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### Temporal Migration Shifts in the Aransas-Wood Buffalo Population of Whooping Cranes (*Grus americana*) Across North America

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**Abstract.**—Birds are altering the phenology of critical life history events, including migration, in response to the effects of global climate change. Whooping Cranes (*Grus americana*) are one of the most critically endangered birds in the world. Their remnant population, referred to as the Aransas-Wood Buffalo Population, numbers between 300-400 individuals and migrates between the U.S. Gulf of Mexico coast and north-central Canada twice each year. Previous analyses suggested Whooping Crane migration was temporally constant in spring and fall. New analyses of observations spanning 1942-2016 show Whooping Crane migration is now occurring earlier in spring by approximately 22 days and later in fall by approximately 21 days. Spring temperatures have also increased in the migration corridor during the same period; however, there is no apparent temperature pattern during the fall. In spring, earlier migrating Whooping Cranes stopped over for longer periods of time compared to late-migrating cranes. This result may be partially explained by single Whooping Cranes migrating with earlier migrating Sandhill Cranes (*Antigone canadensis*). These results have important conservation implications as the timing of Whooping Crane migration and availability of the habitat and foraging resources, including those associated with agriculture, on which this species relies will be increasingly affected by climate change. *Received 6 February 2017, accepted 9 March 2017.*

**Key words.**—agriculture, Central Flyway, climate change, endangered species, *Grus americana*, migration phenology, palustrine wetlands, Whooping Crane.

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Birds are altering the phenology of critical life history events in response to the effects of global climate change (Walther *et al.* 2002; Jenni and Kéry 2003; Visser *et al.* 2009). In the Northern Hemisphere, spring arrival at breeding areas has advanced for many migratory species (Lane and Pearman 2003; Both and Visser 2005; Murphy-Klassen *et al.* 2005; Brown and Brown 2014). Other migratory species have altered their migration phenology by arriving later in spring (Murphy-Klassen *et al.* 2005) or migrating earlier in fall (Guillemain *et al.* 2015) while some have not altered their temporal migration patterns (Both and Visser 2001; Murphy-Klassen *et al.* 2005). In addition to long-term climate trends, migration phenology may be influenced by the occurrence and interaction of resource availability, short-term climate patterns (Brown and Brown 2014; Ward *et al.* 2015), and weather events

(Nisbet and Drury 1968; Shariati-Najafabadi *et al.* 2016) in breeding and wintering areas and along migratory routes (Guillemain *et al.* 2015).

Climate change may alter the availability of resources across a species' range (Both and Visser 2001; Courter *et al.* 2013; Brown and Brown 2014). However, these impacts may not be uniform across wintering, breeding and migratory areas (Both and Visser 2001; Guillemain *et al.* 2015). Since individuals and populations use these areas sequentially throughout their annual cycle, climate change induced consequences in one area may have consequences and repercussions in other areas. In some instances, birds may adapt to these environmental changes with few noticeable consequences (Both and Visser 2005; Murphy-Klassen *et al.* 2005; Ward *et al.* 2015), while in other cases, the changes may have important

consequences. For example, migratory strategies often include arriving at specific locations during specific temporal periods to exploit a specific food resource that historically has predictably been in great abundance for a short time during a certain period of the year (McGowan *et al.* 2011). Changing phenology in either migration or food resource availability can create asynchronies that result in migrating individuals missing the period when key food resources are abundant. These shifts can have cascading effects that impact significant life history events such as reproduction (Both and Visser 2001; Both *et al.* 2009; McKinney *et al.* 2012). Species with small populations and limited geographic ranges may be at particular risk from the additional or additive consequences resulting from climate change (Thomas *et al.* 2004).

Whooping Cranes (*Grus americana*) are one of the most critically endangered species in the world (Urbanek and Lewis 2015). The remnant, self-sustaining population of Whooping Cranes, the Aransas-Wood Buffalo Population (AWBP), numbered as low as 15 or 16 individuals in the early to mid-20th century (Urbanek and Lewis 2015). Due to legal protections, such as the Endangered Species Act (Rohlf 1989) and implementation of extensive conservation efforts, Whooping Crane numbers have increased (Urbanek and Lewis 2015). In 2015, the estimated size of the AWBP was 329 birds (95% CI = 293-371; Harrell and Bidwell 2015).

Whooping Cranes are migratory and use an array of wetland and terrestrial habitats (Urbanek and Lewis 2015). They are omnivorous and feed on animals, such as mollusks, reptiles and amphibians, but also consume vegetative material, such as berries and acorns during winter and waste grain found in croplands, especially during migration (Johns *et al.* 1997; Urbanek and Lewis 2015). The AWBP migrates through the Great Plains of North America between their wintering areas on the U.S. Gulf of Mexico coast to breeding areas in north-western Alberta, Canada, twice each year (Urbanek and Lewis 2015).

