



# Long-term migratory alterations to whooping crane arrival and departure on the wintering and staging grounds

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**ABSTRACT:** Climate change can result in alterations to avian behavior, particularly in migratory species. We assessed long-term changes in the endangered whooping crane *Grus americana* migration phenology in response to temperature, precipitation, and other determinants of migratory behavior. We modeled timing of abundance peaks on the Texas wintering grounds as a function of date and year. During spring and fall migration in central Saskatchewan, we modeled timing of earliest and latest observations, and period of occurrence between them, as a function of year, weather, and wheat production. During winters 1950–2010, the peak abundance period ( $\geq 90\%$  of population) shortened. In winter 1950–1951, the peak was 28 November–12 March, but by winter 2010–2011, it was 18 December–20 February. We predict it will shrink to 2 January–6 February by winter 2035–2036. During fall migration 1972–2021, the period of occurrence in central Saskatchewan lengthened by 20.3 d. In 1971, cranes arrived by 16 September and departed by 17 October, but by 2021 they arrived 12 d earlier (4 September) and departed 17 d later (3 November). We predict a lengthened period of occurrence of 63.8 d by fall 2035 (arrival by 1 September, departure by 8 November). During spring migration 1979–2021, there were no trends in migration phenology (mean period of occurrence was 32 d). Alterations in migration phenology may require modified conservation approaches and consideration of new conservation opportunities. For example, these changes may reduce time cranes spend on the wintering grounds, requiring greater investment in stopover areas.

**KEY WORDS:** Agriculture · Chronology · Climate change · Drought · *Grus americana* · Phenology · Saskatchewan · Temperature · Texas

## 1. INTRODUCTION

Climate change is affecting the life history traits of many wildlife taxa (Isaac 2009, Robinson et al. 2009), and alterations in migration phenology have been documented as a response to climate change (Butler 2003, Robinson et al. 2009). Changes in the timing of migration arrival and departure are of conservation concern, because it can result in mistimed migration schedules with resource availability, molting patterns,

and breeding activities (Hedenström et al. 2007). Changes in migration phenology may often be attributed to climate change, but it can occur for other reasons as well (e.g. changes in land use patterns, trends in abundance, habitat enhancements; Shanni et al. 2018, Koleček et al. 2020). Cranes, family Gruidae, are one of the most endangered bird families, with more than a third of the world's species considered vulnerable to extinction (Johnsgard 1983). For populations of threatened and endangered species, changes in

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their migration phenology can exacerbate extinction risks for vulnerable wildlife species.

One endangered crane species (Canadian Wildlife Service [CWS] & US Fish and Wildlife Service [USFWS] 2007, BirdLife International 2020), the whooping crane *Grus americana*, has an increased extinction risk due to the effects of climate change on juvenile recruitment (Butler et al. 2017). This increase in extinction risk is due to changes in temperature and precipitation regimes at northern latitudes (Butler et al. 2017). However, changes in climate may be influencing other life history traits at other latitudes as well (e.g. food availability, woody species encroachment, wetland availability; Chavez-Ramirez & Wehtje 2012). For example, changes in migration phenology have been observed for Eurasian cranes *G. grus* (Hansbauer et al. 2014), sandhill cranes *Antigone canadensis* (Swanson & Palmer 2009, Harner et al. 2015), and whooping cranes (Jorgensen & Brown 2017), with migration occurring later in the autumn and earlier in the spring. Jorgensen & Brown (2017) examined whooping crane sighting records from 1942–2016 across the US Great Plains states (North Dakota, South Dakota, Nebraska, Kansas, and Oklahoma), and concluded that migration is occurring approximately 21 d later in the autumn and approximately 22 d earlier in the spring.

We used data from long-term monitoring of whooping cranes collected on the wintering grounds in Texas (1950–2010) and on the migratory staging grounds in central Saskatchewan (1971–2021) to examine arrival and departure dates by year in each location. In each case, our objective was to determine if arrival and departure dates changed during the respective 60 or 50 yr periods that whooping cranes were monitored over winter and during migration. On the wintering grounds, we estimated peak abundance date and delay and advancement of arrival and departure dates. During spring and fall on the migratory staging grounds, we used dates of earliest and latest observations to determine if there were trends in arrival date, departure date, or period of occupancy in central Saskatchewan. We discuss implications of changes in migration phenology for ecology and conservation of whooping cranes.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Whooping cranes exist in 1 wild, migratory population; 3 introduced populations; and a captive flock

(French et al. 2019). The wild, migratory population is known as the Aransas–Wood Buffalo population and is the only natural, self-sustaining population. It overwinters along the Gulf of Mexico centered on Aransas National Wildlife Refuge (NWR), Texas, USA, and breeds in and around Wood Buffalo National Park, Alberta, and Northwest Territories, Canada (Canadian Wildlife Service [CWS] & US Fish and Wildlife Service [USFWS] 2007).

