RESEARCH ARTICLE

Heterogeneity in migration strategies of Whooping Cranes

Aaron T. Pearse,[1,*] **Kristine L. Metzger,**[2] **David A. Brandt,**[1] **Mark T. Bidwell,**[3] **Mary J. Harner,**[4,a]
David M. Baasch,[5] **and Wade Harrell**[6]

[1] U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA
[2] U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA
[3] Canadian Wildlife Service, Environment and Climate Change Canada, Saskatoon, Saskatchewan, Canada
[4] The Crane Trust, Wood River, Nebraska, USA
[5] Platte River Recovery Implementation Program, Kearney, Nebraska, USA
[6] U.S. Fish and Wildlife Service, Austwell, Texas, USA
[a] Current address: Department of Biology and Department of Communication, University of Nebraska at Kearney, Kearney, Nebraska, USA
*Corresponding author: apearse@usgs.gov

ABSTRACT

Migratory birds use numerous strategies to successfully complete twice-annual movements between breeding and wintering sites. Context for conservation and management can be provided by characterizing these strategies. Variations in strategy among and within individuals support population persistence in response to changes in land use and climate. We used location data from 58 marked Whooping Cranes (*Grus americana*) from 2010 to 2016 to characterize migration strategies in the U.S. Great Plains and Canadian Prairies and southern boreal region, and to explore sources of heterogeneity in their migration strategy, including space use, timing, and performance. Whooping Cranes completed ~3,900-km migrations that averaged 29 days during spring and 45 days during autumn, while making 11–12 nighttime stops. At the scale of our analysis, individual Whooping Cranes showed little consistency in stopover sites used among migration seasons (i.e. low site fidelity). In contrast, individuals expressed a measure of consistency in timing, especially migration initiation dates. Whooping Cranes migrated at different times based on age and reproductive status, where adults with young initiated autumn migration after other birds, and adults with and without young initiated spring migration before subadult birds. Time spent at stopover sites was positively associated with migration bout length and negatively associated with time spent at previous stopover sites, indicating Whooping Cranes acquired energy resources at some stopover sites that they used to fuel migration. Whooping Cranes were faithful to a defined migration corridor but showed less fidelity in their selection of nighttime stopover sites; hence, spatial targeting of conservation actions may be better informed by associations with landscape and habitat features rather than documented past use at specific locations. The preservation of variation in migration strategies existing within this species that experienced a severe population bottleneck suggests that Whooping Cranes have maintained a capacity to adjust strategies when confronted with future changes in land use and climate.

Keywords: *Grus americana*, heterogeneity, migration strategy, Whooping Crane

Heterogeneidad en las estrategias migratorias de *Grus americana*

RESUMEN

Las aves migratorias usan numerosas estrategias para completar exitosamente los movimientos bianuales entre los sitios reproductivos y de invernada. La caracterización de estas estrategias permite entender el contexto para la conservación y el manejo de estas aves. Las variaciones en las estrategias entre y dentro de los individuos apoyan la supervivencia de la población como respuesta a los cambios en el uso del suelo y en el clima. Usamos datos de ubicación de 58 individuos marcados de *Grus americana* desde 2010 hasta 2016 para caracterizar las estrategias migratorias en las Grandes Llanuras de EEUU y las Praderas canadienses y la región boreal sur, y para explorar las fuentes de heterogeneidad en la estrategia migratoria, incluyendo uso del espacio, fechas y desempeño. *G. americana* completó migraciones de ~3,900 km que promediaron 29 días durante la primavera y 45 días durante el otoño, realizando 11–12 paradas nocturnas. A la escala de nuestro análisis, los individuos de *G. americana* mostraron poca consistencia en los sitios de parada usados entre las estaciones migratorias (i.e. baja fidelidad de sitio). En contraste, los individuos mostraron consistencia en las fechas, especialmente en las fechas de inicio de la migración. *G. americana* migró en diferentes momentos según la edad y el estatus reproductivo, donde los adultos con crías comenzaron la migración de otoño luego de otras aves, y los adultos con y sin crías comenzaron la migración de primavera antes que las aves sub-adultas. El tiempo transcurrido en los sitios de parada estuvo positivamente asociado con la longitud del tramo migratorio y negativamente asociado con el

tiempo transcurrido en los sitios de parada previos, indicando que los individuos de *G. americana* adquirieron recursos energéticos en algunos sitios de parada que usaron para aprovisionar la migración. *G. americana* fue fiel a un corredor migratorio definido, pero mostró menos fidelidad en su selección de los sitios de parada nocturna; por lo tanto, el objetivo espacial de las acciones de conservación puede verse beneficiado al considerar las asociaciones con el paisaje y los rasgos del hábitat más que el uso pasado de los sitios específicos. La preservación de la variación en las estrategias migratorias existentes para esta especie que sufrió cuellos de botella poblacionales severos sugiere que *G. americana* ha mantenido su capacidad de ajustar las estrategias al ser confrontada con futuros cambios en el uso del suelo y el clima.

Palabras clave: estrategia migratoria, *Grus americana*, heterogeneidad

INTRODUCTION

The only self-sustaining and wild population of endangered Whooping Cranes (*Grus americana*), the Aransas–Wood Buffalo population, migrates nearly 4,000 km through central North America during spring and autumn (Kuyt 1992). Recovery efforts for this endangered species include providing protection and habitat during migration (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2005). Whooping Cranes migrate across an extensive area that has been highly modified by urbanization and cultivation as well as hydrological alteration (Dahl 2011, Johnston 2013). Human population growth and continued agricultural and commercial development will lead to additional alteration to the corridor (Lark et al. 2015). Recovery actions include identifying areas to implement conservation actions and determining what kinds of conservation actions would be most effective (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2007). Conservation efforts can be targeted by characterizing migration strategies of Whooping Cranes.

Successfully completing migration is key to fitness of birds that move between seasonal environments as part of their life history strategy. Most individuals that migrate require more than a single flight; therefore, individuals need to stop during migration at sites where they can access resources such as safe roosting sites and high-quality food (Alerstam 2011, Stafford et al. 2014). Distance traveled during migration bouts and time at stopover sites vary greatly among migratory birds and are related to body size, type of flight, energetic and physiological constraints, characteristics of stopover sites (including resources present and disturbance), and distribution of quality stopover sites within the migration pathway (Piersma 1987, Warnock 2010). Constraints birds face during migration (e.g., timing, physiological), resource requirements (e.g., macronutrient), and conservation value and ecological functions of stopover sites visited (e.g., foraging; Mehlman et al. 2005) can be identified by comparing daily distances moved and time spent at stopover sites. Therefore, conservation and recovery actions can be guided by determining where, when, and how birds use migration corridors and stopover sites. Additionally, insight can be gained by identifying variability in migratory strategies employed, both within and among individuals, regarding flexibility

that a population possesses that will be needed for adapting to a changing landscape (Chavez-Ramirez and Wehtje 2012, Gilroy et al. 2016).

We used location data to characterize migration strategies of Whooping Cranes and determined levels and sources of heterogeneity in aspects of migration strategy, including space use (use of geographic locations), timing (initiation and completion of migration), and performance (duration and rate of migration) metrics. This characterization included quantifying use of sites within the migration corridor to understand intensity of use by multiple birds, individual fidelity to stopover sites, and distances between sites. We also estimated migration chronology, length, and variability of these characteristics within and among individuals. Finally, we explored how Whooping Cranes allocated time and energy during migration by comparing distances moved daily and time spent at stopover sites. The answers to these questions will increase our understanding of Whooping Crane migration strategies and help stakeholders make more informed and targeted conservation decisions to support the recovery of this endangered species.

METHODS

Study Area

Whooping Cranes of the Aransas–Wood Buffalo population migrate through the Great Plains of the United States and Canadian Prairies and southern boreal region between wintering and breeding areas (Allen 1952). The central portion of the Whooping Crane migration corridor passes through Canadian provinces of Alberta and Saskatchewan and the states of North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas (Pearse et al. 2018). This region was historically dominated by a grassland biome and mixed-grass prairie. The majority of land is currently used for agricultural production, including annual crops grown for food, livestock feed, and biofuels, and pasture and haylands for ranching (Hartman et al. 2011). Gage et al. (2016) estimated that 82% of the Northern Great Plains has been converted to cropland. Wetlands, rivers, lakes, and reservoirs in the region support a diverse array of aquatic plant and animal communities and support millions of migratory waterfowl and waterbirds

(Laubhan and Fredrickson 1997). Whooping Cranes use grasslands, croplands, wetlands, and rivers as roosting and foraging sites during migration (Pearse et al. 2017).