Since the AWBP population is relatively small, it is vulnerable to environmental changes that may slow or reverse the long-term recovery of the species (Kuyt 1992; Ramirez *et al.* 1993; Urbanek and Lewis 2015). In the species' migration corridor in the Great Plains, economics influence agricultural land use, including the spatial distribution and types of specific crops grown (Higgins *et al.* 2002; Wright and Wimberly 2013) and the amount of waste grain that remains in fields and available to birds following harvest (Krapu *et al.* 2004; Pearse *et al.* 2010). Whooping Cranes, like other migratory birds, use waste corn (*Zea mays*) more so than other crops, such as soybeans (*Glycine max*), during migration (Krapu *et al.* 2004; Pearse *et al.* 2010; Chavez-Ramirez and Wehtje 2012). Climate change is expected to influence agricultural practices and production in the Great Plains, which will affect the availability of crop resources used by Whooping Cranes during migration, including those in important fall staging areas of Saskatchewan (Chavez-Ramirez and Wehtje 2012).

Palustrine wetlands in the Great Plains, which Whooping Cranes use during migration, often as nighttime roost sites, have been reduced in number and altered in physiognomy since settlement by European Americans, primarily due to land use changes associated with agriculture (Higgins *et al.* 2002; Wright and Wimberly 2013). Climate change is also expected to alter temperature and precipitation regimes, which will affect the water volume and hydroperiods of palustrine wetlands in variable and uncertain ways throughout the migration corridor (Johnson *et al.* 2010; Chavez-Ramirez and Wehtje 2012). For example, western areas of the Prairie Pothole Region in North and South Dakota, USA, are expected to become drier in the future (Johnson *et al.* 2010). Collectively, the changes in climate regimes and human land use will result in shifts in the distribution and availability of food and habitat resources, as well as overall habitat connectivity (McIntyre *et al.* 2014; Reese and Skagen 2017), across the AWBP's migration route.

Chavez-Ramirez and Wehtje (2012) evaluated the impacts of climate change scenarios on the AWBP. They noted that changes in temporal patterns of the AWBP migration are likely not influenced by temperature since it has been consistent based on analysis of records from 1943-1999 (Austin and Richert 2001). Chavez-Ramirez and Wehtje (2012) speculated Whooping Crane migration is based on photoperiod. Since the Austin and Richert (2001) analysis, more Whooping Crane sightings have been confirmed (U.S. Fish and Wildlife Service 2017), extending the temporal scale of this study. Many impacts of climate change are relatively recent in occurrence, and changes in some regions, such as the Arctic, are occurring rapidly (Wauchope *et al.* 2017). Other species of waterbirds (e.g., waterfowl, cranes, pelicans, cormorants) have shown temporal shifts in migration, apparently in response to increased temperatures (Murphy-Klassen *et al.* 2005; Guillemain *et al.* 2015), and Whooping Cranes have recently demonstrated unusual migration and wintering patterns (Wright *et al.* 2014).

The objective of this study was to evaluate whether temporal patterns of Whooping Crane migration across the central United States have changed over the past 74 years and whether these changes might be associated with changes in climate. We hypothesize Whooping Cranes are migrating earlier in spring and later in fall throughout the migration corridor in response to warming temperatures.

## METHODS

### Study Area

We studied Whooping Crane migration in the AWBP migratory corridor in the central United States. The migration corridor extends from north to south in the United States for approximately 2,400 km, primarily through western North Dakota, northeastern Montana, west-central South Dakota, central Nebraska, central Kansas, central Oklahoma and east-central Texas (Fig. 1). Individual Whooping Cranes are occasionally observed outside of the migration corridor and, in rare instances, in nearby States, including Colorado, Iowa, Minnesota, Missouri, New Mexico and Wyoming (Austin and Richert 2001).

### Study Species

Whooping Cranes are diurnal migrants traveling in small groups (individuals, mated pairs, family groups, and occasionally larger groups) under favorable conditions (limited cloud cover, tail wind). Since Whooping Cranes rely on thermals and favorable winds to migrate, migratory flights are interrupted each day in late afternoon and evening. During migratory stopovers, which are variable in length, Whooping Cranes use palustrine and riverine wetlands for nighttime roosting and for feeding, self-maintenance, socializing, and resting; agricultural fields are used frequently for feeding (Johns *et al.* 1997; Austin and Richert 2001). Whooping Cranes were formerly (1800s) widespread, but never common, in the north-central United States and southern Canada (Urbanek and Lewis 2015). Individuals in the AWBP migrate primarily from mid-March through early May in spring and from early October through late November in fall (Austin and Richert 2001; Urbanek and Lewis 2015). Individual Whooping Cranes occasionally migrate later or earlier during both spring and fall migration (Austin and Richert 2001).

### Data Collection

We analyzed migration data from the Cooperative Whooping Crane Tracking Project (U.S. Fish and Wildlife Service 2017), which includes all confirmed sighting records since 1942, and temperature data from the National Oceanic and Atmospheric Administration (2017). The Cooperative Whooping Crane Tracking Project is a collaborative effort to collect, evaluate, and archive all Whooping Crane stopover observations in the migratory corridor in the United States. The database includes mostly incidental observations, but also includes data from formalized surveys such as daily aerial surveys along the central Platte River during spring and fall migration (Lingle and Howlin 2015).