The whooping crane's ~4000 km migration leads south–southeast from the southern Northwest Territories through northern Alberta into central Saskatchewan, then continues to the USA–Canada border. From there it leads south from western North Dakota through South Dakota, Nebraska, Kansas, and Oklahoma into central Texas and ends on the gulf coast of Texas. Generally, whooping cranes start arriving on their wintering grounds as early as October and depart as late as May (Johnsgard 1983, Butler et al. 2017). Whooping cranes overwinter in coastal areas on and around Aransas NWR and primarily use coastal saltmarshes, tidal flats, and shallow bay edges (CWS & USFWS 2007). Areas in central Saskatchewan serve as a migratory staging area for resting and refueling during the southward fall migration (Johns et al. 1997), where individual whooping cranes may spend up to 11 wk (range = 0–78 d, mean = 26 d, SD = 19 d; Pearse et al. 2020b, A. Pearse, pers. comm.) before continuing to southern Texas. This area has long been recognized as containing the most important fall staging grounds (Johns 1992) and is where individual whooping cranes have the longest fall residency times throughout the migratory corridor (Pearse et al. 2020b). Spring migration occurs over a shorter time period (2–4 wk) than fall migration, but the staging area in central Saskatchewan receives use during spring migration as well (CWS & USFWS 2007, Chavez-Ramirez & Wehtje 2012, Pearse et al. 2020b). The breeding grounds are remote and inaccessible, and therefore, no long-term data exists on arrival and departure from migration at its northern terminus.

### 2.2. Wintering grounds in Texas

During winter, the Aransas–Wood Buffalo population of whooping cranes (all age and sex classes) was monitored with repeated aerial surveys from October–May of each year beginning in winter 1950–1951 (Stehn & Taylor 2008, Butler et al. 2016, Strobel & Butler 2019) to winter 2010–2011, after which time efforts were redesigned and consolidated into a 2 wk period each winter (Butler et al. 2016, Strobel & Butler 2019).

During those surveys, data were recorded on paper maps. Those data were digitized and archived by Taylor et al. (2015). We summarized those data as the number of whooping cranes counted on each survey date, determined the maximum number counted each winter, and estimated the proportion of the population on the wintering grounds for each survey date (i.e. count/maximum). Surveys were conducted between 9 October and 24 May. We converted dates to days where 9 October was Day 0 for each winter.

We modeled the proportion of the population present on each survey date as a function of day and survey year. Day was treated as a quadratic effect. We scaled variables so model convergence was easier to achieve ( $(\text{Year} - 1950)/10$  and  $\text{Day}/100$ ). We modeled the proportion (count/maximum) using a generalized linear mixed-effects model with the binomial family and logit link (logistic regression; Zuur et al. 2009). Random intercepts for each year were estimated to account for dependencies among subsamples within each year. We analyzed the data with the program R (R Core Team 2022) and the `glmer` function, which was available in the `lme4` package (Bates et al. 2015). We estimated the peak abundance date from the model. We used the model to predict the date on which 50% and 90% of the population had arrived and the date on which 50% and 10% of the population had departed the wintering grounds.

We examined the relationships between arrival and departure dates and mean temperature and a drought index using logistic regression. Data were divided such that surveys conducted on or before the peak abundance date (i.e. 19 January or Day 102) were used in the arrival analysis and data for surveys conducted after that date were used in the departure analysis. The drought index we used was the Palmer hydrological drought index (PHDI), because it is an indicator of long-term moisture supply and was an important indicator of winter loss of whooping cranes and their habitat use (Butler et al. 2014). Mean monthly temperature data were from Aransas County and drought data were from Texas Climatological Division 7 (<https://www1.ncdc.noaa.gov/pub/data/cirs/climdiv/>). We used measurements from November in the arrival analysis and February measurements in the departure analysis. These months mark the beginning of arrival and departure. The proportion of the population present on each survey date was modeled as a function of day, temperature, and drought. The best combination of these variables was determined with Akaike's information criterion adjusted for small sample size ( $AIC_c$ ; Burnham & Anderson 2002).

### 2.3. Migratory staging grounds in central Saskatchewan

During spring and fall migration, a campaign to compile observations of whooping cranes (all age and sex classes are observed but cannot be distinguished in the field) in central Saskatchewan has been conducted since 1940. Coordination and data management of this work was assumed in 1977 by the CWS. Data were obtained from biologists during ground-based surveys, volunteers and landowners, and employees of provincial wildlife and other agencies (Johns 1992). The purpose of the surveys and data compilation is to identify and evaluate specific roosting and feeding sites within staging areas in central Saskatchewan to protect critical migratory habitat used by whooping cranes.

We summarized the CWS database by identifying the earliest and latest observation of whooping cranes at the sites most reliably used by cranes which are within 125 km of Saskatoon, Saskatchewan in the spring (March–May) and fall (September–November) migratory seasons of each year since 1979 and 1971, respectively. Years prior to these cutoffs had sparse data. We used these earliest and latest observations as proxies for arrival and departure of whooping cranes, defining the interval between them as their period of occurrence (in days) in central Saskatchewan.