Field Methods and Data Acquisition

During 2009–2014, we captured 68 Whooping Cranes (~20% of the Aransas–Wood Buffalo population) and marked them with platform transmitting terminals with global position system (GPS) capabilities (North Star Science and Technology, Baltimore, Maryland, USA; Geotrak, Apex, North Carolina, USA), a device that uplinks GPS locations through a global satellite and data collection system (Service Argos 2008). Captures occurred at breeding areas within and near Wood Buffalo National Park and wintering sites along the Texas Gulf Coast. Capture teams consisted of individuals with experience handling endangered birds and a veterinarian. We caught pre-fledged juvenile cranes in the breeding areas by locating adults with young and using a helicopter to position personnel nearby for ground pursuit and hand capture (Kuyt 1979). In Texas, we captured cranes with leg snares that enclosed on their lower tarsus (Folk et al. 2005).

Transmitters logged 4–5 equally timed GPS locations daily, providing daytime and nighttime locations. We initially inspected GPS locations for errors by performing multiple assessments to determine plausibility of locations and omitted locations outside expected time sequences, with an implausible rate of displacement (>100 km h^{-1}), or forming an acute angle ($<5°$) at distances greater than 50 km (distance/angle; Douglas et al. 2012). We identified locations as collected during migration (spring and autumn) based on manual inspection of conspicuous movement patterns north during late winter to early summer (spring migration) or south during late summer to early winter (autumn migration). Fifty-eight of 68 marked cranes provided location data during migration. We classified locations as occurring in flight when instantaneous velocity was >2.6 m s^{-1}. Ground locations were categorized into individual stopover sites for each Whooping Crane by identifying clusters of locations based on distance, movement pattern, and manual inspection. In general, we delineated unique stopover sites if birds moved >10 km between ground locations and spent ≥ 1 night at the site. After identifying locations from each unique stopover site, we calculated stopover centroids by taking the mean of X and Y coordinates from each location identified within the stopover site.

We identified migration paths as complete and assumed all nighttime stopovers were accounted for when no 12-hr gaps in data existed. Migrations that began and ended at the traditional summering and wintering termini (i.e. in or near Wood Buffalo National Park, northern Canada; at or near Aransas National Wildlife Refuge, Texas Gulf Coast) were identified as full migrations. These migrations contrasted with truncated migrations that either did not start

or end at these traditional sites. We organized marked birds into 5 age and social status categories. Individuals <1 yr of age were identified as juveniles with adults, because familial bonds persist beyond summer of hatching into autumn migration, winter, and subsequent spring migration (Urbanek and Lewis 2015). Individuals beginning their second summering period (first full summer >1 yr of age) were classified into a subadult age class for 1 yr. After this point, all birds were considered adults, which could be accompanied by young, without young, or in an unknown social status. We used status at capture, photographic evidence, and observations from project partners to determine social status of adults.

Data Analyses

Migration space use. We estimated a utilization distribution to characterize the spatial distribution of Whooping Cranes during migration and intensity of space use (Worton 1989). We divided the migration area of Whooping Cranes into hexagonal grid cells of 10-km radii (346 km^2) and determined number of stopovers within each cell. After ranking grid cells by stopover frequency, we calculated the cumulative proportion of stopovers found within each cell (i.e. cumulative proportion volume) and cumulative proportion of grid cells (i.e. cumulative distribution area). Volume metrics allowed us to identify and categorize intensity of stopover sites. We plotted utilization distribution area and volume (Powell 2000, Vander Wal and Rodgers 2012), fitted an exponential model to estimate this association, and determined where the slope of this relationship was 1.0. The volume at this inflection point represented a transition where, at cumulative volume values above, the proportion of occupied area increased at a greater rate than use. Thus, we identified grid cells above the critical value as being core migration areas and others as peripheral areas (Pearse et al. 2015).

Heterogeneity in migration timing, space use, and migration performance can be characterized by the degree of synchrony of behaviors that birds express within a population and degree of consistency within individual behaviors (Bauer et al. 2016). To quantify multiple use of sites by individuals by migration season and overall, we determined number of unique marked individuals occupying grid cells for each migration season. In nearly all instances, only one crane was marked within a parental group (i.e. mated pair and associated juvenile if present) or mated pair. If multiple individuals within one of these groups were marked, we removed data from one of the individuals. Therefore, we treated marked individuals as independent observations, which allowed for valid conclusions regarding synchrony in timing and space use during migration. The proportion of grid cells used by multiple marked individuals served as a measure of within-season overlap of space use, and we combined seasons by calculating a mean value. In addition,

we calculated the average number of individuals that used each occupied grid cell. To quantify consistency of use by individuals, first we recorded number of migration seasons that individual marked cranes occurred within every grid cell. Then, for birds monitored for >1 season ($n = 46$), we estimated site fidelity by computing the proportion of all cells ever used by a particular bird that were used in more than one migration season. We also calculated the average number of times that an individual bird occupied a grid cell for all those used at least once.

Timing and migratory performance. We summarized calendar dates of migration initiation and completion for all migrations unless missing data precluded determination of an exact date. Migration time was the elapsed number of days cranes migrated each season. Number of locations cranes used as nighttime stopovers was reported for each migration season. Distance traveled during migration was determined by summing Euclidean distances between nightly stopover sites used by cranes, including beginning and ending locations. Finally, rate of migration was calculated by dividing distance traveled by time in migration (km day^{-1}).

We identified birds in 1 of 4 annual cycle categories: spring migration, summering, autumn migration, or wintering (Krapu et al. 2011, Pearse et al. 2015). We calculated the proportion of cranes in each of these categories by year. We then calculated an average and standard deviation for years 2011–2015, where >10 individuals provided data. We weighted each year equally and censored birds that were not detected during a particular day (i.e. no locations recorded). Averages and standard deviations were plotted by date.

To characterize migration timing in space, we split the migration pathway into 6 equal-sized areas encompassing all identified stopover sites. We categorized locations and stopover sites within each of these analysis zones so that we could determine timing and residency of migrating birds within each spatial zone by migration season (i.e. autumn and spring). We summarized spatially distinct timing with box plots, which included a median, 25th and 75th percentiles defining the box, 10th and 90th percentiles defining the whiskers, and 5th and 95th percentiles as outer points. Residency within spatial zones represented number of days birds were within each spatial zone, and we summarized residency with average days present and 95% confidence intervals. We also calculated site fidelity and spatial overlap metrics for each spatial zone to determine if these dynamics varied in space.

We modeled variation in 4 timing and performance metrics using mixed effects general linear models (*lme4* package, Program R; Bates et al. 2015, R Core Team 2017), including initiation and completion dates, migration time, and rate of migration. Analyses included only migrations in which social status of birds could be determined (i.e.

removed unknown social designations, $n = 78$–105) and for migrations between traditional breeding and wintering grounds, because migrations originating or terminating from other locations were rare and generally had different timing and distances (Table 1). We were interested in timing and performance variation related to age and social status and included this variable as a fixed effect with 3 levels (family group, adult without young, or subadult). We included calendar year of migration event and individual bird as random effects, allowing estimation of variances associated with these effects. We calculated intraclass correlation coefficients (ICC) for individual birds and year to determine relative variation as measures of relative consistency of behaviors for individual birds and synchrony among birds within a particular migration event (*rptR* package; Stoffel et al. 2017). We included a bird's age and social status as fixed effects as described above, with ICC values to be calculated after controlling for variation due to this covariate. Standard errors for ICCs were calculated using 5,000 parametric bootstrap iterations. We used likelihood ratio tests for a fixed effect in linear models and to determine if ICCs were different from zero. We conducted all analyses by migration season (spring or autumn migration).

Migration bout distance and time at stopover sites. Distance between stops was the Euclidean distance between centroids of stopover sites. To explain variation in distance traveled between stopover sites (km), we performed generalized linear models (Proc MIXED, SAS 9.4; SAS Institute, Cary, North Carolina, USA) by season, where we used social status, natural log of days spent at originating stopover site, and total days in migration as independent variables. We used a log transformation of days because the independent variable was log transformed via Poisson regression, and we believed that extended stays would have diminishing effects. Stopover sites within an individual migration were identified as repeated measures.

We calculated time at individual stopover sites by adding up the number of nights that cranes spent at sites. We used general linear models (Proc GLIMMIX) for Poisson distributed data to explain variation in time at stopovers separately for each migration season. The response variable was days spent at a stopover site. Independent variables included social status, the natural log of days spent at a previous stopover site, and total days in migration. All stopovers within an individual migration were identified as repeated measures. Data used in analyses are available in the public domain from the U.S. Geological Survey ScienceBase data repository (Pearse et al. 2019).

RESULTS

We monitored migration of 58 individual Whooping Cranes for 1–11 migration seasons. Monitoring occurred

TABLE 1. Migration phenology and performance summaries for Whooping Cranes in the Great Plains, Prairie Canada, and southern boreal region, 2010–2016.