Even though there may be concerns regarding biases, observational Whooping Crane data (U.S. Fish and Wildlife Service 2017) has been shown to correspond geographically with data from Whooping Cranes outfitted with satellite transmitters, thus indicating biases are minimal (Pearse *et al.* 2015). Individual Whooping Crane occurrences are typically distinguishable from one another during migration because: 1) there are a small number of individuals in the AWBP; 2) they occur over a large geographic area during migration, usually in groups with different numbers and ages of individuals; and 3) a proportion of the AWBP has been banded with unique markers. Without all individuals marked at all times, we cannot completely discount the concern that two or more flocks were successively observed. However, it is estimated that only about 4% of all Whooping Crane stopovers are detected during migration (U.S. Fish and Wildlife Service 2009), and, based on personal observations of cranes and the distribution of the observations across the study area, we do not believe this is a significant problem for our analyses.

We only considered confirmed records, which are observations made by qualified observers or support-

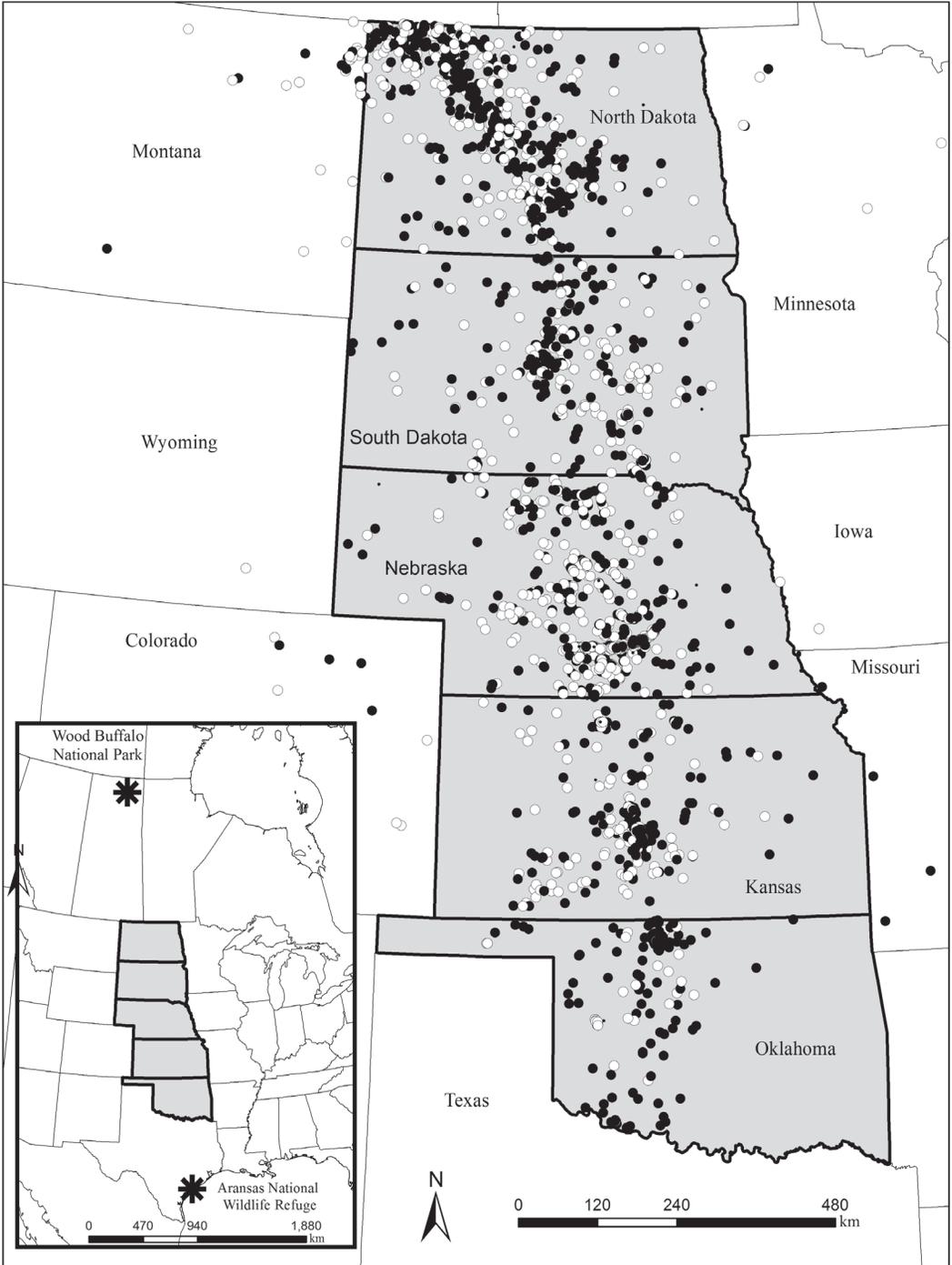


Figure 1. Spatial distribution of Whooping Crane spring (white dots) and fall (black dots) records with focal USA States (gray shading) and adjacent USA States within the Whooping Crane migration route. Inset shows the location of Wood Buffalo National Park, Alberta, Canada, Aransas National Wildlife Refuge, Texas, USA and focal USA States within the migration corridor.