For spring and fall, we examined if there was a trend of increasing or decreasing earliest observation date (arrival), latest observation date (departure), or period of occurrence over the 42 yr interval from 1979 to 2021 (spring) and the 50 yr interval from 1971 to 2021 (fall). We conducted analyses for each migratory season by examining the univariate relationships between earliest observation, latest observation and period of occupancy (3 dependent variables) and survey year (1 independent variable) using linear regression, modeling each dependent variable as linear and quadratic functions of year. For the latest fall observation (fall departure), we also included temperature, precipitation, and cereal crop production on the staging grounds as covariables. We used average October precipitation and temperature obtained from 13 Global Historical Climatology Network (GHCN) stations located across the southern Saskatchewan prairies (i.e. North Battleford: CA004045605 and CA004045600, North Battleford RCS: CA004045607, Yellow Grass: CA004019040, Prince Albert Airport: CA004056240, Regina RCS: CA004016699, Regina University: CA004016640, Waseca: CA004048520, Saskatoon Airport: CA004057120, Meadow Lake Airport:

CA004065060, Meadow Lake Auto8: CA004065058, Estevan Airport: CA004012400, and Muenster: CA004015440; National Centers for Environmental Information [NCEI] 2023). We used total production of wheat (metric tons [t]) beginning in 1976 from Saskatchewan's small area data regions 11, 12, 15 and 16 (Statistics Canada 2023). For the earliest fall observation (fall arrival), we also included temperature and precipitation from the breeding grounds in August. They were based on 4 GHCN stations (Hay River A: CA002202400, Hay River Climate: CA002202402, Fort Smith A: CA002202200, and Fort Smith Climate: CA002202202; NCEI 2023). For the fall period of occurrence on the staging grounds, we examined models containing October temperature and precipitation. Models were fit using the lm function of the program R (R Core Team 2022) and best-supported models identified using AIC<sub>c</sub> (Burnham & Anderson 2002).

### 3. RESULTS

#### 3.1. Wintering grounds in Texas

The Aransas–Wood Buffalo population of whooping cranes comprised 31 birds in winter 1950–1951 and increased to 283 in winter 2010–2011 (Butler et al. 2013). The winter survey data from 1950–2010 contained 38 332 observations of whooping crane groups from 1420 survey days (Taylor et al. 2015). The number of days that surveys were conducted each winter ranged from 5 to 47 (mean = 23.3 d, SD = 8.8 d). The parameter estimates for the model of the proportion of the population present were intercept =  $-2.01$  (SE = 0.13), survey year =  $-0.16$  (SE = 0.04), day = 11.21 (SE = 0.07), and day<sup>2</sup> =  $-5.49$  (SE = 0.03). The model that indicated peak abundance typically occurred on 19 January, and the duration of time spent on the wintering grounds has declined over the last 60 yr (Fig. 1).

In winter 1950–1951, 50% of whooping cranes arrived on the wintering ground by 29 October and remained until 11 April. However, in winter 2010–2011, 50% did not arrive until 10 November and only remained until 31 March. This is a change of approximately 12 d. By winter 2035–2036, the model predicts that the period with

$\geq 50\%$  of the population will shrink to 15 November–25 March. In winter 1950–1951, 90% of whooping cranes arrived on the wintering ground by 28 November and remained until 12 March. However, in winter 2010–2011, 90% did not arrive until 18 December and only remained until 20 February. This is a change of 20 d. By winter 2035–2036, the model predicts that the period with  $\geq 90\%$  of the population will shrink to 2 January–6 February (~5 wk).

For the arrival data, the proportion of the population on the wintering grounds increased with day ( $\beta = 0.05$ , SE = 0.001) and decreased as mean November temperature increased ( $\beta = -0.07$ , SE = 0.01; Fig. 2A). Mean temperature has increased approximately 1.9°C in November ( $\beta = 0.03$ , SE = 0.01,  $p = 0.02$ ) over the 60 yr study period (Fig. 2B). No trend in the PHDI was apparent in November ( $\beta = 0.02$ , SE = 0.02,  $p = 0.31$ ) over the 60 yr study period.

For the winter departure data, the proportion of the population on the wintering grounds decreased with day ( $\beta = -5.39$ , SE = 0.05). As mean February temperature increased, the proportion of the population on the wintering grounds decreased ( $\beta = -0.08$ , SE = 0.04; Fig. 3A). Mean temperature has increased approximately 1.4°C in February ( $\beta = 0.02$ , SE = 0.01,  $p = 0.10$ ) over the 60 yr study period (Fig. 3B). Less of the population remained on the wintering grounds as drought conditions worsened ( $\beta = 0.05$ , SE = 0.03; Fig. 4A). No trend in the February PHDI was apparent ( $\beta = 0.02$ , SE = 0.02,  $p = 0.30$ ) over the 60 yr study period (Fig. 4B).

