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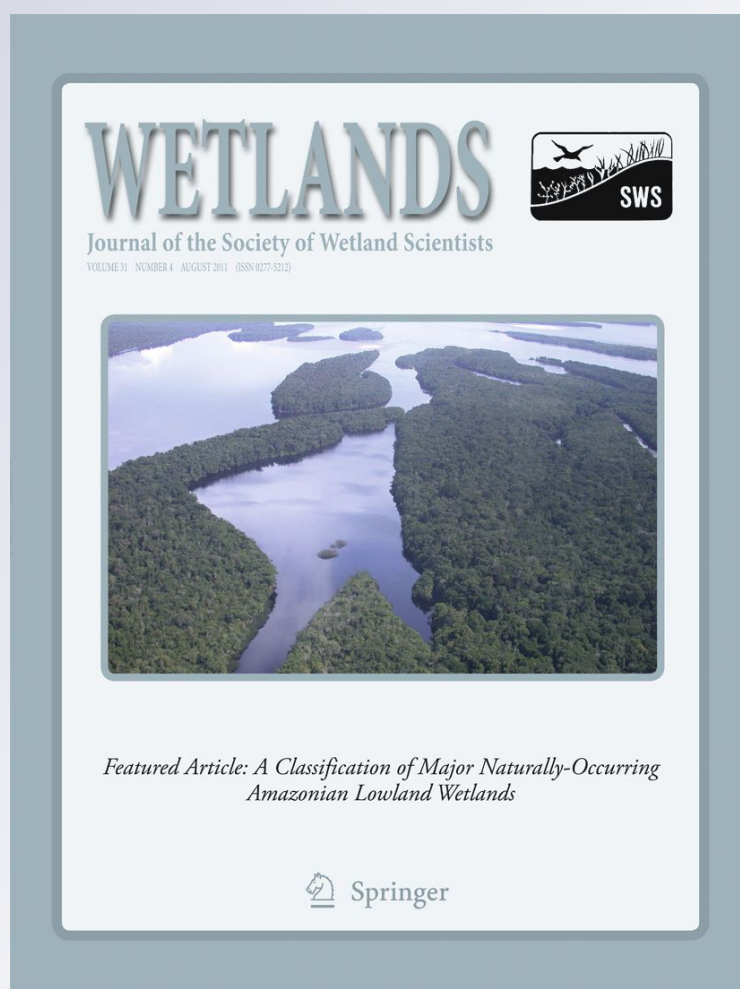
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Potential Impact of Climate Change Scenarios on Whooping Crane Life History

Felipe Chavez-Ramirez · Walter Wehtje

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Abstract Whooping crane (*Grus americana*), a rare and critically endangered species, are wetland dependent throughout their life cycle. The whooping crane's small population size, limited distribution, and wetland habitat requirements make them vulnerable to potential climate changes. Climate change predictions suggest overall temperature increases and significant changes in precipitation regimes throughout North America. At the individual level, temperature changes should have neutral to positive effects on thermoregulation and overall energy expenditure throughout the whooping crane's range. In the breeding grounds, earlier snow melt and increasing temperatures should improve food resources. However, increased precipitation and more extreme rainfall events could impact chick survival if rainfall occurs during hatching. Increased precipitation may also alter fire regimes leading to increased woody plant abundance thus reducing nesting habitat quality. During winter, higher temperatures will lead to a northward shifting of the freeze line, which will decrease habitat quality via invasion of black mangrove. Large portions of current winter habitat may be lost if predicted sea level changes occur. Stopover wetland

availability during migration may decrease due to drier conditions in the Great Plains. Current and future conservation actions should be planned in light of not only current needs but also considering future expectations.

Keywords Aransas National Wildlife Refuge · *Grus americana* · Wood Buffalo National Park

Introduction

Whooping crane (*Grus americana*), North America's tallest bird, are a critically endangered species and one of the world's rarest birds. The current population of 263 individuals, in the Aransas Wood Buffalo population, is the only remaining self-sustaining wild population. While current whooping crane numbers are low, the population is significantly greater than the 16 individuals present during 1941 when the all-time low population was recorded (CWS-USFWS 2007). Historically, the breeding grounds encompassed the prairie wetlands of the northern USA and southern Canada (Allen 1952). Currently, whooping cranes are restricted to boreal forest wetlands in and immediately north of Wood Buffalo National Park (WBNP) in Northern Alberta and Northwest Territories, Canada. Loss of breeding habitat was primarily due to conversion of grasslands and wetlands to agriculture production. Historically, the primary wintering areas for whooping cranes included large sections of the Gulf of Mexico coasts between Tamaulipas, Mexico and Louisiana, USA and large expanses of the central Mexican highlands (Allen 1952). The current winter distribution is limited to a small section of Texas coastal salt marshes in and around Aransas and Matagorda Island National Wildlife Refuges.