ed by documentation (U.S. Fish and Wildlife Service 2006). For all Whooping Crane observations, the database included an initial observation date and a final

observation date. To evaluate temporal migration patterns, we used the initial observation date of each record, since stopover lengths are variable, ranging from

1 to 89 days, which greatly affects the final observation date. Initial observation dates are the first date Whooping Cranes were known to occur at a site. For some historical records, only an approximate time period was known; we did not include records where actual dates were not known. We used the total number of days observed at a location to evaluate whether stopover duration within the migration corridor is changing. The intensity of monitoring across the migration corridor is variable, especially with respect to follow-up monitoring once a record was confirmed. However, for the following analyses, we assumed monitoring was spatially and temporally consistent.

We used all records north of Texas since our focus was migration; areas in Texas within the migratory corridor are relatively close to wintering areas. Adult and/or juvenile Whooping Cranes observed individually or in groups are considered single, separate records. Occasionally, immature non-breeding Whooping Cranes spend the summer (June-August) in the migration corridor, well south of the traditional breeding range, and in rare instances, birds may be found in the migratory corridor during mid-winter (Austin and Richert 2001; Wright *et al.* 2014). Summer and mid-winter records were excluded from our analysis.

To evaluate changes in climate, we used long-term (1942-2016) average monthly temperature data acquired from the National Oceanic and Atmospheric Administration (2017). The temperature data ranged from March-April and October-November for the States lying in the primary migration route for Whooping Cranes: Oklahoma, Kansas, Nebraska, South Dakota and North Dakota. We chose those time periods because they cover the spring and fall Whooping Crane migration months.

#### Statistical Analysis

We used Pearson product-moment correlation using records for both spring and fall to evaluate whether temporal shifts in Whooping Crane migration patterns occurred over the 74-year study period. We evaluated stopover duration during the same period and, using the same approach, assessed whether stopover duration was associated with arrival date at a migratory stopover location. We used correlation to show general relationships since the data were collected opportunistically and not suitable for more complex analyses. We evaluated whether there were noticeable temporal shifts in observed stopover duration and observed stopover duration by latitude across all years by conducting individual analyses for both spring and fall for individual States (North Dakota, South Dakota, Nebraska, Kansas, and Oklahoma) where Whooping Cranes occur as migrants and where a majority (98%) of all records have occurred. To visualize the data, we constructed boxplots for spring and fall and grouped years following the same approach used by Austin and Richert (2001). We used Pearson product-moment correlation to evaluate whether average temperature during principal Whooping Crane migratory periods have changed over time. We used average monthly temperature data by State. All

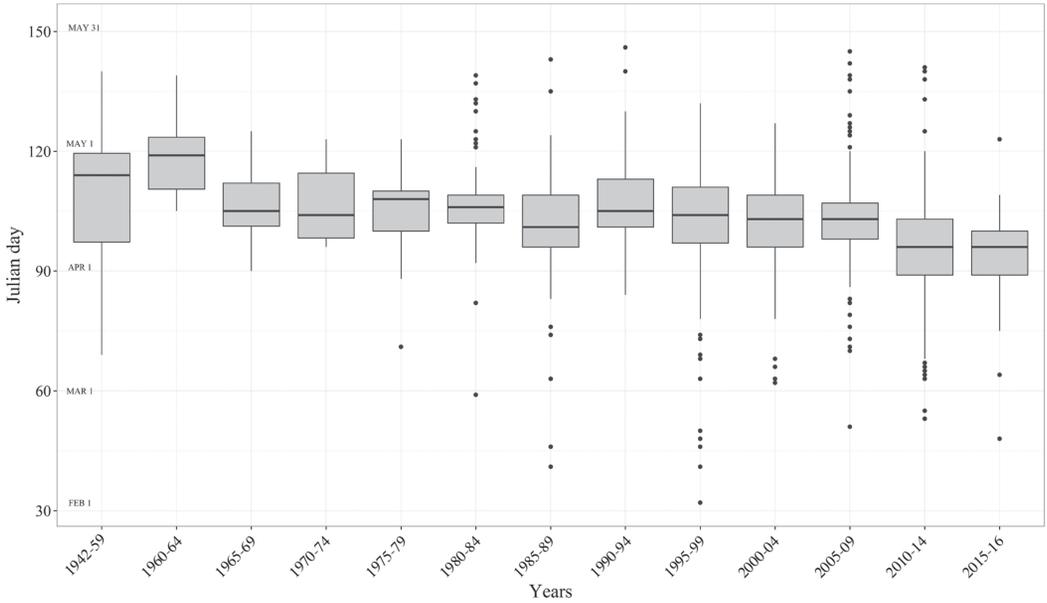
analyses were completed using RStudio (RStudio, Inc. 2015).