Variable	Spring						Autumn					
	n	Mean	Median	SD	5th percentile	95th percentile	n	Mean	Median	SD	5th percentile	95th percentile
Initiation date	122	Apr 6	Apr 6	14	Mar 19	Apr 30	102	Sep 27	Sep 23	18	Sep 2	Oct 25
Completion date	122	May 4	May 5	12	Apr 19	May 23	119	Nov 11	Nov 12	9	Oct 27	Nov 28
Migration time (days)	117	29	27	10	16	47	95	45	48	19	14	79
Migration rate (km day^{-1})	117	149	146	46	83	241	95	107	80	65	51	274
Nighttime stopovers	95	12	12	3	9	15	45	11	11	3	7	15
Multi-day stopovers	95	4	4	2	2	8	45	4	3	2	2	6
Migration distance (km)	109	3,920	3,882	137	3,797	4,172	111	3,881	3,845	114	3,780	4,116
Truncated migration distance (km)	13	3,379	3,244	542	2,758	4,858	11	2,878	2,771	469	2,470	4,181

between spring 2010 and autumn 2016. Each migration season, we monitored an average of 18.3 birds (minimum = 2; maximum = 33).

Migration Space Use

Grid cells contained 0–46 stopover locations, and 1,279 cells contained ≥1 stopover location. An exponential model describing the relationship between utilization area and volume provided an inflection point at 62% cumulative volume as a criterion to identify areas as core and peripheral in use intensity. The closest break point of stopover frequency to this criterion resulted in identifying core use areas as those with ≥3 identified stopover sites (i.e. locations used by a bird for ≥1 day). Core areas represented 25% (319) of grid cells with stopover sites and were generally spread throughout the migration area between summering and wintering areas (Figure 1).

Spatial overlap. Of 1,279 grid cells that had stopover site use, 45% were used by multiple birds across all migration seasons. Within season, proportion of cells occupied by more than one marked bird varied from 0.09 to 0.24 and averaged 0.15 (*n* = 13, SE = 0.01). Average number of birds using occupied grid cells per season was 1.22 (SE = 0.03). The greatest use by multiple birds occurred in analysis zone 2 (Figure 2), and other analysis zones had similar magnitude of use (Table 2).

Spatial consistency. For 46 birds monitored for multiple seasons (mean = 5.3 migrations), 0–0.19 proportion of grid cells were used during ≥2 migrations, and average site fidelity was 0.04 proportion of grid cells (SE = 0.01). Average number of times a bird occupied used grid cells was 1.04 (SE = 0.01). By spatial analysis zone (Figure 2), birds had the greatest fidelity in analysis zones 2 and 5 (Table 2). Zones 3 and 4 had similar fidelity and the lowest fidelity was found at zones 1 and 6.

Timing and Migration Performance

Migration timing. On average, ≥5% of marked birds migrated in spring for 60 days between March 21 and May 19 (Figure 3). Over 50% of cranes were in spring migration for 27 days between April 6 and May 2. Averaged across years, peak spring migration occurred on April 21, with an estimated 84% of cranes in migration status. Annual variation was greater at the second half of spring migration compared to the initial half. During autumn, ≥5% of birds migrated for 89 days between September 2 and November 29 (Figure 3). More than 50% of birds were in migration status for 44 days between September 28 and November 11. Across years, peak autumn migration occurred on October 27, with an estimated 91% of cranes in migration status. Annual variation in autumn migration status peaked at the end of the migration season in mid-November and generally was less than during spring migration.

Variation in timing during spring migration was consistent across zones, with inter-quartile ranges from 17 to
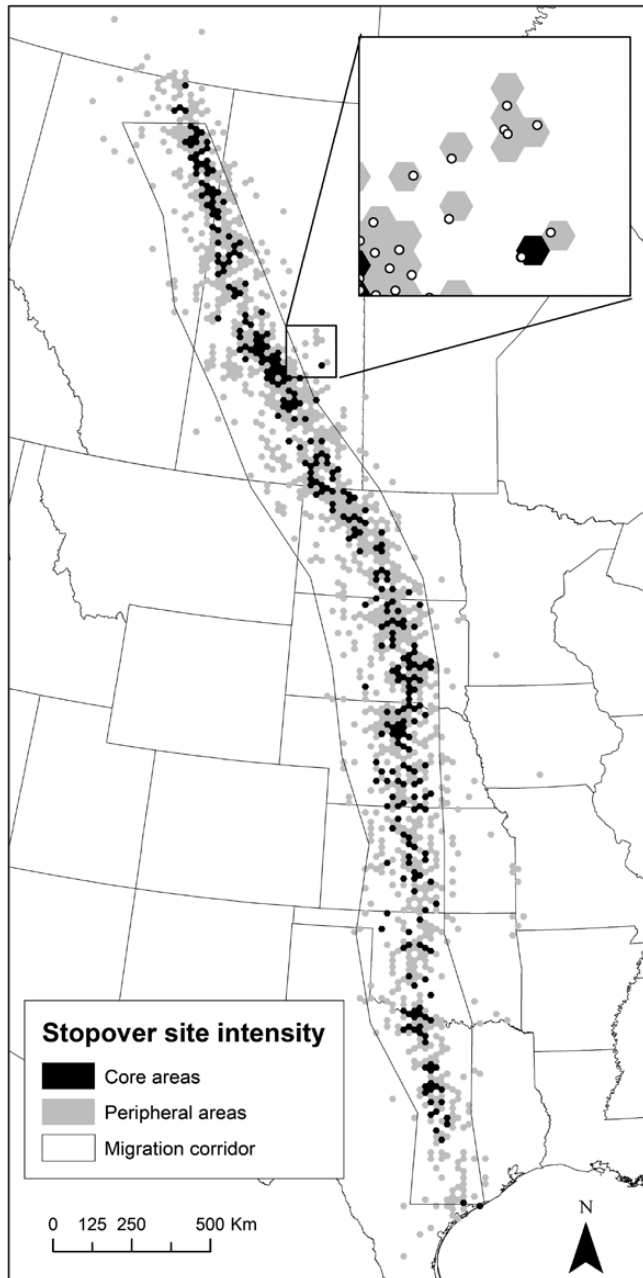
FIGURE 1. Stopover site intensity of areas used by migrating Whooping Cranes in the Great Plains, Prairie Canada, and southern boreal regions, 2010–2016. Migration corridor from Pearse et al. (2018). Insert includes individual stopover locations (white points) overlaying identification of core and peripheral areas).

18 days. Residency within zones 3 and 4 averaged 8.7 days each and was greater than that of other zones, which had averaged residencies of 0.8–5.4 days. Timing among analysis zones in autumn migration revealed considerable overlap in timing of use within the northern 3 analysis zones and within the 3 southern zones (Figure 2). When in the northern zones (4–6), birds resided within

respective areas with greater temporal variability than in the southern zones (1–3). Inter-quartile ranges (IQR) of the 3 northern zones were 24, 23, and 19 days, whereas the IQR of southern zones were 10, 11, and 13 days. Residency was brief for most zones during autumn (1.2–5.6 days on average) as compared to 25.8 days in zone 5.

Spring migration. Average initiation of spring migration occurred on April 6, with 90% of cranes initiating migration during a 42-day period between March 19 and April 30 (Table 1). Mean completion date of spring migration occurred on May 4. Cranes completed spring migrations in an average of 29 days, stopping at an average of 12 nighttime stopover sites. Rate of migration averaged 149 km day^{-1} for average trips of 3,920 km between traditional wintering and summering locations (Table 1).

Subadult Whooping Cranes initiated spring migration 10 days (SE = 2) later than birds in family groups and 8 days (SE = 3) later than adults without juveniles (Figure 4). Cranes showed consistency (ICC$_{bird}$ = 0.41) in initiating spring migration and no synchrony (ICC$_{year}$ = 0.00) during spring migration. Completion dates of spring migration also were later for subadult birds compared to cranes in other social groupings by 6–7 days (Figure 4). We found evidence of both consistency and synchrony in completion dates, with synchrony greater than consistency (Table 3). Time in migration and migration rate varied little due to social status during spring (Table 3). Migration time and rate both had modest and relatively equal levels of correlation within individuals and among birds.

Autumn migration. Autumn migration was initiated by 90% of Whooping Cranes over a 53-day period in September and October (Table 1), and average initiation date was September 27. Termination of autumn migration occurred over a shorter period of 32 days (90% of cranes), generally during November, with an average termination date of November 11. Cranes spent an average of 45 days in autumn migration and stopped at an average of 11 nighttime stopover sites. Rate of migration averaged 107 km day^{-1} (SE = 7), and cranes migrating between traditional summering and wintering locations traveled an average of 3,881 km.

