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# Temporospatial shifts in Sandhill Crane staging in the Central Platte River Valley in response to climatic variation and habitat change

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**ABSTRACT.**—Over 80% of the Mid-Continent Sandhill Crane (*Antigone canadensis*) Population (MCP), estimated at over 660,000 individuals, stops in the Central Platte River Valley (CPRV) during spring migration from mid-February through mid-April. Research suggests that the MCP may be shifting its distribution spatially and temporally within the CPRV. From 2002 to 2017, we conducted weekly aerial surveys of Sandhill Cranes staging in the CPRV to examine temporal and spatial trends in their abundance and distribution. Then, we used winter temperature and drought severity measures from key wintering and early migratory stopover locations to assess the impacts of weather patterns on annual migration chronology in the CPRV. We also evaluated channel width and land cover characteristics using aerial imagery from 1938, 1998, and 2016 to assess the relationship between habitat change and the spatial distribution of the MCP in the CPRV. We used generalized linear models, cumulative link models, and Akaike’s information criterion corrected for small sample sizes (AICc) to compare temporal and spatial models. Temperatures and drought conditions at wintering and migration locations that are heavily used by Greater Sandhill Cranes (*A. c. tabida*) best predicted migration chronology of the MCP to the CPRV. The spatial distribution of roosting Sandhill Cranes from 2015 to 2017 was best predicted by the proportion of width reduction in the main channel since 1938 (rather than its width in 2016) and the proportion of land cover as prairie-meadow habitat within 800 m of the Platte River. Our data suggest that Sandhill Cranes advanced their migration by an average of just over 1 day per year from 2002 to 2017, and that they continued to shift eastward, concentrating at eastern reaches of the CPRV. Climate change, land use change, and habitat loss have all likely contributed to Sandhill Cranes coming earlier and staying longer in fewer reaches of the CPRV, increasing their site use intensity. These historically unprecedented densities may present a disease risk to Sandhill Cranes and other waterbirds, including Whooping Cranes (*Grus americana*). Our models suggest that conservation actions may be maintaining Sandhill Crane densities in areas that would otherwise be declining in use. We suggest that management actions intended to mitigate trends in the distribution of Sandhill Cranes, including wet meadow restoration, may similarly benefit prairie- and braided river-endemic species of concern.

**RESUMEN.**—Más del 80% de la población de grullas canadienses (*Antigone canadensis*), de la zona central del continente (MCP por sus siglas en inglés), estimada en más de 660,000, descansa en el valle central del Río Platte (CPRV por sus siglas en inglés) durante su migración de primavera, desde mediados de febrero hasta mediados de abril. Diversos estudios indican que su distribución espacial y temporal podría estar cambiando dentro del CPRV. Desde el año 2002 hasta el 2017 realizamos sondeos aéreos semanales de grullas canadienses en el CPRV para estudiar las tendencias

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temporales y espaciales relacionadas a su abundancia y distribución. Usamos mediciones de temperatura durante el invierno y de la severidad de la sequía de lugares claves de invernada y de sitios de descanso durante su migración temprana para evaluar el impacto de los patrones climáticos en la cronología migratoria anual del CPRV. También analizamos la amplitud del canal y las características de la cubierta terrestre usando imágenes aéreas de 1938, 1998 y 2016 con el fin de evaluar la relación entre el cambio de hábitat y la distribución espacial de la MCP en el CPRV. Utilizamos modelos lineales generalizados, modelos de enlace acumulativo y el criterio de información de Akaike adecuados a muestras pequeñas (AICc), para comparar modelos temporales y espaciales. Las condiciones climáticas y de sequía en los sitios de invernada y migración más usados por la grulla canadiense mayor (*A. c. tabida*) predijeron mejor la cronología migratoria de la MCP en el CPRV. La reducción de la amplitud del canal principal desde 1938, junto con el porcentaje de cubierta terrestre como hábitat de pradera dentro de los 800 m del río Platte, fue el mejor predictor de la distribución espacial de la grulla canadiense desde el año 2015 hasta el 2017. Nuestros estudios indican que las grullas canadienses adelantaron su migración en un promedio poco más de un día por año entre el 2002 y el 2017 y que continuaron desplazándose hacia el este, concentrándose en los extremos orientales del CPRV. El cambio climático, el cambio de uso del suelo y la pérdida del hábitat probablemente contribuyeron a la migración temprana de esta especie y a su permanencia más prolongada en algunos sectores del CPRV, aumentando la intensidad del uso del sitio. Estas densidades sin precedentes podrían presentar un riesgo de enfermedad para la grulla canadiense y otras aves acuáticas, incluidas las grullas trompeteras (*Grus americana*). Nuestros modelos indican que las medidas actuales de conservación podrían ser la causa de preservación de la densidad poblacional de la grulla canadiense en áreas en las que, de otra forma, su presencia estaría disminuyendo. Sugerimos que las medidas de control destinadas a mitigar la tendencia de distribución de la grulla canadiense, incluyendo la restauración de los prados húmedos, pueden beneficiar de igual manera a las especies endémicas, praderas y ríos trenzados de nuestro interés.

A diversity of avifauna has substantially shifted ranges or migratory paths in response to broad landscape-level changes, such as increased agricultural production (Svedarsky et al. 2000, Coppedge et al. 2001b), modifications in hydrological regimes (Monda and Reichel 1989, Brand et al. 2011), or alterations in forest cover (Dolman and Sutherland 1995, Shaw et al. 2013). Concurrently, long-term research demonstrates that, in response to global climate change, several species of avifauna have altered migratory and breeding chronologies and shifted distributions (Bradley et al. 1999, Swanson and Palmer 2009, Visser et al. 2009). Given the landscape-level and climatic changes being observed in the Anthropocene (Meybeck 2003, Travis 2003), avifauna clearly shift migratory patterns in response to multiple independent factors. However, these factors can interact in their influence on individual species, with habitat loss limiting the ability of wildlife to adapt to global climate change (Travis 2003, Opdam and Wascher 2004).

The Mid-Continent Sandhill Crane (*Antigone canadensis*) Population (MCP) breeds from the eastern edge of Hudson Bay, west to Siberia, and south into the northern Great Plains (Tacha et al. 1984, Krapu et al. 2011). Wintering range of the MCP is also expansive, extending from the coastal plain of eastern Texas, west to southeastern Arizona, south into Chihuahua, Mexico, and north through the Texas Panhandle into central Oklahoma (Tacha et al. 1984, Krapu et al. 2011). However, from late February through the middle of April, over 80% of

the MCP funnels through a relatively narrow stretch of the Central Platte River Valley (CPRV), spanning about 132 km of central Nebraska (Kinzel et al. 2006, Krapu et al. 2014). Individual cranes stage in the CPRV for an average of 3–4 weeks, where they build up fat reserves before continuing their migration north to the breeding grounds (Krapu et al. 1985, 2014, Davis 2003). In recent years, Sandhill Cranes have been observed overwintering in the CPRV, a location well north of their historical wintering range (Tacha et al. 1984, Krapu et al. 2011, Harner et al. 2015). Furthermore, first arrival dates of Sandhill Cranes to Nebraska during northward migration have occurred earlier in recent decades, based on first reported sightings by the public (Harner et al. 2015). Research indicates that crane species have adjusted their migration chronologies in response to climate change, but there has been little investigation linking fluctuations in temperature and drought to variation in migration timing (Alonso et al. 2008, Mingozi et al. 2013, Harner et al. 2015, Jorgensen and Brown 2017).

Since the 1950s, Sandhill Cranes have abandoned large portions of the western CPRV from Overton west to North Platte, Nebraska, following declines in appropriate roosting habitat. Recent research indicates that their abundance in the western half of the CPRV may still be declining (Walkinshaw 1956, USFWS 1981, Faanes and Le Valley 1993, Buckley 2011). Large efforts have been undertaken since the early 1980s to maintain and improve riverine

habitat throughout the CPRV, through the clearing of riparian woodlands, restoration of native meadow habitat, controlled burning, chemical treatment of invasive species, and diking of the river channel during low flows (Currier 1984, 1991, Pfeiffer and Currier 2005, Kinzel 2009, Riggins et al. 2009, Smith 2011, Rapp et al. 2012, Krapu et al. 2014). However, the impact of these efforts on the roosting distribution of Sandhill Cranes remains largely unexamined.

Several studies investigated Sandhill Crane roosting habitat in the CPRV and generally found that Sandhill Cranes prefer channels wider than 150 m, bank vegetation <1.5 m tall, and shallow water depths (<20 cm); they also prefer a lack of human disturbance, including roads, bridges, and structures (Krapu et al. 1984, Iverson et al. 1987, Folk and Tacha 1990, Norling et al. 1992a, Davis 2001, 2003, Pearse et al. 2017). In addition to being an important predictor of Sandhill Crane roosting habitat use, channel width is indicative of broader riverine habitat features in the CPRV, including channel morphology, hydrology, and sinuosity, that can also impact Sandhill Crane habitat suitability (Schumm 1963, Williams 1978, Johnson 1994, Kinzel et al. 2009, Horn et al. 2012). The U.S. Fish and Wildlife Service (USFWS 1981) documented that in the late 1970s, 60% of the CPRV was more than 150 m wide. Over 2 decades later, Davis (2003) found that only 25% of the CPRV was wider than 150 m and that these areas contained 90% of the roosting Sandhill Cranes. Pearse et al. (2017) recently found that about 60% of the available roosting habitat was less than 100 m in width. Channel width may serve as a broad indicator of habitat quality, yet Sandhill Crane declines have been noted in the western portion of the CPRV even where quality roosting habitat still exists (Buckley 2011).

In addition to channel characteristics, land cover features also influence Sandhill Crane roosting distributions (Sidle et al. 1993, Sparling and Krapu 1994, Pearse et al. 2017). Sandhill Cranes require 3 general habitats while in the CPRV: wide channels for roosting, croplands (predominantly cornfields) to meet energetic needs, and wet meadows for protein and other nutrients (Krapu et al. 1982). Sandhill Cranes spend a disproportionate amount of time foraging in areas broadly defined as grasslands compared to their availability in the CPRV

(Krapu et al. 1984, Reinecke and Krapu 1986, Sparling and Krapu 1994). This disproportion is likely a result of their need to accumulate a basic level of protein and other nutrients in their diets that are insufficiently present in corn (Krapu et al. 1982, Reinecke and Krapu 1986). Sidle et al. (1993) documented a negative relationship between the number of Sandhill Crane roosts within a 1.6-km segment of river and the distance to wet meadow habitat. Concurrently, Sparling and Krapu (1994) found that minimum daily flight distances were highest to riverine roosting sites, followed by native meadows, suggesting that these habitats were the most limited resources within the CPRV for Sandhill Cranes. Faanes and Le Valley (1993) also showed that Sandhill Crane roosting densities were increasing in areas with relatively abundant remaining wet meadow habitat.

Pearse et al. (2017) demonstrated that the probability of Sandhill Cranes roosting in a portion of the river is related to the amount of cornfield nearby only when channels are relatively narrow; however, their study did not evaluate the impact of lowland grasslands on roosting distributions. Anteau et al. (2011) found that the use of cornfields by cranes increased with the quantity of wet grassland habitat within 4.8 km. Sparling and Krapu (1994) suggest that native grasslands serve as diurnal activity centers from which cranes base foraging expeditions. Wet grasslands within 800 m of riverine roosting sites are important for pre-roost aggregations, where Sandhill Cranes gather to continue to forage into the evening and engage in important pair-bonding behaviors (Johnsgard 1983, Tacha 1988). Though corn is an important food source, it is widespread (east to west) throughout the CPRV and is not likely restricting the amount of available Sandhill Crane habitat (Sparling and Krapu 1994, Krapu et al. 2014). However, research indicates that waste corn availability may be declining as a result of harvest efficiency and increased populations of arctic-nesting geese; this decline could potentially lead to longer Sandhill Crane flight distances (north and south) to agricultural foraging areas, particularly late in the spring staging period (Pearse et al. 2010, Krapu et al. 2014). Wide channels and wet meadows are the most limited habitat resources in the CPRV and influence the distribution of Sandhill Crane roosts (Krapu et al. 1984, Currier and Ziewitz 1987,

Iverson et al. 1987, Sidle et al. 1989, 1993, Faanes and Le Valley 1993, Davis 2003). However, there has not been a comprehensive habitat assessment estimating the availability of these resources in the CPRV following large-scale restoration efforts over recent decades.

To provide a clear and updated description of the timing and habitat-use patterns of roosting Sandhill Cranes during spring migration in the CPRV, we used aerial survey data spanning 16 years to examine spatial and temporal trends, as well as variation in Sandhill Crane roosting behavior. We then conducted an a priori investigation into the correlates of temporal and spatial shifts and variation in Sandhill Crane roosting within the CPRV. We used weather data from major wintering and early spring migration stopover locations to investigate the impacts of temperature and drought on the arrival dates of significant percentiles of the Sandhill Crane population to the CPRV (Wilson 2013). Finally, we investigated the spatial distribution of Sandhill Cranes in relation to land cover and channel characteristics within segments of the CPRV to assess the effectiveness of recent restoration and management efforts, and to determine which habitat resources may be proximate factors in spatial shifts. Investigating the influences of both climatic variation and landscape-level change together can help elucidate how large-scale independent factors may interact to influence localized patterns of species' temporospatial occurrence.

## METHODS

### Study Area

Our study area focused on the main channel of the Platte River and adjacent land cover within a 132-km reach of the CPRV from Chapman (N 40.984692°, W -98.144053°, WGS 84; 539 m elevation) to Overton (N 40.681662°, W -99.540353°, WGS 84; 702 m elevation), Nebraska, where the majority of the MCP stage during their spring migration (Fig. 1; Kinzel et al. 2006, Krapu et al. 2014). The Platte River provides shallow, secure roosting habitat for migrating Sandhill Cranes and Whooping Cranes (*Grus americana*) (Krapu et al. 1982, Farmer et al. 2005, Kinzel et al. 2006). The CPRV is a highly productive agricultural region, and the landscape largely comprises irrigated corn (*Zea mays*) and soybean (*Glycine max*)

fields in addition to other crops (Dappen et al. 2008, Krapu et al. 2014). The study area also contains significant expanses of riparian woodland and lowland prairie habitats (Currier 1982, Kaul et al. 2006, Krapu et al. 2014). The study area was divided into 11 survey "segments," delineated by bridges often used for reference in both research and conservation efforts in the CPRV (Currier 1991, Buckley 2011, Krapu et al. 2014; Fig. 1). For additional analyses, the 11 segments were grouped into 3 larger "reaches," which include segments 1–4 as the East Reach, segments 5–7 as the Central Reach, and segments 8–11 as the West Reach (Fig. 1).

The Platte River is characterized by a series of submerged and emergent bed-forms that migrate and change depending on river flows, a pattern characteristic of braided river systems (Smith 1971). These bed-forms, commonly referred to as sandbars, can become stabilized by early successional woody vegetation during low-flow conditions that have become increasingly common with the heavy appropriation of river flows for agricultural use and power generation (Williams 1978, Currier 1982, 1997, Johnson 1994, Horn et al. 2012). The impounding and appropriation of river flows over the last century have promoted forest development within former channels throughout the CPRV, leading to widespread declines in channel width (Williams 1978, Currier 1982, Johnson 1994). Dominant tree species in the CPRV include early successional species such as the eastern cottonwood (*Populus deltoides*) and the peachleaf willow (*Salix amygdaloides*), which readily establish seedlings on moist exposed soil (Currier 1982, 1997). These species were the first to colonize within the former high banks of the Platte River in the late 1800s. Eastern cottonwood development peaked between 1935 and 1960, with Russian olive (*Elaeagnus angustifolia*) and eastern red cedar (*Juniperus virginiana*) establishment in the understory beginning 20 years later, on average (Currier 1982, O'Brien and Currier 1987). Active channel area in portions of the CPRV has been reduced by over 90% in the last century, with losses being most pronounced in the western reaches (Williams 1978, Sidle et al. 1989).

The Platte River extends the range of tall-grass prairie habitat west into the central mixed-grass ecoregion of the Great Plains by

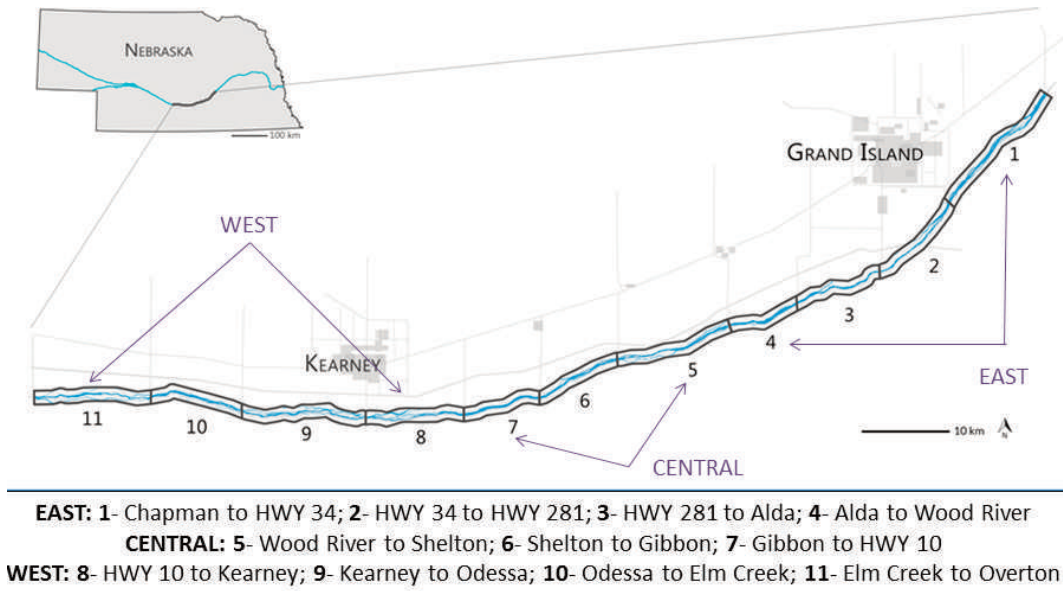


Fig. 1. Study area map showing 11 survey bridge segments and 3 reaches (East, Central, and West) delineating the study area of the Central Platte River Valley, Nebraska, USA.

providing moisture via subirrigation to a relatively deep-rooted herbaceous perennial plant community in the CPRV (Currier 1989, Kaul et al. 2006). Slight changes in elevation within this subirrigated ecosystem provide for a variety of wetland habitats (Currier 1982, 1989, Henszey et al. 2004). Subirrigated prairie systems in the CPRV have been categorized in multiple ways. Brei and Bishop (2008) categorized the drier portions of these subirrigated herbaceous plant communities dominated by big bluestem (*Andropogon gerardii*) and switchgrass (*Panicum virgatum*) as “xeric wet meadows,” whereas Rolfsmeier and Steinauer (2010) considered these systems “Sandhills mesic tallgrass prairies.” Rolfsmeier and Steinauer (2010) categorized wetter portions of these systems dominated by prairie cordgrass (*Spartina pectinata*) and sedges, such as Emory’s sedge (*Carex emoryi*) and woolly sedge (*Carex pellita*), as “northern chordgrass wet prairies.” By contrast, Currier (1982) considered these systems “wet meadows,” Brei and Bishop (2008) categorized them as “mesic wet meadows,” and Henszey et al. (2004) labeled them as “sedge meadows.” For this study we use the term “lowland tallgrass prairie” (Kaul et al. 2006) to refer to slightly higher and drier areas, and the term “wet meadow” (Currier 1982) to refer to lower and

wetter portions of subirrigated herbaceous habitat within the CPRV, where differentiated in the text. Based on current research, it is unclear whether Sandhill Cranes exhibit a strong preference for wet meadows over lowland tallgrass prairie habitats in the CPRV (Sidle et al. 1993, Sparling and Krapu et al. 1994, Davis 2003, Krapu et al. 2014). However, VerCauteren (1998) suggested that cranes used grasslands with shallower ground water to a greater extent. Lowland tallgrass prairie and wet meadow plant communities are not spatially distinct, but rather are integrated with one another, expanding and contracting depending on the moisture regime across several growing seasons (Currier 1989, Henszey et al. 2004). Analyses and discussion referring to lowland tallgrass prairie and wet meadow jointly will be referred to as “meadow-prairie” habitat.