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Whooping cranes are a wetland dependent species. They inhabit freshwater marshes in the boreal forests of Canada for nesting and feeding, shifting to the Texas coast for wintering where they hold territories on coastal brackish wetlands. During migration, between breeding and wintering grounds, whooping cranes use wetlands of varying conditions as stopover sites for overnight roosting and daytime loafing (Howe 1989; Armbruster 1990; Austin and Reichert 2001). Whooping cranes are primarily carnivorous in both breeding and wintering areas, feeding principally on crustaceans, snails, and other saltwater animals in winter (Hunt and Slack 1989; Chavez-Ramirez 1996; Westwood and Chavez-Ramirez 2005) and freshwater invertebrates and vertebrates on the breeding grounds (Allen 1956; Bergeson et al. 2001). Plant items, especially fruits and grains, are also consumed to varying degrees throughout the year. Grains are an important component of the diet during the fall staging period in Saskatchewan, Canada. Fruits appear to be a more significant component of diets when preferred animal prey items are less available (Chavez-Ramirez 1996).

Climate change has been recognized as one of the primary environmental challenges of the 21st century by many scientists and governments (IPCC 2007; Karl et al. 2009). A growing body of scientific literature continues to document effects of climate change on a variety of plant and animal species (Lovejoy and Hannah 2005; IPCC 2007 and references therein). Climate change predictions suggest overall temperature increases and significant changes in precipitation regimes throughout North America (IPCC 2007; Karl et al. 2009).

Climate changes to date and predicted future scenarios could have significant impacts on species tolerance limits and overall development, in addition to modification that may occur to existing habitat conditions. Shifts in range and distribution of many species of insects, birds, and mammals have already been documented due to warming trends (Parmesan 2005). Temperature increases can have significant implications for many aquatic invertebrate and vertebrate life cycles including more rapid development, longer breeding periods, and delayed diapause (Penuelas and Filella 2001; Bale et al. 2002). Higher temperatures could impact energy expenditure required to maintain homeostasis in birds if it leads to ambient temperatures exceeding upper critical temperatures for the species. For migratory species, whose arrival in different areas may be timed to coincide with abundance of prey species, significant changes in life cycles of prey can lead to a lack of synchronization of predator and prey life histories, with a resulting decline in the species' population (Both et al. 2010).

The whooping crane's small population size, limited distribution, wetland habitat requirements, and twice yearly 4,000 km migration route make them particularly vulnerable to changes in habitat conditions in either breeding grounds,

wintering areas, or throughout the migratory corridor. Climate changes that impact the quantity, timing, and intensity of precipitation events could have significant impacts on the habitat availability and wetland food resources for whooping cranes. Climate change models predict significant changes in precipitation and moisture availability within the distribution of whooping cranes in North America (IPCC 2007; Karl et al. 2009). The life cycles and development of most items in whooping crane diets—crustaceans, aquatic invertebrates, and vertebrates—are significantly influenced by temperature, freshwater conditions, and salinity levels. Therefore, temperature changes and alterations in freshwater inflows could have significant impacts on the life histories and phenology of whooping crane food items. The objective of this work was to explore possible consequences of projected climate change scenarios upon whooping cranes in the different geographical locations of their life cycle. Specifically, we wanted to explore the potential consequences of predicted climate change scenarios on: a) nesting habitat conditions, nesting ecology, and chick survival in the Northwest Territories of Canada; b) wetland habitat conditions and food resources based on predicted changes in coastal rainfall and sea level changes along the Texas coast during winter, and c) changes in conditions within the Central Flyway and the possible effects on stopover site availability and quality during spring and fall migrations.

Methods

We used the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (IPCC 2007) as our primary source for predicted scenarios of climate change conditions in the whooping cranes' distribution range. All values in this paper relating to predicted temperature, precipitation, and sea level changes are based on numbers cited in IPCC (2007), except where noted.

We used conceptual ecological models to highlight the relation between different elements in the environment and whooping crane ecology and natural history (Fig. 1, 2, 3). By using these models we were able to evaluate not only potential direct impacts (tolerance limits) of climate change scenarios to cranes but also potential indirect effects (physical habitat and food resources). For example, while a modest increase in temperatures may not exceed upper critical temperature and therefore not impact whooping crane energetics or tolerance limits, they could have significant effect on growth of blue crab (*Callinectes sapidus*) or other invertebrate prey items, which are important foods. Blue crab growth rates are significantly affected by temperature and salinity levels (Costlow 1967). We considered direct effects those that would impact individual condition of birds such as temperature changes that would reach temperatures above or