Whooping Cranes migrating as part of a family group initiated autumn migration 9 days (SE = 5) later than adults migrating without young and 14 days (SE = 4) later than subadult birds (Figure 4, Table 3). Cranes showed more individual consistency compared with yearly synchrony in migration initiation date (ICC$_{bird}$ = 0.48; ICC$_{year}$ = 0.06). Cranes of different age and social status completed autumn migration at similar average dates (November 10–14; Figure 4). Correlations within individuals and among birds during the same years were similar and low, providing little evidence for consistency and synchrony. Compared with cranes as part of family groups, days in autumn migration was 9 days (SE = 5)
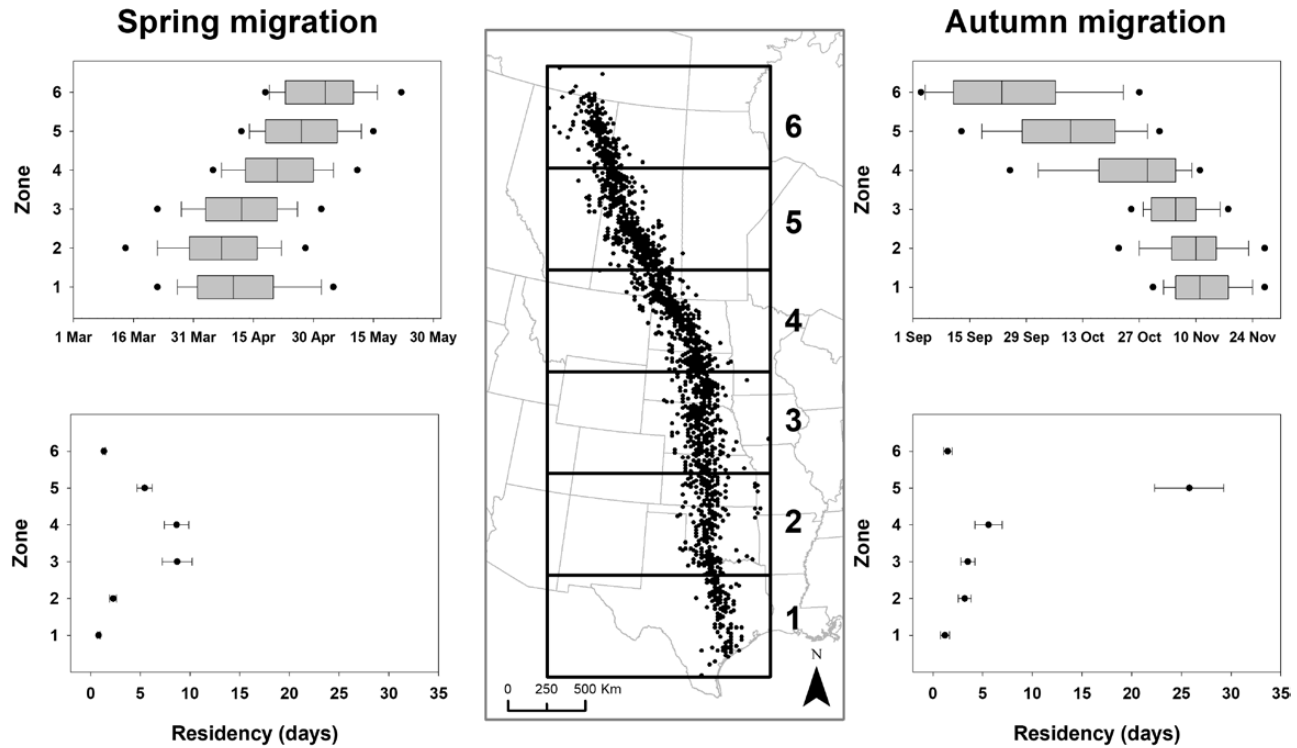
FIGURE 2. Spatial and temporal patterns of spring and autumn migrations of Whooping Cranes in the Great Plains, Prairie Canada, and southern boreal region, 2010–2016. Box plots represent the distribution of dates when individuals occupied each spatial zone during migration. Boxplots were composed of the 25th, 50th, and 75th percentiles, the whiskers were the 10th and 90th percentiles, and outer points represented the 5th and 95th percentiles. Mean residence time (error bars represent 95% confidence limits) that Whooping Cranes spent in each spatial zone in spring and autumn migration.

TABLE 2. Spatial overlap and consistency metrics and 95% confidence limits by analysis zone of Whooping Cranes in the Great Plains, Prairie Canada, and southern boreal region, 2010–2016. Overlap was indexed by the average proportion of grid cells wherein multiple marked birds resided and the average number of marked cranes using each grid cell each migration season. Consistency of use was indexed by the average proportion of grid cells wherein multiple individual birds resided and the average number of times an individual bird used a grid cell across migration seasons monitored.

	Overlap						Consistency					
Zone	Prop.[a]	LCL	UCL	Mean[b]	LCL[c]	UCL[d]	Prop.[e]	LCL	UCL	Mean[f]	LCL	UCL
1	0.16	0.11	0.21	1.23	1.15	1.31	0.02	0.00	0.03	1.02	1.00	1.05
2	0.21	0.16	0.26	1.41	1.28	1.53	0.07	0.04	0.09	1.09	1.05	1.12
3	0.14	0.08	0.20	1.17	1.10	1.25	0.03	0.01	0.05	1.04	1.02	1.06
4	0.16	0.11	0.21	1.19	1.13	1.25	0.03	0.01	0.04	1.03	1.01	1.05
5	0.17	0.12	0.21	1.27	1.16	1.38	0.06	0.03	0.08	1.07	1.04	1.10
6	0.08	0.03	0.13	1.09	1.04	1.14	0.01	0.00	0.02	1.01	1.00	1.02

[a] Mean proportion of grid cells wherein multiple marked birds resided each migration season.
[b] Mean number of marked cranes using each grid cell each migration season.
[c] Lower 95% confidence limit.
[d] Upper 95% confidence limit.
[e] Mean proportion of grid cells wherein individual birds resided across migration seasons.
[f] Mean number of times an individual bird used a grid cell across migration seasons monitored.

longer for adults without young and 11 days longer (SE = 4) for subadult birds (Figure 4, Table 3). Birds showed a similar and relatively low amount of correlation by individual or among birds within a year, suggesting little synchrony or consistency in migration length. Birds within family groups migrated at the greatest rate compared to birds of other social status (Figure 4, Table 3). Like date of initiation, we found evidence of individual
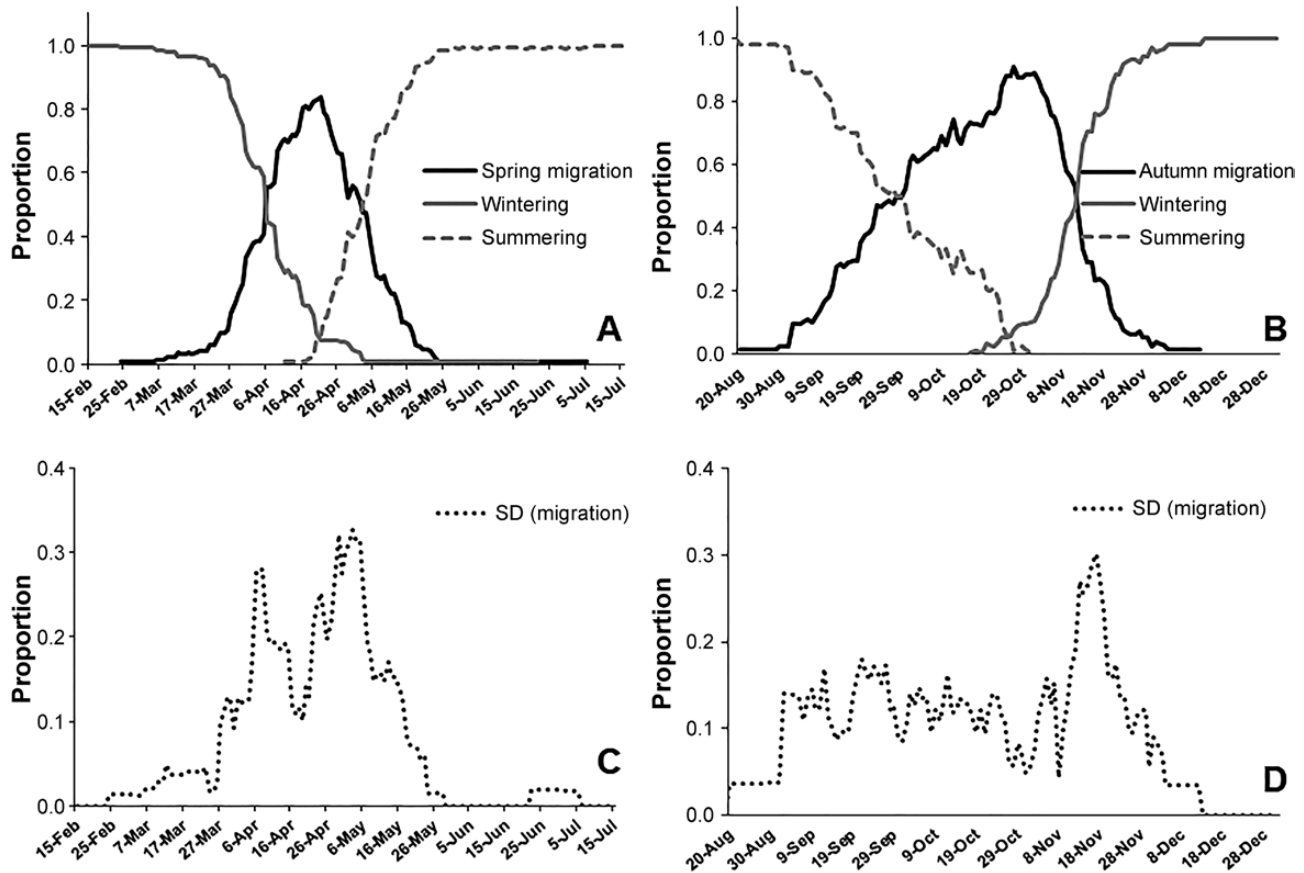
FIGURE 3. Average annual proportion of Whooping Cranes on wintering grounds, breeding grounds, and spring (**A**) and autumn (**B**) migration in the Great Plains, Prairie Canada, and southern boreal region, 2010–2016. Annual variation (standard deviation) in proportion of Whooping Cranes in a spring (**C**) and autumn (**D**) migration status.

consistency in rate of migration (ICC_{bird} = 0.47) and less yearly synchrony (ICC_{year} = 0.04).