#### Aerial Surveys

From 2002 to 2017, we conducted weekly aerial surveys of Sandhill Crane roosts from mid-February (12–18 February) to mid-April (16–22 April). We made every effort to keep the surveys as close to 1 week apart as possible, following the methods described by Buckley (2011). We conducted surveys along a 132-km section of the Central Platte River

from Chapman to Overton, Nebraska (Fig. 1). We conducted between 6 and 9 surveys per year ( $\bar{x} = 7.8$ ,  $SD = 1.0$ ), depending on funding, recent ambient weather conditions (extended periods of weather that preclude surveys), and pilot availability. The surveys were done to gain a better understanding of the spatial and temporal variation in densities and proportions of Sandhill Cranes roosting across different river segments of the CPRV. We began the surveys at civil twilight, approximately 15–25 min before sunrise, contingent upon environmental conditions, when it was light enough to clearly distinguish roosting Sandhill Cranes. Aerial surveys were conducted from a single-engine, fixed-wing aircraft (predominantly a Cessna 172) at an altitude between 200 m and 215 m and a ground speed of 115 to 135 km/h. We completed the majority of surveys in 55–75 min. We generally followed recommendations of Ferguson et al. (1979) for conducting aerial Sandhill Crane surveys on the Platte River; surveys were not flown during reduced visibility conditions (low clouds, fog, precipitation) or during high-wind events ( $>35$  kpm) that could significantly lower detection probabilities.

The route was flown along the south channel of the Platte River, which is generally the largest or “main channel,” where the vast majority of Sandhill Cranes roost (Krapu et al. 2014). Crane groups were considered to be different roosts when they were separated by more than 100 m (Iverson et al. 1987). Because a significant proportion of Sandhill Cranes can leave the roost before sunrise (Lewis 1974, 1978, Norling et al. 1992b), cranes were detected to the limit that they could be positively identified with binoculars in off-channel habitats along the survey path, such as wet meadows and cornfields. These detections were likely reflective of use in adjacent bridge segments (Sparling and Krapu 1994). Research indicates that Sandhill Crane densities peak earlier in eastern survey segments and are generally higher in eastern and central survey segments than in western ones, particularly until late in migration (Krapu et al. 1982, Faanes and Le Valley 1993, Buckley 2011, Krapu et al. 2014, B. Taddicken personal communication). Therefore, surveys were flown from east to west for the first 7–8 survey weeks, and from west to east during the last 2–3 survey weeks, to maximize the total

number of cranes detected at riverine roosting locations. However, in a few of the years, survey directions were rotated weekly. In all, approximately 85% of surveys were conducted by moving from east to west and 15% were completed by moving from west to east. This practice potentially undercounted cranes in western segments for a considerable portion of the migration and in eastern segments near the end of spring staging. Because Sandhill Cranes increase flight distance to foraging sites throughout the spring staging period (Sparling and Krapu 1994, Buckley 2011), survey segments that were assessed latest in the morning and near the end of migration likely sustained the most significant undercounts during individual surveys (i.e., late-season eastern segment surveys).

Two observers and a pilot conducted aerial surveys. One observer counted the number of Sandhill Cranes in river roosts and feeding aggregations in adjacent fields, photographed Sandhill Crane roosts for bias-estimation (beginning in 2016), and directed the course of the pilot (when to circle, etc.). If necessary, large groups were circled and recounted for accuracy. The second observer recorded count data, saved GPS waypoints, spotted forthcoming Sandhill Crane roosts, and assisted with photographing roosts. We recorded GPS waypoints near the center of Sandhill Crane roosts unless the roosting aggregation was large ( $n > 20,000$  Sandhill Cranes), in which case we marked both the beginning and the end of the roost with 2 separate waypoints. Following methods of Gregory et al. (2004) and Bowman (2014), we estimated Sandhill Crane roost sizes by counting a group of between 50 and 100 cranes, and then creating a mental polygon around those groups. The polygon was then multiplied in space to provide counts for small roosts ( $>2000$  cranes), or further grouped into larger units (500–1000 cranes) and multiplied in space to estimate abundance for roost sizes larger than  $\sim 2000$  cranes (Gregory et al. 2004, Bowman 2014).

#### Bias Estimation

The sensitivity of aerial count data to changes in when cranes arrive or depart, and in their distribution within the CPRV, has been significantly improved by the addition of bias estimation procedures, which use photographs of a subset of counted flocks (Ferguson et al.

1979, Johnson et al. 2010). We added a bias estimation component to our aerial survey protocol in 2016, which compared aerial survey counts to photo-interpreted counts of a subset of observed roosts (Ferguson et al. 1979, Gregory et al. 2004). Bias estimates were not conducted until 2016, due to limited staffing resources. Immediately following the aerial count of a designated roost, observers photographed it by circling the area a single time and taking multiple photographs of the entire roost for later bias estimation. The number of photo subplots was proportional to the number of roosts counted per survey, up to a maximum of 10 photo subplots because of time constraints. We selected a variety of roost sizes between 500 cranes and 10,000 cranes, as roosts larger than 10,000 cranes were difficult to photograph with high resolution in a single frame. We averaged percent bias across all subplots, regardless of directionality or roost size, to create a measure of estimated absolute percent bias of cranes observed per aerial survey (e.g.,  $\pm 15\%$ ). We felt this approach was appropriate because our bias estimates were not significantly correlated with roost size estimates ( $r = 0.158$ ). We also calculated a measure of relative percent bias that considered the directionality of error estimates and that could be used to correct estimates up or down (e.g.,  $-11\%$ ; Ferguson et al. 1979, Gregory et al. 2004).

Bias estimates only accounted for the difference between the number of Sandhill Cranes detected in photo subplots and the number detected in aerial roost counts, and did not account for flocks not spotted within the flight path (i.e., all estimates represent minimums present). As bias estimates were not obtained for all years, the 2016 and 2017 aerial Sandhill Crane counts that are used in most of the analyses in this paper were not error-corrected for standardization. However, we used bias estimates collected during peak count dates to approximate the number of Sandhill Cranes counted via our survey methods between Chapman, Nebraska, and Overton, Nebraska, during 2016 and 2017. We then compared our estimates to those produced by the USFWS (Dubovsky 2016, 2017) to determine the degree to which our methods may under- or overrepresent Sandhill Crane densities. We used both proportional metrics and aerial count indices in analyses to serve

as a control accompanying the uncorrected count data, and also to account for some of the variation in accuracy across observers (Gregory et al. 2004). However, we retained basic analyses and summaries of uncorrected abundance indices, when appropriate (i.e., not biased by potential population growth), in order to enhance the interpretability of results and to provide a descriptive account of temporospatial distributions of Sandhill Cranes during the spring staging period in the CPRV.

#### Wintering and Migration Weather Parameters

To examine factors that may influence the phenology of Sandhill Crane migration, temperature and Palmer Drought Severity Index (NOAA–NCDC 2017) data were selected from areas spatially centered within key Sandhill Crane wintering and early spring stopover regions (Fig. 2; Tacha et al. 1984, Iverson et al. 1985, Krapu et al. 2011, 2014). We first selected southern New Mexico (NM division 8; NOAA–NCDC 2017) because it is centered within the western wintering distribution of the MCP, north of wintering concentrations in Chihuahua, Mexico, east of those in southeastern Arizona, and southwest of those in east-central and northeastern New Mexico. A representative aggregation exists within this range that roosts in the backwaters of Caballo Lake, NM (N 32.898267°, W  $-107.295119^\circ$ ; Mitchusson 2003). Much of the Western Alaska–Siberia (WA–S) breeding affiliation winters in this western range, and it includes mostly Lesser Sandhill Cranes (*A. c. canadensis*; Jones et al. 2005, Krapu et al. 2014). Secondly, we selected Coastal Texas (TX division 8; NOAA–NCDC 2017) because it represents the southeastern-most major wintering region for Sandhill Cranes. This region is a major wintering ground for both the Eastern Canada–Minnesota (EC–M) and Western Canada–Alaska (WC–A) breeding affiliations, both of which contain significant numbers of Greater Sandhill Cranes (*A. c. tabida*; Jones et al. 2005, Krapu et al. 2014). A representative aggregation exists within this range that winters in and around Aransas National Wildlife Refuge, Texas (N 28.113560°, W  $-96.888864^\circ$ ; Hunt and Slack 1989). The third wintering location chosen to model the influences of winter and early spring weather on migratory timing of Sandhill Cranes in the CPRV was the Texas Panhandle (TX division 1; NOAA–NCDC 2017).



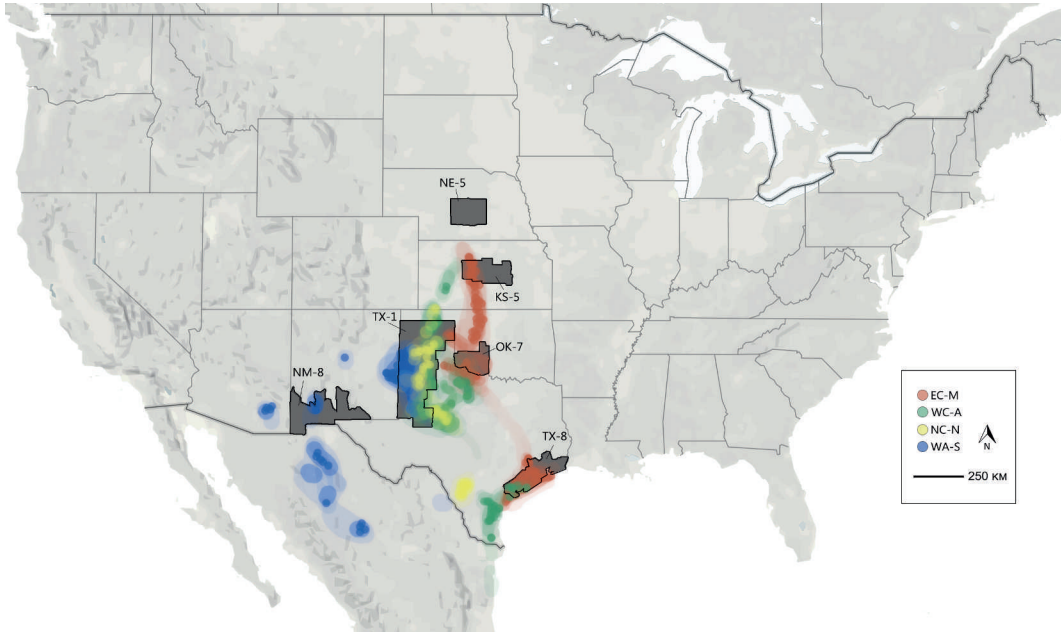


Fig. 2. United States map showing select wintering and stopover locations of the Mid-Century Sandhill Crane Population, wherein breeding affiliation (BA) is presented in color (adapted from Krapu et al. 2011). The east-central Canada–Minnesota BA (EC–M) is depicted in orange; the west-central Alaska BA (WC–A) is in green; the northern Canada–Nunavut BA (NC–N) is in yellow; and the western Alaska–Siberia BA (WA–S) is in blue. Gray outlines broadly surrounding key wintering populations in the U.S. map depict the National Oceanic and Atmospheric Administration’s regional climate divisions used in this study (from south to north): coastal Texas (TX division 8), southern New Mexico (NM division 8), Texas Panhandle (TX division 1), southwest Oklahoma (OK division 7), central Kansas (KS division 5), and central Nebraska (NE division 5).

This location is the largest wintering concentration, and the area serves both as wintering grounds and as an early spring migration stopover location for birds wintering farther to the south (Krapu et al. 2011, 2014). This area contains the largest wintering concentrations of Northern Canada–Nunavut (NC–N) and WA–S breeding affiliation Sandhill Cranes, including mostly Lesser Sandhill Cranes, as well as a large number of WC–A (larger proportion *A. c. tabida*) cranes (Jones et al. 2005, Krapu et al. 2014). A representative aggregation exists within this range that winters in and around Muleshoe National Wildlife Refuge, Texas (N 33.835346°, W –102.755188°; Iverson et al. 1985). Our fourth and final wintering location was sited in southwestern Oklahoma and north-central Texas (OK division 7; NOAA–NCDC 2017). This climate division borders the Red River of north-central Texas to the south, a known wintering location for Sandhill Cranes, but is also close to wetland wintering sites in southwestern Oklahoma, such as at

Washita National Wildlife Refuge (N 35.394310°, W –99.335130°; Lewis 1975). This area serves as a wintering location for the EC–M and WC–A breeding affiliations, as well as a stopover location both for Sandhill Cranes wintering along the Texas Coast and for NC–N birds wintering in the Texas Panhandle (Krapu et al. 2014).

For analyses, we included mean daily average temperatures and the mean Palmer Drought Severity Index (PDSI) values at all wintering sites for the months of January and February. Mean daily average temperatures across seasonal periods have been used to assess the effect of climatic variation and climate change on bird migration distances (Visser et al. 2009), timing of arrival on breeding grounds (McKinney et al. 2012), and a host of other phenological and chronological questions (Thackeray et al. 2016, Pancerasa et al. 2018). Seasonal PDSI values have been linked to the timing of nest initiation (Brown and Brown 2014) as well as habitat use (Igl and Johnson 1999).

We also included in our model, conditions at a key spring migration stopover site south of the Platte River and north of the wintering grounds. Krapu et al. (2011, 2014) indicated that Quivira National Wildlife Refuge in Kansas (KS division 5; N 38.092525°, W -98.488117°; NOAA-NCDC 2017) is one of the most widely used spring migration stopover locations for central and eastern wintering concentrations. We included the mean temperature and mean PDSI for February and March in our model for Quivira National Wildlife Refuge and surrounding wetlands. Finally, we included mean temperature and mean PDSI data averaged across February through April for the CPRV (NE division 5; N 40.708077°, W -98.788742°) to examine the effects of local temperature and drought variables on the phenology of Sandhill Crane staging in the CPRV (Krapu et al 2014).

#### Habitat Assessment

To investigate the changes in landscape features that could affect Sandhill Crane habitat use within the CPRV, we measured unobstructed channel widths and classified key land cover types. We used georeferenced and orthorectified aerial imagery collected in June or early July of 1938, 1998, 2015, and 2016 in order to measure a systematic random sample of unobstructed channel widths across all segments (RWB JV 2017; imagery provided by the Platte River Recovery Implementation Program and the Rainwater Basin Joint Venture's image library). We used aerial imagery from 1998 and 2016 to classify key land cover types within an 800-m buffer to the north and south of the main channel of the Platte River (1.6 km wide). When determining our spatial sampling area, we considered the impacts of human development (disturbances such as buildings, bridges, and roads within ~700 m are associated with decreased use of roost sites within narrow channels; see Pearse et al. 2017), evening pre-roost and morning post-roost aggregation behavior (called "peripheral" or "secondary" roosting and generally occurring in meadows within 800 m of the river; see Wheeler and Lewis 1972, Johnsgard 1983, Tacha 1988), and the estimated distribution of Sandhill Crane roosts in the CPRV (91% of crane roost locations occur in the main channel; see Krapu et al. 2014)

**CHANNEL WIDTH.**—Though a clear trend exists regarding channel losses in the CPRV, many researchers have differentially defined

channel width in this system. Williams (1978) defined channel width as the distance from bank to bank, after subtracting stabilized islands with perennial vegetation. Krapu et al. (1984) similarly defined unobstructed channel width as the breadth of river unbroken by stands of woody vegetation. Pearse et al. (2017) estimated unobstructed channel width from the perspective of cranes, determining it as the distance across the channel, including bare soil and vegetation under 1.5 m in height. Werbylo et al. (2017) considered unvegetated channel width as including sandbars with <25% vegetative cover. For the purposes of this study, we considered the "unobstructed channel width" as the distance from bank to opposite bank, including areas of active flow and unstabilized sandbars. We defined unstabilized sandbars as either those which are bare of vegetation or those which include only early successional vegetation under ~1.5 m in height and significant exposed bare ground (>50%). These sandbars are generally lower elevation and are scoured on a regular basis (Currier 1982). Islands showing signs of initial stabilization (including significant perennial shrub cover [*Salix exigua*, etc.] and perennial exotic plant cover [*Phragmites australis*, etc.]) or islands generally exceeding 1.5 m in height, with limited exposed bare ground, were not included as part of the unobstructed active channel width (Fig. 3).

We manually measured "total unobstructed channel width" (UOCW) in ArcGIS 10.5.1 by broadly following the techniques of Werbylo et al. (2017; Fig. 3). We placed point features every 800 m in the center of the main channel of the Platte River, beginning at a random starting point and using the oldest imagery available to us for each section of river (generally 1938). We then measured the width of the river channel (except for stabilized islands), making every effort to situate the measurement lines as close to perpendicular to each bank as possible. For purposes of comparison between years, we saved channel width measurements for each year of imagery as a unique feature class in ArcGIS 10.5.1. Points randomly landing near bridges were moved 100 m past or before a bridge. We also calculated "maximum unobstructed channel width" (maximum width unbroken by woody encroachment and stabilized islands; MUCW). Islands exceeding 1600 m in length or 400 m in width

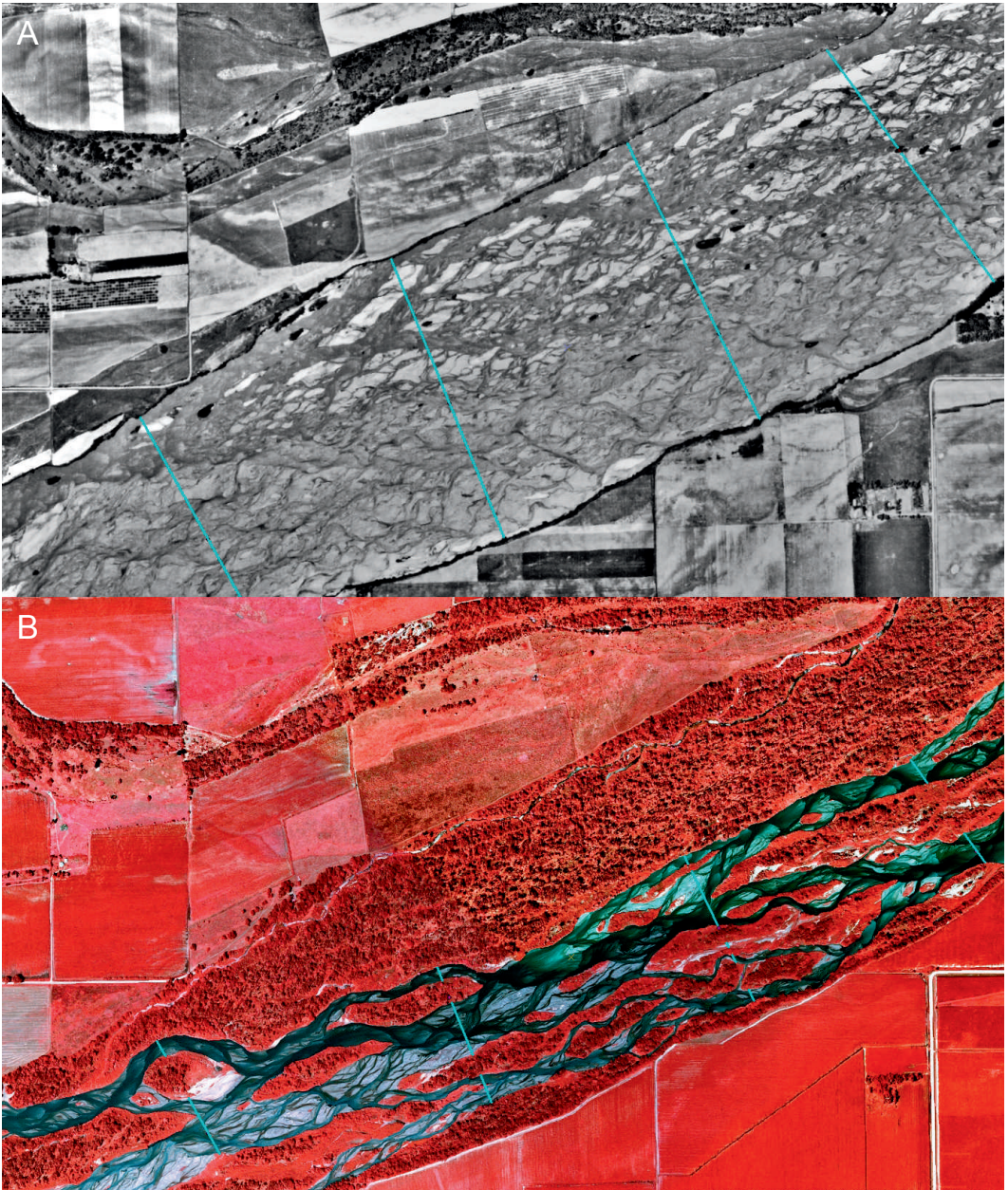


Fig. 3. Caption on page 43.

were considered to separate the Platte River into multiple channels, while vegetated islands smaller than those dimensions were considered obstructions within individual channels. At each point feature, we also recorded the number of active channels of the Platte River in each year of imagery.