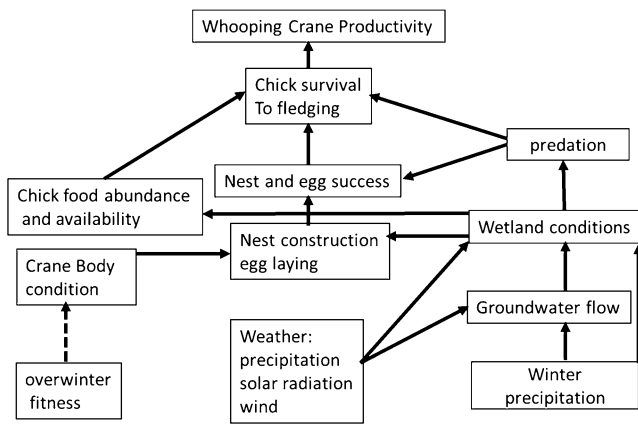


Fig. 1 Conceptual ecological model of whooping crane life history traits and external factors influencing those traits during breeding in Wood Buffalo National Park, Canada

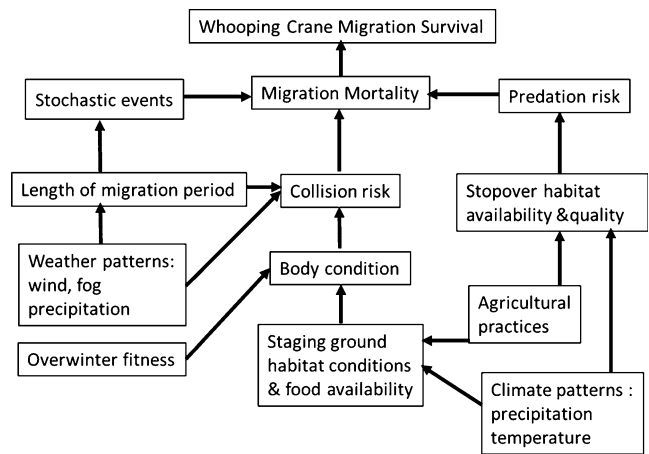


Fig. 3 Conceptual ecological model of whooping crane life history traits and external factors impacting those traits during spring and fall migrations between breeding and wintering grounds

below the crane's thermoneutral zone. Whooping crane upper and lower critical temperatures were previously estimated for adults (Chavez-Ramirez 1996) but are unknown for chicks. In addition, we would consider a change or shift in distribution as a direct impact if it were solely due to a change in tolerance limits. We consider indirect effects those that would influence a physical habitat variable (e.g., changing water levels) or one that impacts abundance and availability of food resources (e.g., changes in development rate of invertebrate larvae due to changes in temperatures).

Future climate change conditions predicted for each of the three distinct geographical locations is presented and explored with respect to potential effects on whooping cranes as described above. Specifically, we explored; a) are distribution and range changes likely to occur; b) will predicted changes exceed whooping crane tolerance limits, particularly temperature; c) are physical features and

characteristics of wetland habitats likely to change and in what direction; and d) what are likely impacts on distribution and abundance of principal food resources.

Results and Discussion

Breeding Grounds

Whooping crane nesting grounds are primarily in the 44,807 km² (17,300 mi²) Wood Buffalo National Park which straddles the border between Alberta and the Northwest Territories, Canada. It lies within the Subhumid Mid-boreal ecoclimatic region, characterized by July mean temperature of 16.3°C, and receives an average of 353 mm of precipitation annually (Timoney et al. 1997; Timoney 1999). The land is usually snow-free by early to mid-May and snow-covered by mid-October (Timoney et al. 1997). Most whooping crane nests in WBNP have been found between 60° and 60.5°N latitude, and 113° and 113.5°W longitude, in a wetland area fed by a groundwater flow system that originates in the Caribou Hills to the southwest (Timoney et al. 1997; Timoney 1999). Wetlands which vary greatly in size, shape and depth, are separated by narrow ridges dominated by an over-story of white spruce (*Picea alauca*), black spruce (*P. mariana*), tamarack (*Larix laricina*), and willows (*Salix* spp.) and an understory of dwarf birch (*Betula glandulosa*), Labrador tea (*Ledum groenlandicum*), bearberry (*Arctostaphylos uva-ursi*), and several species of lichens underlined by *Sphagnum* moss (Novakowski 1966). Whooping crane breeding success oscillates on a cycle, apparently in response to variations in annual precipitation and predation pressure (Boyce et al. 2005; Gil 2006).

