if recruitment declines to < 0.09 (Fig. 5A). Recruitment < 0.09 has occurred during 19.7% of years. However, periodic declines in this population appear normal, and have occurred since its conservation and protection began (Boyce and Miller, 1985; Boyce, 1986; Butler et al., 2013). Indeed, this whooping crane population tends to follow a 10-year cycle similar to other boreal species like lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*; Krebs et al., 2001; Boyce et al., 2005; Butler et al., 2013).

Given the trends in this population's growth, Butler et al. (2013) determined the magnitude and duration of population decline that would delay reaching the downlisting goal of 400 birds by ≥ 5 years (delay measured via comparison with population trends lacking an induced decline; Alternative Criterion 1A; CWS and USWFS, 2007). The scenarios they identified were ≥ 2 consecutive years with -14% population growth or ≥ 3 consecutive years with -9.5% growth. Here we found that if the population had no recruitment, its growth would decline below -9.5% only if drought conditions were moderate to severe (i.e., PHDI ≤ 2.5 ; Fig. 4). By tying our results with Butler et al. (2013), we identified that this scenario (i.e., no recruitment after moderate to severe drought on the wintering grounds) must occur for at least 3 consecutive years to delay reaching the recovery goal by ≈ 7 years. This has not occurred since monitoring began in 1938. Two years of such a scenario would delay that time by ≈ 1 year. Therefore, population growth and delays in population recovery are not only contingent upon extreme drought conditions on the wintering grounds, but rely on a combination of drought and poor recruitment the following year.

Despite this, some may maintain that recruitment depends upon environmental conditions on the wintering grounds, which

could affect whooping crane body condition and therefore reproduction once birds return to the breeding grounds. However, recruitment of HY birds into the winter population was unassociated with drought conditions (as measured by PHDI) on the wintering grounds the previous winter (odds ratio = 0.995, $\hat{\beta} = -0.005$, SE = 0.015, $W = 0.117$, $P = 0.732$). Boyce et al. (2005) found recruitment was associated with predator populations on the breeding grounds, date of egg laying, and was enhanced by egg collection (i.e., removal of one egg from nests for captive breeding and reintroduction projects). Research focused on understanding the associations between recruitment and environmental conditions on the breeding grounds would provide more insight into population growth and species recovery than further investigations of winter loss.

4.4. Components of population growth

We predicted that winter loss contributes 17.2% (95% CI = 13.9–21.1%) to annual mortality during normal drought conditions (i.e., PHDI = 0). Winter loss increased as drought worsened, but annual mortality remained relatively constant ($\approx 9.5\%$) across drought conditions on the wintering grounds (Fig. 7). There are two explanations for this outcome. First, we know that wet winters (i.e., PHDI > 0) experienced the least amount of winter loss (Fig. 1) and whooping crane movement was lower than during dry winters (Fig. 3). Therefore, during wet winters, loss is most likely to represent actual mortality. During wet conditions (PHDI = 4), winter loss is 0.4% (95% CI = 0.3–0.7%) which is 5.5% (95% CI = 3.3–9.0%) of annual mortality (Fig. 7). Perhaps, when winter loss is above 0.4% it represents whooping crane movement or incomplete detection, and not mortality. A second explanation is that additional mortality during drought on the wintering grounds is partially compensated for by reduced mortality during other periods (Fig. 7). Under this scenario, when more whooping cranes are lost during winter drought (Fig. 7, gray area), fewer die during breeding and migration. Likewise, fewer whooping cranes lost during a wet winter means more die during other periods. Otherwise, the proportion of annual mortality due to winter mortality would be constant over a range of drought conditions (i.e., dotted line in Fig. 7). We are unable to tease apart these explanations, and they are not mutually exclusive.

Even with the assumption that winter loss was all death, its contribution was disproportionately low when compared to mortality during other periods. If mortality were constant over the

annual cycle, then winter mortality (December–March) would account for $\approx 33\%$ of annual mortality. Instead, winter loss contributed less (17.3%). Since winter loss was not entirely mortality, the true contribution of winter loss to annual mortality was even lower than 17.3%.

Winter loss was the least important component of population growth (Fig. 6). Most mortality for whooping cranes occurred during the breeding and migratory periods. Mortality during the breeding and migratory periods and recruitment into the winter population explained 42.2% (bootstrap 95% CI = 19.1–61.5%) and 49.9% (bootstrap 95% CI = 20.6–75.2%), respectively, of population growth (Fig. 6).

Effort placed on mitigating winter mortality during extreme drought is probably misplaced since winter mortality was likely overestimated, at least partially compensatory, and only explained 14.4% (bootstrap 95% CI = 3.6–35.8%) of population growth (Fig. 6). Instead, enhancing recruitment or reducing breeding–migratory mortality would have more impact on population growth for this flock of whooping cranes.