**LAND COVER.**—To assess land cover, we classified areas of tree cover and meadow-prairie cover from aerial imagery acquired in the summers of 1998 and 2016 in ArcGIS 10.5.1 (RWB JV 2017). A true-color orthophoto with a 15-cm pixel resolution was used for 2016, and a MrSid (.sid) false-color composite

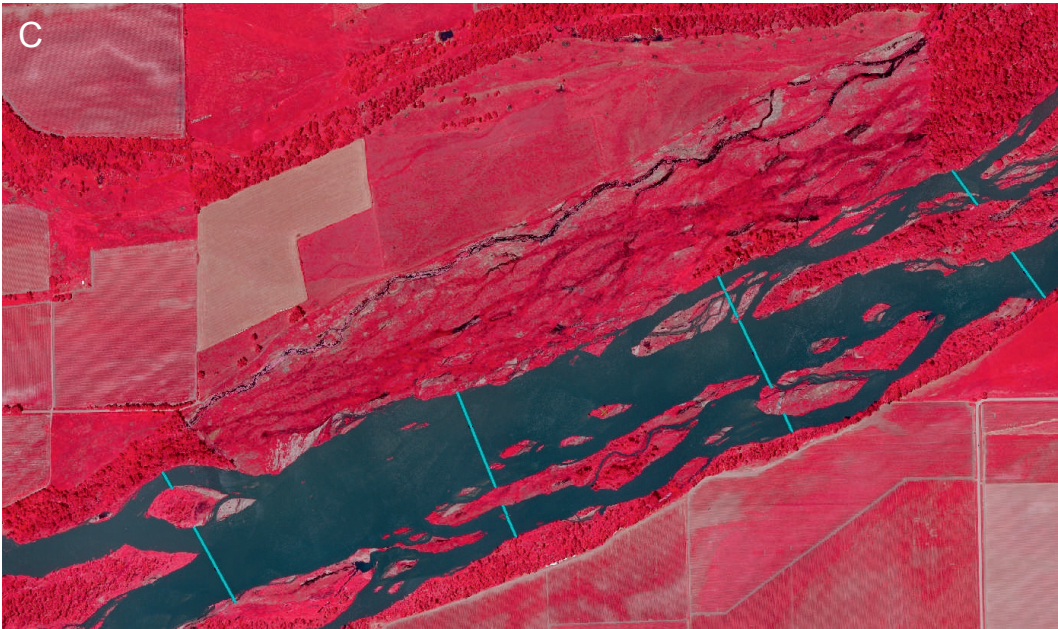


Fig. 3. Total unobstructed channel width measurements. *A*, 1938, black and white imagery. *B*, 1998, color infrared imagery. *C*, 2016, color infrared imagery. Channel width was measured every 800 m near the Dippel Island restoration site, bridge segment 6, southwest of Gibbon, Nebraska, USA (ArcGIS 10.2.1). All images were collected via aerial photography. Unobstructed channel width measurements are presented in blue.

of Landsat data with a pixel resolution of 30 cm was used for 1998. For the purposes of this study, lowland tallgrass prairie (Kaul et al. 2006) and wet meadow (Currier 1982) habitats were not differentiated, and an analysis was performed to classify an aggregated meadow-prairie land cover type. We manually delineated areas of contiguous herbaceous vegetation within 800 m of the Platte River that were dominated by nonwoody species (including grasses [Poaceae], sedges [Cyperaceae], rushes [Juncaceae], and herbaceous forbs [Asteraceae, Lamiaceae, etc.; Currier 1982, Kaul et al. 2006]) using a “heads-up” classification approach on imagery resampled to a 1-ft (30.5-cm) pixel resolution for consistency between years (Cushnie 1987, Grossman et al. 1994, Ghimire et al. 2014). Areas with scattered trees exceeding 30% vegetative cover were considered woodland habitats and were therefore not included in areas of meadow-prairie vegetation (Currier 1982, Grossman et al. 1998). Two individual observers reviewed all “heads-up” classifications of meadow-prairie habitat to ensure accuracy.

To assess tree cover, imagery was resampled to a 3.28-ft (1-m) pixel resolution, and classification methods were broadly based off of work quantifying cedar encroachment (Coppedge et al. 2001a, Ghimire et al. 2014) and delineating range habitats (Cingolani et al. 2004). Using image segmentation in the Spatial Analyst toolbox in ArcGIS 10.5.1, adjacent pixels with similar spectral properties were grouped together. As Cushnie (1987) noted, land cover classification can be improved via the coarsening of image resolution, because creating internally homogenous units can lessen “noise” in the image. We performed pixel-based supervised classification using the interactive maximum likelihood classifier tool in ArcGIS on the segmented images, where pixels were assigned to one of 5 classes: *tree cover*, *water*, *herbaceous* (grassland and agricultural production), *sand/nonvegetated*, or *developed*. Tree cover training samples ( $n = 83$ ) were selected from areas that had been surveyed during habitat-monitoring efforts from 2015 to 2017, which included both deciduous and coniferous species. We used the majority filter, the boundary clean tool, and manual

inspection to correct the raw classification (see Ghimire et al. 2014). Final raster classifications were converted to polygons, visually inspected, and corrected for accuracy (see Ghimire et al. 2014). Tree cover included scattered individuals or groups of trees within woodlands, as well as larger polygons of contiguous forest habitat; we labeled this land cover category as “woodland-forest” for analyses. We then calculated the proportion of land cover within 800 m of the main channel of the Platte River that was classified as woodland-forest and as meadow-prairie in 2016, as well as the change in proportion of meadow-prairie from 1998 to 2016 within each of the 11 bridge-delineated segments (Fig. 1).

#### Data Analyses

We examined the chronology of the spring MCP migration in the CPRV and investigated temporal trends within our data. To summarize seasonal variation, we calculated sample means, standard deviations, and maximum values for Sandhill Crane counts by survey week. We then calculated sample means and standard deviations for peak count and survey week of peak count for each segment. Additionally, we created boxplots of Sandhill Crane counts per survey week for selected individual segments, in order to illustrate the variation in peak timing from east to west across our survey area (ggplot2 package, R Core Team 2015, Wickham 2009). We calculated sample means, standard deviations, and maximum and minimum values for the Julian date (1–365 or 1–366 for leap year) of peak Sandhill Crane migration across all years, as well as Julian date of counts exceeding 125,000, to best approximate the time period when large numbers of Sandhill Cranes are present in the CPRV via our survey data. We used 125,000 Sandhill Cranes, because that number represents approximately 25% of a conservative estimate of the number of cranes in the CPRV (Kinzel et al. 2006, Dubovsky 2017); 25% is a biologically significant proportion (Wilson 2013).

To investigate potential trends in the timing of Sandhill Crane staging in the CPRV, we used bivariate ordinary least squares linear regression to model the yearly change in arrival dates of key proportions of the MCP from 2002 to 2017 (stats package, R Core Team 2015). Wilson (2013) noted that the arrival of “significant percentiles” of migratory

avian populations is more biologically meaningful and sensitive to weather parameters than first detection dates. Therefore, we used 7 Sandhill Crane count metrics to assess arrival: (i–iii) the Julian date that more than 5%, 15%, and 25% of a year’s peak count was first detected via aerial surveys; (iv–v) the percent of the year’s peak count observed in survey weeks 4 (05–11 March) and 5 (12–18 March), which generally predate peak Sandhill Crane abundance in the CPRV but occasionally support large abundances (Krapu et al. 2014, Pearse et al. 2015); (vi) the Julian date of peak Sandhill Crane count; and (vii) the Julian dates that Sandhill Crane counts were greater than 125,000 by survey year in our trend analyses. Although this final metric (vii) uses raw count data, it is likely not biased by potential population growth in its ability to assess an advancing migration. Counts exceeding 125,000 should become more frequent throughout the survey period in the face of population growth in the absence of temporal shifts. However, if counts exceeding 125,000 are becoming more common only early in the migration across years, this metric will be a useful indicator of a shifting migration. We also analyzed the proportion of the peak count detected in survey week 8 (02–08 April) by year to assess whether or not cranes were leaving progressively earlier from 2002 to 2017. Survey week 8 (02–08 April) generally postdates peak Sandhill Crane abundance in the CPRV, but it occasionally supports large numbers of cranes (Krapu et al. 2014, Pearse et al. 2015). Therefore, it may be a good indicator of shifting departure dates.

To summarize the spatial distribution of Sandhill Cranes within the CPRV, we calculated sample means and standard deviations of abundance metrics for each of the 11 segments in our study area from 2002 to 2017, including the count per survey, the maximum value of count per survey during a single study year, the density per kilometer, and the proportion of cranes counted in each segment per survey year. For comparison, we calculated the mean density per kilometer and proportion of Sandhill Cranes per segment from 2015 to 2017. We used data from 2015 to 2017 because it best represented the distribution of Sandhill Cranes following recent restoration efforts, and therefore was likely most reflective of their responses. To further investigate Sandhill Crane distributions and the trends

therein, we calculated the aforementioned summary statistics for larger reaches of the CPRV as well (East: 1–4; Central: 5–7; West: 8–11; Fig. 1). We then used a one-way analysis of variance (ANOVA) test with a Tukey's Honest Significant Differences (HSD) post hoc test to examine differences in Sandhill Crane roosting densities across these larger river reaches and segments (stats package, R Core Team 2015). To determine long-term trends in Sandhill Crane use per segment and in larger river reaches, we used bivariate ordinary least squares linear regression models to examine the relationship between the proportion of the total crane count per segment and survey year.

To investigate the association between winter moisture conditions (PDSI) and temperatures on Sandhill Crane migration phenology, we calculated Pearson's product-moment correlation coefficients for winter and early spring weather data in relation to a number of Sandhill Crane metrics meant to serve as indicators of early migration (Hmisc package, Harrell 2017; R Core Team 2015, NOAA-NCDC 2017). Sandhill Crane arrival metrics included the Julian date that the Sandhill Crane count reached 30,000 via our survey methods (hereafter, >30K), the Julian date that the count reached 100,000 (hereafter, >100K), the Julian date that the count reached 15% or more of the peak count for that year (hereafter, >15%), and the total Sandhill Crane counts during survey week 4 (hereafter, WK4) and week 5 (hereafter, WK5). We hypothesized that the PDSI and mean temperatures across wintering and migration locations would be negatively correlated with the arrival dates of >100K, >30K, and >15% Sandhill Cranes, suggesting that warmer, drier winters are related to earlier arrival dates of larger numbers of cranes (Harner et al. 2015). Following the same logic, we surmised that these same metrics would be positively related to the numbers of cranes in survey weeks 4 and 5.

To determine which wintering locations are most associated with trends in early arrivals of large numbers of Sandhill Cranes in the CPRV, we used Akaike's Information Criterion corrected for small sample sizes (AICc) to compare generalized linear models (GLMs) of weather and drought indices at wintering and migration locations in relation to Sandhill Crane arrival metrics (Nelder and Baker 1972, Hurvich and Tsai 1989, Burnham et al. 2011;

MuMIn package, Barton 2016; stats package, R Core Team 2015). We modeled Sandhill Crane arrival metrics (>30K, >100K, WK4, WK5, >15%) using mean annual winter temperature and PDSI values for major wintering locations, and mean annual late-winter and early spring temperature and PDSI values for major spring migration stopover locations. We included the year as a control variable to account for any long-term trends in migration not driven by annual weather (i.e., population growth, changes in observer, etc.). No mean winter or spring temperatures were substantially correlated ( $r \geq 0.50$ ) with corresponding PDSI values or year for key wintering and migration locations, suggesting that multicollinearity was not an issue in our multivariate models (Dormann et al. 2013). We tested for correlations across sites within years to determine whether any wintering/migration regions were sufficiently similar to warrant combination for analyses. We determined that the climate regions were distinct and should be included individually in the analysis. Most sites were significantly correlated with at least one other site regarding either mean temperatures or PDSI values. However, most sites were not significantly correlated on both metrics. For instance, mean temperatures in Oklahoma and New Mexico were not significantly correlated ( $r = 0.37$ ), but PDSI values were correlated ( $r = 0.81$ ). Similarly, temperatures in Kansas and Oklahoma were significantly correlated ( $r = 0.67$ ), but PDSI values were not correlated ( $r = 0.16$ ). Even those sites that were significantly correlated regarding both metrics did not approach statistical singularity. For instance, temperatures ( $r = 0.86$ ) and PDSI values ( $r = 0.76$ ) on the Texas Coast and in the Texas Panhandle were significantly correlated but appeared sufficiently distinct to warrant individual inclusion in the analysis. We also included a null model regressing the dependent variable by 1. We ran a total of 35 models—7 models (southwest Oklahoma drought [PDSI] and temperature [Temp], Texas coast drought and temperature, Texas Panhandle drought and temperature, southern New Mexico drought and temperature, central Kansas drought and temperature, central Nebraska drought and temperature, and a null model) for each of the 5 Sandhill Crane arrival metrics (>30K, >100K, WK4, WK5,

and >15%). We report only the top-performing models in the results, achieving an Akaike weight of  $\geq 0.10$  (Wagenmakers and Farrell 2004).

To examine the influence of land cover characteristics and channel width measurements on Sandhill Crane habitat use within segments of the CPRV, we summarized the following habitat metrics: (i) percent woodland-forest cover in 2016, (ii) percent meadow-prairie cover in 2016, (iii) change in percent meadow-prairie cover from 1998 to 2016, (iv) percent conservation management in 2016 (% of land within 800 m of the main channel owned or managed by conservation organizations in 2016 including state [i.e., USFWS] and nonstate [i.e., The Nature Conservancy] actors), (v) median longitude per segment, (vi) change in UOCW from 1938 to 2016, (vii) change in MUCW from 1938 to 2016, (viii) change in the number of active channels from 1938 to 2016, (ix) change in UOCW from 1998 to 2016, (x) change in MUCW from 1998 to 2016, (xi) UOCW in 2016, and (xii) MUCW in 2016. Sandhill Crane habitat use metrics included the following: (i) the statistical trend in the proportion of Sandhill Cranes detected per segment from 2002 to 2017, (ii) the mean proportion of Sandhill Cranes per segment from 2015 to 2017, and (iii) the mean density of Sandhill Cranes per segment from 2015 to 2017. We then used Pearson's product-moment correlation analyses between habitat metrics and Sandhill Crane use metrics per segment (Hmisc package, Harrell 2017; R Core Team 2015). After that, we constructed a series of bivariate generalized linear models with Gaussian distributions, using each habitat metric as an explanatory variable and Sandhill Crane use metrics ii and iii (mean proportion and mean density per segment 2015 to 2017, respectively) as dependent variables (26 models total, including null models; Hurvich and Tsai 1989, Burnham et al. 2011; stats package, R Core Team 2015). Because we were limited to 11 observations (one per segment for all spatial analyses variables), we used bivariate models (Vittinghoff and McCulloch 2007) and selected the best-fit model among candidate models by using AICc (Wagenmakers and Farrell 2004; MuMIn package, Barton 2016; stats package, R Core Team 2015). Lastly, we employed ordered logistic regression with a cumulative "probit" link function to determine

the habitat metrics that best explained the trend in the proportional use of segments from 2002 to 2017 (use metric iii, 13 models total, including null model; McCullagh 1980, Christensen 2015, R Core Team 2015). Trends in the proportional use of each segment were coded as ordered factors ( $-1$  = negative,  $0$  = no trend,  $1$  = positive) and models were compared using AICc (Wagenmakers and Farrell 2004; MuMIn package, Barton 2016; stats package, R Core Team 2015).

## RESULTS

From 2002 to 2017, we conducted 108 aerial survey counts between the dates of 11 February and 16 April, surveying a total of 1162 segments (11 segments multiple times) and counting a total of 12,831,526 cranes across 14 survey years; our surveys were not conducted in 2011 and 2012 due to lack of financial resources and staffing. Our mean estimate per segment was  $11,043 \pm 21,336$  Sandhill Cranes across all years. Comparisons of aerial ocular estimates with bias-corrected estimates derived from photo subplots in 2016 and 2017 revealed a mean absolute error of  $\pm 9.44\%$  (SD = 3.42%, range  $\pm 3.20\%$  to  $\pm 14.0\%$ ) across surveys ( $n = 14$ ), with a relative error of  $-3.42\%$ , considering the directionality of error estimates (SD = 8.4%, range  $-14.0\%$  to 13.5%). Our bias-corrected peak count of Sandhill Cranes roosting between Chapman and Overton was  $418,759 \pm 46,901$  in 2016 and  $429,916 \pm 27,386$  in 2017.

### Temporal Trends

Mean Sandhill Crane counts per survey week from 2002 to 2017 for the survey region from Chapman to Overton, Nebraska, demonstrated that survey week 7 (26 March–01 April) had the highest mean Sandhill Crane count, followed by weeks 8 (02–08 April) and 6 (19–25 March); all exceeded an average of 200,000 Sandhill Cranes (Table 1). High counts of over 400,000 Sandhill Cranes were observed in all weeks from week 4 (05–11 March) to week 8 (02–08 April) (Table 1). Mean date of peak Sandhill Crane count per year was 25 March ( $\bar{x} =$  day 84.1), with a standard deviation of approximately 9 days (SD = 9.2 days). However, we observed peak numbers from as early as 8 March (day 67) to as late as 8 April (day 98). Aerial counts of Sandhill Cranes exceeding

TABLE 1. Mean (with standard deviation) and maximum Sandhill Crane counts by survey week (1–10) on the main channel of the Platte River from Chapman to Overton, Nebraska, from spring 2002 through spring 2017.  $N = 108$  aerial surveys with 103 calendar weeks surveyed (when multiple surveys were conducted in a calendar week, the highest count was used). The total number of survey years was 14, and surveys were not conducted in 2011 and 2012. Not all segments were flown every week, primarily because of in-flight changes in weather.

Survey week	$n$	Dates	$\bar{x}$	SD	Maximum
1	2	12 Feb to 18 Feb	8073	103	8146
2	6	19 Feb to 25 Feb	15,891	24,948	66,017
3	10	26 Feb to 04 Mar	41,298	60,212	194,825
4	12	05 Mar to 11 Mar	73,560	119,180	405,857 <sup>^</sup>
5	13	12 Mar to 18 Mar	112,672	112,971	404,170 <sup>^^</sup>
6	13	19 Mar to 25 Mar	206,241 <sup>^</sup>	105,679	410,066 <sup>^^</sup>
7	11	26 Mar to 01 Apr	254,468 <sup>^</sup>	110,734	541,100 <sup>^^</sup>
8	14	02 Apr to 08 Apr	212,017 <sup>^</sup>	125,183	567,525 <sup>^^</sup>
9	11	09 Apr to 15 Apr	94,891	75,866	270,015
10	11	16 Apr to 22 Apr	19,346	36,667	109,025

<sup>^</sup> Indicates a mean aerial count of >200,000 Sandhill Cranes within a survey week.

<sup>^^</sup> Indicates a maximum aerial count of >400,000 Sandhill Cranes within a survey week.

TABLE 2. Bivariate ordinary least squares linear regression analyses of Julian date of peak Sandhill Crane count (Peak), Julian dates of all Sandhill Crane counts over 125,000 (>125K), Julian date when Sandhill Crane counts first reached 5%, 15%, and 25% of peak yearly count (>5%, >15%, >25%), and the proportion of peak Sandhill Crane count observed during survey week 4 (05 Mar–11 Mar; %WK 4), 5 (12 Mar–18 Mar; %WK 5), and 8 (02 Apr–08 Apr; %WK 8) by survey year (coefficient) from 2002–2017.  $n = 45$  for the SACR > 125,000 analysis and  $n = 14$  for all other analyses. “DV” = dependent variable.