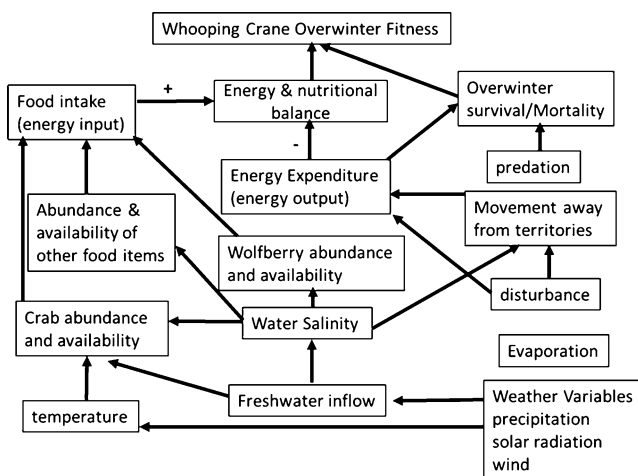


Fig. 2 Conceptual ecological model of whooping crane life history traits and external factors impacting those traits in wintering grounds along the Texas coast

Predicted changes on the breeding grounds include annual temperature increases in North Central Canada by 5°C and as much as 8°C in winter by the end of this Century. The predicted ensemble-mean northern warming varies from more than 7°C in winter (nearly all Atmosphere-Ocean General Circulation Models project a warming exceeding 4°C) to as little as 2°C in summer. Snowmelt is expected to advance by 1–2 weeks, allowing stream flows and thawing of potential whooping crane nesting ponds to occur earlier than at present. Precipitation is expected to increase by 20% overall and by 30% during winter. Precipitation patterns are expected to be more extreme with more precipitation occurring in less days. As temperatures increase there will be an increase in evaporation rates as well, but considering the slight increases predicted for the summer (2°C) when whooping cranes are present, the influence of additional evaporation may not alter the water regime of wetlands to a significant extent.

Direct Impacts

A 2°C to 5°C warming in summer temperature is not likely to exceed whooping crane's higher critical temperature and therefore unlikely to impact thermoregulatory capabilities. Whooping cranes appear to have a wide thermoneutral zone (estimated lower critical temperature (LCT) –13.5°C, Chavez-Ramirez 1996), therefore small changes in ambient temperature should not have significant direct impacts on thermoregulatory energy expenditure of individuals. Upon arrival on breeding grounds, the landscape can be frozen and snow covered. Warmer temperatures should result in less likelihood of cold weather events (those where temperature exceeds the LCT) occurring once the cranes have arrived in breeding grounds, reducing the possibility of exceeding LCT as occurs in some years at present.

Many avian species have shifted distribution ranges northward as a result of warming conditions in temperate regions and others are expected to do so (Review in Crick 2004; Parmesan 2005). This is not expected for whooping cranes. Most whooping crane breeding range was formerly farther south in southern Canada and northern US. In addition, whooping cranes have high cultural inheritance with male whooping cranes tending to establish territories close to their natal territories, reducing the speed and distance of range expansion (Johns et al. 2005).

The predicted pattern of more rain in fewer rainfall events could have significant implications for whooping crane chick survival depending on timing of precipitation events. Heavy rainfall during hatching or first weeks after hatch could lead to chicks drowning or succumbing to health problems. Pneumonia and other respiratory diseases appear in chicks in captive rearing facilities following rainy weather (Olsen and Langenberg 1996) and appear to be a common cause of mortality among chicks exposed to heavy

precipitation or flooding conditions in Cuban sandhill cranes (*Grus canadensis nesiotis*) (Chavez-Ramirez pers. observ). Novakowski (1966) noted that low precipitation on the nesting grounds during the breeding period were most likely to produce good hatch years for whooping cranes.

Indirect Impacts

More precipitation could mean more and higher quality nesting ponds. Water is the primary driver in wetland ecosystem dynamics including plant and animal growth (Weller 1999). Higher water levels are considered indicators of good breeding conditions in WBNP (Boyce et al. 2005; CWS and USFWS 2007), while low water levels are associated with higher levels of depredation of young whooping cranes (Kuyt 1981). Groundwater provides most of the water in this system, so increased winter precipitation and resulting infiltration should not have a negative impact upon the breeding grounds. On a longer-term scale, the encroachment of the cranes' preferred open breeding habitat by taller vegetation is controlled by forest fires occurring on a decadal to centennial recurrence interval (Timoney 1999). In the long term, an increase in moisture may reduce this fire interval, perhaps decreasing suitable breeding habitat for the cranes.

A 1–2 week earlier thawing of frozen wetlands (and higher temperatures) could lead to earlier and greater development of aquatic invertebrates and amphibians. This may be beneficial for cranes as it may mean greater abundance of prey items would be available earlier for adults and may mean greater abundance of prey items during chick rearing period. However, if crane hatching is synchronized to prey life cycles at present, a 1–2 week advance in prey species development may mean that they are less palatable and/or vulnerable to young whooping crane chicks. In the specific case of odonates, a 2-week period in the growth and development of dragonfly nymphs is unlikely to have an effect as the majority of species present have multiyear development cycles (K. Tennessen, pers. comm.). For amphibians it could mean earlier emergence, calling, and abundance in wetlands, which could translate into more potential food resources for whooping cranes. Because little is known about the food habitats of adult or young whooping cranes on the breeding grounds, climate change may cause alterations to their food base that we are unable to assess at present.