## RESULTS

We evaluated 2,806 Whooping Crane records from 1942 through 2016. The largest proportion (25.4%) of records were from Kansas followed by Nebraska (25.3%), North Dakota (23.5%), Oklahoma (13.1%), South Dakota (10.4%), Montana (1.4%), Colorado (0.4%), Minnesota (0.2%), Iowa (0.1%), New Mexico (0.1%), Illinois (< 0.1%) and Wyoming (< 0.1%). More observations (1,727; 61%) were recorded during fall compared to spring (1,079; 39%).

We found a negative relationship between spring observation date and year when all data were considered ( $r = -0.29$ ,  $P < 0.001$ ; Fig. 2). Negative relationships occurred for North Dakota ( $r = -0.29$ ,  $P < 0.001$ ), South Dakota ( $r = -0.46$ ,  $P < 0.001$ ), Nebraska ( $r = -0.32$ ,  $P < 0.001$ ), and Kansas ( $r = -0.33$ ,  $P < 0.001$ ). The relationship for Oklahoma was also negative, but not significant ( $r = -0.04$ ,  $P = 0.76$ ). The linear relationship of our analysis suggests spring migration occurs approximately 22 days earlier at the end of the study period (2016) compared to the beginning of the study period (1942). The results do not suggest the variation is a directional shift associated with latitude since the relationship is not consistently stronger in States located north or south in the flyway.

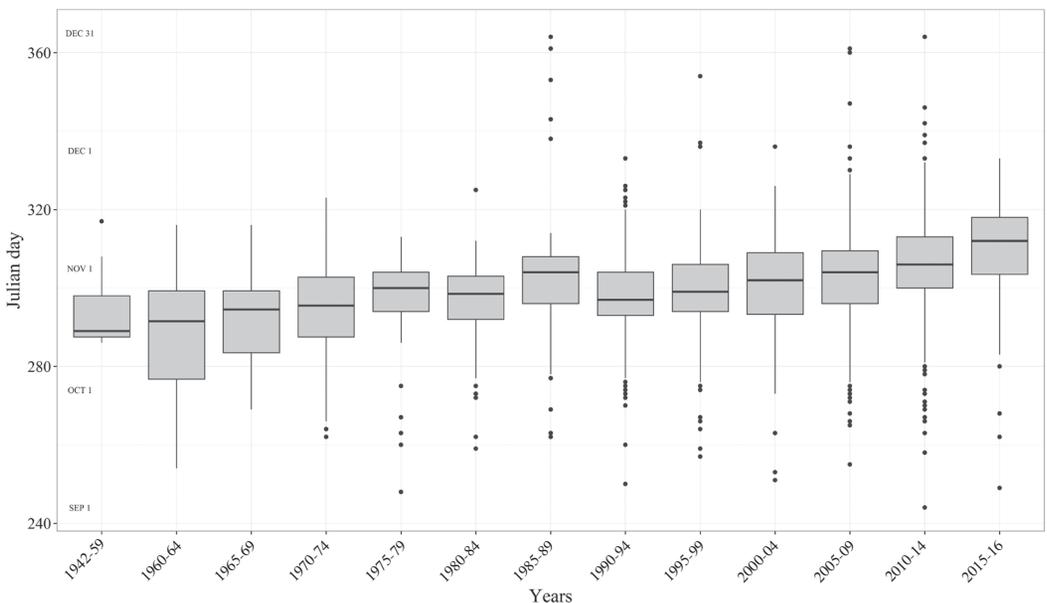
As hypothesized, we found a significant positive relationship between fall migration dates and year ( $r = 0.29$ ,  $P < 0.001$ ; Fig. 3). Analysis by individual States showed significant positive relationships for North Dakota ( $r = 0.24$ ,  $P < 0.001$ ), South Dakota ( $r = 0.36$ ,  $P < 0.001$ ), Nebraska ( $r = 0.26$ ,  $P < 0.001$ ), Kansas ( $r = 0.39$ ,  $P < 0.001$ ) and Oklahoma ( $r = 0.30$ ,  $P < 0.001$ ). The linear relationship of our analysis suggests fall migration occurs approximately 21 days later at the end of the study period (2016) compared to the beginning of the study period (1942). The results do not suggest the variation is a directional shift associated with latitude since the relationship is not consistently stronger in States located north or south in the flyway.



**Figure 2.** Boxplot showing the distribution of confirmed Whooping Crane spring observations by Julian day from 1942 to 2016. Most Whooping Crane records occur between Julian day 60 (March 1) and 120 (April 30). Box plots show median (horizontal line in box), 25th and 75th percentiles (box), 10th and 90th percentiles (bars) and outliers (dots). Grouping of years follow Austin and Richert (2001).

