Migratory Ecology and Movement Patterns of Mid-Continent and Eastern Sandhill Cranes

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Table of Contents

List of Figures

Chapter 1:

Chapter 2:

List of Appendices

Chapter 1

Range Overlap between Mid-Continent and Eastern Sandhill Cranes Revealed by GPS-Tracking

***Overview*:** Sandhill cranes (*Antigone canadensis*) are long-lived birds with relatively low recruitment rates, making accurate knowledge of abundance and distribution critical for well-informed harvest management. Minnesota is one of few states containing portions of 2 distinct breeding populations of greater sandhill cranes (*A. c. tabida*)—the Mid-continent Population (MCP) and the Eastern Population (EP). Historically, the breeding range of MCP cranes in Minnesota was restricted to the extreme northwestern portion of the state, whereas the breeding range of EP cranes was limited to the east-central part of the state with a large area of separation between the 2 populations. Whereas MCP cranes have exhibited stable population estimates over time, EP cranes are currently experiencing a significant increase in population size and a concurrent expansion of breeding range. Our objectives were to evaluate the current range boundaries of the 2 populations in Minnesota and to determine whether the populations overlap on their breeding areas and fall staging grounds. We captured and attached Global Positioning System-Global System for Mobile Communications (GPS-GSM) transmitters to 50 cranes in the zone between the historical breeding range boundaries of the 2 populations. Movements of captured cranes revealed that EP cranes have greatly expanded their breeding range in Minnesota while MCP cranes have experienced more moderate range expansion in the state. Results of this study provide the first documentation of overlap between the breeding ranges of EP and MCP sandhill cranes. Our results also suggest that staging areas in northwestern Minnesota, where recreational harvest targeted at MCP

cranes was allowed beginning in 2010, are being used by both populations and there is overlap in migration corridors, as evidenced by 4 cranes that used both the Mississippi and Central flyways.

Key Words: *Antigone canadensis*, Minnesota, range overlap, sandhill crane, satellite telemetry

INTRODUCTION

Sandhill cranes (*Antigone canadensis*) are long-lived birds with delayed sexual maturity and the lowest recruitment rates of any avian species hunted in North America (Tacha et al. 1989, Drewien et al. 1995), making accurate knowledge of distribution critical for well-informed harvest management. Sandhill cranes (hereafter cranes) in North America are designated into 6 migratory and 2 non-migratory populations for management purposes based on their geographic distributions (Tacha et al. 1994). Minnesota is one of few states containing portions of 2 distinct breeding populations of sandhill cranes: the Mid-continent Population (MCP) that breeds and migrates through northwestern Minnesota, and the Eastern Population (EP) that breeds throughout much of the rest of the state. This distinction has particular relevance to harvest management because MCP cranes breeding in Minnesota are hunted locally whereas EP cranes are not.

Historically, the breeding ranges of MCP and EP cranes in Minnesota were geographically distinct with MCP cranes restricted to the extreme northwestern portion of the state (Johnson 1976) and EP cranes limited to the east-central part of the state (C. Henderson, Minnesota Department of Natural Resources, unpublished report; Johnsgard 1983; Tacha and Tacha 1985) (Fig. 1). Estimates of the number of breeding cranes in Minnesota have recently increased (A. Hewitt, U.S. Fish and Wildlife Service, unpublished data), and widespread documentation of breeding cranes throughout the state suggests that breeding-range boundaries of EP and MCP cranes may be in close proximity or overlapping (Minnesota Breeding Bird Atlas 2014). Because harvest strategies for these 2 breeding populations differ, it is necessary from a management

perspective to be able to distinguish between populations (Kruse et al. 2015). Sandhill cranes are monomorphic; therefore, the most viable option of delineating current geographic range boundaries is to capture cranes that breed near the edge of each population's range and track them throughout their annual migration cycle.

Eastern Population and MCP cranes have substantially different population sizes. The latest photo-corrected 3-year average for the MCP was approximately 405,000 and analyses of population abundance indicate the population grew at a 0.8% annual rate from 1982-2012 (Dubovsky 2016). The EP was reduced to a historical low in the 1930s, (Henika 1936) but has since rebounded with the latest 3-year average at approximately 80,000 individuals (likely an underestimate of total population size, see Fronczak et al. 2017), and an average growth rate of 3.9% per year between 1979 and 2009 (Dubovsky 2016).

Hunting of MCP cranes in Canada and the United States was gradually re-established starting in 1961 and a harvest season was first established in Minnesota in 2010 (Kruse et al. 2015). Minnesota is the only state in the contiguous United States in which MCP cranes are hunted within their breeding range (Lawrence et al. 2012). Although Manitoba and Saskatchewan also have harvest seasons and breeding crane populations, most MCP cranes are hunted while on their migration and wintering grounds (Krapu et al. 2011). Limited hunts of EP cranes were established in Kentucky in 2011 and in Tennessee in 2013, but there is not currently a harvest season targeted at EP cranes in Minnesota.

Cranes in the MCP winter in western Oklahoma, Texas, New Mexico, southeastern Arizona, and northern Mexico before migrating north during the spring to breed throughout central and western Canada, Alaska, eastern Siberia, and northwestern Minnesota (Krapu et al. 2011, Dubovsky 2016) (Fig. 1). A relatively small proportion of the total MCP breeds in Minnesota, with aerial-survey-based estimates of 2,300-7,200 cranes from 2012-2014 (Lawrence et al. 2014). Eastern Population cranes winter in the southeastern United States before migrating to summer breeding areas in the Great Lakes states and Ontario (Walkinshaw 1973, Lewis 1977). However, the EP has recently expanded its breeding distribution throughout the Great Lakes region and northeastern United States and Quebec, and the wintering distribution has expanded north and west into Georgia, Alabama, Tennessee, Kentucky, and Indiana (Melvin 2002, Sauer et al. 2014, Lacy et al. 2015, Fronczak et al. 2017).

Our objective was to characterize the breeding, staging, and migratory distributions of cranes that breed within the zone between historical EP and MCP range boundaries in Minnesota. Specifically, our goals were to (1) ascertain population affiliation of GPS-tagged cranes based on migratory pathways and wintering areas, and (2) determine if EP and MCP cranes breeding in Minnesota overlap in breeding or fall staging distributions, and if so, identify regions of overlap. We expected the northwestern expansion of EP cranes would likely result in overlap of breeding range boundaries within Minnesota and that the majority of breeding cranes found between historical range boundaries would be EP cranes. We also hypothesized that we would observe increases in the number and geographic extent of EP staging areas concurrent with their expanding population.

METHODS

Study Area and Field Methods

We captured and marked cranes in 9 counties in central Minnesota during April-October 2014-2015 (46° to 48° N, -96° to -93° W). We focused our capture efforts in the zone between historical boundaries of breeding ranges of MCP and EP cranes in Minnesota (Fig. 2). We also captured cranes near Sherburne National Wildlife Refuge (NWR), Minnesota (45.5° N, -93.8° W), a fall staging area of cranes, during October-November 2015. Central Minnesota is at the confluence of several ecological sections, including the Northern Minnesota Drift and Lake Plains and Minnesota and Northeast Iowa Morainal sections (Cleland et al. 1997). The western half of the study area is in the ecocline between eastern tallgrass prairie and northern hardwood forest. The landscape is a mosaic of wetlands and lakes in the lowlands, and pasture, agricultural crops, second-growth forest patches, and residential development in the uplands. Wetland areas consist of primarily emergent vegetation communities dominated by cattails (*Typha* spp.) and sedge (*Carex* spp.)-meadows. The predominant agricultural crops are corn, soybeans, wheat, and alfalfa (National Agricultural Statistics Service 2016).

In 2014 and 2015 we captured and equipped cranes with Global Positioning System-Global System for Mobile Communications (GPS-GSM) transmitters (Cellular Tracking Technologies, Somerset, PA). In 2014, we located crane nests by soliciting information from land managers and the general public, and also searched potential nesting areas on the ground from both vehicles and on foot. In 2015, we conducted aerial

surveys during 2 sessions in the first and last week of April from a Bell OH-58 helicopter to identify crane nests in the zone we presumed to be the likely area of overlap.