Wintering Grounds

Whooping cranes spend 6–7 months between October and April in the salt marshes along the central Texas coastline and around Aransas and Matagorda Island National Wildlife Refuges. This coastal estuary lies between the Texas mainland

and the barrier islands of Matagorda and San Jose Islands. On the mainland side, habitat consists of a gradient from upland grasslands dominated by marsh hay cordgrass (*Spartina patens*) and scrub live oak (*Quercus virginianus*); salt-brackish marsh consists of vegetated flats dominated by glasswort (*Salicornia virginiana*), saltwort (*Batis maritima*), sea oxeye daisy (*Borrchia frutescens*), saltgrass (*Distichlis picata*), wolfberry (*Lycium carolinianum*), and smooth cordgrass (*Spartina alterniflora*); and wind tidal flats dominated by mudflat grass (*Elocharis parvula*), saltgrass, and cordgrass; and open bay (Chavez-Ramirez 1996). On the barrier island side the gradient runs from beach-barrier, salt-brackish marsh, wind tidal flats, and open bay. Changes in sea level and freshwater inflows from the Guadalupe and San Antonio rivers affect the extent, location, and composition of these habitat types (Montagna et al. 2007).

Whooping cranes maintain and defend winter territories in the salt marshes. Here they feed predominantly on blue crabs (Chavez-Ramirez 1996; Westwood and Chavez-Ramirez 2005) in the salt-brackish marsh and wind tidal flats. When blue crabs are not available due to cold water temperatures or high water levels, the cranes switch their diet to wolfberries in the salt-brackish marsh and marine invertebrates such as clams and annelids in the wind tidal flats. While whooping cranes do use these other food resources in the marsh (Hunt and Slack 1989; Westwood and Chavez-Ramirez 2005), and other upland habitats (Chavez-Ramirez et al. 1996), years with low blue crab availability are associated with high winter mortalities (Chavez-Ramirez and Slack 1999; Pugsek et al. 2008).

Minimum winter temperature increases of <1.6 to $>5.5^{\circ}\text{C}$ for southern portion of the USA are predicted. The winter freeze line is therefore likely to move farther north. Precipitation is expected to decrease, leading to drier conditions throughout the region. Total runoff expectations are not consistent among different models (IPCC 2007) with some having significant increases while others predict significant decreases (Karl et al. 2009).

Rising sea levels are an ongoing concern along the Texas coast and are likely to continue into the future. Since 1948, average sea level at the Rockport tidal gauge has risen by 4.6 mm/year, due to a combination of absolute sea level rise and local land subsidence (Montagna et al. 2007; Snay et al. 2007). By combining the rate of local land subsidence with IPCC climate models, the projected relative sea-level rise at Rockport for 2000 to 2100 is estimated at 0.46 to 0.87 m (Montagna et al. 2007). These estimates only reflect sea level rises due to the thermal expansion of Earth's ocean waters. If high latitude temperatures approach levels seen during the last interglacial period (124,000–119,000 years ago), much of the Greenland Ice Sheet and/or the West Antarctic Ice Sheet could disintegrate, each of which would

cause an average sea level rise of up to 5 m (IPCC 2007; Rohling et al. 2008). However, without quantitative information with which to formulate ice sheet models, the fourth IPCC report decided against making any predictions regarding the likelihood of these events occurring by 2100 (Meehl et al. 2007).

Direct Impacts

Warmer winter temperatures would be neutral to positive for whooping cranes' thermoregulation. Currently, low temperatures rarely exceed LCT in winter (Chavez-Ramirez 1996), which would become rarer in future higher temperature scenarios. Whether a more northern freeze line would impact winter distribution is not known. New winter territories are generally established adjacent to existing territories (Stehn and Prieto 2010) so the likelihood of range expansion or shift due to temperature changes alone are not considered likely. Whooping cranes have high winter territory fidelity; one male bird has occupied the same winter territory for the past 30+ years (T. Stehn pers. comm.).

Decreased precipitation in the wintering area may lead to increased water salinities in whooping crane wetland territories. Whooping cranes drink brackish marsh water when salinities are below 20 ppt (parts per thousand). If salinities increase and remain >23 ppt, all whooping cranes must leave their saltmarsh territories and fly to drink freshwater in upland sources leading to increased energy expenditure and potentially greater predation (USFWS reports, pers. Observ.). Most depredation events recorded in reintroduced whooping cranes in Florida were related to cranes spending time in uplands away from wetland habitat.