We found no evidence that the observed stopover duration changed for either spring ( $r = 0.00$ ,  $P = 0.94$ ) or fall ( $r = 0.01$ ,  $P = 0.78$ ).

Results for spring were similar for South Dakota ( $r = 0.00$ ,  $P = 0.98$ ), Nebraska ( $r = 0.03$ ,  $P = 0.54$ ), Kansas ( $r = -0.05$ ,  $P = 0.45$ ) and Okla-



**Figure 3.** Boxplot showing the distribution of confirmed Whooping Crane fall records by Julian day from 1942 to 2016. Most Whooping Crane records occur between Julian day 274 (October 1) and 330 (November 26). Box plots show median (horizontal line in box), 25th and 75th percentiles (box), 10th and 90th percentiles (bars) and outliers (dots). Grouping of years follow Austin and Richert (2001).

homa ( $r = -0.13$ ,  $P = 0.36$ ). However, results for North Dakota ( $r = -0.12$ ,  $P = 0.06$ ) suggested a slight, albeit non-significant, negative relationship. Results for fall showed no discernible relationship for North Dakota ( $r = -0.03$ ,  $P = 0.50$ ), South Dakota ( $r = -0.05$ ,  $P = 0.50$ ), Nebraska ( $r = -0.01$ ,  $P = 0.83$ ), Kansas ( $r = 0.06$ ,  $P = 0.21$ ) or Oklahoma ( $r = -0.06$ ,  $P = 0.23$ ).

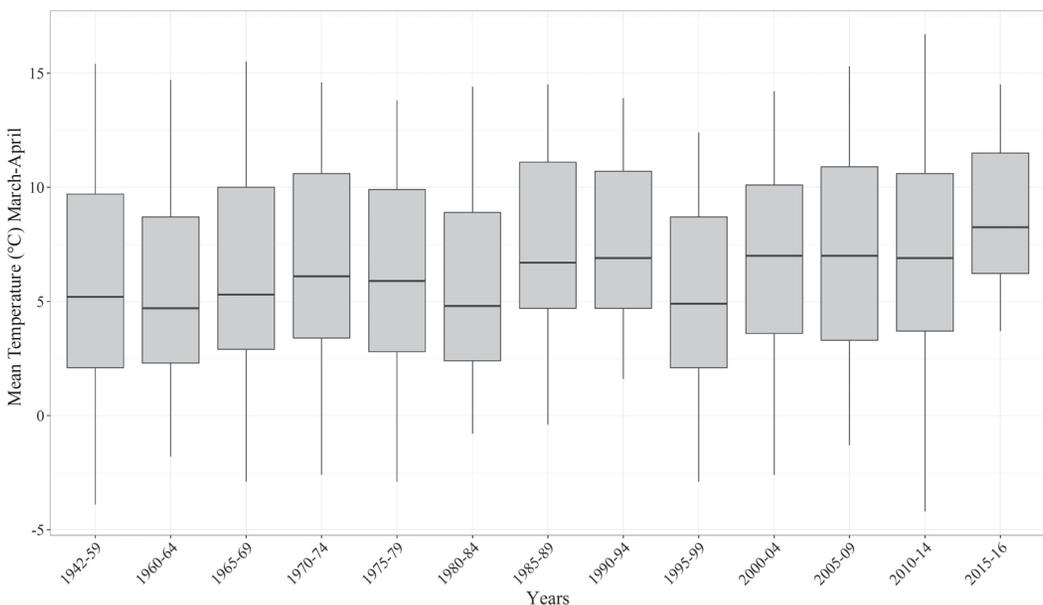
Observed stopover duration in spring was negatively related to Julian date when all data were considered ( $r = -0.24$ ,  $P < 0.001$ ). However, a negative relationship was found only for Nebraska ( $r = -0.37$ ,  $P < 0.001$ ) and Oklahoma ( $r = -0.30$ ,  $P = 0.02$ ); results for North Dakota ( $r = 0.04$ ,  $P = 0.54$ ), South Dakota ( $r = 0.01$ ,  $P = 0.89$ ) and Kansas ( $r = 0.08$ ,  $P = 0.29$ ) showed no discernible relationship. A proportion of earlier migrating birds in the southern portion of the migration corridor were stopping over for longer periods. In fall, we found no relationship between Julian date and observed stopover length when all data were considered ( $r = -0.02$ ,  $P = 0.38$ ), but again the relationship varied among States. We found a negative relationship for North Dakota ( $r = -0.13$ ,  $P < 0.01$ ), but a positive relationship for Okla-

homa ( $r = 0.12$ ,  $P = 0.02$ ). South Dakota ( $r = -0.01$ ,  $P = 0.93$ ), Nebraska ( $r = 0.00$ ,  $P = 0.96$ ), and Kansas ( $r = 0.02$ ,  $P = 0.62$ ) showed no discernible relationship.