We captured cranes via night-lighting as described by Drewien and Clegg (1992) and modified by Fox (2011). We mounted a portable spotlight capable of 5,000 lumens and 640 meters of throw (Olight, Smyrna, GA) on a hard hat and a pair of 100-watt weatherproof speakers to an external frame backpack. We approached cranes on foot at night, using the spotlight and broadcast white noise to disorient roosting cranes. We captured adult cranes on their roost sites in emergent-vegetation wetlands from 2 hours after dusk until 2 hours before dawn. We avoided attempting to capture cranes on dates within a week of a full moon to decrease the likelihood of cranes flushing before capture under conditions of relatively high ambient light levels.

To increase efficacy of locating adult cranes on their roosts while night-lighting, we captured pre-fledged hatch-year cranes (colts) by hand during the day and marked these individuals with 6.7-g glue-on VHF radio transmitters (Advanced Telemetry Systems [ATS], Isanti, MN). We sewed each transmitter into the center of a fabric patch, which was colored to approximate the plumage of a colt, and attached the fabric square to the colt's mid-dorsal region using waterproof, non-toxic, quick-drying eyelash adhesive (Andrea Lashgrip Eyelash Adhesive, Ardell, Los Angeles, CA; Spalding et at. 2001, Fox 2011). We tracked radio-marked colts using an ATS receiver and a hand-held 3-element antenna to roost locations. If necessary, we recaptured colts 2-3 weeks after application and reapplied adhesive to ensure relocation of the tagged colt until we captured an adult.

We equipped colts with GPS-GSM transmitters just prior to fledging (approximately 50-60 days old).

In October-November 2015, we captured and marked cranes using rocket nets (Wheeler and Lewis 1972) near a staging area at Sherburne NWR. We assembled a 13.1 x 19.7-m rocket-propelled net along the edge of natural vegetation and obscured it from sight. We conducted trapping on sites that cranes consistently used either for primary feeding shortly after dawn or for daytime loafing later in the morning and we used replica crane decoys to increase crane interest in the capture area. We randomly selected and then equipped up to 3 cranes with transmitters from each successful rocket-netting attempt to limit the number of cranes marked from the same family unit and also minimize stress to cranes and potential capture myopathy. We used a Coda NetLauncher (Coda Enterprises Inc., Mesa, AZ) as an alternative to rocket-netting in areas where a smaller propelled net was more appropriate.

We marked cranes with 60-g GPS-GSM transmitters (Models CTT-1060a-LB and CTT-1060-LM-BT3; Cellular Tracking Technologies, Somerset, PA) above the left tibio-tarsus joint using a 2-piece leg band (Krapu et al. 2011). Legs bands consisted of 2 7.6-cm, color-coated, polyvinyl chloride (PVC), flanged halves; one half bonded to the transmitter and the other half engraved with a unique alpha-numeric code (Haggie Engraving, Crumpton, MD). We lined the leg bands with 1-mm-thick closed-cell neoprene to minimize abrasion (Krapu et al. 2011). We collected a blood sample from the metatarsal vein just below the tibio-tarsus joint of the right leg to subsequently determine sex of captured cranes by DNA analysis (Avian Biotech, Tallahassee, FL). We weighed

all captured cranes and attached aluminum butt-end bands (size 8 or 9, U.S. Geological Survey Bird Banding Laboratory) above the right tibio-tarsus joint. We released all processed cranes within 30 min of capture. All capture and handling methods were approved by the University of Minnesota Institutional Animal Care and Use Committee (Protocol #1403-31362A).

Transmitters were programmed to collect GPS locations at 15-min intervals between sunrise and sunset each day. Horizontal precision of GPS locations was < 5 m. Locations were stored temporarily in the transmitter memory and once a day, the transmitter attempted to upload the entire batch of locations to the Cellular Tracking Technologies database by way of a cell phone network. We assigned the population affiliation (i.e., MCP or EP) for each crane *post hoc* based on migratory patterns and overwintering locations. Mid-continent Population cranes historically use the Central Flyway for both fall and spring migration (Krapu et al. 2011, Dubovsky 2016), and EP cranes use the Mississippi Flyway (Walkinshaw 1973, Lewis 1977, Fronczak et al. 2017). We considered cranes that used multiple flyways during migration in a separate category.

We determined the presence of overlap on breeding and fall staging areas by first filtering telemetry locations for each period: 1 April- 1 August for breeding, and 1 August – 1 October for fall staging. The number of locations and movement characteristics (e.g., mean step length) varied among cranes during these periods. We focused our efforts on roost locations, both to standardize data across individuals (i.e., 1-2 observations/night) and to allow for simple polygon-based summaries of overlap among individuals from the 2 populations. We extracted the last location of each night

and the first location of each morning to represent roost-site locations, provided they were within an hour of dawn or dusk. We buffered each roost location by 3 km and merged these areas to derive a single polygon layer for each crane using package rgeos (Bivand and Rundel 2013) in program R (R Core Team 2014). We then intersected these layers to identify regions of spatial overlap among individuals from the 2 populations or overlap with individuals that used multiple migration flyways and therefore could not be classified as an MCP or EP crane.

RESULTS

We captured 72 cranes (19 by night-lighting, 34 by hand [all colts], 18 using rocket-propelled nets, and 1 crane with a Coda NetLauncher) during 2014-2015. We deployed 50 GPS-GSM transmitters on cranes (26 female, 24 male) from 35 separate family groups.

Population Affiliation

We excluded 14 (28%) cranes with incomplete migratory pathway information due to transmitter failure or potential mortality from assessment of migration movements and assignment to population. Of the 36 cranes (21 adults, 15 colts) observed over ≥1 winter, we classified 9 as MCP cranes and 23 as EP cranes based on their use of either the Central or Mississippi Flyway during migration. We assigned 4 cranes to neither population because they used multiple flyways during migration (Fig. 2). The migratory patterns of these 4 cranes did not conform to the traditional migration framework of cranes in North America (Fig. 3). Two cranes used the Mississippi (EP) Flyway for fall

and spring migrations in fall of 2015 and spring of 2016, but switched to the Central (MCP) Flyway during the fall of 2016. One crane used the Mississippi Flyway in the fall of 2015, continued to Texas to spend the winter in MCP range, then used the Central Flyway to migrate north in the spring of 2016. One crane migrated to Florida in December 2016 before continuing west to settle for the remainder of the winter on the Texas Gulf Coast.

Regions of Overlap

During the breeding season, we identified 3 areas of overlap in northwestern Minnesota that were used by both MCP and EP cranes and cranes that used both flyways (Mississippi and Central; Fig. 2); 2 nearby regions in northwestern Becker and southwestern Mahnomen counties and one area in central Clearwater County. We identified 4 fall-staging areas in northwestern Minnesota that were used by both EP and MCP cranes (Fig. 4). Of these, 3 were used in both 2015 and 2016, and 1 was used only in 2016 (Fig. 4 and Fig. 5). The northwestern Minnesota staging area that had the highest use by EP cranes in both the fall of 2015 and fall of 2016 was a large, 25-km^2 wetland complex in northern Clearwater County (47.9° N, -95.5° W). Ten GPS-marked EP cranes roosted there during fall staging, whereas only 2 GPS-marked MCP cranes roosted at this staging area (Fig. 5, labeled Red Lake Reservation).

DISCUSSION

Our study is the first account of EP and MCP cranes exhibiting overlap on both their breeding areas and fall staging grounds. The EP has expanded its breeding

distribution in Minnesota to the northwest, and most of the breeding cranes we captured in the area between historical breeding range boundaries were EP cranes. The MCP has expanded its breeding distribution southeast in Minnesota, but not to the extent that breeding EP cranes expanded to the northwest. The relatively modest expansion of MCP range in Minnesota is not likely to change management implications for that population; however, the continued expansion of the EP breeding range may influence management considerations, such as bag limits and timing of the harvest season in northwestern Minnesota, on a state level.

Several crane telemetry studies have captured cranes on staging and wintering grounds (Wheeler and Lewis 1972, King et al. 2010, Krapu et al. 2011, Fronczak 2014, Fronczak et al. 2017) with the objective of obtaining a sample of marked cranes representative of the entire population (e.g., the entire EP; Fronczak et al. 2017). In contrast, we focused our capture efforts on breeding grounds, which allowed us to only sample cranes breeding within the geographic area of interest between historical population boundaries in Minnesota. We attempted to evenly distribute capture locations across our study area to maximize our ability to assess population affiliation across the zone where both EP and MCP cranes breed; however, due to logistic constraints, we were unable to sample uniformly across this zone. Also, because we focused our capture efforts in the presumed zone of overlap between the MCP and EP, our sample of marked cranes was not representative of all EP and MCP cranes in Minnesota. As a consequence, we were able to document areas used by cranes of both populations, but the areas of overlap we identified do not necessarily adequately represent overlap at the

population level. Therefore, we used relatively simple, polygon-based methods to identify areas of overlap among individuals rather than attempt to quantify population-level overlap using measures of space-use intensity (e.g., Fieberg and Kochanny 2005).