Indirect Impacts

Higher winter temperatures are likely to be positive for whooping crane prey as well as making them more abundant or available to cranes. Low temperatures ($<17^{\circ}\text{C}$), for example, cause prey (blue crab) to burrow into bottom substrate (Chavez-Ramirez 1996) making them difficult to find, so fewer cold days and higher temperatures would keep blue crabs available for greater periods. Other factors, however, such as high water and crab movements could still influence availability. While warmer temperatures may tend to make crabs more available, they may lead to decreased abundance overall. It has been theorized that the warming temperature of the Gulf of Mexico may be causing a decline in juvenile crab survival (P. Montagna pers. comm.). Abundance of several species of snails and clams could also be affected by temperature, but what the actual effect to overall whooping crane diets may be is unknown.

Warmer temps and northward movement of the freeze line could mean greater and more rapid growth of mangrove along coastal marshes, which are unlikely to benefit whooping cranes. Black mangrove (*Avicennia germinans*) has steadily increased in the last few decades in and around Aransas National Wildlife Refuge (Stehn pers. comm.), with die-offs occurring about once every 10 years due to freezing temperatures. In the Mission-Aransas estuary, black mangrove has increased from 26 ha in the early 20th century to 2,428–3,520 ha in 2007 (Montagna et al. 2007). A northward movement of the winter freeze line could allow this trend to continue. While mangrove forests are biologically rich environments, they are not likely to be used by whooping cranes (Chavez-Ramirez 1996). An added process, that may speed the conversion of saltmarsh to mangrove forest, has been identified in the Mississippi Delta of Louisiana. There, reduced freshwater inflows have been associated with die-offs of the saltmarsh grass *Spartina alterniflora* (McKee et al. 2004). In response, black mangroves quickly invaded much of the newly opened areas (USGS 2004; Perry and Mendelssohn 2009).

Sea level rise will increase the volume of the estuaries by deepening the bays and also increasing the extent of open water. This will most likely lead to an increase in estuary salinities due to increased evaporation, greater inflows of ocean water, and decreases in freshwater inflow due to predicted changes in precipitation (Montagna et al. 2007). Future climate change scenarios may therefore alter the current wintering grounds of the whooping crane to resemble the higher salinity Laguna Madre Estuary (Montagna et al. 2007). Such a shift would have a devastating impact upon blue crabs, the whooping crane's preferred winter food source.

Rising sea levels will decrease the extent of saltmarsh habitat available to wintering whooping cranes. Montagna et al. (2007) plotted the impact of lower and upper sea level rise estimates for Mustang Island, a barrier island just south of Aransas and Matagorda Island National Wildlife Refuges. Even at the lowest projected sea level rise, lateral shifts of 1 to 2 km of bay-side wetland environments will occur (Montagna et al. 2007). At the high end of projected sea level rise, several upland portions of the island will be less than 200 m wide, and much of central Port Aransas, on the north end of the island, will be flooded (Montagna et al. 2007). These lateral shifts of wetlands will reduce the amount of all habitat types on the barrier islands, and most likely increase the rate of saltmarsh erosion, as an increase in the width of Aransas Bay and the extent of deep water will increase fetch, leading to larger waves (Price 2006; USGS 2007). The higher sea level will reduce the relative height of the barrier islands, making them more vulnerable to overwash by tropical storms (Montagna et al. 2007). This has already occurred

in Louisiana, where the Chandeleur Islands were almost completely eliminated by hurricanes Katrina and Rita in 2005 (Fearnley et al. 2009). Based upon current trends, we believe sea level rise will reduce and eventually eliminate the bayside saltmarshes currently found along Texas barrier islands.

In the past, rising sea levels led to the conversion of uplands to saltmarsh habitat (Montagna et al. 2007). It is unknown whether saltmarshes can develop to keep pace with current rates of sea level rise. Such shifts will also be constrained by the seawalls, cultivated fields, industrial development, housing, and roads that dominate much of the central Texas coastline. Given the desirability of living near the coast, shoreline communities will probably try to armor their immediate coastline rather than consider relocating farther inland. These factors will most likely prevent a sufficient amount of upland habitat conversion to compensate for the loss of existing saltmarshes.

In addition to losing overall area of whooping crane habitat, the remaining saltmarshes will change character. In a study of wetland and aquatic habitats on Texas barrier islands, White et al. (2006) found that the area of Matagorda Island, Matagorda Peninsula, and the Colorado River Delta had lost 1,842 ha of tidal flats between 1950s and 2001. Most of this habitat turned into seagrass beds, mangroves, or marsh vegetation (White et al. 2006). However, at water levels >1 m, seagrass beds become unvegetated as insufficient light penetrates to sustain this vegetation type (Montagna et al. 2007). We can expect existing saltmarsh habitats to experience significant changes in their relative abundance.