4.5. Monitoring considerations

Poorly designed monitoring programs can lead to inadequate or inappropriate inference and misplaced conservation actions. Regrettably, this issue is pervasive and often overlooked by field biologists and decision makers (Legg and Nagy, 2006; Nichols and Williams, 2006; Field et al., 2007; Lindenmayer and Likens, 2009, 2010). For example, unrepresentative sampling misled monitoring assessments of green sea turtle (*Chelonia mydas*) populations (Kittinger et al., 2013), unstandardized monitoring practices may have resulted in inappropriate recovery targets for endangered species such as snail kites (*Rostrhamus sociabilis plumbeus*; Martin et al., 2006), and coarse monitoring of African elephant (*Loxodonta africana*) populations has diminished the appropriateness of data to inform regulatory decisions on ivory bans (van Aarde and Ferreira, 2009). Further, survey assumptions are often overlooked in long-term monitoring efforts, and their violation can compromise results (Anderson, 2001; Mazerolle et al., 2007; Butler et al., 2010; Collier et al., 2013; Harris et al., 2013).

In our case, the technique for monitoring whooping cranes was trusted to produce information that it could not credibly provide (i.e., winter mortality; Lewis et al., 1992; Stehn and Haralson-Strobel, 2014). We were fortunate with our scenario because we could identify the biases that inflated winter mortality estimates,

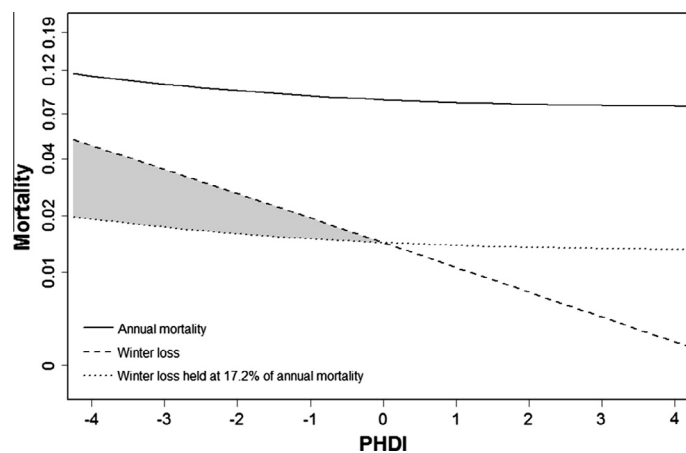


Fig. 7. Relationship between drought (PHDI), winter loss, and annual mortality (log-scale). Winter loss increased as drought worsened but annual mortality was relatively constant across drought conditions on the wintering grounds. This indicates the potential for additional mortalities during drought on the wintering grounds to be compensated for by reduced mortality during other periods (gray shading). Annual mortality was derived from the PHDI-based models of winter loss and the contribution of winter loss to annual mortality (see Eq. (1)).

and despite them, demonstrated that winter mortality was a minor component of the whooping crane's population dynamics. It may not be possible to derive meaningful results from other poorly designed monitoring programs.

Monitoring efforts should use rigorous techniques and be based in good science, beginning with well-defined questions (Nichols and Williams, 2006; Field et al., 2007; Lindenmayer and Likens, 2009, 2010). Successful, long-term monitoring programs build strong relationships between field and quantitative biology, and rely on critical thinking to ensure monitoring results and data limitations are understood. These steps help ensure that monitoring is relevant, logistically feasible, statistically appropriate and provides meaningful information. The U.S. Fish and Wildlife Service recognized these issues and committed to a purposeful inventory and monitoring effort to address them (USFWS, 2011). This effort enables science to better address priority topics, such as focusing conservation strategies for whooping cranes and ensuring that future monitoring informs such strategies (Butler et al., 2014; Strobel and Butler, 2014).

5. Applications

Our results focus conservation on the most appropriate places and periods while identifying the research areas required to advance understanding of this whooping crane population's demographics. Management focused on reducing mortality during winter would produce little gain in population growth. Instead, over 80% of annual mortality occurred during the migratory or breeding periods. Those periods should garner management emphasis. Mortality estimates for the breeding and migratory periods would help identify when mortality has the greatest impact on population growth. Cause-specific estimates of mortality would be most useful for identifying appropriate management strategies (e.g., marking of power lines, predator management, or restoration and/or protection of wetland habitats along the migratory route; Brown and Drewien, 1995; CWS and USFWS, 2007).

Recruitment was as important to whooping crane population growth as mortality during breeding and migration. Examining the associations between environmental conditions on the breeding grounds and recruitment would help identify the major factors influencing fledgling survival. Boyce et al. (2005) found $\approx 28\%$ of whooping crane fledglings that lived to August ended up dying during autumn migration to the wintering grounds. Perhaps reducing mortality during migration would also improve recruitment, making this issue an important research and management priority for this whooping crane population.

By placing winter mortality in an annual context, we identified that winter drought has little influence on this population's recovery. Therefore, on the wintering grounds in Texas, conservation and management priorities should focus on maintaining and protecting coastal, upland, and interior habitats for whooping cranes to use, given the wide range of climatic conditions that cranes experience. Such actions will ensure that enough, sustainable habitat exists to support this expanding population of whooping cranes.

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firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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