Generally, overlap among our sample of marked cranes from these 2 populations was minimal during the breeding season and more pronounced during fall staging. Migratory cranes tend to move from their breeding territories to staging areas (see Fronczak et al. 2017) in late summer and their movements during that period are no longer constrained by relatively immobile young or association with breeding territories. The increased period of overlap in the fall coincides with the Minnesota crane-hunting season, which occurs during September and October, thereby potentially affecting EP cranes that are in the Minnesota Northwest Goose and Crane Zone (Fig. 4), where they would be vulnerable to harvest.

We identified 4 fall staging areas in Minnesota where MCP and EP cranes co-occurred (Fig. 4). However, each staging area received predominant use by 1 population and only brief visitations by cranes from the other population (Fig. 5). These short visits correspond with an increase in relatively long-distance movements by cranes in the fall, possibly to investigate staging areas that are optimal for foraging (Sparling and Krapu 1994). Two commonly used staging areas (Agassiz NWR and Pembina WMA) were within the Northwest Goose and Crane Zone, whereas another (Red Lake Reservation) was just outside the boundary (Fig. 4). In addition to 2 EP cranes that used the Agassiz NWR staging area for 1 night during the 2015 crane-hunting season, 1 EP colt spent the summer there and was still present in mid-September, further indicating that there is the

potential for harvest of EP cranes in MCP hunting seasons in Minnesota. Additional monitoring of movements from cranes breeding in northern and northwestern Minnesota is necessary to better understand the extent of this co-mingling. Although the incidental take of EP cranes during the MCP hunting season is not likely to have a substantial effect on the EP's rapidly increasing population in Minnesota, it is a necessary consideration when making management regulations.

Eastern Population and MCP cranes currently show significant genetic differentiation (Jones et al. 2005) despite the presence of gene flow between them. Our results suggest that EP and MCP cranes are currently in contact during breeding in northwestern Minnesota, which may result in increased interbreeding between the 2 populations. Such increased interbreeding would have implications for the genetic diversity of cranes in both the area near range boundaries and across both populations. Johnson et al. (2005) speculated that cranes in North America once had a contiguous breeding range, which became fragmented into distinct breeding populations as numbers decreased and portions of the larger population were extirpated. Jones et al. (2005) found a lack of genetic heterozygosity in both the EP and MCP, which may be explained in the MCP by the existence of multiple localized demes (Wahlund 1928); however, for the EP, a more likely cause is the severe reduction in population size during the 1900s and near extirpation during the 1930s, causing a genetic bottleneck event (Henika 1936; Walkinshaw 1949, 1973; Jones et al. 2005). Cranes are thought to copulate primarily at spring staging areas, and to a lesser extent at wintering areas (Tacha 1988, G. Krapu personal communication). However, Hayes (2015) reported that at breeding areas with

high territory density such as central Wisconsin, cranes reform pair bonds following death and divorce. Therefore, in areas where cranes from both the EP and MCP breed (i.e., the current zone of overlap between EP and MCP cranes in Minnesota), it is likely that as territory density increases, the opportunity for mating between EP and MCP cranes will also likely increase. If that is the case, genetic heterozygosity will likely increase and current genetic structure between these 2 populations may begin to break down.

We used observed crane migratory patterns and overwintering areas for *post hoc* determination of population affiliation. In 4 cases, individual cranes used the migratory flyways of both populations (Fig. 3). Crane populations are defined in part by the migratory paths linking summer and winter ranges, and therefore use of multiple flyways by these cranes precluded us from assigning population affiliation. Annual variation in migration pathways such as this is previously undocumented and could be a result of increasing co-mingling between populations on staging and breeding grounds. Fluid use of multiple flyways may increase social interaction between crane populations and effectively produce a separate category of cranes breeding in overlap zones to which current management definitions do not apply. Although cranes that used multiple flyways only represented 8% of our sample of marked cranes, as crane densities in northwestern Minnesota increase, it is likely that the use of multiple flyways will become more commonplace, further complicating management.

MANAGEMENT IMPLICATIONS

Temporal and spatial overlap of EP and MCP cranes on both staging and breeding areas suggests the need for updated management strategies in Minnesota that no longer assume separation between the 2 populations. Currently, use of northwestern Minnesota fall staging areas by EP cranes is limited during the hunting season targeted at MCP cranes. However, if EP cranes continue to increase in numbers and expand their range, Minnesota crane harvest management and regulations will need to account for the possibility of EP crane take in the Northwest Goose and Crane Zone during hunting seasons. The potential for incidental take of EP cranes in MCP crane hunting seasons also has implications for EP harvest management in that it is currently an unknown component of total harvest. Our results also suggest that if the spatial and temporal overlap we observed during breeding and fall staging increases, and if cranes breeding near the zone of overlap between the MCP and EP use multiple migratory flyways, delineation of migratory cranes breeding at mid-latitudes into distinct populations (i.e., MCP or EP) may at some point no longer be useful as a management tool.

Figure 1. Primary breeding and migratory/wintering ranges for Mid-Continent and Eastern Populations of sandhill cranes (*Antigone canadensis*). Black arrows indicate the predominant migration routes for each population. Pink dots indicate sporadic breeding records of Eastern Population sandhill cranes in the northeastern U.S.

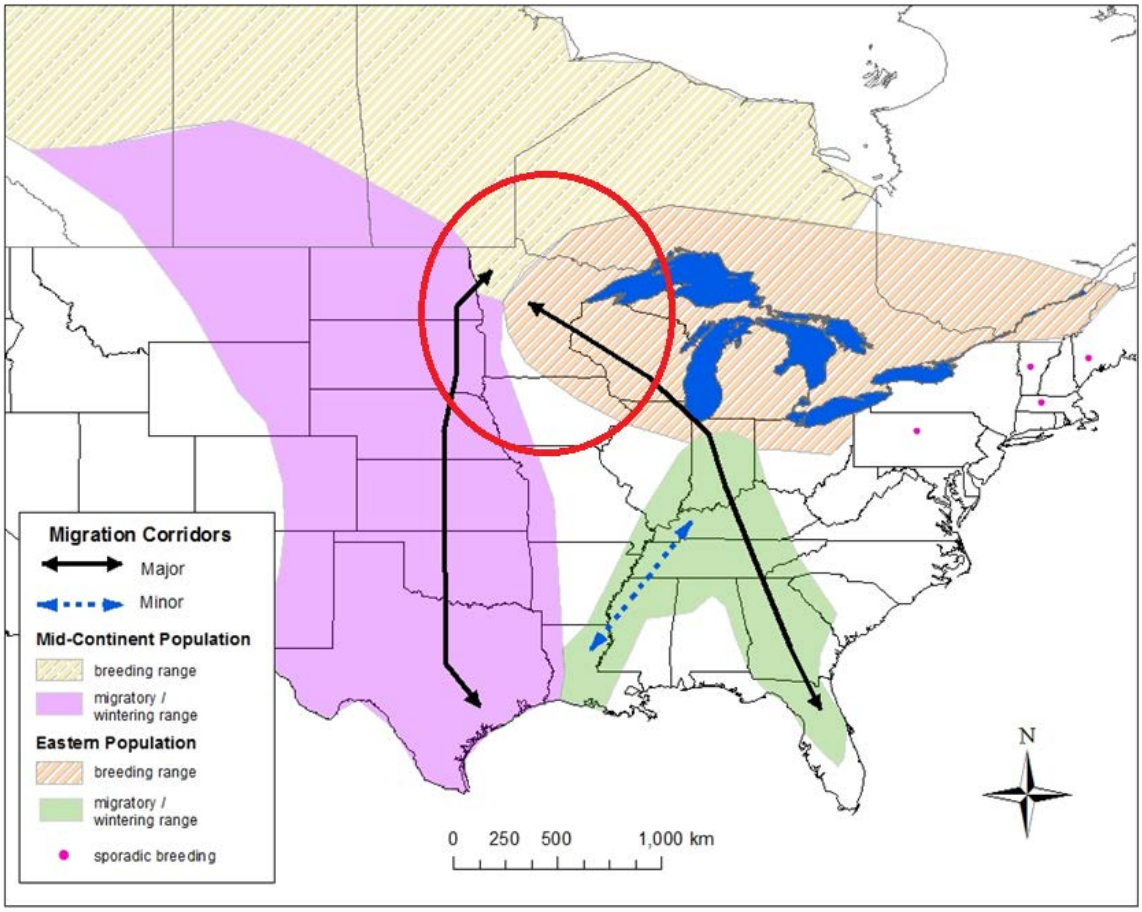


Figure 2. Capture locations of sandhill cranes (*Antigone canadensis*) during May-October 2014 and April-November 2015. Color of points represent population affiliation assigned based on migratory flyway (Central Flyway = Mid-Continent Population [MCP], Mississippi Flyway = Eastern Population [EP]), with MCP sandhill cranes in green (n=9), EP sandhill cranes in blue (n=23), and cranes that used both migration flyways in orange (n=4). Historical range boundaries are shown with corresponding color affiliation. Areas used by cranes from multiple population segments (EP, MCP, both flyways) during 1 April - 1 August of 2015 or 2016 are represented with yellow polygons.