Migration Period

Beginning in early September and no later than freeze-up in early October, whooping cranes leave their breeding grounds and fly southeast to their fall staging area in the farming landscape of central and southern Saskatchewan (CWS and USFWS 2007). Here the birds spend 2–4 weeks foraging in agriculture fields and roosting in wetlands before continuing their southeastward migration (CWS and USFWS 2007).

Once the birds reach the Canada-USA border, the whooping crane migration corridor consists of a 320 km wide corridor that runs through the central portions of North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas (Austin and Reichert 2001). During migration, whooping cranes migrate during daylight, alighting on wetland areas in late afternoon to dusk where they roost overnight (Austin and Reichert 2001). Except for their extensive use of riverine systems in Nebraska, more than 75% of roost sites are palustrine with seasonal and semipermanent water regimes (Austin and Reichert 2001).

While moving through the USA the cranes tend to fly 400–600 km/day during favorable weather conditions and spending up to a week at a time on the ground when encountering unfavorable winds (Howe 1989; Kuyt 1992).

There are no staging grounds in the USA that equal the importance of south-central Saskatchewan, but several areas, including the central Platte River in Nebraska, Quivira National Wildlife Refuge (NWR) and Cheyenne Bottoms in Kansas, and the Salt Plains NWR in Oklahoma are used frequently enough that they are designated as Critical Habitat by the U. S. Fish and Wildlife Service (CWS and USFWS 2007). The southbound migration ends at the central Texas coast, and can be completed in as little as a week after leaving Saskatchewan (Kuyt 1992). Some birds linger along the way, with the last birds arriving at Aransas NWR as late as mid-December (CWS and USFWS 2007). In spring, birds begin leaving the Aransas area by late March, with most birds gone by 1 May (CWS and USFWS 2007). Spring migration doesn't include any traditional staging areas and is concluded in 2–4 weeks (CWS and USFWS 2007). Despite increasing temperatures recorded during the last few decades along the Great Plains (Karl et al. 2009), evaluation of sightings of migrant whooping cranes in the United States detected no trend in when birds were observed in different states (Austin and Reichert 2001).

The Canadian prairies have warmed at a faster rate than the global average, with their future climate predicted to vary outside the current range of natural variability (IPCC 2007). Warmer and wetter winters are predicted for this region, which may lead to the formation of more seasonal wetlands due to increased runoff from the winter precipitation. Summers will be warmer, leading to increases of the growing season. In the Saskatchewan staging area increased growing season and warmer temperatures are expected to improve the agricultural conditions for much of the region. Corn may become a crop in this area and wheat and barley cultivation may shift farther north but none of the models predict conditions that will eliminate grain farming in this region (Sauchyn et al. 2009). To the south, in the USA, projected warming is forecast to range between 3°C and 5°C. Predictions include precipitation increases by as much as 20% in the northern portions of the Great Plains, the whooping cranes' migratory route in Canada and northern US. Precipitation in the southern half of the US is expected to decrease 5–10% overall. Increased temperature will lead to increased evaporation as warmer climate allow more moisture to be held in the atmosphere. For every 0.5°C rise in temperature, the water holding capacity of the atmosphere increases by about 4%.

Historically, the central Great Plains consisted of grasslands, with a cline from tallgrass prairie in the wetter eastern portions through mixedgrass and then shortgrass prairie in the drier western reaches of the region (Samson

and Knopf 1994). The northern tier of states include portions of the Prairie Pothole Region (PPR), an area of 5–8 million glacially formed wetlands that are filled by winter precipitation and groundwater (Millett et al. 2009). These potholes are extremely sensitive to climate variability, during drought years large portions of this region support few if any wetlands with water (Millett et al. 2009). Beginning with the Rainwater Basin in south-central Nebraska, playa lakes become the primary wetland type in the southern Great Plains (Smith 2003). Less abundant than the potholes of the northern Great Plains, playa wetlands number only in the tens of thousands (Guthery and Bryant 1982; Smith 2003). These intermittent lakes and wetlands are dependent upon precipitation, during drought periods many of them are dry year-round (Smith 2003).

Most of the Great Plains region has been transformed into cropland or pasture, with many of the wetlands drained (Samson and Knopf 1994; Askins et al. 2007). In addition, government policies during the late 19th and early 20th centuries encouraged the settlement of this region, resulting in most of it being in private ownership (Samson and Knopf 1994). The result of these actions is that most whooping crane stopover habitat is on private property (Howe 1989)—more than 60% ($n=695$) of all historic stopover sites (Austin and Reichert 2001).

On a more regional scale, the PPR is expected to experience lower rainfall in its western portion and more rainfall farther east (Millett et al. 2009). In addition, the Great Plains have experienced recurring drought cycles during the last 8,000 years; future droughts are expected and may be exacerbated by climate change (Clark et al. 2002). The implications of the IPCC predictions are that whooping crane stopover habitat may become less common in the future as so many of the wetlands in the Great Plains are intermittent and dependent upon precipitation (Smith 2003). With so much of the region in private ownership, there are limited opportunities for government agencies to provide wetland habitat for whooping cranes and other migratory water birds. Continued existence of wetland habitats will therefore depend upon the willingness of farmers and ranchers to maintain such areas on their property.