Migration Bout Distance and Time at Stopover Sites

Migration bout distance. Distance between stopover sites in spring averaged 307.7 km (n = 1,379, SD = 187.6, median = 308.0, 95th percentile = 632.7, maximum = 884.0). Whooping Cranes flew an average of 305.0 km between stopover sites during autumn migrations (n = 1,056, median = 256.4, SD = 222.5, 95th percentile = 730.3, maximum = 1,479.0).

During spring, migration flight distances between stopovers varied little by social status ($F_{2,109}$ = 1.0, P = 0.367; Figure 4). Cranes flew farther for each day they spent at the originating stopover site in the spring (ln[days]: β = 19.5, SE = 6.9, $F_{1,1056}$ = 8.0, P = 0.005; Figure 5B). They also flew 2.5 km less per migration flight bout during the spring for each additional day of their entire migration (β = −2.5, SE = 0.5, $F_{1,109}$ = 24.2, P < 0.001). Distances between stopover sites in autumn varied little among birds composed of family groups, adults without young, or subadults during autumn migration events ($F_{2,84}$ < 0.1, P = 0.975; Figure 4).

Time spent at the originating stopover site was positively related to travel distance during autumn (ln[days], β = 40.4, SE = 7.7, $F_{1,661}$ = 27.4, P < 0.001; Figure 5A). On average, birds flew 1.2 km less per migration bout for each additional day cranes spent in their entire migration during autumn (β = −1.2, SE = 0.4, $F_{1,84}$ = 7.9, P = 0.006).

Time at stopover sites. During spring, stopover time averaged 2.5 days (n = 1,405, SD = 3.6, median = 1, 95th percentile = 8, maximum = 49). Whooping Cranes averaged 4.1 days at autumn migration stopovers (n = 1,179, SD = 8.7, median = 1, 95th percentile = 27, maximum = 62). Stopovers lasting a single night were most common overall (64% of stopovers), during spring migration (61%) and autumn migration (67%). For stopovers that were >1 night, average duration was 4.7 days in spring (n = 545, SD = 5.0, median = 3, 95th percentile = 15) and 10.2 days in autumn (n = 392, SD = 13.1, median = 3, 95th percentile = 40).

Time at spring stopover sites varied little by social status ($F_{2,109}$ = 0.6, P = 0.533; Figure 4). Natural log of time at previous stopover site also had little influence on time spent at the current stopover (β = −0.08, SE = 0.05,
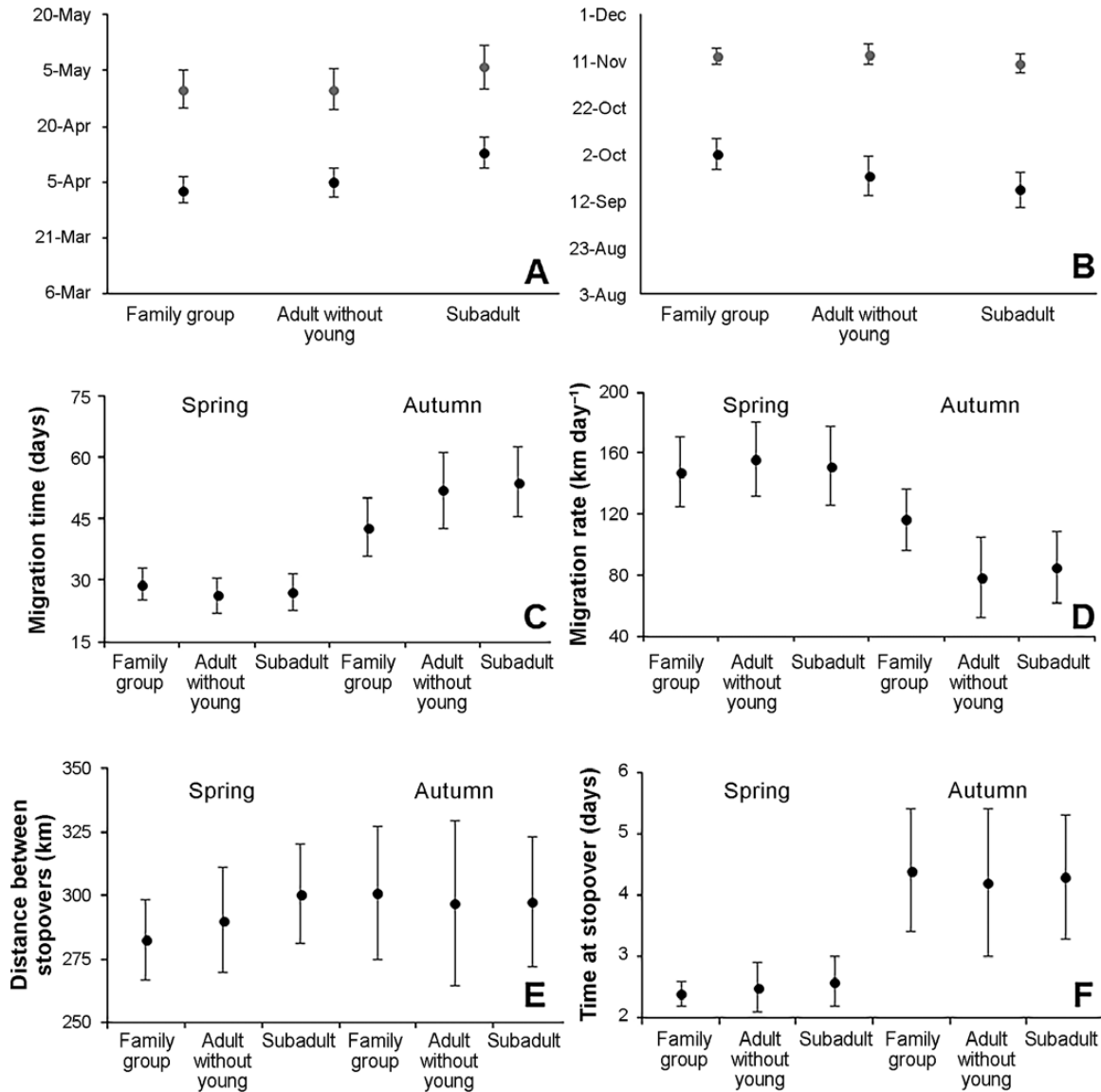
FIGURE 4. Model predicted means and standard errors of migration initiation (black) and completion dates (gray) in spring (**A**) and autumn (**B**) migrations, days in migration (**C**), migration rate (**D**), distance between stopovers (**E**), and time at stopover sites (**F**) by age and social status and migration season for Whooping Cranes migrating in the Great Plains, Prairie Canada, and southern boreal region, 2010–2016.

$F_{1,1070}$ = 2.7, P = 0.102; Figure 5C). Total migration time was positively related to time spent at individual spring stopover sites (β = 0.024, SE = 0.003, $F_{1,109}$ = 60.1, $P < 0.001$). Time at autumn stopover sites varied little due to social or age status of birds ($F_{2,84} < 0.1$, $P = 0.975$; Figure 4). Days spent (ln) at the immediate previous stopover site negatively influenced time at current stopover site (β = −0.23, SE = 0.08, $F_{1,714}$ = 9.0, $P = 0.003$; Figure 5D). Total migration time was positively related to time at autumn stopover sites (β = 0.019, SE = 0.004, $F_{1,84}$ = 24.3, $P < 0.001$).

DISCUSSION

Whooping Cranes migrated within a defined migration corridor but exhibited low levels of fidelity to specific stopover sites, suggesting they commonly select novel stopover locations each migration season. Fidelity to a general migration route but not to specific sites has been observed in another thermal soaring migrant, the Black Stork (*Ciconia nigra*), and this behavior was attributed to temporal variability in resource availability at stopover sites (Chevallier et al. 2011). Whooping Cranes primarily rely upon wetlands at stopover

TABLE 3. Results of generalized linear models explaining variation in migration initiation date, completion date, migration time, and migration rate of Whooping Cranes in the Great Plains, Prairie Canada, and southern boreal region, 2010–2016.