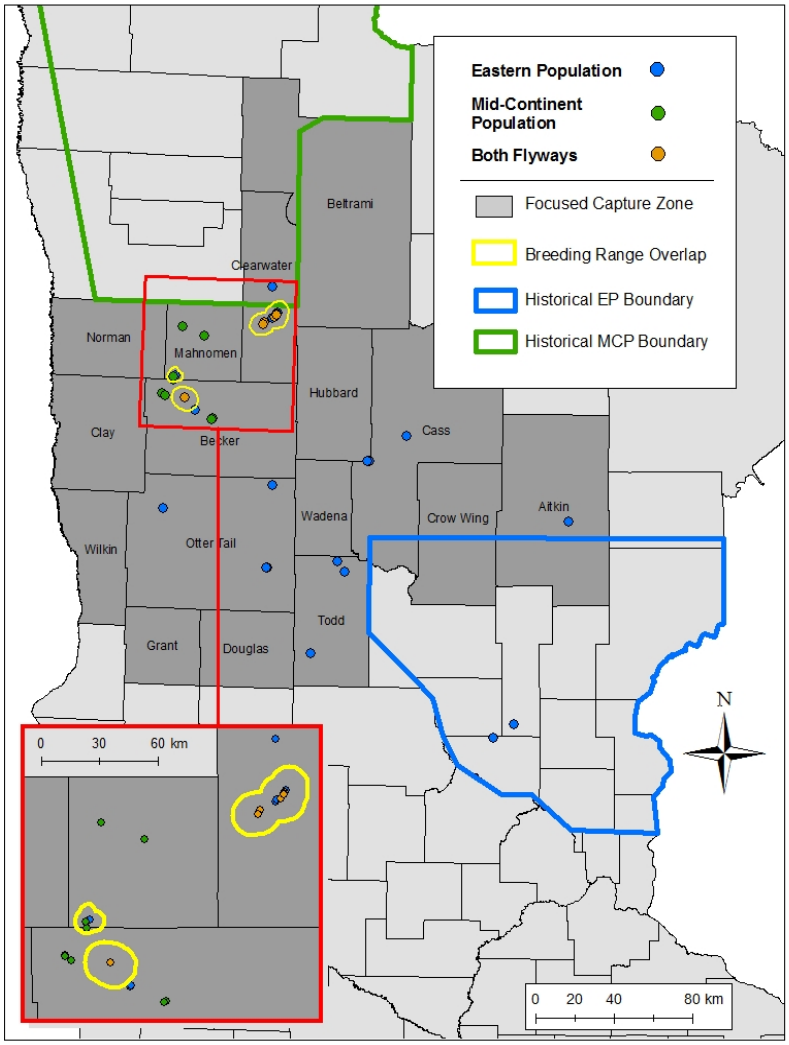

Eastern Population
Mid-Continent Population
Both Flyways
Focused Capture Zone
Breeding Range Overlap
Historical EP Boundary
Historical MCP Boundary
Beltrami
Clearwater
Norman
Mahnomen
Hubbard
Clay
Becker
Cass
Wadena
Crow Wing
Aitkin
Wilkin
Otter Tail
Todd
Grant
Douglas
N
0 30 60 km
0 20 40 80 km

Figure 3. Migration routes of sandhill cranes (*Antigone canadensis*) in 2014 (*n*=4) and 2015 (*n*=36). Color of lines represent population affiliation, assigned based on migratory flyway (Central Flyway = Mid-Continent Population [MCP], Mississippi Flyway = Eastern Population [EP]), with Mid-Continent Population sandhill cranes in green (*n*=9), Eastern Population sandhill cranes in purple (*n*=23), and cranes that used both flyways in orange (*n*=4).

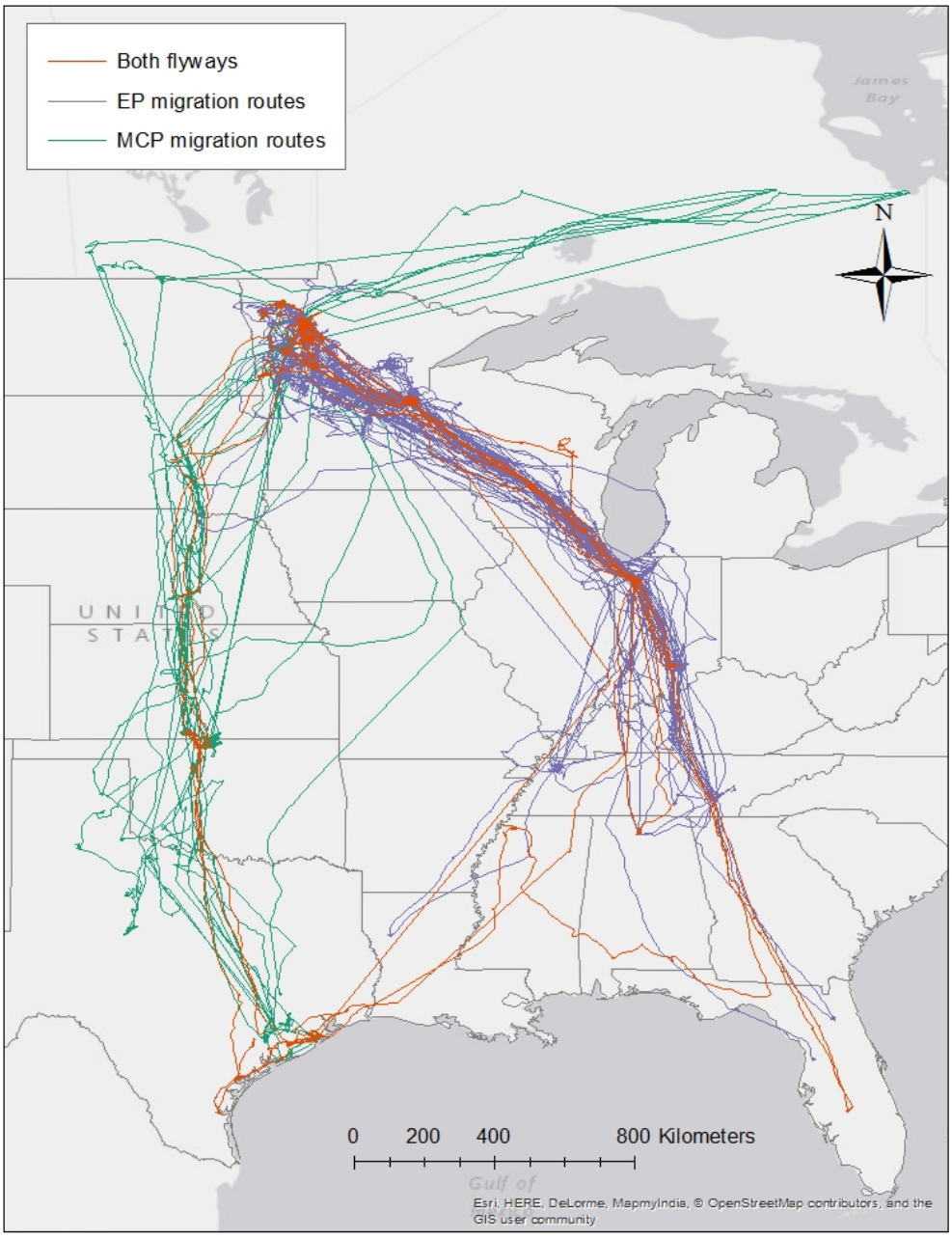

Both flyways
EP migration routes
MCP migration routes
N
0 200 400 800 Kilometers
Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 4. Areas of overlap between Eastern Population and Mid-Continent Population sandhill cranes (*Antigone canadensis*) during the fall staging periods of 1 August - 1 October 2015 and 2016. Red polygons represent overlap during 2015 and blue polygons represent overlap during 2016. The Northwest Goose and Crane Zone (open to MCP crane hunting) in northwestern Minnesota is indicated by the cross-hatched polygon. The historical Mid-Continent Population range boundary is indicated by the green polygon.