Metric	DV	$B$	SE	$t$	$P$	$R^2$	df
Peak	Julian date	-1.324	0.364	-3.63	0.0034**	0.524	12
>125K	Julian date	-1.134	0.277	-4.10	0.0002***	0.281	43
>5%	Julian date	-1.413	0.428	-3.30	0.0063**	0.476	12
>15%	Julian date	-1.155	0.309	-3.73	0.0029**	0.537	12
>25%	Julian date	-1.434	0.334	-4.29	0.0010**	0.605	12
%WK 4	Proportion	0.034	0.013	2.59	0.0268*	0.402	10
%WK 5	Proportion	0.035	0.012	2.89	0.0151*	0.430	11
%WK 8	Proportion	-0.039	0.016	-2.38	0.0343*	0.322	12

\* $P < 0.05$

\*\* $P < 0.01$

\*\*\* $P < 0.001$

125,000 were observed from 27 February to 11 April, with a mean date of 24 March ( $\bar{x} =$  day 82.6,  $SD = 9.9$  days). Median Sandhill Crane counts were highest in week 7, exceeding the 75th percentile of both weeks 6 and 8. However, the 1.5 times interquartile range of Sandhill Crane counts for week 6, denoting extreme but not outlying values, exceeded weeks 7 and 8 (see Wickham 2009).

Bivariate ordinary least squares linear regression analyses demonstrated that counts of more than 125,000 Sandhill Cranes advanced an average of approximately 1.13 days per year across the 16-year survey period ( $P < 0.01$ ; Table 2, Fig. 4). Similarly, peak Sandhill Crane count advanced on average 1.32 days per year ( $P < 0.001$ ), and the Julian date on which more than 15% of the year's peak Sandhill Crane count was first observed advanced on average

1.16 days per year ( $P < 0.01$ ; Table 2, Fig. 4). The proportion of the peak Sandhill Crane count observed during survey week 5 (12–18 March) increased by 3.5% per year from 2002 to 2017 ( $P < 0.05$ ; Table 2, Fig. 4). The proportion of the peak Sandhill Crane count observed during survey week 8 (02–08 April) decreased 3.9% per year ( $P < 0.05$ ; Table 2).

Cranes in the survey area did not demonstrate a uniform temporal peak among segments; instead, there was a distinct difference in eastern and western portions. From 2002 to 2017, easternmost segments 1–3, spanning from Chapman to Alda, Nebraska, had the highest mean counts during survey week 6 (19–25 March); segment 4 had the highest mean counts during week 7 (26 March–01 April); and central and western segments 5–11, from Wood River to Overton, Nebraska,



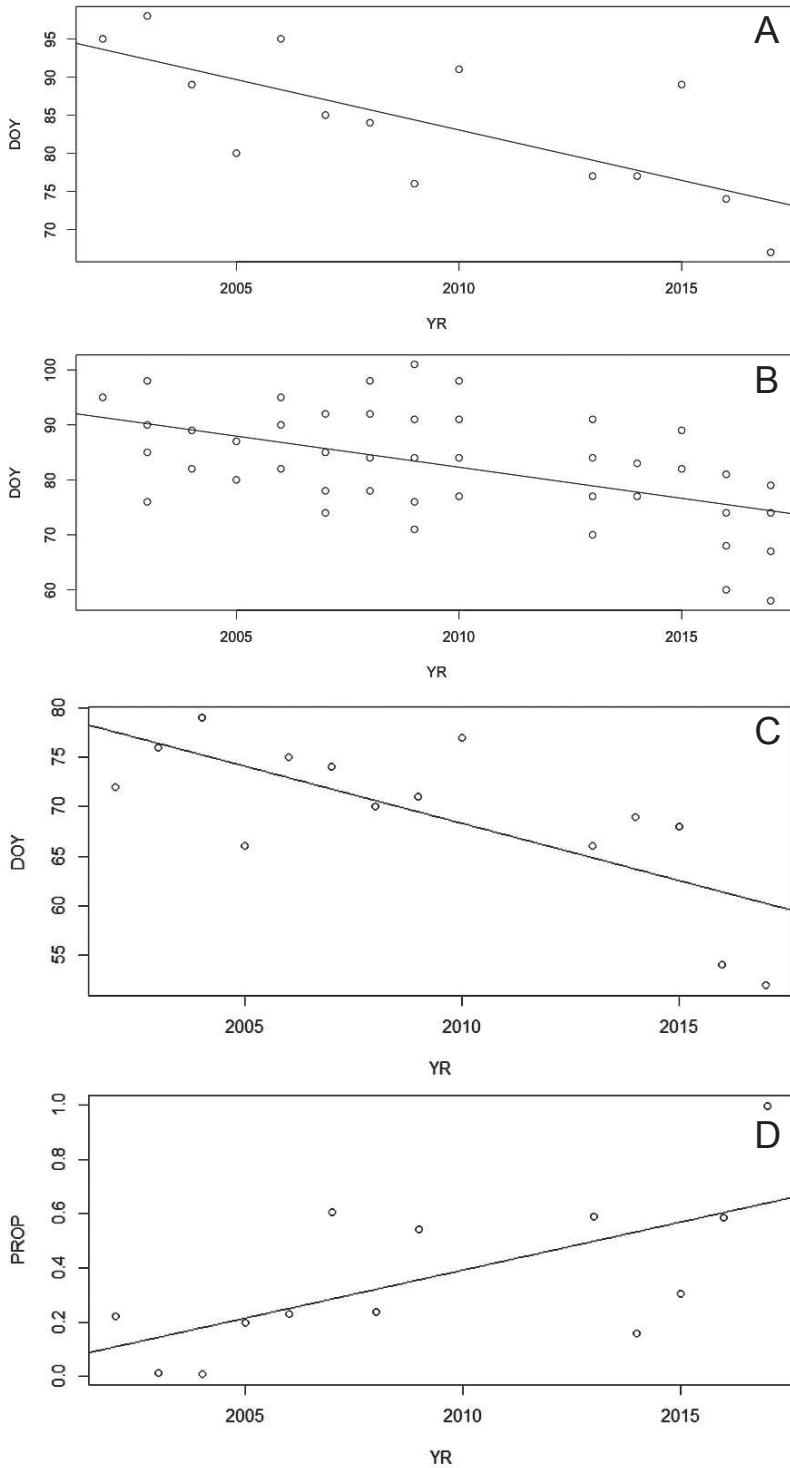


Fig. 4. Sandhill Crane abundance and arrival metrics fit with ordinary least squares bivariate regression lines by survey year, 2002–2017. A, Julian date (DOY) of peak Sandhill Crane count by year (YR). B, Julian dates (DOY) of Sandhill Crane counts exceeding 125,000 by year (YR). C, Julian date (DOY) when Sandhill Crane counts exceeded 15% of peak by year (YR). D, Proportion of the peak Sandhill Crane count observed in week 5 (12–18 March; PROP) by year (YR).

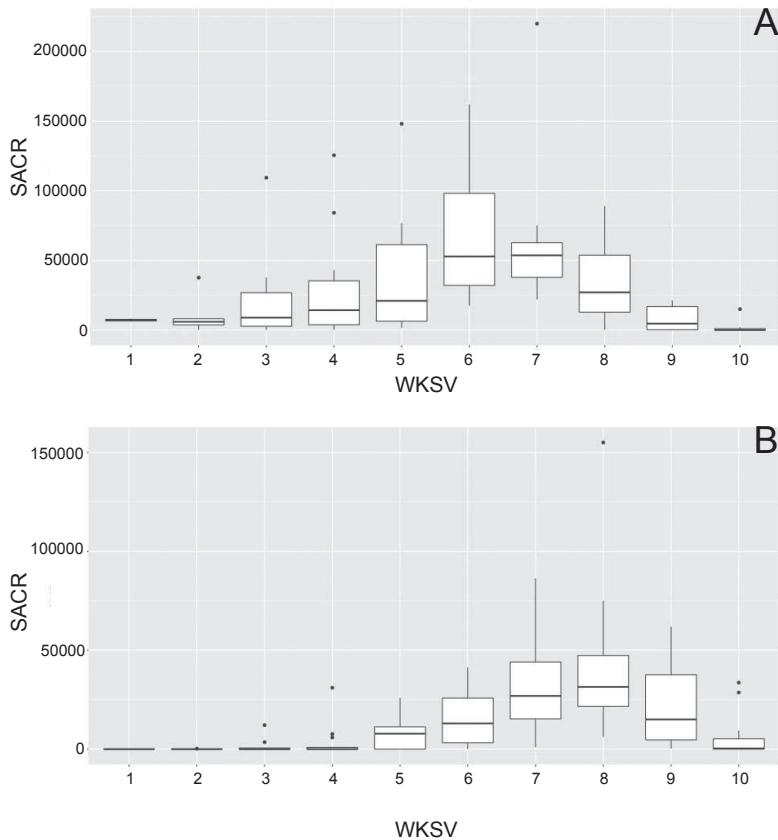


Fig. 5. Weekly Sandhill Crane counts. *A*, Bridge segment 3 (HWY 281 to Alda Rd.). *B*, Bridge segment 7 (Gibbon to HWY 10). In bridge segment 3, median counts are statistically similar for weeks 6 and 7, but the upper interquartile range and whisker are highest for week 6. In bridge segment 7, median and upper quartile counts are highest during week 8, though the whisker in week 7 slightly exceeds that in week 8. SACR = Sandhill Crane, WKS = survey week.

peaked during survey week 8 (02–08 April; Table 3). High counts in eastern segments (1–4) began to decline just as central and western segments (5–11) reached peak numbers (Table 3; Fig. 5). Segments 3 and 7 have historically held some of the highest densities of cranes, and they were separated from east to west by areas of relatively lower density (Krapu et al. 2014). The median weekly count was highest during week 6 in segment 3, but farther west in segment 7, the median weekly count was highest during week 8 (Fig. 5).

#### Spatial Trends

From 2002 to 2017, mean counts of Sandhill Cranes per segment were highest for segments 3, 4, and 7, respectively (Table 4). These segments also had the highest observed Sandhill Crane densities per kilometer of river

channel (Table 4, Figs. 6, 7) and, along with segments 2 and 5, each averaged over 10% of the recorded Sandhill Cranes per survey season (Table 4). Sandhill Crane densities per kilometer from 2002 to 2017 varied significantly across survey segments ( $F = 22.13$ ,  $P < 0.001$ ; Appendix 1). Tukey HSD post hoc tests revealed that segment 3 (HWY 281 to Alda) had a significantly higher density than all other segments, excluding segment 4 (Alda to Wood River). Segment 4 had a higher density of cranes than all segments with the exceptions of segments 7 and 3 (Gibbon to HWY 10). However, a comparison of data from the most recent surveys (2015 to 2017) to those of earlier years suggests that Sandhill Crane densities are increasing over time in the east (Table 4, Fig. 6). The 3 highest Sandhill Crane densities for 2015 to 2017 were

TABLE 3. Mean yearly peak Sandhill Crane count and mean survey week of yearly peak across aerial surveys ( $N = 108$ ) and years by survey bridge segment and length, 2002–2017. When multiple average Sandhill Crane counts by survey week were within one standard deviation of each other, we used the median count to determine peak survey week. See Fig. 1 for map of segments. SACR = Sandhill Crane.

Segment/location	km	$\bar{x}$ peak SACR	$\bar{x}$ peak survey week
1 Chapman–HWY 34	17.1	18,423	6 (19 Mar to 25 Mar)
2 HWY 34–HWY 281	11.6	36,114	6 (19 Mar to 25 Mar)
3 HWY 281–Alda	10.7	68,913	6 (19 Mar to 25 Mar)
4 Alda–Wood River	8.5	39,561	7 (26 Mar to 01 Apr)
5 Wood River–Shelton	13.9	38,180	8 (02 Apr to 08 Apr)
6 Shelton–Gibbon	10.1	25,046	8 (02 Apr to 08 Apr)
7 Gibbon–Hwy 10	9.1	42,457	8 (02 Apr to 08 Apr)
8 HWY 10–Kearney	11.4	10,107	8 (02 Apr to 08 Apr)
9 Kearney–Odessa	14.7	4065	8 (02 Apr to 08 Apr)
10 Odessa–Elm Creek	11.0	3971	8 (02 Apr to 08 Apr)
11 Elm Creek–Overton	13.6	851	8 (02 Apr to 08 Apr)

TABLE 4. Mean weekly Sandhill Crane count ( $\bar{x}$ ), maximum mean weekly count for a single survey year (max), mean count per kilometer of river channel ( $\bar{x}/\text{km}$ ), and mean proportion of the yearly Sandhill Crane counts ( $\bar{x}$  Prop.) during 108 aerial surveys in 2002–2017; mean count per kilometer of river channel ( $\bar{x}/\text{km}$  15–17) and mean proportion of the yearly Sandhill Crane counts ( $\bar{x}$  Prop. 15–17) during 2015–2017. Metrics are shown by survey bridge segment and reach of river from Chapman to Overton, Nebraska<sup>a</sup>. “Reach” refers to a larger section of the study area and includes multiple bridge segments. The East Reach includes segments 1–4, the Central Reach includes segments 5–6, and the West Reach includes segments 8–11. See Table 3 for a description of bridge segments and Fig. 1 for a map of segments and reaches.

Reach/ segment	$\bar{x}$	SD	max	$\bar{x}/\text{km}$	$\bar{x}$ Prop.	$\bar{x}/\text{km}$ 15–17	$\bar{x}$ Prop. 15–17
East	75,085	35,350	140,269	1568	59.6%	2107	75.8%
1	5786	3838	13,335	338	5.2%	523	7.4%
2	14,168	6501	29,952	1221	11.7%	1918 <sup>3</sup>	17.6%
3	33,203 <sup>1</sup>	20,188	81,583 <sup>1</sup>	3103 <sup>1</sup>	25.4%	4023 <sup>1</sup>	32.2%
4	21,928 <sup>2</sup>	10,316	43,507 <sup>3</sup>	2580 <sup>2</sup>	17.3%	3137 <sup>2</sup>	18.6%
Central	42,640	21,975	96,515	1288	33.8%	812	20.3%
5	15,672	7698	26,923	1128	13.2%	546	5.8%
6	9623	6238	23,769	953	7.8%	382	3.2%
7	17,345 <sup>3</sup>	11,510	47,233 <sup>2</sup>	1906 <sup>3</sup>	12.8%	1697	11.3%
West	7173	3538	13,331	141	5.7%	100	4.0%
8	4002	2168	9119	351	3.1%	311	2.8%
9	1539	1081	4204	105	1.3%	47	0.6%
10	1419	1534	4707	129	1.1%	45	0.4%
11	213	410	1316	16	0.2%	25	0.2%

<sup>a</sup>Superscripts 1, 2, and 3 are used to rank Sandhill Crane abundance per bridge segment via the various metrics.

segments 3, 4, and 2, respectively, with segment 7 being the only segment in the western two-thirds of the survey area to support over 10% of the Sandhill Cranes (Table 4, Fig. 6). The same pattern is clear when comparing discrete survey periods; the mean proportion of Sandhill Cranes counted per survey year from 2013 to 2017 was higher than from 2002 to 2010 in each of the eastern segments (1–4) and lower in each of the central and western segments (5–11; Fig. 8). Comparing 2013 to 2017 and 2002 to 2010, increases were most pronounced in segments 1 (mean  $\pm$  SD; 8.5%  $\pm$  4.9% vs. 3.3%  $\pm$  2.5%)

and 3 (32.2%  $\pm$  2.9% vs. 21.6%  $\pm$  8.2%), while decreases were most prominent in segments 5 (16.3%  $\pm$  6.6% vs. 7.6%  $\pm$  2.7%) and 6 (10.2%  $\pm$  4.3% vs. 3.6%  $\pm$  1.3%; Fig. 8).

When 11 survey segments were grouped into 3 larger reaches of the CPRV (East [1–4], Central [5–7], and West [8–11]), survey data from 2002 to 2017 showed that the East Reach accounted for 59.6% of the Sandhill Cranes counted (Table 4). When the most recent surveys from 2015 to 2017 were examined, the eastern segments accounted for 75.8% of the Sandhill Cranes counted (Table 4). Concurrently, when the discrete survey periods were

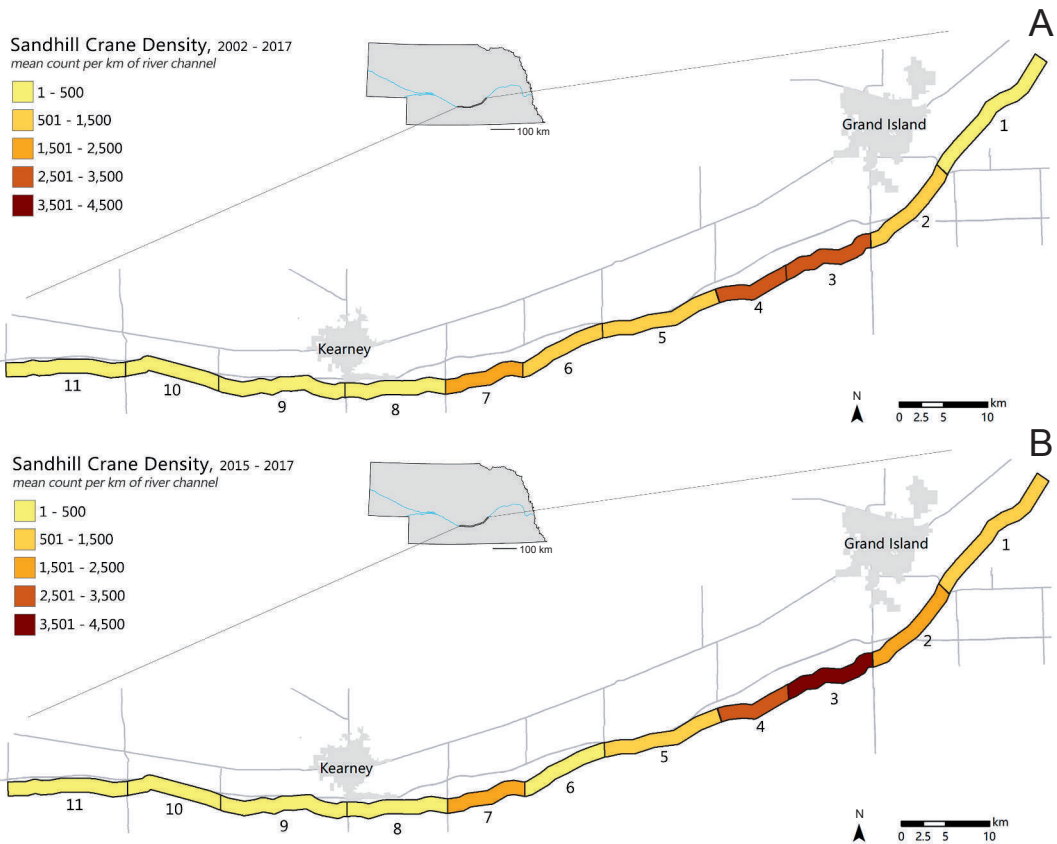


Fig. 6. Mean Sandhill Crane density per kilometer by bridge segment. A, 2002 to 2017. B, 2015 to 2017.

compared, 73.4% of Sandhill Cranes were detected in eastern segments from 2013 to 2017, compared to 51.8% from 2002 to 2010 (Fig. 8). Sandhill Crane densities varied widely across East, Central, and West reaches of the CPRV ( $F = 27.7$ ,  $P < 0.001$ ; Appendix 1). Densities in the East and Central reaches were significantly higher than in the West reach, but not significantly different from each other across all data from 2002 to 2017 (Table 4, Fig. 7, Appendix 1).

Bivariate ordinary least squares linear regression models showed statistically significant trends in the proportion of Sandhill Cranes using particular segments from 2002 to 2017 (Table 5). Segment 1 (Chapman to HWY 34) demonstrated a positive trend in the proportion of cranes using it on a yearly basis (+0.5% annually,  $P < 0.05$ ; Table 5). The proportion of cranes using segment 3 (HWY 281 to Alda Road) increased 1.4% per year ( $P < 0.001$ ; Table 5). Segment 5 (Wood River to Shelton)

demonstrated a significant decline in the proportion of cranes using it annually (−1.2% annually,  $P < 0.001$ ; Table 5). Negative trends were also noted in segments 6 (Shelton to Gibbon; −0.7% annually,  $P < 0.01$ ) and 9 (Kearney to Odessa; −0.1% annually,  $P < 0.01$ ; Table 5). Analysis of larger reaches showed that the proportion of Sandhill Crane use in the eastern segments increased 2.3% annually ( $P < 0.001$ ). By contrast, there was a significant decline in the proportion of Sandhill Cranes using the central segments (−2.0% annually,  $P < 0.001$ ) and a marginal decline in the proportion of cranes using the western segments (−0.2% annually,  $P < 0.10$ ; Table 5).