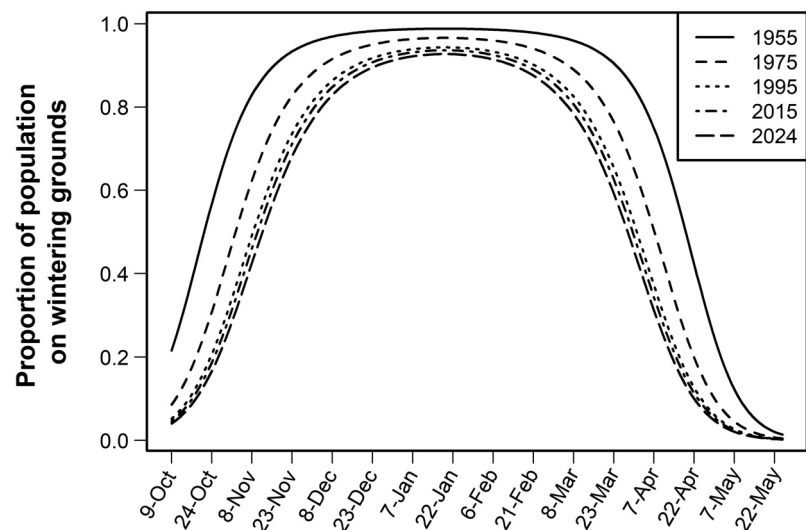


Fig. 1. Predicted changes in whooping crane migration phenology as indicated by the proportion of the population occurring on the wintering grounds along the Texas coast, USA. Model based on whooping crane aerial surveys conducted from 1950–2010

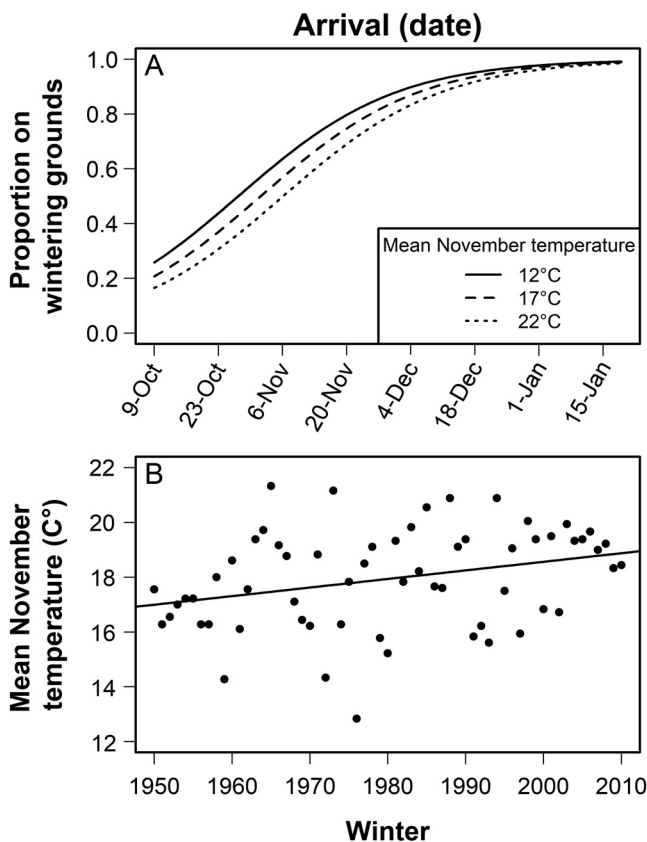


Fig. 2. (A) Relationships between proportion of whooping crane population on the wintering grounds during the arrival period (9 October–19 January) and mean temperature in November for Aransas County, Texas, USA. (B) Trend in Aransas County mean November temperature from winter 1950–1951 through winter 2010–2011