Response variable	Effect	Spring migration					Autumn migration				
		Estimate	SE	df	λ[a]	P	Estimate	SE	df	λ	P
Initiation date	Intercept	95.5	1.9				265.6	3.8			
	Status (FMG)[b]	−2.0	2.2	2	14.6	<0.001	9.1	4.1	2	15.5	<0.001
	Status (SBA)[c]	7.8	2.5				−5.2	4.4			
	ICC bird[d]	0.41	0.12	1	10.3	<0.001	0.48	0.13	1	5.3	0.011
	ICC year[e]	0.00	<0.1	1	0.0	1.0	0.06	0.06	1	0.8	0.190
Completion date	Intercept	119.7	2.6				317.7	2.0			
	Status (FMG)	0.6	1.6	2	16.3	<0.001	−0.8	2.2	2	2.7	0.253
	Status (SBA)	6.7	1.8				−3.9	2.5			
	ICC bird	0.25	0.11	1	6.4	0.006	0.17	0.12	1	2.3	0.066
	ICC year	0.43	0.16	1	41.2	<0.001	0.09	0.08	1	1.6	0.101
Migration time	Intercept	26.3	2.0				51.9	4.2			
	Status (FMG)	2.6	1.5	2	3.0	0.219	−9.1	4.6	2	8.4	0.015
	Status (SBA)	0.7	1.7				2.1	5.0			
	ICC bird	0.27	0.11	1	10.3	<0.001	0.19	0.14	1	1.0	0.160
	ICC year	0.29	0.14	1	25.5	<0.001	0.12	0.1	1	2.1	0.076
Migration rate	Intercept	156.2	11.4				78.4	12.2			
	Status (FMG)	−8.3	8.2	2	1.0	0.609	38.1	13.3	2	10.8	0.005
	Status (SBA)	−4.4	9.1				7.0	14.3			
	ICC bird	0.28	0.11	1	13.5	<0.001	0.47	0.13	1	3.5	0.032
	ICC year	0.34	0.15	1	31.0	<0.001	0.04	0.05	1	0.8	0.193

[a] Likelihood ratio test statistic.
[b] Birds within confirmed family groups (intercept represents adults without young).
[c] Subadult cranes.
[d] Intraclass correlation coefficient for consistency.
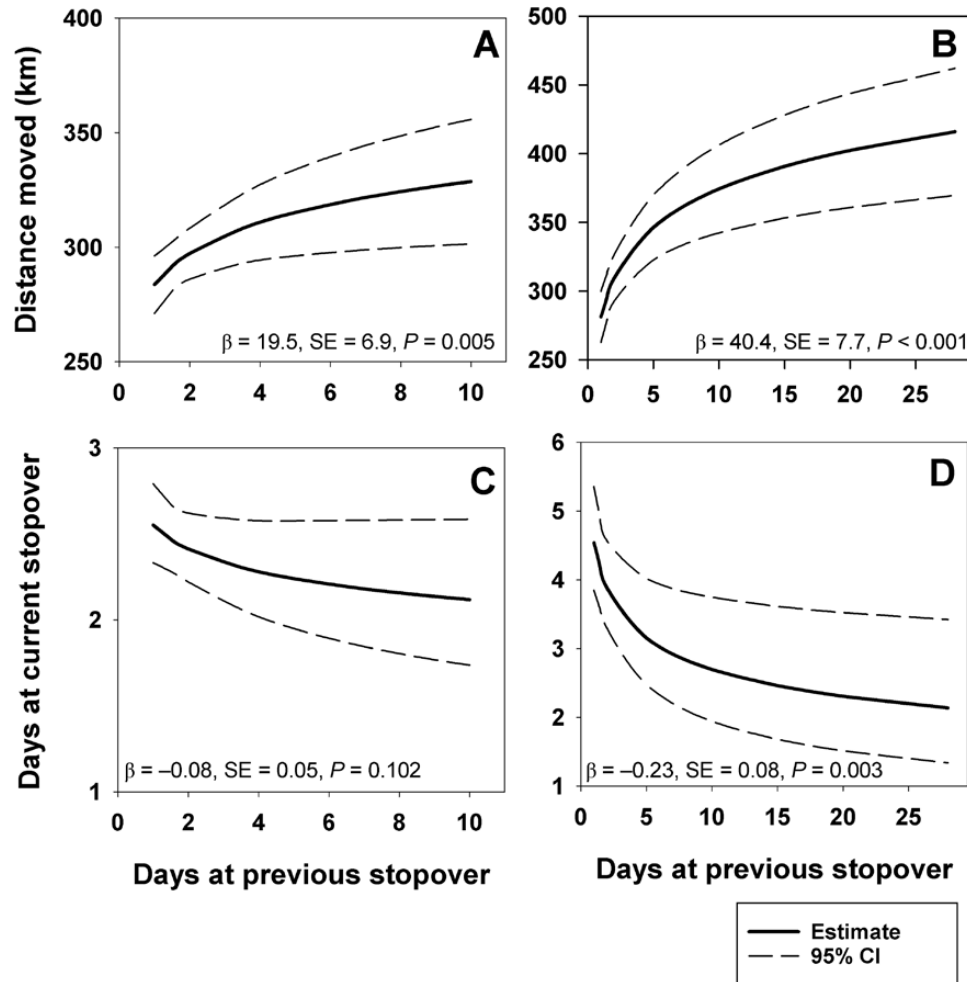[e] Intraclass correlation coefficient for synchrony.

FIGURE 5. Estimates and 95% confidence limits describing migration strategies of Whooping Cranes in the Great Plains, Prairie Canada, and southern boreal region, 2010–2016. Predicted distances moved per migration bout increased with number of days at initial stopover during spring (**A**) and autumn (**B**) migrations. Number of days spent at current stopover sites in relation with days spent at previous stopover site during spring (**C**) and autumn migrations (**D**).

sites for foraging and nocturnal roosting (Austin and Richert 2005, Pearse et al. 2017). The ephemeral nature of surface water in wetlands may require cranes to be flexible in finding suitable stopover sites that are sufficient to meet their needs. Even at sites with more permanent and predictable surface water, foraging resources may vary among migrations, necessitating flexible site-selection behavior. Use of sites by multiple marked cranes not traveling together within the same year (i.e. spatial overlap) was more pronounced than site fidelity, averaging 16% of grid cells occupied by more than one marked bird and as great as 24% in a migration season. Birds not traveling together but using the same places in a migration season also supports the notion that birds responded to seasonal conditions or conspecific attraction in choosing stopover sites more so than relying on knowledge of sites used in previous years.

Because of the general nontraditional site selection across most of the migration corridor, conservation prioritization and targeting schemes may be more effective if they consider documented stopover site conditions (i.e. landscape and habitat features) rather than geographic locations used by Whooping Cranes in different parts of their migration corridor. For example, Whooping Crane sightings in the northern Great Plains were more likely at locations with greater wetland density, wetland types, and cropland area (Niemuth et al. 2018). Conservation strategies that rely entirely on prioritizing sites with a history of prior use may not be as effective across most of the migration corridor. However, site fidelity varied spatially and was more pronounced in some locations. For example, individuals expressed greater probability of reusing sites in Saskatchewan (zone 5; Table 2, Figure 2). Sites in this region were used by many of the marked birds for extended periods in autumn, which may allow for development of greater familiarity with high-quality sites within the region increasing the chance that they come back to these

places in future migrations. Site fidelity also was more pronounced in a southern section of the migration corridor (zone 2), where core use sites were fewer (Figure 1), which may be an indication of more limited suitable site availability. Fewer choices coupled with the presence of large wildlife management areas of considerable past Whooping Crane use, including Salt Plains National Wildlife Refuge, Quivira National Wildlife Refuge, and Cheyenne Bottoms Wildlife Area, likely promoted higher fidelity to sites in this portion of the migration corridor.

Cranes showed consistency in migration initiation, but variation increased with completion of the migration. Migration strategies reflecting temporal, but not spatial, consistency have been observed in other species (Conklin et al. 2013, Thorup et al. 2013, López-López et al. 2014), but this pattern seems to be species-specific (Vardanis et al. 2016, Hasselquist et al. 2017). Consistency can suggest certain behaviors are controlled innately, which may reduce capacity for adaptation in the face of changing conditions. We found that initiation of migration during both seasons had more consistency, yet completion dates were less consistent, suggesting birds were able to modify consistent behaviors based on environmental cues. Therefore, variation in migratory strategy persists in this small population, indicating a capacity for adaptation. Long-term data suggests some directional changes in migration timing and route have occurred (Jorgensen and Brown 2017, Pearse et al. 2018), and reintroduced birds with genetic origins from the Aransas–Wood Buffalo Population have expressed a high capacity to modify migration and wintering behaviors in novel environments (Teitelbaum et al. 2016).