#### Temporal Factors

Daily average winter (January–February) and early spring (February–March/April) temperatures from major Sandhill Crane wintering and migratory stopover regions were negatively correlated with the arrival date of >30K

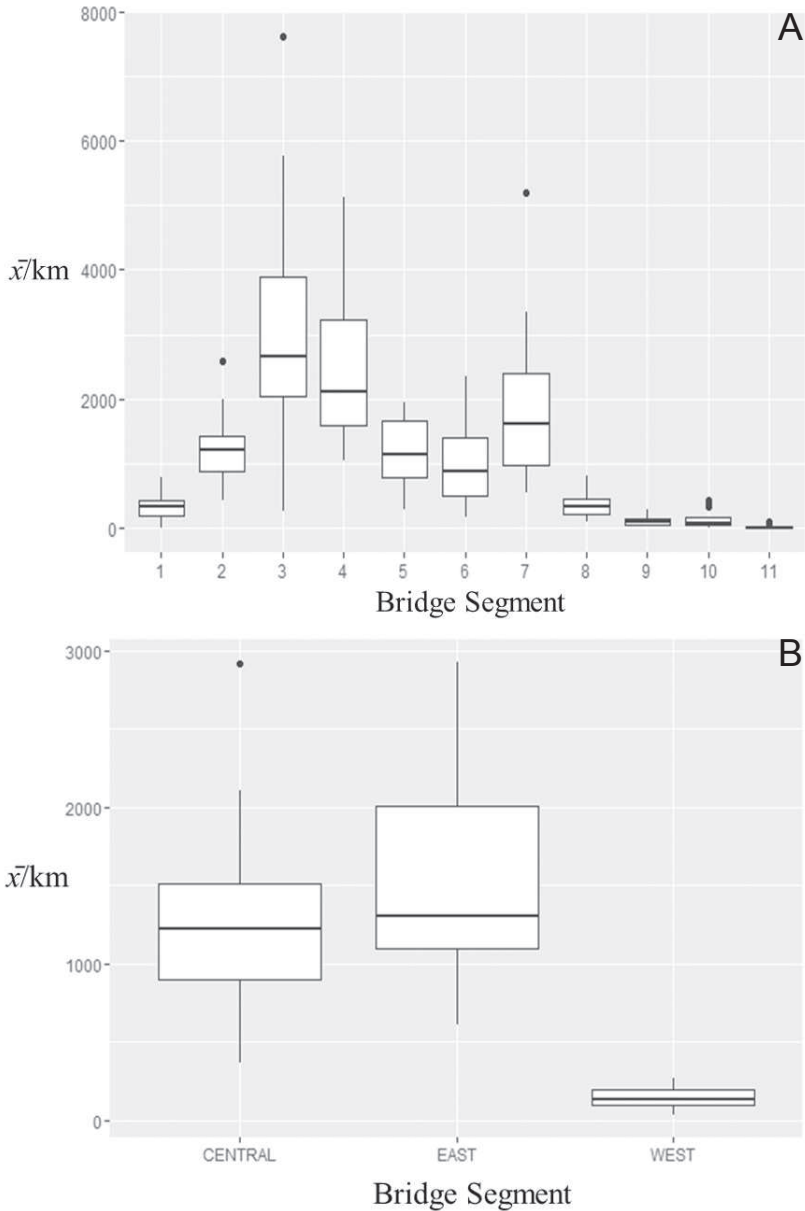


Fig. 7. Sandhill Crane density (mean count per kilometer;  $\bar{x}/\text{km}$ ) from 2002 to 2017. A, Density by bridge segment (1–11). B, Density by river reach (Central, East, and West). Black horizontal lines denote median values, while the tops and bottoms of boxes denote the upper and lower interquartile ranges (75th and 25th percentiles), respectively. Extending “whiskers” denote values of 1.5 times the interquartile range; areas outside of this range constitute outliers and are marked with points. For a description of bridge segments and reaches, see Fig. 1.

Sandhill Cranes in all locations but southern New Mexico (Table 6). Average temperatures from southwestern Oklahoma ( $r = -0.84$ ,  $P < 0.001$ ), the Texas Panhandle ( $r = -0.81$ ,  $P < 0.001$ ), and the Texas Coastal Plain ( $r = -0.80$ ,  $P < 0.001$ ) demonstrated the strongest

correlations, suggesting that as temperatures increased in these locations, Sandhill Cranes arrived earlier in the CPRV (Table 6). Similarly, the arrival date of >15% and the Sandhill Crane counts during survey week 4 were significantly correlated with temperatures at

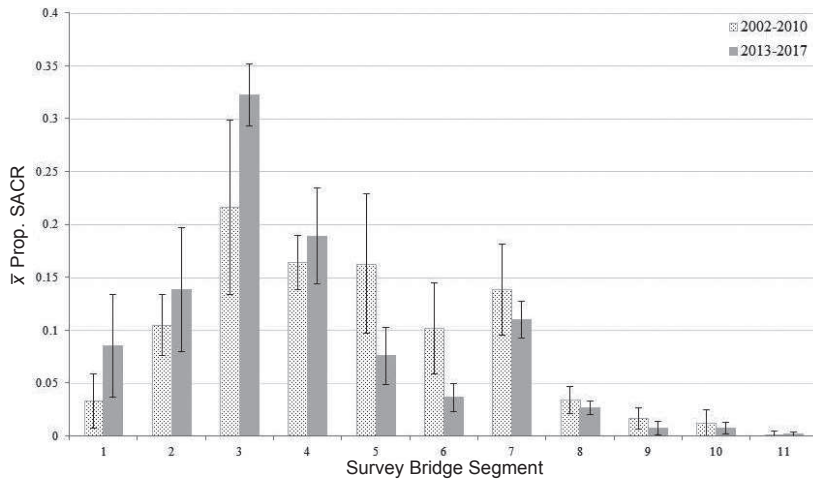


Fig. 8. The mean proportion of Sandhill Cranes ( $\bar{x}$  Prop. SACR) counted in each survey bridge segment per year from 2002 to 2010 (patterned bars) and from 2013 to 2017 (gray bars). Error bars represent one standard deviation from the mean.

TABLE 5. Bivariate ordinary least squares linear regression models for trends in the proportion of Sandhill Cranes per bridge segment (1–11) and river reach (including East [1–4], Central [5–7], and West [8–11]) by survey year, 2002–2017. See Table 3 for a description of bridge segments and Fig. 1 for a map of segments and reaches.

Reach/segment	DV	<i>B</i>	SE	<i>t</i>	<i>P</i>	R <sup>2</sup>	df
East	Prop.	0.0233	0.0028	8.25	0.001***	0.850	12
1	Prop.	0.0049	0.0020	2.51	0.027*	0.344	12
2	Prop.	0.0023	0.0024	0.99	0.343	0.075	12
3	Prop.	0.0135	0.0029	4.63	0.001***	0.641	12
4	Prop.	0.0025	0.0018	1.39	0.190	0.138	12
Central	Prop.	-0.0200	0.0035	-5.76	0.001***	0.735	12
5	Prop.	-0.0116	0.0021	-5.56	0.001***	0.720	12
6	Prop.	-0.0072	0.0017	-4.15	0.001**	0.589	12
7	Prop.	-0.0011	0.0021	-0.54	0.601	0.023	12
West	Prop.	-0.0021	0.0010	-1.98	0.071	0.246	12
8	Prop.	-0.0007	0.0006	-1.19	0.256	0.101	12
9	Prop.	-0.0013	0.0004	-3.12	0.009**	0.449	12
10	Prop.	-0.0001	0.0005	-0.20	0.846	0.003	12
11	Prop.	0.00004	0.0002	0.28	0.784	0.006	12

\**P* < 0.05

\*\**P* < 0.01

\*\*\**P* < 0.001

all locations except southern New Mexico, and most strongly correlated with temperatures in the Texas Coastal Plain ( $r = -0.64$ ,  $P < 0.05$ , and  $r = 0.73$ ,  $P < 0.01$ , respectively; Table 6). The average February and March temperatures in central Kansas had the strongest correlation with >100K Sandhill Cranes ( $r = -0.68$ ,  $P < 0.01$ ) and Sandhill Crane counts in survey week 5 ( $r = 0.75$ ,  $P < 0.001$ ; Table 6). The Palmer Drought Severity Index in Oklahoma averaged for January and February had a marginal negative correlation with >100K, as well as >15% Sandhill Cranes ( $P <$

0.10; Table 6). New Mexico weather data was not related to arrival dates in the CPRV for any metric. Average temperatures in central Kansas were related to all crane arrival metrics (Table 6).

Sandhill Cranes >30K was best predicted by weather and drought conditions in the Texas Panhandle (wt = 0.59), closely followed by weather conditions in southwestern Oklahoma (wt = 0.40; Table 7). Both of these models demonstrated a highly significant negative relationship between average temperature and arrival date on the Platte River, but they

TABLE 6. Pearson’s product-moment correlation coefficients relating average temperature (Temp) and Palmer’s Drought Severity Index (PDSI) measures for key wintering areas (January–February) and migration locations (February–March/April) to the Julian date (JD) when Sandhill Crane counts (SACR) reached 30,000 (30K), 100,000 (100K), and 15% of a respective year’s peak count, as well as Sandhill Crane counts for survey week 4 (WK4; 5 March–11 March) and week 5 (WK5; 12 March–18 March), 2002–2017. J–F = January–February, F–M = February–March, and F–A = February–April.

Wintering/ stopover area	Coefficient (months)	JD SACR >30K	JD SACR >100K	SACR WK4	SACR WK5	JD SACR >15%
SW Oklahoma	Temp (J–F)	–0.84***	–0.35	0.65*	0.60*	–0.59*
	PDSI (J–F)	–0.37	–0.53	0.46	0.42	–0.46
Texas Panhandle	Temp (J–F)	–0.81***	–0.36	0.58*	0.46	–0.54*
	PDSI (J–F)	–0.37	–0.44	0.31	0.33	–0.40
Texas Coastal Plain	Temp (J–F)	–0.80***	–0.50	0.73**	0.70**	–0.64*
	PDSI (J–F)	–0.12	0.01	0.12	0.12	–0.08
S. New Mexico	Temp (J–F)	–0.40	–0.23	0.28	0.10	–0.31
	PDSI (J–F)	–0.24	–0.34	0.18	0.34	–0.24
Central Kansas	Temp (F–M)	–0.78**	–0.68**	0.70*	0.75**	–0.62*
	PDSI (F–M)	–0.12	–0.33	0.02	0.29	0.03
Central Nebraska	Temp (F–A)	–0.61*	–0.51	0.62*	0.50	–0.53*
	PDSI (F–A)	–0.21	–0.18	0.06	0.34	0.03

\*P < 0.05  
 \*\*P < 0.01  
 \*\*\*P < 0.001

TABLE 7. All generalized linear models with a delta weight  $\geq 0.10$  used to predict the relationship between temperature (Temp) and Palmer Drought Severity Index (PDSI) at key Sandhill Crane wintering areas (Location) and the Julian date (JD) when Sandhill Crane counts (SACR) reached 30,000 (30K), 100,000 (100K), and 15% of a respective year’s peak count (top), as well as Sandhill Crane counts (bottom) for survey week 4 (WK4; 05–11 March) and week 5 (WK5; 12–18 March) at the staging grounds in the Central Platte River Valley, Nebraska, 2002–2017. In the models, survey year functions as a control variable along with average temperature (Temp) and drought (PDSI) from particular locations functioning as covariates. “logLik” refers to log likelihood.

Dependent variable	Location	Temp. <i>B</i>	PDSI <i>B</i>	logLik	AICc	delta	weight
JD SACR >30K	TX Panhandle	–2.6848***	–0.4317	–36.72	90.9	0.00	0.59
JD SACR >30K	Southwest OK	–2.5137***	–0.4121	–37.11	91.7	0.78	0.40
JD SACR >100K	Central KS	–1.2798**	–1.3338^	–37.32	92.1	0.00	0.90
JD SACR >15% PK	TX Coast	–1.2768***	–1.1903*	–33.68	84.9	0.00	0.71
JD SACR >15% PK	Southwest OK	–1.2665**	–1.0991*	–34.90	87.3	2.43	0.21
SACR WK4 (05–11 Mar)	TX Coast	21,624**	16,910*	–145.80	311.6	0.00	0.84
SACR WK4 (05–11 Mar)	Southwest OK	21,035*	14,572	–147.90	315.8	4.19	0.10
SACR WK5 (12–18 Mar)	TX Coast	21,059**	15,189^	–159.46	337.5	0.00	0.55
SACR WK5 (12–18 Mar)	Central KS	18,694**	10,487	–159.93	338.4	0.94	0.35

^P < 0.10  
 \*P < 0.05  
 \*\*P < 0.01  
 \*\*\*P < 0.001

also included PDSI as a nonsignificant variable (Table 7). For every unit increase in average temperature across January and February in the Texas Panhandle, the model predicted a 2.7-day earlier arrival of at least 30,000 Sandhill Cranes (Table 7). Sandhill Cranes >100K was best predicted by climate conditions in central Kansas (wt = 0.90), and included both average temperature ( $P < 0.01$ ) and, marginally, PDSI ( $P < 0.10$ ) as significant variables, suggesting that increased temperatures and drought in Kansas (to some degree) were associated with advanced

arrival dates of 100,000 Sandhill Cranes to the CPRV.

Average temperatures ( $P < 0.001$ ) and PDSI ( $P < 0.05$ ) in Coastal Texas (wt = 0.71), followed by average temperatures ( $P < 0.01$ ) and PDSI ( $P < 0.05$ ) in southwestern Oklahoma (wt = 0.21), best predicted the >15% Sandhill Crane arrival dates. For every unit increase in the average winter temperature in Coastal Texas, the model predicted that >15% of Sandhill Cranes would arrive 1.3 days earlier to the CPRV, and that for every unit increase in the PDSI, cranes would arrive

TABLE 8. Summary of the percent of land owned and managed by conservation organizations within 800 m of the main channel of the Platte River in 2016, the percent land cover classified as woodland-forest and meadow-prairie in 2016, and the percent change in land cover classified as meadow-prairie from 1998 to 2016 per survey bridge segment. See Fig. 1 for map of segments and study area.

Segment/ location	Woodland 2016 (%)	Meadow-prairie 2016 (%)	$\Delta$ Meadow-prairie 1998–2016 (%)	Conservation mgmt. 2016 (%)
1 Chapman–HWY 34	21.5	20.7	–0.42	0.0
2 HWY 34–HWY 281	13.3	12.7	–0.78	0.7
3 HWY 281–Alda	3.4	49.6	1.32	67.4
4 Alda–Wood River	9.8	29.4	6.89	43.0
5 Wood River–Shelton	21.3	6.9	–0.60	16.7
6 Shelton–Gibbon	11.9	16.2	6.26	14.1
7 Gibbon–HWY 10	4.3	25.9	3.38	60.7
8 HWY 10–Kearney	18.8	13.3	12.11	38.2
9 Kearney–Odessa	30.7	2.0	–0.93	13.1
10 Odessa–Elm Creek	29.1	10.3	1.97	34.2
11 Elm Creek–Overton	30.6	7.0	1.48	40.5

1.2 days earlier (Table 7). In addition, week 4 Sandhill Crane counts were best predicted by environmental conditions in Coastal Texas ( $wt = 0.84$ ), including both temperature ( $P < 0.01$ ) and PDSI ( $P < 0.05$ ) as significant independent variables in the model. Our model suggests an increase of 21,624 Sandhill Cranes in survey week 4 (05–11 March) with every degree increase in average winter temperatures in Coastal Texas, and a 16,910 increase in Sandhill Cranes for a one-unit increase in PDSI (Table 7). Temperature in southwestern Oklahoma also demonstrated a notable impact on week 4 Sandhill Crane counts ( $wt = 0.10$ ). Week 5 Sandhill Crane counts were best predicted by environmental conditions in Coastal Texas ( $wt = 0.55$ ), including both average temperature ( $P < 0.01$ ) and, marginally, drought conditions ( $P < 0.10$ ), followed by conditions in central Kansas ( $wt = 0.35$ ; Table 7).

#### Spatial Factors

Our land cover analysis revealed that in 2016, the proportion of woodland-forest cover and the proportion of wet meadow–tallgrass prairie (meadow-prairie) cover within 800 m of the main channel of the Platte River varied widely across the CPRV (Table 8, Fig. 9). Segments 9, 10, and 11 each had approximately 30% woodland-forest cover, whereas segments 3 and 7 both had <5%, and segment 4, <10% woodland-forest cover (Table 8). There was over 25% meadow-prairie cover in segments 3, 4, and 7, whereas segments 5, 9, and 11 each contained <10% (Table 8, Fig. 9). Efforts by conservation organizations to restore wet meadow and tallgrass prairie throughout the

CPRV were evident in the percent change of meadow-prairie from 1998 to 2016; segment 8 increased in meadow-prairie cover by 12.1%, while segments 4 and 6 saw between a 6% and 7% increase. The proportion of area within 800 m of the main channel of the Platte River managed by conservation organizations ranged from 0% in segment 1 to over 60% in segments 3 and 7 (Table 8).

On average, from 1938 to 2016, UOCW of the main channel of the Platte River decreased 59%, MUCW decreased 57%, and the number of total active channels of the Platte River increased 12% (Appendix 2, Fig. 10). It is important to note that our channel width analysis did not consider peripheral channels, which have arguably demonstrated greater losses in portions of the CPRV (Williams 1978, Currier 1991, Johnson 1994). The greatest decrease in channel width of the main channel was evident in segment 9 (Kearney to Odessa), which decreased 82% in UOCW and 79% in MUCW (Appendix 2). Concurrently, segment 9 increased 140% in the number of active channels, because the once singular and wide channel ( $\bar{x} = 1110$  m,  $SD = 121$  m, in 1938; Appendix 2, Fig. 10) became fragmented by several stabilized and relatively large wooded islands (Figs. 3, 9; Appendix 2). By contrast, segment 4 decreased the least, with a loss of 15% of UOCW, a loss of 11% of MUCW, and a decrease in the number of active channels. This pattern was also observed for segment 3, which decreased 21% in the number of active channels and largely maintained its channel width (Figs. 3, 9; Appendix 2). Historically, segments 3 and 4 were narrower than the western segments



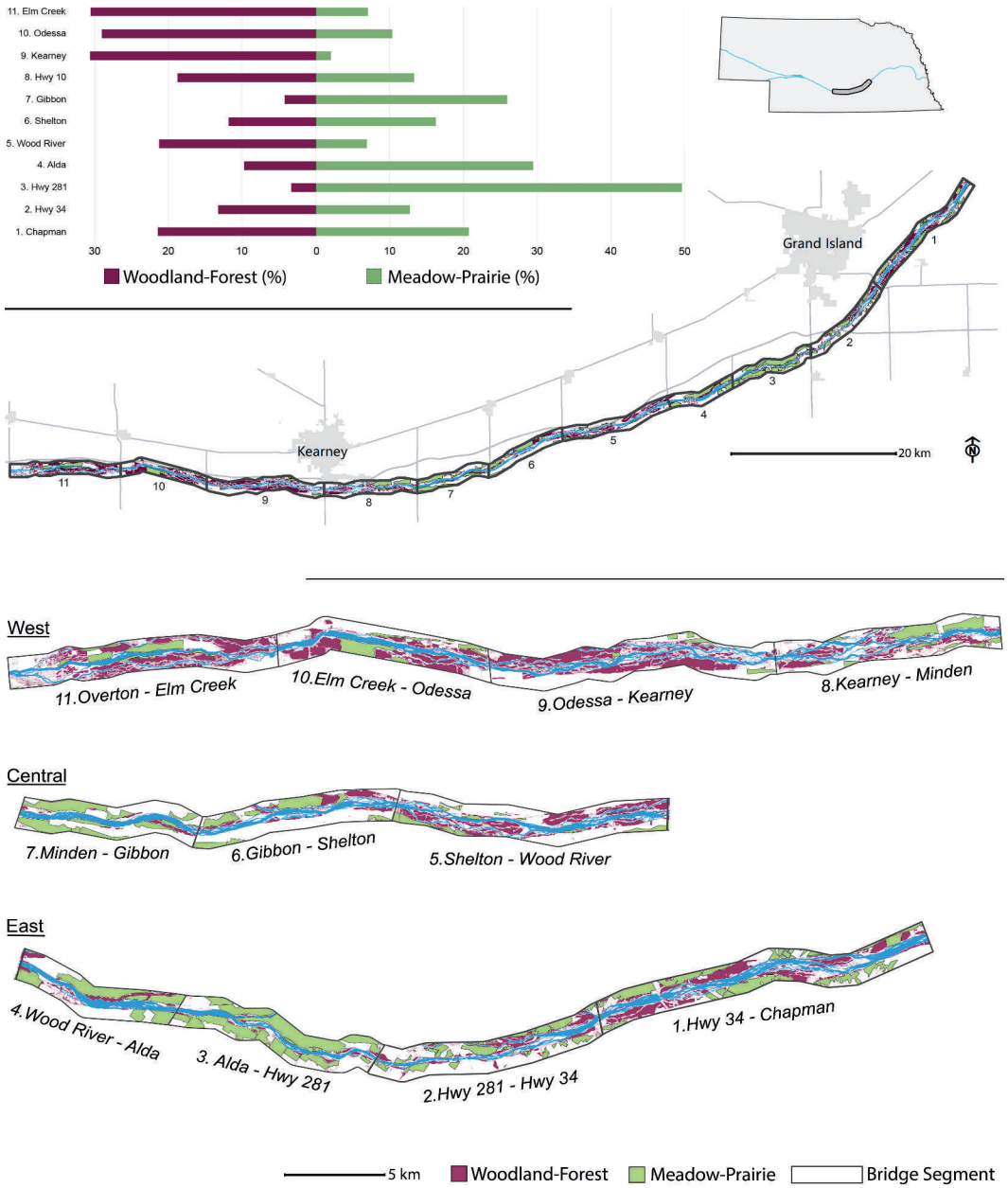


Fig. 9. Proportion of meadow-prairie and woodland-forest land cover within 800 m of the main channel of the Platte River per bridge segment within the Central Platte River Valley in 2016.