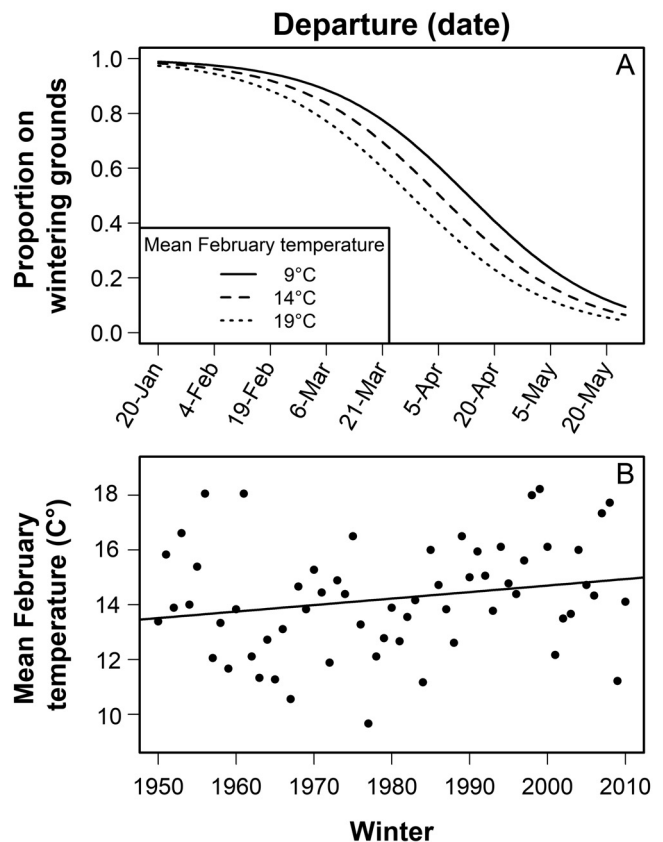


Fig. 3. (A) Relationships between proportion of whooping crane population on the wintering grounds during the departure period (20 January–24 May) and mean temperature in February for Aransas County, Texas, USA. Drought conditions were held constant at normal moisture (Palmer hydrological drought index = 0). (B) Trend in Aransas County mean February temperature from winter 1950–1951 through winter 2010–2011

### 3.2. Migratory staging grounds in central Saskatchewan

For spring migration in central Saskatchewan, there were no trends for arrival ( $\beta = -0.06$ ,  $SE = 0.10$ ,  $p = 0.57$ ; Fig. 5A), departure ( $\beta = -0.04$ ,  $SE = 0.14$ ,  $p = 0.76$ ; Fig. 5A) or period of occupancy ( $\beta = 0.02$ ,  $SE = 0.18$ ,  $p = 0.93$ ) over the 42 yr interval from 1979–2021. During that interval, the mean arrival and departure dates in spring were 10 April ( $SD = 8.0$  d) and 11 May ( $SD = 10.6$  d), respectively, with a 32 d period of occurrence. In fall migration in central Saskatchewan, the best model for arrival indicated a linear trend for earlier arrivals ( $\beta = -0.23$ ,  $SE = 0.08$ ,  $p = 0.005$ ; Fig. 5B). The best model for departure indicated a linear trend for later departures ( $\beta = 0.35$ ,  $SE = 0.10$ ,  $p = 0.001$ ; Fig. 5B), with delays increasing as average temperature increased ( $\beta = 1.46$ ,  $SE = 0.78$ ,  $p = 0.066$ ). This resulted in an increasing period

of occurrence in fall ( $\beta = 0.43$ ,  $SE = 0.10$ ,  $p < 0.001$ ) over the 50 yr interval from 1971–2021, with the period of occurrence increasing as temperature increased ( $\beta = 2.19$ ,  $SE = 0.77$ ,  $p = 0.007$ ). Fall departure was not associated with wheat production ( $\beta = -3.37 \times 10^{-6}$ ,  $SE = 2.26 \times 10^{-6}$ ,  $p = 0.143$ ).

The arrival and departure models suggested that in 1971, whooping cranes arrived in central Saskatchewan by 16 September and departed by October 17, but by 2021 they were arriving 12 d earlier, by 4 September, and departing 17 d later, by 3 November. The period of occurrence in central Saskatchewan during fall increased from 36.3 d in 1971 to 57.8 d in 2021 (an increase of 21.5 d over the 50 yr period). By fall 2035, the models predict that the period of occurrence will increase to 63.8 d, with birds arriving by 1 September and departing by 8 November.