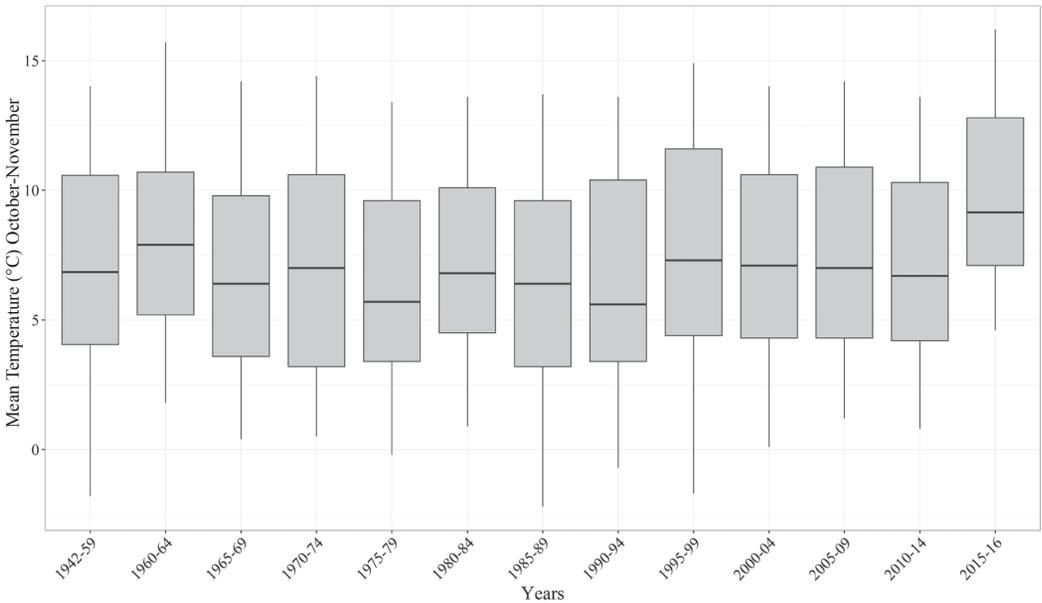
Average monthly temperatures during March-April have increased during 1942-2016 throughout the study area ( $r = 0.12$ ,  $P = 0.01$ ; Fig. 4) and in all States examined (North Dakota,  $r = 0.26$ ,  $P = 0.02$ ; South Dakota,  $r = 0.37$ ,  $P = 0.001$ ; Nebraska,  $r = 0.38$ ,  $P < 0.001$ ; Kansas,  $r = 0.32$ ,  $P = 0.01$ ; and Oklahoma,  $r = 0.23$ ,  $P = 0.05$ ). Average temperatures during October-November also tended to be stable or increase slightly throughout the study area ( $r = 0.03$ ,  $P = 0.51$ ; Fig. 5). However, no trend was observed in any of the States (North Dakota,  $r = 0.07$ ,  $P = 0.53$ ; South Dakota,  $r = 0.08$ ,  $P = 0.08$ ; Nebraska,  $r = 0.12$ ,  $P = 0.30$ ; Kansas,  $r = 0.08$ ,  $P = 0.47$ ; and Oklahoma,  $r = 0.11$ ,  $P = 0.36$ ).

## DISCUSSION

Previous analyses (Austin and Richert 2001; Chavez-Ramirez and Wehtje 2012) suggested Whooping Crane migration patterns were temporally constant and influenced by



**Figure 4.** Boxplot showing average temperature data for March and April for all USA States from 1942 to 2016. Box plots show median (horizontal line in box), 25th and 75th percentiles (box) and 10th and 90th percentiles (bars). Grouping of years based on Figure 2.



**Figure 5.** Boxplot showing average temperature data for October and November for all USA States from 1942 to 2016. Box plots show median (horizontal line in box), 25th and 75th percentiles (box) and 10th and 90th percentiles (bars). Grouping of years based on Figure 3.

photoperiod rather than weather and climate. Our results contradict those studies and demonstrate that the temporal patterns of Whooping Crane migration have shifted from the 1940s to the present; birds are migrating earlier (22 days) in spring and later (21 days) in fall throughout the central United States. These results also show that average temperatures have increased in spring during the same period, which suggests a link between climate change and Whooping Crane migration phenology. Temperatures during fall migration also suggest a slight increase, although any patterns related to migration phenology were inconclusive. The earliest median migration date in spring and the latest in fall during the period of record (1942-2016) occurred recently in years in which record warmth was recorded in March-April (2012) and October-November (2016) in the migration corridor (National Oceanic and Atmospheric Administration 2017). Our results align with observations of the Common Crane (*Grus grus*) in Eurasia, where the species is migrating earlier in spring and later in fall throughout its range (Hansbauer *et al.* 2014). Sandhill Cranes

(*Antigone canadensis*) are also migrating progressively earlier in spring in the mid-continent of North America in recent years (Harner *et al.* 2015).