Timing and performance metrics reflected greater consistency than synchrony. Synchrony corresponds to how temporally distributed individuals were during migration. Autumn migration had little temporal synchrony and was more protracted than spring, where we observed synchrony in some metrics. Whooping Cranes regularly migrated at different times based on social status and age, and these temporal differences were the likely explanation for a lack of synchrony. Different temporal migration dynamics by age classes and protracted migrations resulted in individuals migrating for ~20% of the year (2.5 mo) whereas, from the perspective of the entire population, at least some birds were in migration status for ~40% of the year (5 mo). Although migrations may make up the shortest life stage each year for individual birds, conservation practices targeting migration can affect the population for nearly half the year.

Average migration flight bouts between stopover sites were similar seasonally and comparable to distances observed in other species with thermal soaring migration flight in White-naped Crane (*Grus vipio*), White Stork (*Ciconia ciconia*), and Osprey (*Pandion haliaetus*) (Ueta and Higuchi 2002, Alerstam et al. 2006, Rotics et al. 2016).

Conservation planners can use these flight capabilities when determining spacing and distribution of stopover habitat necessary for completion of successful migration. The time Whooping Cranes spent at stopover sites was positively related with their subsequent flight distance. Lislevand et al. (2016) found a similar relationship in migration bout distances and time at stopover sites for Common Ringed Plovers (*Charadrius hiaticula*) during autumn migration. For Whooping Cranes this effect was greater in autumn than spring, which may be related to birds minimizing spring migration time, allowing arrival on the breeding grounds with enough time to complete breeding season events. We suspect cranes were able to build energy reserves during longer stays to fuel extended flights. The greater need for extended stays before longer migration flights in autumn also could be because the birds in autumn had just finished breeding and may be in poorer body condition when initiating migration as compared to birds initiating spring migration.

Time spent at stopover sites, not in flight, constitutes the majority of the time in the migratory period; therefore, to minimize total time in migration (Hedenström and Alerstam 1997), Whooping Cranes should limit length of migration stops, a behavior observed in other crane species (Kanai et al. 2002). During autumn migration, the correlation between length of stop and length of subsequent stops (e.g., shorter stops were followed by longer stops) indicated energy expenditure was an important consideration in autumn (Nilsson et al. 2013). The extended residency Whooping Cranes have during autumn in Saskatchewan, coupled with observations of diurnal habitat use and foraging behavior (Johns et al. 1997), provides evidence that Whooping Cranes acquire resources for migration at these sites. Continued conservation and management of wetlands and upland foraging resources in this region serve as a key recovery action to maintain important migration habitats (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2007). In spring, we speculate that migration was fueled from resources garnered during the end of the wintering period, as we documented few extended stays at stopover sites during spring where significant resources could be acquired. Whooping Cranes resided for the longest time during spring in mid-latitudes from northern Kansas to North Dakota, where they likely acquired food resources but to a lesser extent than autumn in Saskatchewan. Conservation actions in this mid-latitude area also would support continued recovery of Whooping Cranes but may be more difficult given the larger area in which cranes are dispersed.

We quantified migration timing and distances for birds that made migrations between traditional wintering areas along the Texas Gulf Coast and summering areas near Wood Buffalo National Park in Canada. Our exclusion of <10% of migrations that did not begin or end at these

locations underestimated the variability in migration timing and performance metrics. These truncated migrations were most common for subadult birds that do not return to natal areas until their second or third summer to begin breeding. Therefore, our inferences pertain to the portion of the population that migrates between traditional wintering and summering locations, which constitutes most of the population of breeding individuals.

Conservation Implications

Conservation of habitats used by migratory birds throughout their annual cycle has been a common goal for landscape-scale conservation plans (e.g., U.S. Department of the Interior and Environment Canada 1986, Rosenberg et al. 2016), yet considerable efforts remain to meet these goals globally (Runge et al. 2015). A need exists to understand migration and migratory stopover sites to assist conservation and determine where and what types of habitats to conserve for birds in migration (Mehlman et al. 2005). These deficiencies partially arise because of difficulty in conducting research and conservation activities during times when individuals are migrating over large areas (Webster et al. 2002). For Aransas–Wood Buffalo Whooping Cranes, conservation actions directed at birds during migration will be inherently more challenging than actions at other times of the year. Whooping Cranes spread out over a much larger area in migration compared to their much more limited and predictable use of areas during breeding or wintering seasons (Allen 1952, Kuyt 1992). In addition, >50% of lands used by Whooping Cranes on summering and wintering grounds have some level of land protection (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2005), as compared to 10% in migration (Pearse et al. 2015). Therefore, conservation protection in the migratory corridor remains a priority. Because most land in the Great Plains is in private ownership and most stopover sites occurred on these lands (Pearse et al. 2017), working with landowners will be required for success.

Even with these challenges, our work supports numerous opportunities to expand conservation for migrating Whooping Cranes and benefit other wetland-dependent species. Our findings indicate that Whooping Cranes have a relatively large migration distribution and revisit sites rarely. Therefore, cranes will have a continued need for a variety of well-distributed stopover habitats available along the migration corridor. To meet this need, land protection programs over extensive areas, such as through easement programs, may be more beneficial than intensive conservation actions at specific locations. Distances Whooping Cranes were able to migrate each day can provide partial insight as to the distribution of these habitats, although redundancy and diversity of wetlands may help mitigate pressures associated with seasonal and interannual dynamics, such as drought and fluctuating water levels.

Prioritizing locations within the migration corridor could be directed by interpreting the amount of time cranes spent at various places within the migration corridor each season. Specifically, locations in mid-latitude locations from Kansas to North Dakota in spring and southern Saskatchewan in autumn were used for longer periods, providing support for their prioritization.

The ability for a species to adapt to change is partially dependent on variation in its behavior. We found that Whooping Cranes had flexible aspects to their migration strategy that will be necessary as the landscape continues to undergo conversion, such as from oil and gas extraction (Allred et al. 2015), wind energy development (Wiser and Bolinger 2017), and cropland expansion (Lark et al. 2015). Even with this flexibility, Whooping Cranes and other wetland obligate species likely have little ability to adapt to large-scale loss of wetlands and will continue to require an adequate network of wetlands to persist. Continued adaptation to climate change will remain necessary and, although Whooping Cranes have shown the ability to modify migration timing (Jorgensen and Brown 2017), their continued ability to adapt to intensified future climate change scenarios is unknown, as it is for numerous other species worldwide (Bellard et al. 2012).

Permit NWT-SCI-10-04, Parks Canada Agency Research and Collection Permit WB-2010-4998, and Northwest Territories Wildlife Research Permits WL004807, WL004821, and WL500051. Procedures were approved by Animal Care and Use Committee at Northern Prairie Wildlife Research Center and Environment Canada's Animal Care Committees.

LITERATURE CITED

Alerstam, T. (2011). Optimal bird migration revisited. Journal of Ornithology 152:5–23.

Alerstam, T., M. Hake, and N. Kjellén (2006). Temporal and spatial patterns of repeated migratory journeys by Ospreys. Animal Behaviour 71:555–566.

Allen, R. P. (1952). The Whooping Crane. National Audubon Society, New York, NY, USA.

Allred, B. W., W. K. Smith, D. Twidwell, J. H. Haggerty, S. W. Running, D. E. Naugle, and S. D. Fuhlendorf (2015). Ecosystem services lost to oil and gas in North America. Science 348:401–402.

Austin, J. E., and A. L. Richert (2005). Patterns of habitat use by Whooping Cranes during migration: Summary from 1977–1999 site evaluation data. Proceedings of the North American Crane Workshop 9:79–104.

Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bauer, S., S. Lisovski, and S. Hahn (2016). Timing is crucial for consequences of migratory connectivity. Oikos 125:605–612.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp (2012). Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Canadian Wildlife Service and U.S. Fish and Wildlife Service (2005). International Recovery Plan for the Whooping Crane. Recovery of Nationally Endangered Wildlife (RENEW), Ottawa, ON, Canada, and U.S. Fish and Wildlife Service, Albuquerque, NM, USA.

Chavez-Ramirez, F., and W. Wehtje (2012). Potential impact of climate change scenarios on Whooping Crane life history. Wetlands 32:11–20.

Chevallier, D., Y. L. Maho, P. Brossault, F. Baillon, and S. Massemin (2011). The use of stopover sites by Black Storks (*Ciconia nigra*) migrating between West Europe and West Africa as revealed by satellite telemetry. Journal of Ornithology 152:1–13.

Conklin, J. R., P. F. Battley, and M. A. Potter (2013). Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. PLOS One 8:e54535.

Dahl, T. E. (2011). Status and trends of wetlands in the conterminous United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC, USA.

Douglas, D. C., R. Weinzierl, S. C. Davidson, R. Kays, M. Wikelski, and G. Bohrer (2012). Moderating Argos location errors in animal tracking data. Methods in Ecology and Evolution 3:999–1007.