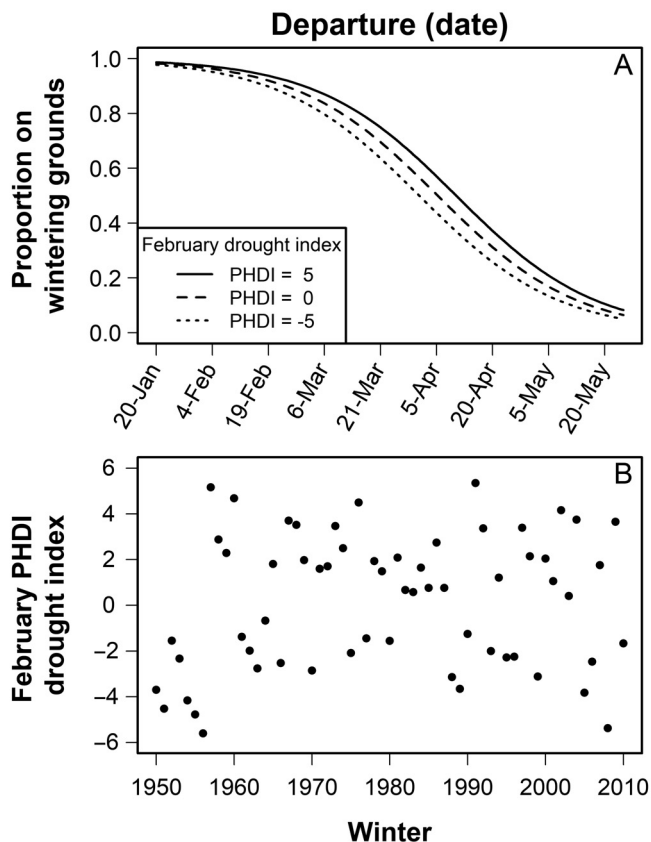


Fig. 4. (A) Relationships between proportion of whooping crane population on the wintering grounds during the departure period (20 January–24 May) and the Palmer hydrological drought index (PHDI) in February for Aransas County, Texas, USA. Negative PHDI values are indicative of drought, 0 is normal moisture, and positive values are above normal moisture. Temperature was held constant at 14°C. (B) No trend was observed in Aransas County February PHDI from winter 1950–1951 through winter 2010–2011

#### 4. DISCUSSION

Our results suggest that whooping cranes, on average, are arriving later at the wintering grounds and leaving them earlier. Arrival of 50% of the population occurred approximately 13 d later in 2010 than it did in 1950. Arrival of 90% has been delayed approximately 20 d. During fall migration, there is a trend of whooping cranes arriving earlier in central Saskatchewan and departing later, resulting in a period of occurrence that is now about 20 d longer than at the beginning of the 50 yr period we studied. We observed no such trends during spring in Saskatchewan. Similar delays have been documented for whooping cranes (~22 d) during fall migration at stopover locations across the US Great Plains (Jorgensen & Brown 2017). Eurasian cranes have shifted spring migration

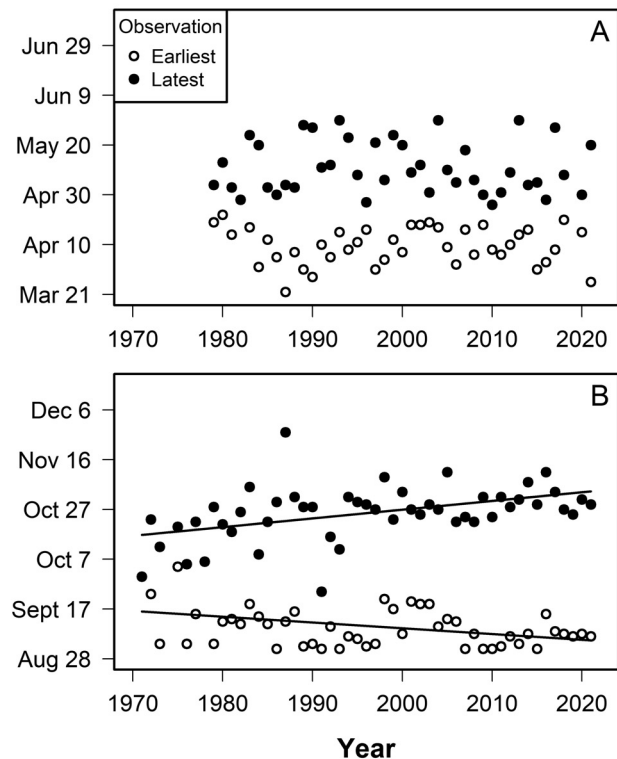


Fig. 5. Earliest and latest detections of whooping cranes in central Saskatchewan, Canada during (A) spring migration, 1979–2021, and (B) fall migration, 1971–2021. Lines represent predictions of best-supported linear models with temperature held constant at the mean (4.1°C)

approximately 18 d earlier in Estonia (Hansbauer et al. 2014) and 20 d earlier in the fall in Israel (Shanni et al. 2018). Also, sandhill crane spring arrival dates are approximately 0.7 d earlier each year based on the finding of Swanson & Palmer (2009).

Trends in changing migration phenology can be driven by many factors. Such factors may include climate change, changes in population size and structure through time, habitat enhancements, and changes in land use patterns (e.g. Shanni et al. 2018, Koleček et al. 2020). For example, Eurasian cranes started using the Hula Valley of northeastern Israel after creation of a shallow wetland, establishment of a feeding program, and changes in agricultural practices in the valley, and habitat lost on their traditional wintering grounds in Ethiopia (Shanni et al. 2018). Changes other than habitat or climatic conditions may explain some changes in migration phenology as well.

For example, during times of abundance for a species, changes in migration phenology may be more easily detected, allowing arrival to be detected earlier than in times of lower abundance (Koleček et al. 2020). However, the reverse would be true too, allow-

ing departure to be detected later in times of greater abundance. If changes in detection due to abundance were the cause of the changes in migration phenology that we observed, we would expect earlier arrivals and later departures. We observed earlier arrivals and later departures dates on the migratory staging grounds in central Saskatchewan during fall, but we did not observe that pattern on the wintering grounds on the coast.