(8–11) because the river was divided into multiple channels in those areas ( $\bar{x}$  = 304 m, SD = 40 m, and  $\bar{x}$  = 377 m, SD = 106 m, respectively, in 1938; Appendix 2), and the complete loss of some northern side channels to woody accretion between 1938 and 2016 absorbed much of the declines in flow (Figs. 3, 9;

Appendix 2). The western segments (8–11) observed the greatest declines in channel width and the highest increases in the number of active channels (Fig. 10, Appendix 2). All segments improved when both MUCW and UOCW from 1998 to 2016 were considered (Appendix 2).

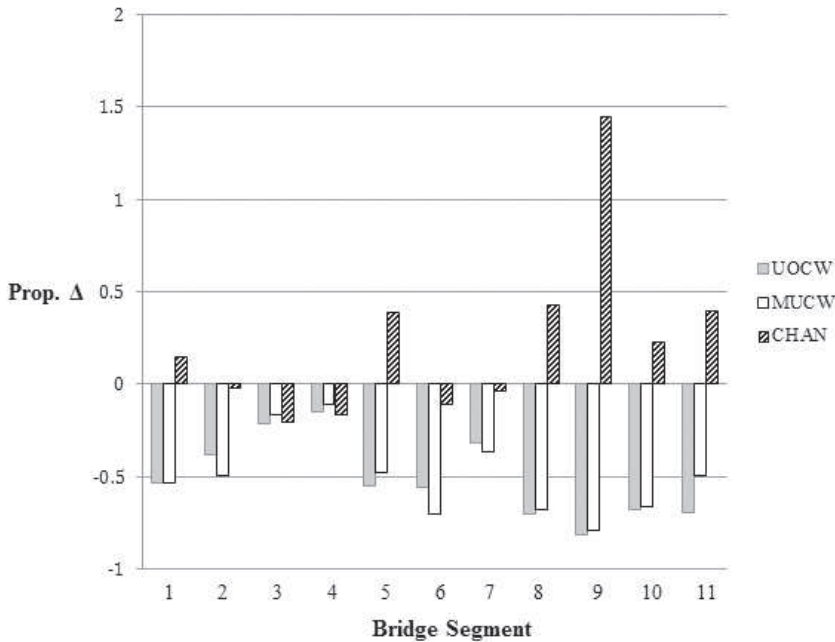


Fig. 10. Proportional change in total (UOCW) and maximum (MUCW) unobstructed channel width within the main channel of the Central Platte River, as well as the proportion change in the total number of active channels of the Platte River (CHAN), 1938–2016.

TABLE 9. Pearson's product-moment correlation coefficients for the relationships between habitat covariates and Sandhill Crane abundance metrics per bridge segment, including channel width measurements, percent meadow-prairie, percent woodland-forest, and percent of conservation managed area in 2016, channel width changes observed since 1938 and 1998, respectively, and change in meadow-prairie from 1998 to 2016. Sandhill Crane abundance variables include the trend in proportional use from 2002 to 2017 (Trend) as well as the mean proportion ( $\bar{x}$  Prop.) and density of Sandhill Cranes ( $\bar{x}$ /km) observed per bridge from 2015 to 2017. Segments (1–11) include all bridge segments between Chapman and Overton, Nebraska; Longitude (E–W) = median longitude;  $\Delta UOCW$  1938–2016 = percent change in unobstructed channel width from 1938 to 2016;  $\Delta MUCW$  1938–2016 = percent change in maximum unobstructed channel width from 1938 to 2016;  $\Delta$ No. Active Channels = percent change in the number of active channels of the Platte River;  $\Delta UOCW$  1998–2016 = percent change in unobstructed channel width from 1998 to 2016;  $\Delta MUCW$  1998–2016 = percent change in maximum unobstructed channel width from 1998 to 2016;  $\bar{x}$  UOCW 2016 = mean unobstructed channel width in 2016;  $\bar{x}$  MUCW 2016 = mean maximum unobstructed channel width in 2016; % Woodland 2016 = percent woodland within 800 m of the main channel of the Platte River in 2016; % Meadow 2016 = percent meadow-prairie within 800 m of the main channel of the Platte River;  $\Delta$ Meadow 1998–2016 = percent change in meadow-prairie from 1998 to 2016; % Conservation 2016 = percentage of land owned or managed by conservation organizations within 800 m of the main channel of the Platte River.

Covariate	Trend	$\bar{x}$ Prop.	$\bar{x}$ /km
Segments (1–11)	-0.43	-0.67*	-0.58
Longitude (E–W)	0.41	0.68*	0.59
$\Delta UOCW$ 1938–2016	0.44	0.88***	0.92***
$\Delta MUCW$ 1938–2016	0.51	0.82**	0.88***
$\Delta$ No. Active Channels	-0.48	-0.60*	-0.60*
$\Delta UOCW$ 1998–2016	-0.46	-0.37	-0.34
$\Delta MUCW$ 1998–2016	-0.42	-0.53	-0.44
$\bar{x}$ UOCW 2016	0.22	0.17	0.20
$\bar{x}$ MUCW 2016	0.31	0.29	0.37
% Woodland 2016	-0.31	-0.78**	-0.80**
% Meadow 2016	0.67*	0.87***	0.88***
$\Delta$ Meadow 1998–2016	-0.04	-0.09	0.03
% Conservation 2016	0.33	0.42	0.52

\* $P < 0.05$

\*\* $P < 0.01$

\*\*\* $P < 0.001$

The proportion of meadow-prairie per segment in 2016 was the only land cover metric significantly correlated with the trend in the annual proportion of Sandhill Cranes per segment from 2002 to 2017 (Fig. 9, Table 9). The 2 habitat metrics having the strongest correlations with the mean proportional use of bridge segments from 2015 to 2017 were the change in UOCW from 1938 to 2016 and the proportion of meadow-prairie in 2016 (Table 9). The change in MUCW from 1938 to 2016 and the proportion of woodland-forested area in 2016 also demonstrated strong relationships with proportional use from 2015 to 2017 (Table 9). The density of Sandhill Cranes from 2015 to 2017 was highly correlated with change in UOCW ( $r = 0.92$ ,  $P < 0.001$ ) and MUCW ( $r = 0.88$ ,  $P < 0.001$ ) from 1938 to 2016, and with the proportion of meadow-prairie ( $r = 0.88$ ,  $P < 0.001$ ) and woodland-forest in 2016 ( $r = -0.80$ ,  $P < 0.01$ ) (Table 9). These variables also demonstrated strong correlations among themselves (Appendix 3): change in UOCW from 1938 to 2016 was highly correlated with both meadow-prairie cover ( $r = 0.82$ ,  $P < 0.001$ ) and woodland-forest cover ( $r = -0.86$ ,  $P < 0.001$ ), while meadow-prairie cover and woodland-forest cover exhibited a strong negative correlation ( $r = -0.81$ ,  $P < 0.001$ ; Appendix 3).

The top bivariate model for predicting Sandhill Crane density from 2015 to 2017 was the change in UOCW (wt = 0.81) followed by the change in MUCW (wt = 0.10) from 1938 to 2016 (Table 10). Change in UOCW from 1938 to 2016 (wt = 0.48) and the proportion of meadow-prairie in 2016 (wt = 0.41) best determined the proportion of Sandhill Cranes using each segment from 2015 to 2017 (Table 10). The proportion of meadow-prairie in 2016 (wt = 0.42) was the best predictor of the statistical trend in the proportional use of segments by Sandhill Cranes from 2002 to 2017 (Table 10, Fig. 11).

## DISCUSSION

Our investigation of 14 years of Sandhill Crane aerial survey data suggested that the migration chronology in the CPRV has high annual variation. We documented peak counts over a wider range of dates than the majority of published records; this range is likely a result of our long-term data set (Davis 2001,

Pearse et al. 2010, Buckley 2011, Krapu et al. 2014). Annual weather influenced chronology of migration to the CPRV, and we found indications of advancing migration arrival, with the most recent years showing significant numbers of Sandhill Cranes arriving in late February. By contrast, variation in the spatial distribution of Sandhill Cranes roosting along the Platte River was relatively patterned. Sandhill Crane distributions were related to the availability of quality river roost sites and meadow-prairie habitats that are important for foraging and social behavior. Long-term changes in hydrology and land cover were related to roosting Sandhill Cranes shifting eastward, creating higher densities in eastern segments. Our results demonstrated how temporospatial changes in a species' regional occurrence may be simultaneously associated with multiple independent processes that can interact in their influence; in this case, these processes are landscape-level habitat changes within the MCP's main spring staging area and wamer and drier winters associated with climate change on Sandhill Crane wintering grounds (see Runkle et al. [2017] and Fitzpatrick and Dunn [2019] for climate data and projections). Our results indicated that Sandhill Cranes are arriving at the CPRV earlier, staying longer, and concentrating in limited reaches with higher-quality riverine and meadow-prairie habitats in increasing densities. In this way, climatic variation and landscape-level habitat change are related to increasing site use intensity in portions of the CPRV.

## Temporal Dynamics

Our population indices were generally lower than those produced by the USFWS-coordinated spring survey of the MCP for the CPRV (Kinzel et al. 2006, Dubovsky 2016, 2017), suggesting that density estimates derived from our study may have negative bias. The USFWS predawn aerial surveys of the river were ceased in the early 1980s in favor of a daytime survey composed of transects running perpendicular to the river because the daytime surveys were deemed to provide more reliable population abundance indices (Ferguson et al. 1979, Benning and Johnson 1987). However, repeated predawn aerial surveys of the Central Platte River can produce useful depictions of river roosting distributions and relative densities over time (Davis 2003, Buckley 2011), and can

TABLE 10. Statistical models, with a delta weight  $\geq 0.10$  as measured by AICc, used to predict average density of Sandhill Cranes from 2015 to 2017 ( $\bar{x}/\text{km}$ ), average proportional use from 2015 to 2017 ( $\bar{x}$  Prop.), and trends in use from 2002 to 2017 (Trend) within bridge segments 1–11 in response to habitat variables. Coefficients include change in unobstructed channel width between 1938 and 2016 ( $\Delta\text{UOCW}$ ), change in maximum unobstructed channel width between 1938 and 2016 ( $\Delta\text{MUCW}$ ), and percent meadow-prairie land cover in 2016 (% Meadow-Prairie). An ordered logistic regression model with a cumulative “probit” link function was used to predict “Trend” ( $-1$  = negative,  $0$  = no trend,  $1$  = positive), and generalized linear models with Gaussian distributions were used to predict “ $\bar{x}/\text{km}$ ” and “ $\bar{x}$  Prop.”

Dependent variable	Coefficient	<i>B</i>	SE	<i>t/z</i>	Log likelihood	AICc	delta	weight
$\bar{x}/\text{km}$	$\Delta\text{UOCW}$	5840.2***	818.7	7.1	-84.1	177.7	0.00	0.81
	$\Delta\text{MUCW}$	5590.5***	988.4	5.7	-82.1	178.8	1.14	0.10
$\bar{x}$ Prop.	$\Delta\text{UOCW}$	0.41***	0.07	5.5	18.2	-26.9	0.00	0.48
	% Meadow-Prairie	0.66***	0.12	5.4	18.0	-26.6	0.30	0.41
Trend	% Meadow-Prairie	1.27*	0.64	1.9	-7.6	24.7	0.00	0.42

\* $P < 0.05$

\*\* $P < 0.01$

\*\*\* $P < 0.001$

be used to assess Sandhill Crane relative abundance and distribution in the CPRV (assuming that detection probability is relatively constant). Our results indicated that the average day of peak Sandhill Crane abundance in the CPRV was 25 March, one day earlier than the estimate provided by Pearse et al. (2015). We documented peak counts as early as 8 March and as late as 8 April across 14 survey years. Pearse et al. (2015) estimated peak counts between 13 March and 3 April from 2001 to 2007 using data from Sandhill Cranes tracked with platform transmitting terminals (PTTs). From 2001 to 2007, between 71% and 94% of PTT-marked Sandhill Cranes were present within the CPRV during the USFWS spring coordinated survey, suggesting that the yearly population indices reflected varying proportions of the MCP in the CPRV to a greater degree than real changes in the population (Pearse et al. 2015). Our results documented even wider temporal variation in Sandhill Crane peak abundance than the USFWS survey did. As Ferguson et al. (1979) recommended, conducting photo-corrected spring surveys weekly over a period of at least 3 weeks would likely reduce fluctuation in the USFWS population abundance index. However, doing so would need to be weighed against financial costs and the prospective value of finer-resolution but less frequent data. One solution could be to conduct surveys across 3 weeks every 3 years, which would equate to roughly the same effort and may produce a more robust abundance index. Another option may be to conduct replicate surveys in only the densest Sandhill Crane roosting areas annually; a combination of both alternative strategies could also work. It will

be important to consider the potential impacts of changing survey methods on the integrity of the USFWS’s long-term data set as well as harvest regulation management.

Distributions of Sandhill Cranes that were developed during the peak of migration (e.g., Kinzel et al. 2006, Dubovsky 2016) may underestimate eastern segments, which our findings indicate peaked in use 1–2 weeks ahead of western segments (Table 3, Fig. 5). Krapu et al. (2014) found some evidence for this underestimation, because WC–A and EC–M breeding affiliation Sandhill Cranes, which are predominantly Greater Sandhill Cranes, are more likely to roost in eastern segments (EC–M = 97.8% and WC–A = 76.8% east of Shelton). They also tend to have shorter total migrations, leaving the CPRV 3–12 days earlier than WA–S and NC–N breeding affiliation Sandhill Cranes, which comprise mostly Lesser Sandhill Crane subspecies (Krapu et al. 2014). Our findings also suggest that the early arrival of significant proportions of the MCP to the CPRV is associated with seasonal weather trends on the wintering grounds and southern stopover locations (Tables 6, 7). This trend seems particularly pronounced for EC–M, WC–A, and (to some degree) NC–N breeding affiliations of Sandhill Cranes that use the Texas Coastal Plain, the Texas Panhandle, southwestern Oklahoma, and central Kansas for their wintering grounds and migration routes (Krapu et al. 2011, 2014; Fig. 2). Our models indicated that an increase in the mean winter temperatures of a key wintering region by 1 °F (0.56 °C) was associated with an increase in the abundance index of Sandhill Cranes in the CPRV by tens of thousands of cranes in early

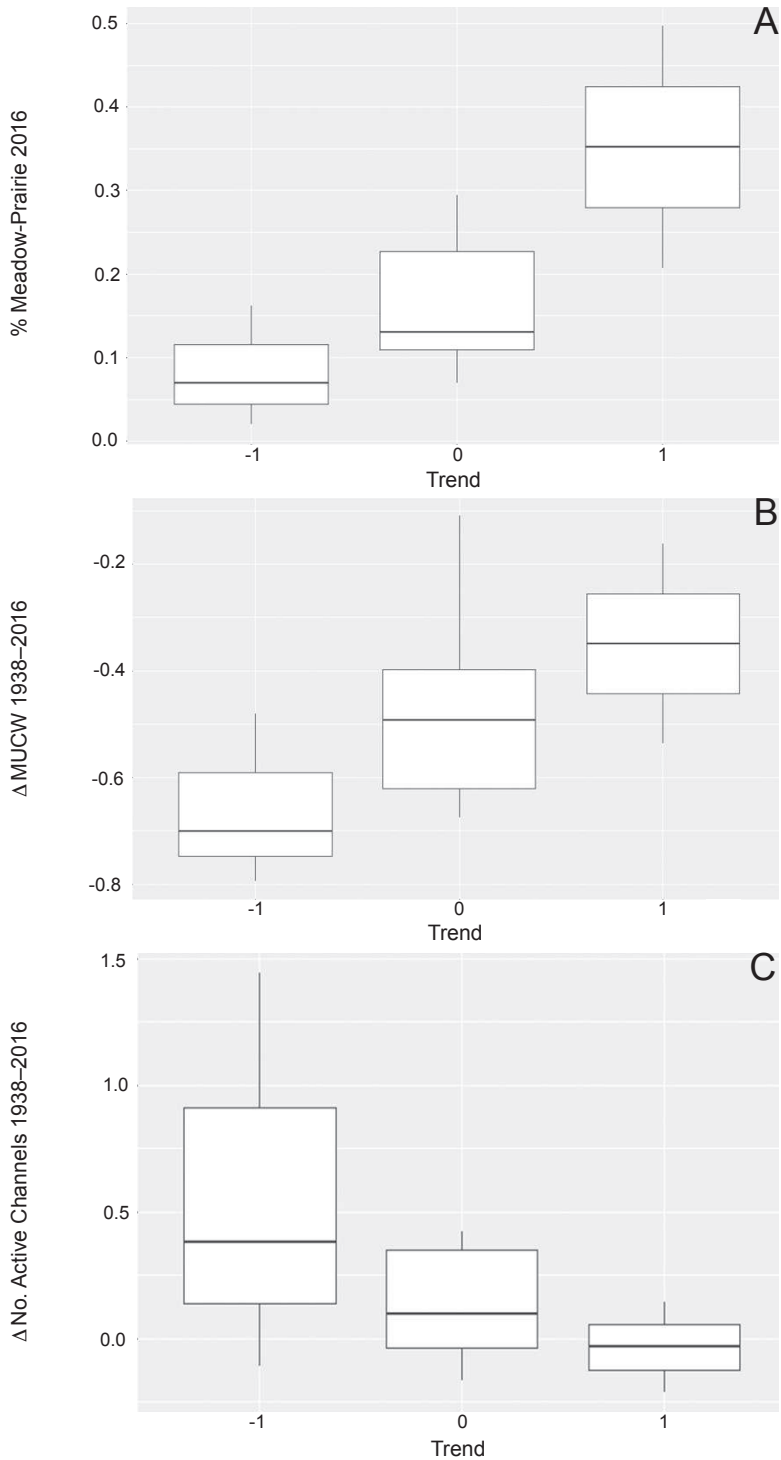


Fig. 11. Habitat parameters by bridge segments with statistically significant positive (1), stable (0), or negative (–1) trends (Trend) in the proportional use by Sandhill Cranes across survey years 2002–2017. Black horizontal lines denote median values, while the top and bottom of boxes denote the upper and lower interquartile ranges (75th and 25th percentiles), respectively. Extending “whiskers” denote values of 1.5 times the interquartile range; areas outside of this range constitute outliers and are marked with points. (Caption continued on page 61.)