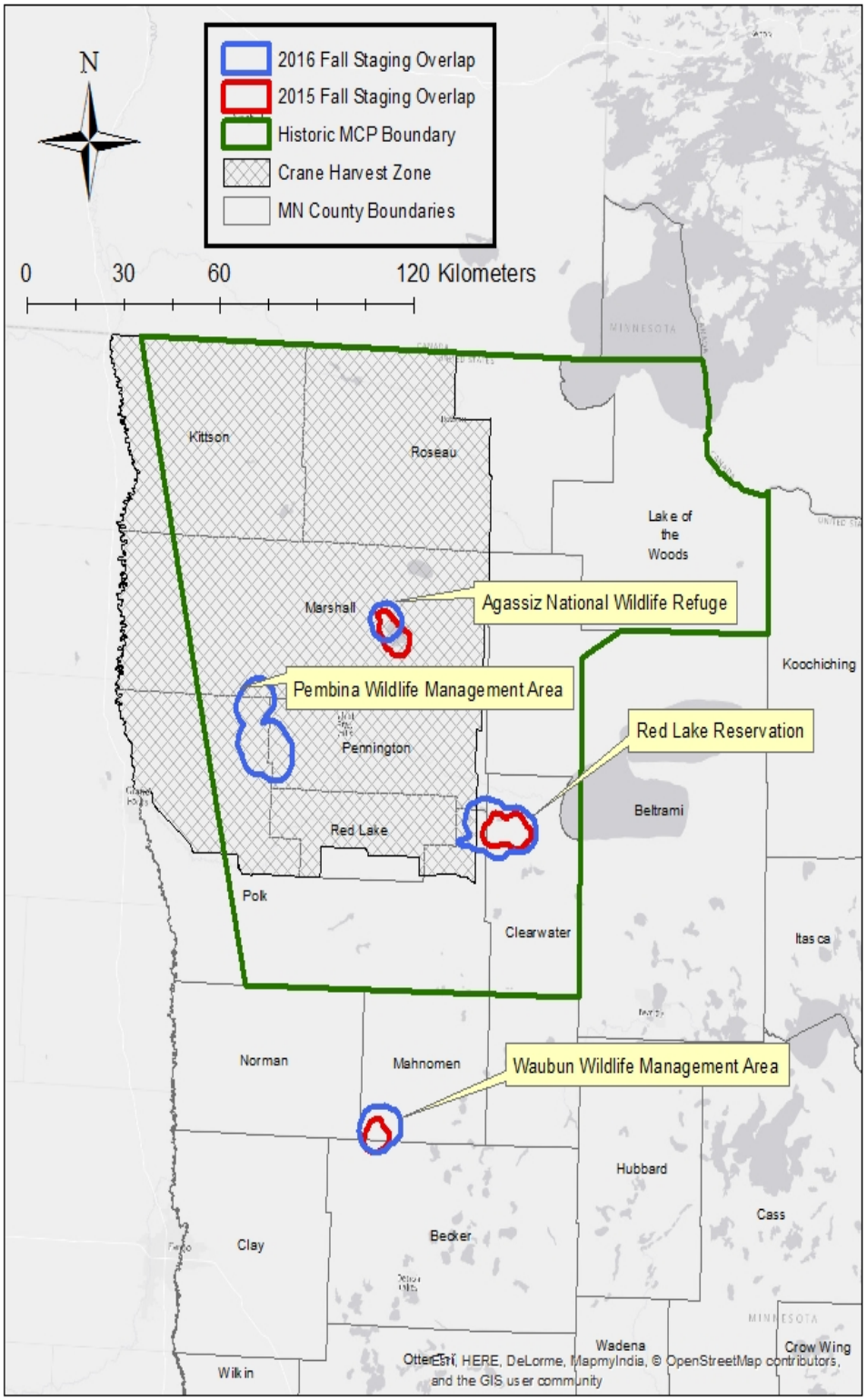
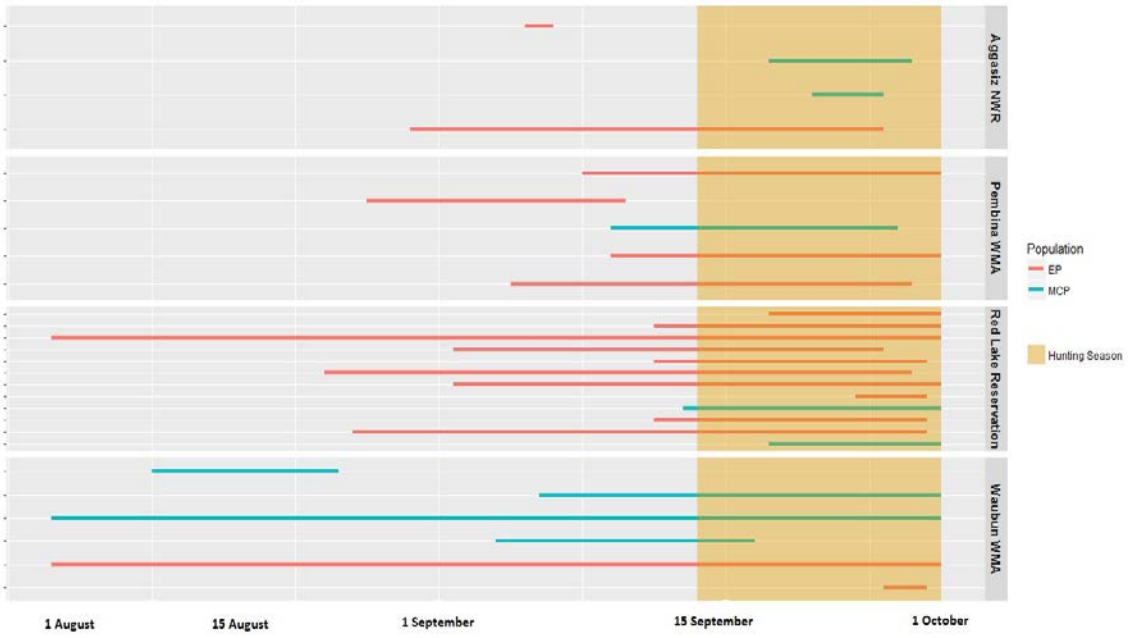

N
2016 Fall Staging Overlap
2015 Fall Staging Overlap
Historic MCP Boundary
Crane Harvest Zone
MN County Boundaries
0
30
60
120 Kilometers
Kittson
Roseau
Lake of the Woods
Marshall
Agassiz National Wildlife Refuge
Koochiching
Pembina Wildlife Management Area
Red Lake Reservation
Pennington
Beltrami
Red Lake
Polk
Clearwater
Itasca
Norman
Mahnomen
Waubun Wildlife Management Area
Hubbard
Cass
Clay
Becker
Wadena
Crow Wing
Wilkin
Otter Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 5. Temporal overlap between Eastern Population (EP) and Mid-Continent (MCP) sandhill cranes (*Antigone canadensis*) during the fall staging periods of 1 August - 1 October 2015 and 2016. Orange lines represent use by EP cranes and green lines represent use by MCP cranes. The period of the fall hunting season within the Northwest Goose and Crane Zone (NWGCZ) in Minnesota, where MCP cranes are hunted, is highlighted in orange beginning on 15 September. The first and second staging areas (Agassiz NWR and Pembina WMA) are within the NWGCZ, the third staging area (Red Lake Reservation) is just outside the boundary of the NWGCZ, and the last staging area is further south of the NWGCZ.