Other characteristics of the population's structure might affect changes in migration phenology as well. For example, Kuyt (1992) noted that subadults tended to leave the breeding grounds approximately 17 d earlier than adults ( $n = 10$ ). Telemetry data from 2010–2017 (Pearse et al. 2020a) suggested subadults ( $n = 19$ ) arrive on the wintering grounds only 5.5 d (95% CI = 1.4–9.7 d) before adults ( $n = 34$ ). We observed arrival dates changing on the wintering and staging grounds by 13–20 d, more than the differences observed between adult and subadult migration, though changes in the age structure of the population could have contributed to variation in migration phenology.

Alterations in migration phenology have been documented in many taxa and are often considered a response to climate change (Butler 2003, Isaac 2009, Robinson et al. 2009, Swanson & Palmer 2009). Our results for winter suggested that arrival is delayed, and departure occurs earlier as temperatures rise. On the staging grounds in central Saskatchewan, we observed delayed departure and longer periods of occurrence with increased temperatures in the fall. Warmer fall temperatures probably caused wetlands to remain unfrozen for a longer period, allowing cranes to extend their period of occupancy in order to take advantage of abundant food resources. This relationship has been observed for sandhill cranes in Minnesota, USA (Swanson & Palmer 2009); whooping cranes in the US Great Plains states during spring (Jorgensen & Brown 2017); pink-footed geese *Anser brachyrhynchus* in western Europe during spring (Bauer et al. 2008); multiple species of ducks and geese (Anseriformes) in Manitoba, Canada, during spring (Murphy-Klassen et al. 2005); and white storks *Ciconia ciconia* during autumn and spring migration in Spain (Gordo & Sanz 2006). White storks also arrive earlier to the breeding grounds in Slovakia during years with warmer temperatures (Gordo et al. 2013).

Precipitation and drought affect migration as well. For whooping cranes, we found that departure from the wintering grounds occurred earlier as drought conditions worsened. Drought conditions on the wintering grounds may limit food availability, requiring

whooping cranes to seek food resources further inland (Wright et al. 2014). This may allow new wintering areas to be established outside of the traditional wintering grounds along the coast (Butler et al. 2022, 2023). Similar relationships have been observed for other species. For example, during dry years in the Sahel region of Africa, common cuckoo *Cuculus canorus*, common swift *Apus apus*, barn swallow *Hirundo rustica*, and common nightingale *Luscinia megarhynchos* had later arrivals, and barn swallow had earlier departures (Gordo & Sanz 2006). American redstarts *Setophaga ruticilla* depart wintering grounds earlier in Jamaica during years with less precipitation (Studds & Marra 2011). However, timing of migration appears to be modified by the local environmental conditions surrounding an individual animal (Studds & Marra 2011).

Changes in precipitation regimes due to climate change have been implicated in increased extinction risk for whooping cranes. Butler et al. (2017) found that changes in precipitation on the breeding grounds and northern portions of the migratory route resulted in reduced juvenile whooping crane recruitment, which could result in declining populations. Alterations in migration phenology due to climate change may affect other aspects of whooping crane ecology and conservation as well. For example, it could result in decreased migration distances, more time using stopover areas during migration; mistimed migration with food availability, other habitat resources, or weather events; and a smaller window of time for monitoring abundance on the wintering grounds.

Visser et al. (2009) found shorter migration distances over time for 12 bird species in northwestern Europe. They found migration distance was inversely related to winter temperature, and therefore, decreases in migration distances a consequence of climate change. Recently some whooping cranes have been observed overwintering further inland (e.g. short-stopping; Wright et al. 2014). Historically, overwintering whooping cranes have been confined to an area < 1000 km<sup>2</sup> in and around Aransas NWR. Increased geographic range during winter would reduce the population's vulnerability to stochastic catastrophic events like disease, hurricanes, or chemical spills (Wright et al. 2014). Also, it could expose individuals to greater mortality risks not currently encountered or encountered at lower rates on the wintering grounds. Traditionally, conservation practitioners have focused on protection and creation of habitat in coastal areas near current wintering grounds (Metzger et al. 2020). However, future expansion of the geographic range during winter requires broadening the scope of conservation activities on the wintering grounds. For example, pro-

tection and enhancement of non-traditional habitats used by wintering whooping cranes and education of hunters in areas newly frequented by whooping cranes will be necessary. If short-stopping at migratory stop-over locations allows whooping cranes to overwinter in areas within the migratory corridor, conservation focus may need to change to development and implementation of planning tools that inform land use activities (e.g. Boggie et al. 2023).