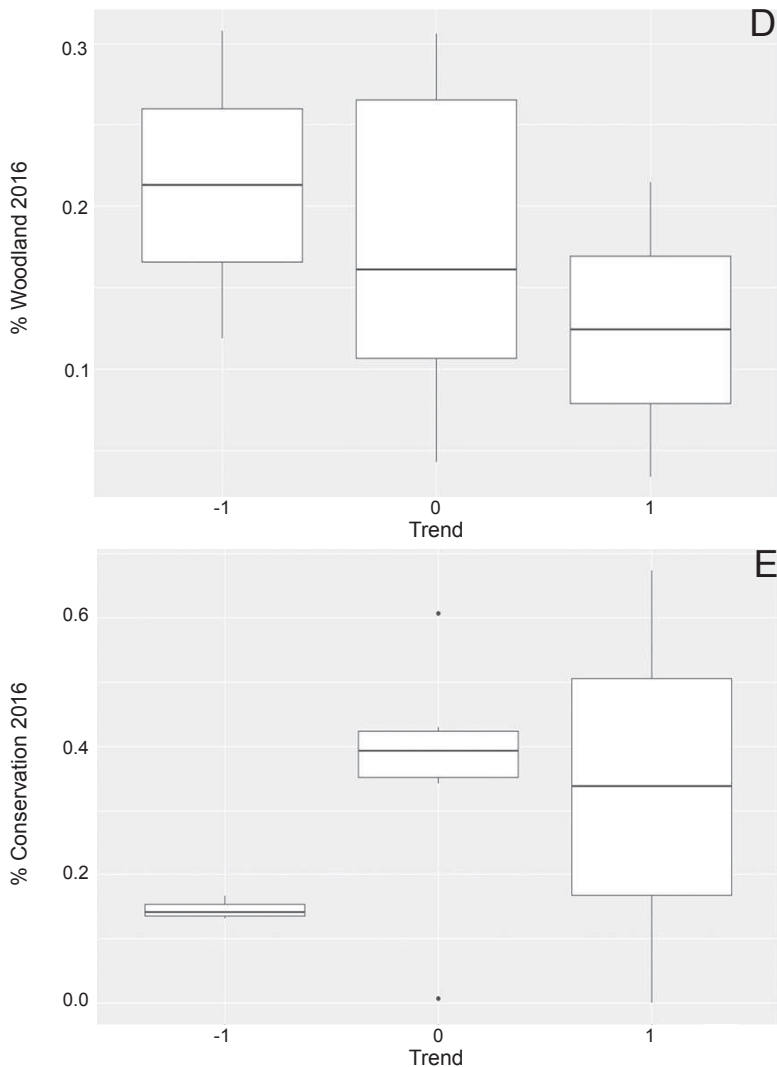


Fig. 11. Continued. A, Proportion of meadow-prairie land cover within 800 m of the main channel of the Platte River in 2016 (% Prairie-Meadow 2016). B, Percent change in maximum unobstructed channel width from 1938 to 2016 on the main channel of the Platte River ( $\Delta$ MUCW 1938–2016). C, Percent change in the number of active channels of the Platte River from 1938 to 2016 ( $\Delta$  No. of Active Channels 1938–2016). D, Proportion of land cover within 800 m of the main channel of the Platte River classified as woodland in 2016 (% Woodland 2016). E, Proportion of land within 800 m of the main channel of the Platte River owned or managed by conservation organizations in 2016 (% Conservation 2016). The highest median value for conservation ownership is where trends are flat.

March (Tables 6, 7). This association suggests that relatively small temperature changes could result in large temporal shifts in the timing of the MCP's spring migration, especially considering that average temperatures in Texas are projected to increase by  $\sim 4$  °F (2.22 °C; low-emissions scenario) to  $\sim 10$  °F (5.56 °C; high-emissions scenario) by 2100, compared to mean values from 1901–1960

(Runkle et al. 2017; mean temperatures in Texas have already increased 1 °F). Our results also demonstrated that a one-unit increase in PDSI values at some wintering locations (such as Coastal Texas) was associated with an increase of over 10,000 Sandhill Cranes in the CPRV in early March (Tables 6, 7). Coastal Texas is projected to receive between 5% and 10% less annual precipitation by 2050 (Runkle et

al. 2017). Along with temperature and recent available water content in soils, precipitation is a major determinant of soil moisture balance and therefore drought indices such as PDSI (Hayes et al. 2007). Consistent increases in temperature, along with decreases in precipitation, will increase the risk for drought and decrease available wetland area that Sandhill Cranes depend on throughout their wintering range (Hayes et al. 2007, Harner et al. 2015, Reese and Skagen 2017, Runkle et al. 2017).

A number of studies indicate that shorter-distance migrants, like those in the WC–A and EC–M breeding affiliations, are more flexible and responsive to local conditions in their migration timing and routes (Temple and Cary 1987, Adamík and Pietruszková 2008, Palm et al. 2009, Swanson and Palmer 2009). Given the relatively shorter migration distance of Greater Sandhill Cranes compared to Lesser Sandhill Cranes, it is possible that the former disproportionately comprises increases in early arrivals and potentially in overwintering occurrences (Harner et al. 2015). Mean winter temperatures and drought conditions on the Coastal Plain of Texas, predominantly a wintering location for Greater Sandhill Cranes, appeared to be a factor influencing early arrivals of significant numbers of cranes (Table 7). Concurrently, Krapu et al. (2014) found that departure dates from the CPRV were correlated with daily ambient temperatures in late March and early April for Greater Sandhill Cranes but not for Lesser Sandhill Cranes. Our research indicated a decline in Sandhill Cranes remaining in the CPRV through the first week of April (survey week 8, 02–08 April; Table 2). It is possible that this decline is influenced by Greater Sandhill Cranes departing the CPRV earlier in recent years. Krapu et al. (2014) also noted that staging length in the CPRV was negatively correlated with arrival dates, suggesting that early arrivals tend to stay longer. A high number of Sandhill Cranes extending the period in which they stage at the CPRV will likely put additional pressure on agricultural foraging resources (Pearse et al. 2010, Salvi 2012), as well as increase the disease risk for cranes and other waterbird species that overlap in wetland habitat use (Vogel et al. 2013, Bertram et al. 2017).

All metrics of migration chronology demonstrated an advancement of between 1.1 days

and 1.4 days per year (Table 2, Fig. 4). For instance, counts of over 125,000 Sandhill Cranes advanced during our study, while becoming scarcer later in the migration season across years, demonstrating that trends in early arrival were not the result of population growth but likely of a temporal shift in migration (Table 2, Fig. 4). From 1942 to 2016, Whooping Cranes advanced their spring and fall migration dates by approximately 21 and 22 days, respectively, in the central Great Plains (Jorgensen and Brown 2017), whereas Common Cranes (*Grus grus*) in France have advanced their spring migration by about 20 days over a period of 30 years (Filippi-Codaccioni et al. 2011). The first reported sightings of Sandhill Cranes submitted to the Nebraska Bird Review from 1914 to 2013 have advanced from approximately late March to early February (Harner et al. 2015). Our data suggest that the MCP has advanced its migration by between 18 and 23 days over the last 16 years. Despite the different temporal scopes of the data sets used to model changes in the migratory chronology of crane species, the various data sets each achieve a very similar result. The Common Crane, Whooping Crane, and Sandhill Crane have all advanced their spring migration in the Northern Hemisphere over historically recorded dates (Alonso et al. 2008, Prange 2012, Harner et al. 2015, Jorgensen and Brown 2017). Research suggests that climate in the CPRV during the last few decades has been anomalous compared to the climate record of the last 150 years, being more variable and showing a rapid warming trend (Hughes 2000, Mann et al. 2016, Pittock 2017, Runkle et al. 2017). Therefore, it is possible that a large portion of these migration advances have taken place over the last 2 decades, and that the increased climatic variation may also result in wider variation in the timing of spring staging in the CPRV (Harner et al. 2015, Pittock 2017). Increasing spring temperatures have been related to advancing migration chronology (Filippi-Codaccioni et al. 2011, Jorgensen and Brown 2017); our results corroborate these findings in that warmer temperatures at key wintering and early spring stopover locations explained variation in arrival dates and migration chronology of the MCP to the CPRV.

Despite the consistency of advancement in migration chronology across various metrics in our data, it is important to note that research

from the late 1970s and early 1980s described the Sandhill Crane migration as spanning from late February to mid-April with a peak in abundance most often in late March (Ferguson et al. 1979, USFWS 1981, Krapu et al. 1982). Our data demonstrate that the majority of the migration still occurs in March, with the peak often occurring in late March. However, the tail of the distribution has switched from April to February in our data, with more individuals arriving early in February in recent years, and fewer staying past peak abundance into mid-April. For example, from 2002 to 2005, counts from week 9 (09–15 April) consistently exceeded counts from survey week 4 (05–11 March), and from 2014 to 2017, the opposite was true, with variation in the intervening years. In 2016 and 2017, week 3 (26 February–04 March) exceeded week 9 for the first time in our data, which suggests that Sandhill Cranes are likely coming earlier to the CPRV and staying longer, but that their stopover is now less commonly extending into mid-April.

Long-term changes in wind and storm patterns associated with climate change have also been linked to shifting avian migration patterns (Adamík and Pietruszková 2008, Mingozi et al. 2013). Cranes migrate primarily by thermal soaring and therefore are dependent on favorable wind conditions (Swanberg 1987, Volkov et al. 2016). Shifts in the spring wind regime (Catto et al. 2014) or precipitation patterns (Trenberth 2011) that provide moisture to basin wetlands, which are important to the MCP in the southern plains, could result in further temporal or spatial shifts in spring migration (La Sorte et al. 2019). Drought conditions at wintering and early spring stopover locations, particularly in Coastal Texas and southwestern Oklahoma, predicted MCP arrival metrics in the CPRV, suggesting that weather patterns aside from temperature are also important (Table 7). Periods of extended drought in the southern plains may have been a major factor in irregular wintering distributions of both Whooping Cranes and Sandhill Cranes (Wright et al. 2014, Harner et al. 2015).

Sandhill Cranes require flooded herbaceous emergent wetlands for breeding; agricultural expansion led to the regional extirpation of Sandhill Cranes from significant portions of their former breeding range, particularly within the Great Plains (Walkinshaw 1949, Baker et al. 1995, Gerber et al. 2014, Silcock and Jorgensen

2018). However, the replacement of native grasslands and wetlands with agricultural lands provided Sandhill Cranes with a greater carrying capacity at a range-wide scale, particularly by improving foraging opportunities on the wintering grounds and at stopover locations, because corn provides more fat per ounce than native plant resources (Krapu et al. 1984, Iverson et al. 1987, Pearse et al. 2010, Gerber et al. 2014). Sandhill Cranes and Common Cranes in Europe, two of the world's most granivorous crane species, have likely become more spatially and temporally flexible in wintering habitat use in response to the increased production of cereal grains, including corn and rice (*Oryza sativa*) (Alonso et al. 1994, 2008, Miene and Archibald 1996, Pearse et al. 2010, Prange 2012). Research indicates that the wintering distribution of Common Cranes in Europe has shifted north as a result of warmer winters and agricultural waste grain availability (Alonso et al. 1994, 2008, Prange 2012). The advances in Sandhill Crane migration described during this study are probably the interactive result of recent above-average winter temperatures associated with climate change, periods of relative drought, and the availability of waste grain on key wintering grounds and stopover locations. Parsing out the influences of these particular factors is beyond the scope of this study, but it should be a consideration when interpreting our results, and an area for future research.

#### Spatial Dynamics

Our findings demonstrated increasing proportional use and densities in eastern segments (Tables 4, 5). These increases suggest the continuation of a trend associated with habitat loss that began prior to the 1938 aerial imagery used in this study (Eschner et al. 1983, O'Brien and Currier 1987). Channel width losses had already been noted from 1938 to 1965 near Cozad, Nebraska, an area abandoned by Sandhill Cranes well before CPRV conservation efforts began in the 1970s (Walkinshaw 1956, Williams 1978, O'Brien and Currier 1987, Krapu et al. 2014). Sandhill Cranes have been moving east since at least the 1950s, and they have abandoned much of the western CPRV (Walkinshaw 1956, Faanes and Le Valley 1993, Buckley 2011). Faanes and Le Valley (1993) noted a negative trend (−0.5% per year) in the density of Sandhill Cranes between Kearney and Wood River, and a positive trend



(+0.7% per year) farther east from Wood River to HWY 34. We demonstrated a continuation and acceleration of this trend with a 2.3% per year increase in the total proportion of Sandhill Cranes detected from Wood River to Chapman, Nebraska, and a 2.0% per year decrease in the total proportion of Sandhill Cranes detected from Kearney to Wood River, Nebraska (Table 5).

Buckley (2011) found that segment 1 (HWY 34 to Chapman) had low Sandhill Crane use from 2002 to 2010 despite having some of the best habitat in the CPRV, presumably because it was isolated east of major roosting densities. Segment 1 now exemplifies one of the strongest positive trends in proportional use per year (Table 5). Segments 1 and 2 supported about 13.8% of the Sandhill Cranes from 2002 to 2010, and supported 22.4% from 2013 to 2017 (Fig. 8). However, these segments have <1% of the total area within 800 m of the main channel of the Platte River in conservation ownership or management, such as easements. Gaining protections from development on these lands should be a top priority for ensuring the ecological integrity of migratory Sandhill Crane habitat in the CPRV (Tables 4, 5; Figs. 1, 6; Faanes and Le Valley 1993). Central segments still hold densities of Sandhill Cranes comparable to eastern segments on average (Fig. 7b); nevertheless, significant declines in the proportional use per year may be concerning for conservation managers (Tables 4–5; Figs. 6–8). Our findings suggest that significant conservation ownership in particular western and central segments may be responsible for maintaining stable roost densities adjacent to unmanaged areas of declining density (Fig. 11e). This is exemplified by segment 7, where over 60% of the land within 800 m of the river is under conservation management. We estimated little change in crane use in this river segment, despite it being bordered to the east by a segment declining in crane use and having low conservation ownership (14%) and to the west by a segment with low densities (Tables 4, 5, 8; Figs. 6, 7). However, recent increases in conservation ownership in some western and central segments and the associated habitat restoration efforts have not significantly redistributed densities of Sandhill Cranes, potentially because the extent of wet meadow and braided river restorations may not have been large enough to make an impact (Tables 4, 5, 8). For instance, following conservation land purchases and restorations within

segment 8 from 1998 to 2016, we found that meadow-prairie cover increased 12.1% but still totaled only 13.3% in 2016, which is well below the cover associated with segments 1 (20.7%) and 3 (49.6%) where Sandhill Crane use appears to be increasing most significantly (Tables 5, 8). Further concentration of Sandhill Crane densities along the CPRV promotes a potential increase in disease risk for Sandhill Cranes and other organisms, including Whooping Cranes (Lu et al. 2013, Bertram et al. 2017, Fenton et al. 2018). Additionally, increased densities of Sandhill Cranes in fewer reaches of the CPRV escalates the potential risk for mass mortality incidents resulting from extreme weather events like hail and ice storms (Higgins and Johnson 1978, Lingle 1997, Narwade et al. 2014). Increasing the spatial footprint of habitat restoration efforts may encourage dispersal of the MCP throughout the CPRV.

Our spatial model demonstrated that large proportional declines in total unobstructed channel width (UOCW) and maximum unobstructed channel width (MUCW) per segment from 1938 to 2016 were associated with reduced proportional use and densities of Sandhill Cranes from 2015 to 2017, despite generally wide channel widths in 2016 in some locations (Tables 9, 10). The percent of channel width loss in the main channel of the Platte River from 1938 to 2016 may serve as an effective proxy for multiple dimensions of habitat change associated with woodland accretion and channel morphology alteration (Schumm 1963, Williams 1978, Johnson 1994, Horn et al. 2012). Sandhill and Whooping Cranes use the Platte River in great part to take advantage of quality sandbar roosting habitat characteristic of braided rivers (Krapu et al. 1982, Kinzel 2009). However, the Platte River has been transitioning from a braided river to a more anabranching river system (sections where the channel is split by stabilized islands) as a result of reductions in sediment load and discharge (Williams 1978, Eschner et al. 1983, O'Brien and Currier 1987, Horn et al. 2012).

Change in channel width from 1938 to 2016 is likely a top explanatory variable because it reflects that segments which have changed the least from historic widths, have maintained a more braided nature than reaches which have seen large percent losses of channel width; these least-changed segments have become more anabranching (O'Brien and Currier 1987,

Horn et al. 2012). Our findings demonstrate that segments that exhibited the greatest losses in UOCW from 1938 to 2016 also had the highest levels of woodland-forest land cover in 2016 and saw the largest increases in the number of active channels from 1938 to 2016 (Fig. 10; Appendixes 2, 3). Percent change in the number of active channels and the percent cover of woodland-forest were negatively correlated with Sandhill Crane proportional use and densities per segment from 2015 to 2017 (Table 9). Heavily wooded and anabranching reaches of the Platte River have more stabilized banks (O'Brien and Currier 1987, Johnson 1994); have comparatively incised (steeper banks and deeper channels), fragmented, and sinuous channels (Schumm 1963, Williams 1978, Eschner et al. 1983, Horn et al. 2012); have less exposed sandbar habitat (Kinzel 2009, Horn et al. 2012); and are therefore lower-quality Sandhill and Whooping Crane roosting habitat, despite occasionally having UOCWs in 2016 appropriate for crane roosting (Eschner et al. 1983, O'Brien and Currier 1987, Farmer et al. 2005, Pearse et al. 2017). These reaches also have less meadow-prairie or agricultural habitat adjacent to the river for pre-roost aggregations important to both the pair bonding and the safety of Sandhill Cranes (Currier 1982, Johnsgard 1983, Tacha 1988). Additionally, mature cottonwoods adjacent to the river provide quality habitat for Bald Eagles (*Haliaeetus leucocephalus*), which have increased significantly in abundance in the CPRV over the last 3 decades and pose a potential depredation risk to Sandhill Cranes (Silcock and Jorgensen 2017, Caven et al. 2018).

Though the rate of woodland-forest development in the former riverbed stabilized by the early 1970s, the abundance of vegetated islands within the existing high banks of the channel and the number of anabranches have continued to increase from 1984 to 2009 (Currier 1982, O'Brien and Currier 1987, Johnson 1994, Horn et al. 2012). These hydro-ecological changes have not occurred uniformly throughout the CPRV, because sediment load, flow regime, and the intensity of active management for conservation purposes differ throughout the CPRV (Williams 1978, Eschner et al. 1983, O'Brien and Currier 1987, Pfeiffer and Currier 2005, Rapp et al. 2012). These changes have been most pronounced in the western portion of the CPRV (Table 8; Figs. 3, 8, 9).

Kearney to Odessa (segment 9), an area that has experienced continued declines in Sandhill Crane use (Faanes and Le Valley 1993; Tables 4, 5), provides a clear example of drastic channel loss; UOCW averaged over 1 km in 1938 and has declined by over 80% as of 2016.

The other factor that best predicted the proportion of Sandhill Cranes using individual segments and trends therein was the proportion of meadow-prairie land cover within half a mile of the river. Faanes and Le Valley (1993) suggested that Sandhill Crane habitat in the CPRV was limited by the availability of appropriately wide channels and wet meadow habitat. Sidle et al. (1993) also found a correlation between selected roost sites and distance to wet meadow. These results are further corroborated by Sparling and Krapu (1994), who used flight distances to particular habitat resources as a proxy for their importance. Sparling and Krapu (1994) found that distances to roost sites were highest followed by distances to wet meadows. We found that meadow-prairie land cover was the best predictor of a positive annual trend in proportional use per segment from 2002 to 2017. It was also strongly associated with mean proportional use and density from 2015 to 2017, providing evidence that meadows (particularly those within 800 m of the main channel of the Platte River) represent a habitat resource influencing the distribution of Sandhill Cranes in the CPRV.