Chapter 2

Movement Strategies of Adult and Juvenile Sandhill Cranes during the Breeding Season

Overview: The movement patterns of juveniles, which are influenced by a combination of both internal and external factors unique to their age class, affect both range expansion of populations and patterns of spatiotemporal overlap, yet are not well-studied in birds and other vertebrates. Recent technological advances in animal biotelemetry have made it possible to quantify movements of juvenile birds prior to settlement on breeding areas. We used fine-scale GPS telemetry data to characterize movements of adult and juvenile sandhill cranes (*Antigone canadensis*) in and near the transition zone between breeding Eastern and Mid-Continent Populations from arrival on natal areas until staging prior to fall migration. We segmented the movement trajectory of each crane into a series of behavioral states indicative of either roaming or settled movement patterns. Juvenile and adult sandhill cranes utilized different movement strategies throughout the breeding season. Juveniles were more likely than adults to display long-distance roaming movements and also traversed much larger areas than adults when roaming. Roaming was most common during spring (i.e., April-May), early in the breeding season and soon after juvenile cranes returned to natal areas. Adult cranes revisited areas at higher rates than juveniles regardless of behavioral state. Adults visited areas for longer durations than juveniles during roaming periods but for shorter durations during settled periods. We hypothesize that the differences in frequency and intensity of space-use between juvenile and adult cranes may be attributed to differences in both biological requirements and

familiarity with the landscape. Adult cranes are constrained by association with breeding areas during spring and early summer, but also likely have prior experience with foraging and roosting sites within their home ranges. In contrast, juvenile cranes are not associated with a nest during this period, and they are learning where and how to independently secure resources.

Key Words: *Antigone canadensis*, long-distance roaming, movement ecology, sandhill crane, segmentation, telemetry

INTRODUCTION

Recent attention has focused on understanding movements of birds throughout their annual cycle (Hostetler et al. 2015, Kramer at al. 2018) to elucidate season-specific drivers that affect demographic rates and population dynamics (Rushing et al. 2017). Similarly, understanding intra-annual movements of different age classes, which have varying biological requirements (e.g., obtaining and defending a territory, attracting a mate, rearing offspring, etc.), can provide insights into how these differences inform spatio-temporal patterns of landscape use. Of particular interest is the role juvenile avian movement plays in determining range dynamics (Clobert et al. 2001), especially for long-lived species with delayed sexual maturity. The seasonal movements and dispersal strategies of juveniles, which are influenced by a combination of both internal and external factors unique to their age class, affect both population range expansion and patterns of spatiotemporal overlap (Clobert et al. 2008, Nathan et al. 2008, Jonsson et al. 2016). For example, long-distance dispersal events by juveniles may inform future breeding site establishment and provide opportunities for intermingling of otherwise spatially isolated populations (Morrison and Wood 2008).

Despite the importance of understanding intra-annual movements of juvenile birds (defined here as birds pre-breeding, but after individuals have become independent from adults), these movements are poorly understood because of difficulties capturing and marking juvenile birds, and because juvenile mortality rates are often much higher than those of adults (Peron and Gremillet 2013, Schillinger et al. 2012). Recent reductions in the mass of satellite transmitters and advances in other technology (e.g.,

light-level geolocators, McKinnon et al. 2013) have made it more feasible to study movements of juveniles (Bridge et al. 2011, Margalida et al. 2013, Geary et al. 2015, Flack et al. 2016, Harel et al. 2016). As a result, several recent studies have demonstrated that juvenile movements tend to be less directed during different periods relative to adults (Brown and Taylor 2015, de Grissac et al. 2017). These differences have been attributed to exploratory behaviors associated with prospecting during the post-fledging period in juvenile blackpoll warblers (*Setophaga striata*; Brown and Taylor 2015), or increased foraging efficiencies of adults and competitive exclusion of juveniles in wandering albatrosses (*Diomedea exulans*; de Grissac et al. 2017).

Juvenile dispersal is considered to have 3 distinct phases: 1) departure from parental care, 2) transience, during which individuals investigate the landscape, and 3) settlement, where individuals first defend a breeding territory (Bowler and Benton 2005, Murphy et al. 2017). The first phase of dispersal has been well-studied for some avian species; however, most studies have focused on small-scale, post-fledging movements of species that exhibit short-duration parental care in only the first year of life (White and Faaborg 2008, Small et al. 2015). Short-lived avian species, such as songbirds, spend relatively little time between the onset of independence and successful breeding. By contrast, long-lived species may spend several years in this transient phase, with juveniles moving long distances from natal areas before eventually returning as they approach sexual maturity; however, this transient period is neither well described nor understood (Ferrer 1993, Poessel et al. 2016).

Sandhill cranes (*Antigone canadensis*; hereafter cranes) have delayed sexual maturity and low recruitment rates (Tacha et al. 1989, Drewien et al. 1995), which results in juveniles comprising a significant portion of the population (Melvin 1978, Tacha and Vohs 1984), providing a useful system to compare and contrast movement strategies among different age classes in a long-lived species. Adult cranes have high annual breeding site fidelity and defend (often the same) breeding territories each spring/summer, which constrains their movements to a relatively small area (Nesbitt and Williams 1990, Drewien et al. 1999, Krapu et al. 2011). After young of the year have fledged, adult cranes use a larger area, including fall staging areas, which generally provide abundant food resources in preparation for migration, and then most cranes move considerable distances between breeding and non-breeding (i.e., wintering) areas (Krapu et al. 2011, Fronczak et al. 2017, Wolfson et al. 2017).

In contrast, little is known about juvenile crane movements and habitat use following the end of parental care until they enter the breeding population. Most juvenile cranes dissociate from their parents at some point between the onset of their first fall (southward) migration and the completion of spring (northward) migration the following year (Hayes 2015). Because cranes do not typically successfully reproduce until they reach 4 to 5 years of age, they spend a large portion of their lives in a non-breeding state (Radke and Radke 1986, Tacha et al. 1989, Nesbitt 1992, Hayes 2015). While on summer breeding grounds, juvenile cranes exhibit lower philopatry than adults, and often spend time in large groups likely developing social bonds with other juveniles, and possibly

prospecting for potential breeding areas (Lovvorn and Kirkpatrick 1982, Drewien et al. 1999, Hayes 2015).

Breeding adult crane movements are spatially constrained due to the need to defend territories, incubate eggs, and raise pre-fledged young. However, juvenile cranes do not have these constraints, and therefore may exhibit markedly different behavioral patterns than adults. There is a paucity of information on movements of pre-breeding juvenile cranes and most other long-lived birds, and existing information derives only from studies involving VHF transmitter-equipped cranes (Bennett 1989, Drewien et al. 1999, Hayes 2015), which limits the resolution of information about their movements. The advent of GPS-GSM transmitters offers the potential to study juvenile movements at finer temporal resolution and over greater spatial and temporal extents.

To better understand how juvenile cranes used landscapes during the period following arrival on their natal areas in spring, we marked and monitored juvenile cranes from 2 populations whose breeding distributions come into contact in Minnesota (Wolfson et al. 2017). We used fine-scale GPS telemetry data to characterize movements of juveniles in and near the transition zone between breeding Eastern and Mid-Continent Populations from arrival on natal areas until staging prior to fall migration. We further evaluated whether and how these movements differed from those of adults. Our specific objectives were to 1) quantify the frequency and intensity of space-use across the landscape by cranes during this period, using the metrics of revisitation rate and duration of time in areas used, 2) classify crane movements into behavioral states (i.e.: settled versus roaming), and 3) quantify age-specific differences in movement strategies. We

expected that biological requirements would dictate movement strategies, and therefore hypothesized that adult cranes would display intensive space use on relatively small territories throughout the summer whereas juveniles would exhibit low-frequency use over a much greater spatial extent, and potentially exhibit more variability in movement strategies.

METHODS

Study Area

We captured and marked cranes in 9 counties in central Minnesota during April–October 2014–2015 (46° to 48°N, −96° to −93°W). We focused our capture efforts in the zone between the historical boundary separating breeding ranges of the Mid-Continent and Eastern populations in Minnesota (Fig. 2; Wolfson et al. 2017). We also captured and marked six adult cranes near Sherburne National Wildlife Refuge, Minnesota (45.5°N, −93.8°W), an autumn staging area of cranes, during October–November 2015. Central Minnesota is at the confluence of several ecological sections, including the Northern Minnesota Drift and Lake Plains and Minnesota and Northeast Iowa Morainal sections (Cleland et al. 1997). The western half of the study area was in the ecocline between eastern tallgrass prairie and northern hardwood forest. Land cover in our study area was a mosaic of wetlands and lakes in the lowlands, and pasture, agricultural crops, second-growth forest patches, and residential development in the uplands. Wetland areas consisted of primarily emergent vegetation communities dominated by cattails (*Typha* spp.) and sedge (*Carex* spp.)-meadows. The predominant agricultural crops were corn,

soybeans, wheat, and alfalfa (National Agricultural Statistics Service 2016).