The weaker relationship in fall may be an artifact of the available climate data. Average temperature data are only available by month (National Oceanic and Atmospheric Administration 2017), but in fall during many years, all or most Whooping Cranes migrated out of the study area (i.e., into Texas) before the latter part of November. Inclusion of temperature data recorded beyond the primary migration period may be masking a stronger relationship between seasonal climate patterns and migration. Finer scale analysis of these data or movement data for individually marked birds may reveal a stronger relationship. Alternatively, the changing availability of food resources (e.g., waste grain) may be causing birds to delay their fall migration and remain further north later into the season independent of temperature. Future research should consider the effects of food (e.g., energetics) and proximate weather events, along with climate change, on the migration of Whooping Cranes.

These results have important implications for Whooping Crane conservation. The potential impacts of climate change on Whooping Cranes were discussed by Chavez-Ramirez and Wehtje (2012), but these potential impacts should be re-evaluated in light of changes in migration phenology, in apparent response to warming temperatures. One of the principal impacts of climate change on Whooping Crane migration will be changes to stopover habitat (palustine wetlands), used for roosting and foraging, found over much of their migration corridor. Changing temperature and precipitation regimes are expected to affect availability and quality of wetlands, and possibly reduce the number of wetlands in some areas of the migration corridor (Chavez-Ramirez and Wehtje 2012). However, impacts to wetland habitats caused by climate change are not expected to be uniform across the migration corridor or across migration seasons (Johnson *et al.* 2010). These changes, along with those associated with agricultural practices and distribution of crops may spatially and temporally redistribute the resources upon which Whooping Cranes depend. Conservation practitioners should work to identify and mitigate areas of reduced resource availability within the migration corridor to maintain their suitability for migrating Whooping Cranes.

Whooping Crane migration patterns in the central United States may also be affected by changes in winter habitat and the species' winter distribution. During the winter of 2011-2012, a number of Whooping Cranes were observed during and throughout the winter well north of the traditional wintering areas along the Texas coast, which was suffering from severe drought at the time (Wright *et al.* 2014). Wright *et al.* (2014) suggested that birds may have migrated later in the fall of 2011 in response to mild temperatures or dispersed from wintering areas along the Texas coast because of poor habitat and foraging conditions and overcrowding at traditional wintering sites as a result of population increases. Wright *et al.* (2014) also suggested that Whooping Cranes may be more flexible in selecting and using habitats and food resources than previously believed, which may be beneficial as an increasing population requires additional habitat.

Warming temperatures in spring are likely to make certain food resources (e.g., amphibians, invertebrates, seeds) available earlier in the season since wetlands, cultivated fields, and other substrates may thaw earlier in the season (Gibbs and Breisch 2001; Parmesan 2006). A possible reflection of Whooping Crane flexibility is the notable relationship that earlier-migrating birds in spring are stopping over for longer periods in southern portions (Oklahoma and Nebraska) of the migration route. This relationship was strongest in Nebraska, but may be explained by the fact that 56% of the 79 Nebraska records for February and March involved single birds along the central Platte River observed among, and apparently migrating with, flocks of Sandhill Cranes. The central Platte River is a major staging area for Sandhill Cranes, which arrive earlier than Whooping Cranes (Sharpe *et al.* 2001) and generally stop over an average of 25 days in this area (Krapu and Brandt 2008). The remaining February and March records for Nebraska were distributed throughout migration areas in the State and involved groups ranging from 2-11 individuals and stopover durations ranging from 1-37 days.

Later timing of migration and declining stopover lengths in North Dakota in fall may suggest Whooping Cranes are spending longer periods in important staging areas in Saskatchewan (Johns *et al.* 1997; Chavez-Ramirez and Wehtje 2012), allowing them to take advantage of food resources resulting from changes in agricultural practices, and migrating quickly through the northern United States, possibly in response to adverse weather. Later migration in fall and earlier migration in spring may increase the likelihood birds could experience late spring or early fall blizzards. The possibility of late spring and early fall storms are also a concern for Common Cranes in Eurasia (Hansbauer *et al.* 2014). Relationships between stopover lengths, migration phenology and food resources at different latitudes should remain a focus of research in future years to determine whether spatial, as well as temporal, patterns are shifting.

Whooping Crane spatial and temporal patterns have shifted over the past 74 years and most noticeably during the past two decades. The patterns are likely to continue to evolve into the future as climate changes throughout the species range and affects resource availability. It is likely that future changes in and relationships between wintering and migration habitat and Whooping Crane distribution will increasingly interact with migration patterns observed in the central United States. Temporal and spatial patterns of a number of migratory birds have changed in unanticipated ways as changes in climate, land use, and habitat and food resources interact (Guillemain *et al.* 2015). Regulatory agencies, non-governmental organizations, and citizens must be prepared to adapt conservation efforts to these changes to maintain, continue, and secure the ongoing recovery of this critically endangered species.

#### ACKNOWLEDGMENTS

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