Our top models suggested that the distribution of Sandhill Cranes in the CPRV, and therefore their distributional shifts from west to east, are best explained by the availability of limited habitat resources, specifically meadow-prairie habitat and channels that have changed the least in width and character since 1938. Despite increases in meadow-prairie land cover in most western segments and mean UOCWs in all western segments from 1998 to 2016 (Table 8, Appendix 2), Sandhill Cranes continued to shift east from 2002 to 2017. This suggests that improvements made since 1998 may not be large enough in scale to redistribute densities of Sandhill Cranes. Sandhill Cranes move, on average, 5.7 km between roost sites from night to night, and contiguous areas of quality habitat allow for a wider selection of important resources (Sparling and Krapu et al. 1994, Krapu et al. 2014) and consistently support higher densities of cranes (Davis 2003, Buckley 2011). Nonetheless, our findings demonstrated

declines in some segments that include areas of high-quality riverine and meadow habitat. Buckley (2011) argues that Sandhill Crane declines in western segments where quality habitat exists may be reflective of roosting habitat isolation. Although not a variable in top models, the median longitude was significantly correlated with the proportional use of segments increasing from west to east (Table 9). Seager et al. (2018) recently documented the eastern shift of the climactic conditions historically associated with the 100th meridian, which demarcates the longitudinal start of the arid west on the North American continent, to what is about the 98th meridian. This broad shift in climate could negatively impact basin wetlands and the water birds that depend on this habitat in the southern plains (Covich et al. 1997, Reese and Skagen 2017). Pearse et al. (2018) recently documented an eastern shift of about 1.2 km per year in the migratory corridor of the Whooping Crane over the last 8 decades. It is possible that eastward shifts in the distribution of Sandhill Cranes since the 1950s, which we continued to document in our research, are reflective not only of habitat change in the CPRV, but also of increasingly arid conditions in the western portion of the traditional Sandhill Crane migration corridor (Covich et al. 1997, Reese and Skagen 2017).

Though our study did not critically evaluate the effect of waste corn availability on the distribution of Sandhill Cranes in the CPRV, research suggests that cornfields nearer to significant complexes of wet meadow and lowland tallgrass prairie receive more use (Sparling and Krapu 1994, Anteau et al. 2011). Concurrently, research indicates that waste corn availability in the CPRV, which Sandhill Cranes depend on, has declined as a result of harvest efficiency and competition with growing numbers of Snow Geese (*Chen caerulescens*) and other waterfowl (Krapu et al. 2004, Pearse et al. 2010). Interestingly, Pearse et al. (2010) found that competition for waste corn resources was highest in the eastern portion of the CPRV, where we demonstrated increased Sandhill Crane relative abundance and density from 2002 to 2017. Krapu et al. (2005a) suggest that fat storage in Sandhill Cranes may have declined within the CPRV from the late 1970s to the mid-1990s, likely as a result of additional energy expenditure associated with increased flight

distances to waste grain foraging sites. Dependence upon market-driven products, such as particular cultivated grains, poses a risk to wildlife populations at various spatial scales (Krapu et al. 2004, Salvi 2012). For instance, Salvi (2012) found that decreases in corn production in favor of rapeseed (*Brassica napus*) were associated with negative trends in Common Crane abundance at some historic wintering areas in southern France. Increases in soybean (*Glycine max*) cultivation in the CPRV could pose similar risks for Sandhill Cranes, because they do not forage on it regularly and soybeans are nutritionally deficient (Krapu et al. 2004, 2005b). Pearse et al. (2010) suggest that efforts to improve riverine habitat to redistribute Sandhill Cranes could decrease competition for waste grain resources near high-quality sites and help Sandhill Cranes energetically by decreasing the distance from riverine roosting areas to agricultural foraging areas.

#### Management Implications

To promote the redistribution of Sandhill Cranes throughout the CPRV, managers could restore lowland tallgrass prairie and wet meadow within 800 m of the main channel of the Platte River (Pfeiffer 1999, Riggins et al. 2009, Meyer et al. 2010). As much of these lands are wooded, reducing woodland-forest cover (particularly areas of more recent woodland accretion dominated by invasive species) and restoring it to meadow-prairie habitat could prove an effective strategy. Also, restoring croplands to native habitats adjacent to existing tracts of prairie-meadow habitat could maximize the footprint of contiguous herbaceous land cover and protect its ecological integrity (Rowe et al. 2013). Russian olive and eastern redcedar are problematic invasive species that did not become established to a significant extent in the CPRV until the 1950s, and they can negatively impact the structure and function of riverine and prairie ecosystems (Currier 1982, Huddle et al. 2011, Coppedge et al. 2001a, Nagler et al. 2011). Areas with high densities of these species provide a target for riverine meadow-prairie habitat restoration efforts focused on improving Sandhill Crane habitat. Though there is some debate regarding the historic density of eastern cottonwood and peachleaf willow trees in the CPRV (Currier 1982, Currier and Davis 2000, Johnson

and Boettcher 2000), it is clear that woodland-forest cover far exceeds that from before the large-scale development of Nebraska's water resources beginning in the late 1800s (Williams 1978, Currier 1982, Eschner et al. 1983, O'Brien and Currier 1987, Johnson 1994). Restoration efforts will be most acceptable if they maximize the benefit to Sandhill Cranes and other native prairie species while minimizing the financial costs of such an endeavor and the risks to species of concern that utilize woodlands.

Sandhill Cranes are an effective "umbrella species" in the CPRV because their habitat preferences reflect the historic structure of the ecosystem (Currier 1982, Currier and Davis 2000, Davis 2003), mirror the needs of a number of species of concern (Faanes et al. 1992, Kirsch 1996), and delineate an ecologically significant area (Caro and O'Doherty 1999, Suter et al. 2002). Whooping Cranes and Least Terns (*Sterna antillarum*) both prefer wide unobstructed channel widths (Faanes et al. 1992, Farmer et al. 2005, Kirsch 1996); Regal Fritillary (*Speyeria idalia*) populations can become isolated in prairies fragmented by woodland edges (Ries and Debinski 2001, Caven et al. 2017); and woody encroachment also limits habitat suitability for grassland birds (Grant et al. 2004, Ellison et al. 2013). The Bobolink (*Dolichonyx oryzivorus*), Henslow's Sparrow (*Ammodramus henslowii*), Upland Sandpiper (*Bartramia longicauda*), Greater Prairie-Chicken (*Tympanuchus cupido*), and several other grassland endemic avian species need large contiguous areas of prairie (Winter and Faaborg 1999, Grant et al. 2004). Samson et al. (2004) estimated that only about 4.4% of the original extent of "central tallgrass prairie" remains, and Samson and Knopf (1994) estimated that only 2% of Nebraska's tallgrass prairie remains. Habitat restoration efforts focused on improving habitat for Sandhill Cranes could potentially create a network of tallgrass prairies and wet meadows adjacent to the Platte River that could benefit a host of regionally declining species (Rosenberg et al. 2016, Caven et al. 2017).

Riparian woodlands in the CPRV provide breeding and migratory habitat for a diversity of avifauna; however, the dominant species are widespread forest-edge and woodland generalists (Davis 2005a, 2005b). Furthermore, Davis (2005b) indicates that productivity and recruitment for breeding birds is relatively low in

CPRV's riparian woodlands, and that most migrant species demonstrated weight loss during stopover periods between 1998 and 2001. However, Scharf et al. (2008) argue that these habitats provide an important forest stepping stone for migrating woodland birds moving through the central Great Plains that is superior to the surrounding grassland habitats. Furthermore, species of regional concern, such as the Red-bellied Snake (*Storeria occipitomaculata*), rely upon eastern cottonwood-dominated riparian forests along the Platte River (Geluso and Harner 2013, Tye et al. 2017). Strategically reducing the density of woodland-forests (particularly areas dominated by invasive species) to increase meadow-prairie land cover where quality Sandhill Crane roosting habitat can be restored would leave significant habitat to meet the needs of woodland species. Many side channels of the Platte River, mostly north of the main channel, have been completely replaced by woodland-forest habitat in the last century and reflect a localized ecological regime shift, ensuring the continued presence of woodland in the CPRV (Williams 1978, Currier 1982, O'Brien and Currier 1987, Johnson 1994, Bunn and Arthington 2002, Biggs et al. 2009). Grassland birds are the fastest declining avian community in continental North America (Rosenberg et al. 2016). Ellison et al. (2013) demonstrated that the removal of linear tree rows from fragmented prairies increased bird and nesting densities for Henslow's Sparrows and Bobolinks, as well as nesting densities for Eastern Meadowlarks (*Sturnella magna*) in Wisconsin. Where appropriate, Sandhill Cranes and a host of prairie and braided river endemic species could likely benefit from targeted efforts to restore herbaceous habitats in place of linear woodlands and areas dominated by invasive tree species near the main channel of the Platte River (e.g., Farmer et al. 2005, Caven et al. 2017).

Our findings suggest that large-scale efforts to maintain wide channels within the CPRV will have positive habitat consequences for Sandhill Cranes. An extensive body of research demonstrates that mechanical river management improves and maintains quality Sandhill Crane roosting habitat (Faanes and Le Valley 1993, Currier 1997, Pfeiffer and Currier 2005, Kinzel 2009). Our results suggest that these efforts may need to be expanded

and accelerated to improve contiguous areas of quality habitat large enough to counter landscape-level trends. Conservation organizations should continue to increase limited habitat resources, such as wet meadow habitat and wide channels, with the intention of redistributing densities of Sandhill Cranes into larger areas of connected high-quality habitat. Resource managers should continue to monitor the impacts of restoration efforts on the distribution of roosting Sandhill Cranes in the CPRV to determine whether objectives are being met and resources are being expended judiciously. Unprotected relict meadow-prairie and quality riverine roosting habitats showing increased crane use, particularly east of HWY 281 (segments 1 and 2), where <1% of the land is currently safeguarded from development, should be targeted for strategic conservation efforts, such as conservation easements, to protect the habitats' ecological integrity (Theobald 2003). Conservation organizations should also plan for larger numbers of Sandhill Cranes arriving earlier and staying longer within the CPRV, given recent advances in arrival dates. Earlier arrivals reinforce the need to expand contiguous areas of quality habitat, as earlier and longer stays could mean increased pressure on the CPRV ecosystem, as well as increased risks posed to Sandhill Cranes by disease agents and extreme weather events.

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APPENDIX 1. Comparisons of density per bridge segment and river reach using one-way analyses of variance (ANOVAs).

TABLE 1A. Comparison of mean Sandhill Crane density per kilometer by reach of the Central Platte River: East (bridge segments 1–4), Central (bridge segments 5–7), and West (bridge segments 8–11).

Variable	df	Sum of squares	Mean square	<i>F</i>	<i>P</i>
Reach	2	$3.23e^{+10}$	$1.62e^{+10}$	27.77	$3.17e^{-8***}$
Residuals	39	$2.27e^{+10}$	$5.87e^{+10}$		

\*\*\**P* < 0.001

TABLE 1B. Tukey's Honest Significance Difference Test to assess significance of differences between pairs of individual river reaches (East, Central, West) regarding Sandhill Crane density.

Comparison	Difference	95% CI lower limit	95% CI upper limit	<i>P</i>
East–Central	279.29	–249.76	808.36	0.411
West–Central	–1146.75	–1675.81	–617.69	<0.0001***
West–East	–1426.05	–1955.11	–896.99	<0.0001***

\*\*\**P* < 0.001

TABLE 1C. Comparison of mean Sandhill Crane density per kilometer across survey bridge segments.

Variable	df	Sum of squares	Mean square	<i>F</i>	<i>P</i>
Bridge segment	10	155,855,630	15,585,563	22.13	$2e^{-16***}$
Residuals	143	100,712,703	704,285		

\*\*\**P* < 0.001

APPENDIX 2. Total unobstructed channel width (UOCW) and maximum unobstructed channel width (MUCW) for the main channel of the Platte River, as well as the total number of active channels per bridge segment (CHAN) from aerial imagery taken in 1938, 1998, and 2016. For description of segments, see Fig. 1.  $n = 164$  measurements of UOCW and MUCW per year for 1998, 2015, and 2016, and  $n = 136$  for 1938. TTL = total.

SEG-VAR	% CHG 16			2016			2015			1998			1938		
	98	38	SD	$\bar{x}$	min-max	SD	$\bar{x}$	min-max	SD	$\bar{x}$	min-max	SD	$\bar{x}$	min-max	SD
1	UOCW	0.09	0.53	363	198-509	83	363	207-511	84	332	133-449	157	776	601-904	157
	MUCW	0.20	-0.54	268	80-509	117	272	79-511	99	224	73-391	142	579	488-743	142
	CHAN	0	0.14	1.1	1-2	0.4	1.1	1-2	0.4	1.1	1-2	0.0	1.0	1-1	0.0
2	UOCW	0.11	-0.39	224	116-372	80	216	110-373	71	201	129-318	171	364	229-762	171
	MUCH	0.19	-0.50	170	66-360	68	153	63-290	60	143	58-256	175	336	148-762	175
	CHAN	0	-0.03	3.3	1-4	1.0	3.3	1-4	1.0	3.3	1-4	1.0	3.4	1-4	1.0
3	UOCW	0.08	-0.21	239	161-359	53	231	160-365	48	221	153-343	40	304	218-349	40
	MUCH	0.03	-0.16	196	94-359	75	183	91-355	65	190	84-343	81	234	92-336	81
	CHAN	0	-0.21	3.5	2-5	1.1	3.5	2-5	1.1	3.5	2-5	0.7	4.4	3-5	0.7
4	UOCW	0.15	-0.15	323	206-449	79	322	208-447	66	281	184-418	106	377	268-536	106
	MUCH	0.30	-0.11	287	169-449	85	296	208-447	65	222	112-304	133	323	218-536	133
	CHAN	0	-0.17	2.0	2-2	0.0	2.0	2-2	0.0	2.0	2-2	0.9	2.4	2-4	0.9
5	UOCW	0.37	-0.55	275	137-423	98	268	136-416	89	201	70-331	263	608	129-1010	263
	MUCW	0.45	-0.48	216	107-352	79	203	103-337	75	150	62-284	203	416	92-775	203
	CHAN	-0.06	0.38	1.7	1-2	0.5	1.7	1-2	0.6	1.8	1-3	0.4	1.2	1-2	0.4
6	UOCW	0.13	-0.56	298	247-379	47	289	231-385	31	264	193-309	192	679	360-895	192
	MUCW	0.24	-0.70	188	138-283	53	188	111-274	58	151	68-286	193	627	358-895	193
	CHAN	0	-0.11	1.3	1-2	0.5	1.3	1-2	0.5	1.3	1-2	0.8	1.5	1-3	0.8
7	UOCW	0.20	-0.32	305	232-373	44	300	230-356	33	254	212-330	65	449	306-524	65
	MUCW	0.40	-0.37	261	98-336	61	255	100-315	56	186	83-255	103	411	158-513	103
	CHAN	0	-0.04	2.0	2-2	0.0	2.0	2-2	0.0	2.0	2-2	0.3	2.1	2-3	0.3
8	UOCW	0.04	-0.70	191	64-276	65	197	64-282	75	183	62-372	359	633	252-1185	359
	MUCW	0.21	-0.68	138	64-248	51	138	63-248	39	114	60-191	314	425	99-1144	314
	CHAN	0	0.42	2.6	1-5	1.0	2.7	2-5	1.0	2.6	1-5	0.9	1.9	1-3	0.9
9	UOCW	0.20	-0.82	201	125-369	72	205	125-365	57	168	91-266	121	1110	902-1286	121
	MUCW	0.28	-0.79	159	103-254	45	160	105-258	48	124	63-218	308	776	185-1190	308
	CHAN	-0.04	1.4	2.4	1-3	0.6	2.4	1-3	0.7	2.6	1-4	0.0	1.0	1-1	0.0
10	UOCW	0.16	-0.68	264	194-316	38	262	195-314	46	228	152-292	236	829	286-1183	236
	MUCW	0.21	-0.66	215	93-316	67	214	93-312	58	177	92-254	228	638	270-1109	228
	CHAN	0	0.22	1.6	1-3	0.8	1.6	1-3	0.8	1.6	1-3	0.5	1.3	1-2	0.5
11	UOCW	0.37	-0.69	186	115-373	82	192	122-415	41	135	80-229	210	602	144-879	210
	MUCW	0.61	-0.49	166	67-310	66	166	65-312	28	103	57-165	227	327	43-740	227
	CHAN	-0.04	0.39	2.9	1-4	0.8	3.0	1-4	0.8	3.1	1-4	0.8	2.1	1-4	0.8
TTL	UOCW	0.17	-0.59	260	64-509	90	258	63-511	84	223	62-449	310	639	129-1286	310
	MUCW	0.28	-0.57	205	64-509	86	201	63-511	74	161	57-391	271	473	43-1190	271
	CHAN	-0.02	0.12	2.2	1-5	1.0	2.2	1-5	1.0	2.2	1-5	1.2	2.0	1-5	1.2

APPENDIX 3. Pearson's product-moment correlation coefficients for relationships between land cover and channel width metrics collected at bridge segments within the Central Platte River Valley using aerial imagery from 1938, 1998, and 2016. All significant correlations ( $P < 0.05$ ) are bolded. For site descriptions, see Fig. 1.

Variable <sup>a</sup>	1	2	3	4	5	6	7	8	9	10	11	12
LON <sup>1</sup>	1	<b>0.66</b>	0.47	-0.51	-0.43	-0.53	0.56	0.43	<b>-0.61</b>	0.53	-0.18	-0.26
X38UOCW <sup>2</sup>	<b>0.66</b>	1	<b>0.91</b>	<b>-0.78</b>	-0.25	-0.28	0.47	<b>0.61</b>	<b>-0.86</b>	<b>0.82</b>	0.06	0.42
X38MUCW <sup>3</sup>	0.47	<b>0.91</b>	1	<b>-0.65</b>	-0.01	-0.06	0.32	0.57	<b>-0.67</b>	<b>0.78</b>	0.01	0.58
X38CHAN <sup>4</sup>	-0.51	<b>-0.78</b>	<b>-0.65</b>	1	0.29	0.25	-0.5	-0.47	<b>0.74</b>	<b>-0.68</b>	-0.24	-0.32
X98UOCW <sup>5</sup>	-0.43	-0.25	-0.01	0.29	1	<b>0.88</b>	-0.16	0	0.43	-0.47	-0.42	-0.01
X98MUCW <sup>6</sup>	-0.53	-0.28	-0.06	0.25	<b>0.88</b>	1	-0.13	0.03	0.4	-0.53	-0.11	0.02
UOCW2016 <sup>7</sup>	0.56	0.47	0.32	-0.5	-0.16	-0.13	1	<b>0.9</b>	-0.37	0.34	-0.06	-0.14
MUCW2016 <sup>8</sup>	0.43	<b>0.61</b>	0.57	-0.47	0	0.03	<b>0.9</b>	1	-0.37	0.42	-0.1	0.14
PWOOD16 <sup>9</sup>	<b>-0.61</b>	<b>-0.86</b>	<b>-0.67</b>	<b>0.74</b>	0.43	0.4	-0.37	-0.37	1	<b>-0.81</b>	-0.27	-0.45
PMEAD16 <sup>10</sup>	0.53	<b>0.82</b>	<b>0.78</b>	<b>-0.68</b>	-0.47	-0.53	0.34	0.42	<b>-0.81</b>	1	0.15	<b>0.62</b>
X98PMEAD <sup>11</sup>	-0.18	0.06	0.01	-0.24	-0.42	-0.11	-0.06	-0.1	-0.27	0.15	1	0.35
PCONS <sup>12</sup>	-0.26	0.42	0.58	-0.32	-0.01	0.02	-0.14	0.14	-0.45	0.62	0.35	1

<sup>a</sup>Variable definitions

1: Median longitude.

2: Change in unobstructed channel width from 1938 to 2016.

3: Change in maximum unobstructed channel width from 1938 to 2016.

4: Change in the number of active channels of the Platte River from 1938 to 2016.

5: Change in unobstructed channel width from 1998 to 2016.

6: Change in maximum unobstructed channel width from 1998 to 2016.

7: Unobstructed channel width in 2016.

8: Maximum unobstructed channel width in 2016.

9: Proportion of land cover designated as woodland-forest within 800 m of the Platte River in 2016.

10: Proportion of land cover designated as meadow-prairie within 800 m of the Platte River in 2016.

11: Change in meadow-prairie land cover within 800 m of the Platte River from 1998 to 2016.

12: Percent of land within 800 m of the main channel of the Platte River owned or managed through easement by conservation organization.