Capture and Marking

We captured cranes using a variety of methods including night-lighting, rocket-nets, and hand-capture of pre-fledged juveniles. For a full description of capture and handling methodology, see Wolfson et al. (2017). We marked cranes with 60-g GPS-GSM transmitters (Models CTT-1060a-LB and CTT-1060-LM-BT3; Cellular Tracking Technologies, Somerset, PA) above the left tibio-tarsus joint using a 2-piece leg band. All capture and handling methods were approved by the University of Minnesota Institutional Animal Care and Use Committee (Protocol #1403-31362A).

Transmitters were programmed to collect GPS locations at 15-min intervals between sunrise and sunset each day. Horizontal precision of GPS locations was < 5 m (Wolfson, unpublished data). Locations were stored temporarily in the transmitter memory and once a day, the transmitter attempted to upload the entire batch of locations to the Cellular Tracking Technologies database by way of a cellphone network, resulting in near-continuous diurnal locations for marked cranes.

Data Analysis

We excluded all crane locations east of -93 longitude (WGS84; roughly the eastern boundary of Minnesota) to focus our analysis on crane movements subsequent to arrival on summer ranges used by breeding cranes in Minnesota and association with natal areas for non-breeding, juvenile cranes. We visually inspected plots of successful GPS fixes for each crane and excluded cranes with extended periods of missing fixes

(missing ≥50% of expected fixes over the period of interest). We also excluded locations recorded during spring migration to breeding areas, and all locations associated with staging behavior in the fall.

We used the T-LoCoH package in R (R Core Team 2014) to examine patterns of space use over time for each crane. We constructed convex polygons, or hulls, around each GPS location using a pre-defined number of nearest-neighbor points that were close together in both time and space, using the metric Time-Scaled Distance (TSD). The TSD value (Ψ) for any 2 points *i* and *j* is given by:

$$\Psi_{ij} = \sqrt{\Delta x_{ij}^2 + \Delta y_{ij}^2 + \left(s * v_{max} * \Delta t_{ij}\right)^2},$$

where Δx_{ij} and Δy_{ij} measure the difference between *x* and *y* coordinates of points *i* and *j*, v_{max} is the maximum observed velocity between any 2 consecutive points, Δt_{ij} is the change in time between locations, and *s* is a dimensionless tuning parameter used to scale the importance of temporal differences relative to spatial differences; if s = 0, TSD is equivalent to Euclidean distance. As the value of s increases, the influence of the time interval between points is given increasing weight versus Euclidean distance in the calculation of TSD. We selected *s* so that 60% of hulls were time-selected (i.e., hulls were determined using only sequential points in time) as suggested by Lyons et al. (2013).

We then selected the set of nearest-neighbor points used to create each hull by using both temporal and spatial separation; therefore, points close in space may not be

considered nearest neighbors if they are far apart in time. We used the "a-method", which includes all neighboring points up to a certain cumulative TSD value, because it is recommended when points are sparse in some areas and dense in other areas (Getz and Wilmers 2004). We used the "auto.a" function to find values of "a" such that 98% of all points had ≥20 nearest neighbors (Lyons et al. 2013). Once we created hulls, we calculated revisitation rates and duration of stay for each hull by assigning an inter-visit gap (the amount of time that must pass before an occurrence within the hull is considered a separate visit) of 24 hours so that we could analyze daily patterns of space use.

We segmented each crane's movement trajectory during spring and summer (1 April to 1 September) into one of two behavioral states, settled or roaming, to facilitate comparison of movement strategies between juveniles and adults. We measured the distance between each GPS location and the centroid of all points for each crane using code customized from the T-LoCoH package (Lyons et al. 2013). We used these distance-to-centroid (D2C) values to quantify the extent of long-distance roaming behavior for each individual.

We segmented each resulting time-series of D2C values using the Lavielle method of segmentation in the adehabitatLT package in program R (Calenge 2006, Lavielle 1999). The Lavielle method is a non-parametric method that finds the optimal segmentation of a time series using K segments, by minimizing a function that measures the contrast between a value of interest (in this case, mean D2C values) for segments in an observed time series versus a theoretical model with K (user-defined) possible segments. We graphically inspected the contrast function and chose the optimal K value

that produced a clear break in the decrease of this function (Barraquand and Benhamou 2008, Fig 1). We next segmented each time series of locations using the chosen K value and visually inspected the corresponding segmented time-series of D2C values to confirm that breakpoints coincided with apparent changes in D2C values. We then assigned a behavioral state of settled to the segments with lower D2C values and roaming to the segments with higher D2C values.

The segmentation approach was occasionally problematic when cranes utilized multiple areas over the course of the season instead of a single high-use area. If the use of an additional area was relatively short (< 3-4 weeks), D2C plots showed a plateau for that period (this happened on 3 occasions with 3 cranes). In the case of multiple areas with extended use, the centroid of the entire trajectory was located between the multiple areas and the Lavielle method did not help discriminate useful breakpoints (this happened on 5 occasions with 4 different cranes). For these 8 cranes, we segmented the trajectory following visual inspection of D2C values.

After classifying all locations into a behavioral state (settled or roaming), we calculated a variety of animal-specific summary statistics (mean, median, maximum, standard deviation, and inter-quartile range) of the D2C values for each behavioral state. We also calculated animal-specific summaries (mean, maximum, and standard deviation) for the T-LoCoH derived time-use estimates (revisitation rate of hulls visited, and duration of time spent at each hull) for each behavioral state.

We conducted a principal components analysis (PCA) using the mean D2C values, mean revisitation rate, mean duration length, and the number of observations in

each behavioral state to evaluate differences in movement characteristics by age class and behavioral state. We used the prcomp function in the stats package in R to conduct the PCA with centered and scaled variables.

RESULTS

From the 50 cranes deployed with GPS-GSM transmitters during 2014-2015, there were sufficient data for analysis from 29 cranes (13 juveniles and 16 adults) during the period 1 April-1 September 2016, and 16 cranes (5 juveniles and 11 adults) during the period 1 April-1 September 2017. The average distance-to-centroid (D2C) value, which represents the geographic area over which an individual moved, was much greater for juvenile cranes (25,500 meters) than for adults (3,850 meters), indicating that juveniles used a much larger geographic extent throughout the season. Adult D2C values remained stable and relatively small throughout the season whereas juvenile D2C values were highest during April and May and lower during the rest of the season. (Fig. 2)

In 2016, 10 (77%) of 13 juveniles exhibited roaming, while only 2 (12%) of 16 adults roamed. In 2017, 3 (60%) of 5 juveniles roamed, and 2 (15%) of 13 adults roamed (Fig. 3). Over both years, juveniles spent 88.2% of their time in a settled state and 11.8% roaming, whereas adults spent 96.5% of their time settled and 3.5% roaming. Juvenile cranes exhibited roaming behavior on 13% of days, whereas adults exhibited roaming behavior on 2% of days during the period between arrival on breeding or natal areas and fall staging (Appendix A).

Juveniles revisited fewer hulls than adults both while roaming and also when settled. Juveniles revisited hulls, on average, 3 times while roaming and 11 times while settled. Adults revisited hulls, on average, 8 times while roaming and 19 times while settled (Appendix B). Juveniles tended to use areas for shorter durations than adults while roaming and longer durations than adults while settled (Fig. 4). For juveniles, the average animal-specific mean duration length of hulls was 54 locations per visit while roaming and 127 locations per visit while settled. For adults, the average animal-specific mean duration length of hulls was 90 locations per visit while roaming and 114 locations per visit while settled (Appendix B); these summaries only include individuals that spent at least some time in the roaming state.