Across the US Great Plains states, Jorgensen & Brown (2017) found no evidence that stopover duration was increasing through time during autumn or spring even though winter arrival and departure dates were changing. In contrast, our results indicate that during fall migration, whooping cranes have occurred in central Saskatchewan for a longer period of time over the 50 yr interval we studied. Migration can be energetically costly, requiring whooping cranes to acquire resources at stopover sites (Pearse & Selbo 2012). Central Saskatchewan provides an important combination of high densities of semi-permanent and permanent wetlands used for roosting in close proximity to croplands used for feeding (Johns et al. 1997). As agricultural conditions improve in Saskatchewan with increased growing season and warmer temperatures (Sauchyn et al. 2009), the region may become more important as stopover habitat for whooping cranes seeking food resources provided by some types of agricultural crops (Chavez-Ramirez & Wehtje 2012). Wheat and other cereal grains are abundant in central Saskatchewan ( $3\,135\,344 \pm 662\,077$  t wheat  $\text{yr}^{-1}$  [mean  $\pm$  SD] produced 2012–2021; Statistics Canada 2023); and cranes forage on waste cereals after harvest. We did not observe a relationship between departure date and wheat production, probably because wheat is very abundant relative to the small whooping crane population size, so cranes are not limited by it. However, changes in cropping patterns at local scales have caused observed declines in occurrence and abundance of whooping cranes where production of oilseeds is predominant (M. T. Bidwell unpubl. data), likely due to the preference of whooping cranes to feed in cereal crop fields (Johns et al. 1997). More widespread conversion from production of cereal grains to oilseeds (Carlyle 2002) may have negative consequences for whooping cranes, potentially resulting in local declines in abundance on historically important staging grounds. Negative responses to changes in agricultural practices, including shifts in crop type, have been demonstrated for Eurasian cranes in Germany, sandhill cranes in the southwestern United States, and red-crowned cranes *Grus japonensis* in Korea (Ilyashenko & King 2018).

In spring, we observed no trend for whooping cranes arriving earlier in central Saskatchewan during the 42 yr interval we studied, as might be expected given their earlier departure from the wintering grounds we report here. Instead, whooping cranes may be spending more time further south in the migratory corridor, although no such trends for longer occurrence during spring migration were observed by Jorgensen & Brown (2017). However, a trend for a longer spring occurrence period in central Saskatchewan may have gone undetected given the relatively short residency times of individual cranes there in spring (Pearse et al. 2020b). Alternatively, whooping cranes could be tending to fly over central Saskatchewan in spring to arrive earlier on the breeding grounds, but data to test these hypotheses do not exist over the 42 yr interval we studied.

A primary consequence of changes in whooping crane migration phenology may be timing and length of stopover habitat use. If migration is mistimed with food, other habitat resources (e.g. water levels in wetlands), or weather events, whooping crane population dynamics could be affected (Møller et al. 2008, Robinson et al. 2009, Miller-Rushing et al. 2010). For example, Jorgensen & Brown (2017) noted that earlier spring and later autumn migration could subject whooping cranes to increased chances of encountering storms and blizzards. Butler et al. (2017) found that, as precipitation during autumn migration in the northern US Great Plains states increased, whooping crane recruitment declined. They hypothesized that inclement weather reduces foraging activity and increases juvenile mortality risk (Clark 2009). Alternatively, increasing length of stopovers could help mitigate winter habitat losses that may occur due to sea level rise in the future (Metzger et al. 2020).

For some bird species, feather molt could become mistimed as weather phenology changes (Gordo 2007, Hedenström et al. 2007). However, the timing of molting for whooping cranes should not create mismatches, because flight-feather replacement occurs on the breeding grounds starting in June (Urbanek & Lewis 2015). A food resource of whooping cranes on the wintering grounds is wolfberry *Lycium carolinianum* fruit (Hunt & Slack 1989). Wolfberry fruit production typically peaks in November (Butzler & Davis 2006), though its phenology appears to be driven in part by temperature and salinity (Wozniak et al. 2012). With whooping cranes arriving to the wintering ground later, this food source may become less available when whooping cranes occur on the wintering grounds, though other food sources may compensate for its lower availability.



Since winter 2011–2012, USFWS has conducted aerial surveys of wintering whooping cranes with spatially explicit distance sampling during an approximate 2 wk period, to monitor change in population size (Strobel & Butler 2019). The protocol used by USFWS called for surveys during mid-December (Butler et al. 2016). However, over the last few years it has become evident that all whooping cranes had not arrived on the wintering grounds until later, which prompted moving the surveys to late January through early February (Butler & Harrell 2018). As the peak abundance period (>90% of the population) on the wintering grounds shrinks from >15 wk to approximately 5 wk, it may be necessary to conduct surveys more intensively within a narrower window, if winter surveys are to remain an effective tool for estimation of population size of this endangered species.

Whooping crane conservation has been a success over the last century, resulting in the Aransas–Wood Buffalo population expanding from 16 birds in winter 1941–1942 to 543 (95% CI = 426–781) in winter 2021–2022 (Butler et al. 2013, 2022). However, alterations in migration phenology due to climate and habitat changes may require new thinking and innovations in population management (Chavez-Ramirez & Wehtje 2012, Butler et al. 2017). Conservation activities on the wintering grounds may have to broaden in geographic scope, and conservation of stopover sites in the fall migratory staging areas of central Saskatchewan may become a greater priority in the future.

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