Folk, M. J., S. A. Nesbitt, S. T. Schwiker, J. A. Schmidt, K. A. Sullivan, T. J. Miller, S. B. Baynes, and J. M. Parker (2005). Techniques employed to capture Whooping Cranes in central Florida. Proceedings of the North American Crane Workshop 9:141–144.

Gage, A. M., S. K. Olimb, and J. Nelson (2016). Plowprint: Tracking cumulative cropland expansion to target grassland conservation. Great Plains Research 26:107–116.

Gilroy, J. J., J. A. Gill, S. H. M. Butchart, V. R. Jones, and A. M. A. Franco (2016). Migratory diversity predicts population declines in birds. Ecology Letters 19:308–317.

Hartman, M. D., E. R. Merchant, W. J. Parton, M. P. Gutmann, S. M. Lutz, and S. A. Williams (2011). Impact of historical land-use changes on greenhouse gas exchange in the U.S. Great Plains, 1883–2003. Ecological Applications 21:1105–1119.

Hasselquist, D., T. Montràs-Janer, M. Tarka, and B. Hansson (2017). Individual consistency of long-distance migration in a songbird: Significant repeatability of autumn route, stopovers and wintering sites but not in timing of migration. Journal of Avian Biology 48:91–102.

Hedenström, A., and T. Alerstam (1997). Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Johns, B. W., E. J. Woodsworth, and E. A. Driver (1997). Habitat use by migrant Whooping Cranes in Saskatchewan. Proceedings of the North American Crane Workshop 7:123–131.

Johnston, C. A. (2013). Wetland losses due to row crop expansion in the Dakota Prairie Pothole Region. Wetlands 33: 175–182.

Jorgensen, J. G., and M. B. Brown (2017). Temporal migration shifts in the Aransas–Wood Buffalo population of Whooping Cranes (*Grus americana*) across North America. Waterbirds 40:195–206.

Kanai, Y., M. Ueta, N. Germogenov, M. Nagendran, N. Mita, and H. Higuchi (2002). Migration routes and important resting areas of Siberian Cranes (*Grus leucogeranus*) between northeastern Siberia and China as revealed by satellite tracking. Biological Conservation 106:339–346.

Krapu, G. L., D. A. Brandt, K. L. Jones, and D. H. Johnson (2011). Geographic distribution of the mid-continent population of Sandhill Cranes and related management applications. Wildlife Monographs 175:1–38.

Kuyt, E. (1979). Banding of juvenile Whooping Cranes on the breeding range in the Northwest Territories, Canada. North American Bird Bander 4:24–25.

Kuyt, E. (1992). Aerial radio-tracking of Whooping Cranes migrating between Wood Buffalo National Park and Aransas National Wildlife Refuge, 1981–84. Ottawa, Ontario, Canada: Canadian Wildlife Service.

Lark, T. J., J. M. Salmon, and H. K. Gibbs (2015). Cropland expansion outpaces agricultural and biofuel policies in the United States. Environmental Research Letters 10:044003.

Laubhan, M. K., and L. H. Fredrickson (1997). Wetlands of the Great Plains: Habitat characteristics and vertebrate aggregations. In Ecology and Conservation of Great Plains Vertebrates (F. L. Knopf and F. B. Samson, Editors). Springer, New York, NY, USA. pp. 20–48.

Lislevand, T., M. Briedis, O. Heggøy, and S. Hahn (2016). Seasonal migration strategies of Common Ringed Plovers *Charadrius hiaticula*. Ibis 159:225–229.

López-López, P., C. García-Ripollés, and V. Urios (2014). Individual repeatability in timing and spatial flexibility of migration

routes of trans-Saharan migratory raptors. Current Zoology 60:642–652.

Mehlman, D. W., S. E. Mabey, D. N. Ewert, C. Duncan, B. Abel, D. Cimprich, R. D. Sutter, and M. Woodrey (2005). Conserving stopover sites for forest-dwelling migratory landbirds. The Auk 122:1281–1290.

Niemuth, N. D., A. J. Ryba, A. T. Pearse, S. M. Kvas, D. A. Brandt, B. Wangler, J. E. Austin, and M. J. Carlisle (2018). Opportunistically collected data reveal habitat selection by migrating Whooping Cranes in the U.S. Northern Plains. The Condor: Ornithological Applications 120:343–356.

Nilsson, C., R. H. G. Klaassen, and T. Alerstam (2013). Differences in speed and duration of bird migration between spring and autumn. The American Naturalist 181:837–845.

Pearse, A. T., D. A. Brandt, M. T. Bidwell, K. L. Metzger, M. J. Harner, D. M. Baasch, and W. Harrell (2019). Data from: Characterization of Whooping Crane migrations and stopover sites used in the Central Flyway, 2010–2016: U.S. Geological Survey data release. https://doi.org/10.5066/P9NRAY6F

Pearse, A. T., D. A. Brandt, W. C. Harrell, K. L. Metzger, D. M. Baasch, and T. J. Hefley (2015). Whooping Crane stopover site use intensity within the Great Plains. U.S. Geological Survey Open-File Report 2015–1166.

Pearse, A. T., M. J. Harner, D. M. Baasch, G. D. Wright, A. J. Caven, and K. L. Metzger (2017). Evaluation of nocturnal roost and diurnal sites used by Whooping Cranes in the Great Plains, United States. U.S. Geological Survey Open-File Report 2016–1209.

Pearse, A. T., M. Rabbe, L. M. Juliusson, M. T. Bidwell, L. Craig-Moore, D. A. Brandt, and W. Harrell (2018). Delineating and identifying long-term changes in the Whooping Crane (Grus americana) migration corridor. PLOS One 13:e0192737.

Piersma, T. (1987). Hop, skip or jump? Constraints on migration of Arctic waders by feeding, fattening and flight speed. Limosa 60:185–194.

Powell, R. A. (2000). Animal home ranges and territories and home range estimators. In Research Techniques in Animal Ecology: Controversies and Consequences (L. Boitani and T. K. Fuller, Editors). Columbia University Press, New York, NY, USA. pp. 65–110.

R Core Team. (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee. https://www.partnersinflight.org/resources/the-plan/

Rotics, S., M. Kaatz, Y. S. Resheff, S. F. Turjeman, D. Zurell, N. Sapir, U. Eggers, A. Flack, W. Fiedler, F. Jeltsch, M. Wikelski, and R. Nathan (2016). The challenges of the first migration: Movement and behaviour of juvenile vs. adult White Storks with insights regarding juvenile mortality. Journal of Animal Ecology 85:938–947.

Runge, C. A., J. E. M. Watson, S. H. M. Butchart, J. O. Hanson, H. P. Possingham, and R. A. Fuller (2015). Protected areas and global conservation of migratory birds. Science 350:1255–1258.

Service Argos. (2008). User's Manual. Servos Argos, Inc., Landover, MD, USA.

Stafford, J. D., A. K. Janke, M. J. Anteau, A. T. Pearse, A. D. Fox, J. Elmberg, J. N. Straub, M. W. Eichholz, and C. Arzel (2014). Spring migration of waterfowl in the northern hemisphere: A conservation perspective. Wildfowl 2014:70–85.

Stoffel, M. A., S. Nakagawa, and H. Schielzeth (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution 8:1639–1644.

Teitelbaum, C. S., S. J. Coverse, W. F. Fagan, K. Böhning-Gaese, B. R. O'Hara, A. E. Lacy, and T. Mueller (2016). Experience drives innovation of new migration patterns of Whooping Cranes in response to global change. Nature Communications 7:12793.

Thorup, K., Y. Vardanis, A. P. Tøttrup, M. W. Kristensen, and T. Alerstam (2013). Timing of songbird migration: Individual consistency within and between seasons. Journal of Avian Biology 44:486–494.

Ueta, M., and H. Higuchi (2002). Difference in migration pattern between adult and immature birds using satellites. The Auk 119:832–835.

Urbanek, R. P., and J. C. Lewis (2015). Whooping Crane (Grus americana), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.153

U.S. Department of the Interior and Environment Canada (1986). North American Waterfowl Management Plan, Washington, DC, USA.

Vander Wal, E., and A. R. Rodgers (2012). An individual-based quantitative approach for delineating core areas of animal space use. Ecological Modelling 224:48–53.

Vardanis, Y., J.-Å. Nilsson, R. H. G. Klaassen, R. Strandberg, and T. Alerstam (2016). Consistency in long-distance bird migration: Contrasting patterns in time and space for two raptors. Animal Behaviour 113:177–187.

Warnock, N. (2010). Stopping vs. staging: The difference between a hop and a jump. Journal of Avian Biology 41:621–626.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: Unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

Wiser, R. H., and M. Bolinger (2017). 2016 wind technologies market report. Electricity Markets & Policy Group. https://www.energy.gov/eere/wind/downloads/2016-wind-technologies-market-report

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.