Although fall and spring migration only span 9 weeks (17%) of the birds' annual cycle, 60–80% of whooping crane mortality occurs during this time (CWS and USFWS 2007). There are few documented causes of death during migration, but the collisions with power lines has been identified as a major cause of death for young birds (Howe 1989; Lewis et al. 1992). Such collisions are believed to be more common when birds are flying in unfamiliar surroundings during low light conditions, such as after sunset (CWS and USFWS 2007) and decreased availability of roosting wetlands in the future may cause whooping cranes to fly greater distances in lower light conditions.

Possible impact of warming temperatures on departure from wintering grounds does not appear to be an issue. Whooping cranes leave around the same dates consistently year after year so are more likely to be using photoperiod rather than temperature as a migratory initiation cue. It is not known if delayed snow cover dates (currently by mid-October) in fall on breeding grounds will delay movement of whooping cranes to the staging area in Saskatchewan. Also, initiation of movement from staging areas southward is not likely to be influenced by temperature shifts as it has been consistent in the past, so likely based on photoperiod. As mentioned previously evaluation of sightings of migrant whooping cranes in the United States detected no trend in when birds were observed in different states over the past five decades (Austin and Reichert 2001).

Conclusions

Whooping crane recovery will require significant population increases via high survival, greater reproductive output, and reduced mortality rates. As a migratory species whose breeding and wintering range are at temperate latitudes, the species will be exposed to significant alterations in its habitat conditions in all areas of its life cycle. At the individual level it appears that overall temperature changes should have little to no effects on thermoregulation and overall energy expenditure for whooping cranes. Instead, it appears that predicted climate change scenarios will alter habitat conditions and modify habitat quality to varying degrees in different areas. Overall predicted climate change scenarios are likely to have mixed results for whooping cranes in different area of its range.

The predicted climate change scenarios in breeding grounds are likely to be positive overall in regards to potential increases in habitat conditions for nesting sites and food availability. However, two elements of predicted climate change scenarios in this region could have significant negative impacts. One issue is whether more rainfall occurs during the summer months in more extreme events. Large rainfall events during, and shortly after hatching, could lead to chick mortality via drowning and pneumonia. Increased precipitation overall could reduce fire frequency and result in increased woody plant cover which may reduce overall nesting habitat quality. However, the net effect of this change for overall reproductive output is unknown.

Significant changes are expected throughout the Great Plains regions where whooping cranes migrate during spring and fall, in regards to rainfall pattern and quantity. It appears that no negative impacts will result from warming in the staging area in Saskatchewan unless warmer temperatures and longer growing season alter the types of crops to those that may not serve as food for

whooping cranes. The predicted decreased rainfall in most of the Great Plains could lead to stopover wetlands being less available for migrating whooping cranes. It is believed that less stopover wetlands and therefore increased movement of cranes may lead to greater mortality in migration. However, as how and where most migration mortality occurs on migration is unknown we cannot predict actual effects of decreased stopover wetlands. The limited number of protected areas for whooping cranes is a concern as most stopover sites are on private lands, where conservation and management actions may not be as likely or possible as on protected areas.

In the wintering grounds some elements of food resources may be enhanced based on predicted temperature changes alone. However, warmer temperatures and more northern freeze line can also impact habitat quality via invasion of black mangrove and other species. Habitat area is likely to be greatly impacted by sea level rises as described above. Habitat alterations due to climate change alone are only one aspect of concern for long-term survival of the whooping crane. Human development has been and continues to be a concern in the wintering grounds where housing developments continue and more are planned for large areas of the coastal zone of Texas. The area currently available for whooping crane expansion contiguous with the current range is limited, estimated to support no more than 142 total nesting pairs (Stehn and Prieto 2010). The total area of brackish marsh would be further reduced by human development and expected sea level rises that are occurring throughout the coastal zone in and around the whooping crane winter distribution.

It is not clear whether predicted climate changes would exacerbate or limit the amount of human development in Texas coastal areas or change land use patterns in the Great Plains. What is clear, based on expected climate change scenarios and current human development, is that recovery targets for whooping cranes will be compromised if no preemptive actions are taken to alleviate future expected problems. Actions are required to protect whooping cranes not only within the limits of national wildlife refuges and national parks where they are already protected, but throughout the species complete current distribution and in consideration of future scenarios. Because protected area systems are designed to address current stable climate conditions for biodiversity protection they should be reevaluated in light of current knowledge and future expectations. This is particularly true in regards to whooping cranes whose increasing population is no longer limited to present day protected area boundaries, particularly during migrations.

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