The first principal component, which explained 58% of the variance among the movement metrics (number of observations in a state, mean D2C value, mean duration of use value, and mean revisitation value), had high positive factor loadings for number of observations in the behavioral state (i.e., roaming or settled) and mean revisitation rate, and high negative loading for mean D2C values, suggesting that cranes revisited more of the same areas when in a settled state (Appendix C). The second principal component, which explained 27% of the variance, had a high negative factor loading for mean duration of use and low loading for the other 3 variables, which indicated that mean duration of use was not highly correlated with the other variables of interest. The third and fourth principal components explained 9% and 5% of the variance, respectively (Fig. 5).

DISCUSSION

We found that juvenile and adult cranes utilized different movement strategies during spring and summer. Juveniles were more likely than adults to display long-distance roaming movements and also traversed much larger areas than adults when roaming. Juveniles often had multiple bouts of roaming during the season, although roaming was most common during spring (i.e., April-May), early in the breeding season and soon after juvenile cranes returned to natal areas. Adult cranes had higher revisitation rates than juveniles regardless of behavioral state, and higher duration of use when roaming than juveniles, but lower duration when settled.

We hypothesize that differences in frequency and intensity of space-use between juvenile and adult cranes may be attributed to differences in both biological requirements and familiarity with the landscape. Adults have accumulated knowledge over many years and have experience with specific breeding areas, and are therefore likely able to more efficiently navigate to and make use of preferred areas for breeding, foraging, and loafing. During the 2016 field season, 11 of the 13 juveniles were on the breeding grounds for the first year without parental care (2 juveniles were captured as hatch-year birds during the summer of 2014), and therefore had much less familiarity with their surroundings than adults, which likely had multiple years of experience with breeding areas. The highest revisitation rates of adults were all during the settled state, likely due to informed use of their defended breeding territory.

As we expected, juveniles had a high incidence of long-distance roaming in the first part of the breeding season, especially in their first summer without parental care.

These movements may be indicative of prospecting behavior, in which potential breeding sites are investigated for use in future years (Reed et al. 1999). Prospecting has been well studied among colonial breeders because of the relative ease of field observation (Boulinier et al. 1996, Danchin et al. 1998, Dittmann et al. 2005, Calabuig et al. 2010). Although prospecting movements have been documented at a fine spatial scale, long-distance movements, especially those of juveniles, may also need to be considered in the context of potential prospecting (Ponchon et al. 2013).

We observed less roaming among third-year cranes (i.e., cranes in their second summer following independence) compared to second-year cranes (i.e., cranes in their first summer following independence; Fig. 3). That pattern is consistent with other studies of juvenile dispersal of long-lived avian species (Gonzalez et al. 1989, Soutullo et al. 2006). Cranes can reproduce for the first time as early as age 2, but more commonly occupy breeding areas and nest between ages 4 and 6 (Radke and Radke 1986, Tacha et al. 1989). Therefore, juvenile cranes experience multiple seasons on the breeding range before acquiring and defending a breeding territory, and appear to exhibit less roaming as they age.

Hayes and Barzen (2016) considered the role of prospecting in Eastern Population sandhill cranes in Wisconsin. They used VHF telemetry, and were therefore not able to detect long-distance movements. However, they found that second-year cranes had the largest home-range sizes, which then decreased each year until cranes bred. However, their study design resulted in 60-100 locations per individual each season, whereas our

study resulted in an average of about 6,000 locations per crane per season, providing us with the ability to evaluate more fine-scale patterns within a year.

Although the incidence of long-distance roaming by adults was drastically less than that of juveniles, there were periods of roaming by adults that occurred during both years of our study. These roaming periods may be part of a movement strategy that predominantly relies on well-informed, intensive use of a local area, but also includes occasional long-distance forays, similar to the mixed movement distribution investigated by Spiegel et al. (2015). These authors tracked adults of 3 long-lived species of vultures, and found their movements operated at 3 different scales: central-place Brownian motion, highly-directional ballistic motion, and long-range forays, with steps far greater than the first 2 states. These first 2 movement states, small-scale localized search and directional travel, comprise the Levy flight foraging hypothesis, which had been thought to be an optimal foraging strategy for an unpredictable and resource-poor environment, although more recent literature suggests that separate behavioral states can better explain animal movement (Viswanathan et al. 1999, Edwards et al. 2007, Bazazi et al. 2012, Pike 2015). Spiegel et al. (2015) found that long-range forays conducted by adult vultures had step lengths far exceeding those expected under the Levy hypothesis. To test mechanistic drivers, Spiegel et al. (2015) examined the relationship between long-range forays and optimal foraging behavior, sexual dimorphism in wing loading, weather, population genetics, and potential breeding dispersal and rejected all potential hypotheses with the exception of breeding dispersal.

We observed a lower incidence of long-distance roaming among adult cranes compared to juveniles, but we were unable to confirm whether adults successfully bred in years subsequent to capture. Of the 16 adult cranes in our study, 10 were associated with a nest and/or hatch-year young at the time of capture, and we were unable to ascertain the breeding status of the other 6 adults. We observed long-distance roaming in 3 adults, 2 of which were among the 6 adults for which we were not certain of breeding status when marked.

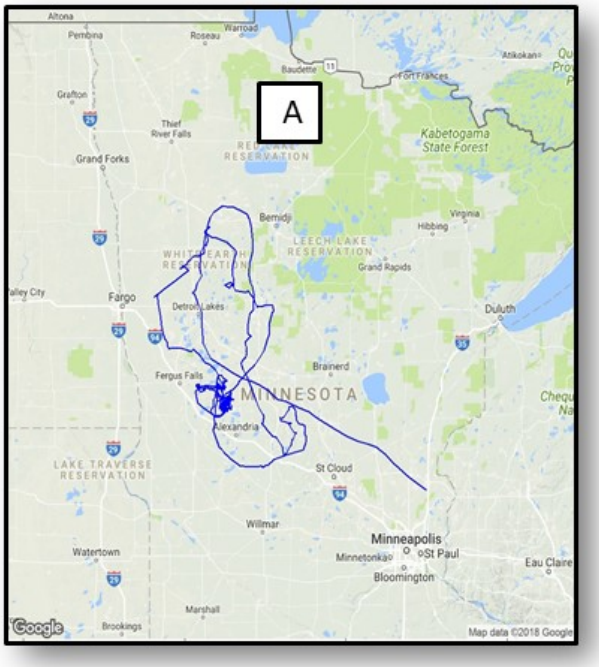
Our analytical approach is novel, and provides a more flexible process of segmentation than alternative approaches, allowing individuals to shift their designated behavioral state on a daily basis. Other approaches for assessing movement patterns include tools such as Net-Squared Displacement to fit the trajectory of individuals to a single movement strategy (i.e., localized, migratory, disperser, nomadic) over an entire season (Fryxell et al. 2008, Bunnefeld et al. 2011, Singh et al. 2012, Cagnacci et al. 2015), or home-range estimates applied over regular time intervals (i.e., weekly or monthly; Borger et al. 2006, Signer et al. 2015, Blanchet et al. 2016, Murphy et al. 2017). The drawback to such techniques is it forces an arbitrary choice of analysis window that may not be biologically relevant. Our approach allowed us to consider each individual's trajectory over the entire period of interest (1 April through 1 September), thus avoiding some of these issues of scale (Bissonette 2016).

Because we were unable to evaluate subsequent reproductive success of both juvenile and adult marked cranes, we can only speculate to what extent these long-distance roaming movements may have influenced future nesting locations and breeding

strategies. However, knowledge of extent and intensity of space-use can help inform estimates of the distance and rate of colonization of unoccupied areas on the landscape and perhaps, breeding range expansion. Our study focused on cranes whose breeding range was in Minnesota, where breeding distributions of Eastern and Mid-Continent populations converge (Wolfson et al. 2017). The period with the highest degree of long-distance roaming behavior was in April and May, shortly after the conclusion of northbound spring migration. If this is an important period for developing pair bonds between juvenile cranes, long-distance dispersal may increase the potential for intermingling of pre-breeders among these 2 populations. Improved knowledge of how juveniles use the landscape provides insight as to where and when the breeding range of cranes may expand. Given the northwestern orientation of most long-distance roaming in this study, it seems likely that Eastern Population cranes will continue to expand their breeding range in that direction.

Juvenile cranes that have separated from their parents need to balance time and energy expenditure devoted to establishing a territory, foraging, and predator avoidance. Dispersing juvenile cranes likely gather information that will improve both foraging and breeding opportunities (Dall et al. 2005). Multiple other factors influence behavioral decisions, including intraspecific competition, kin competition, mate choice, and habitat quality (Clobert et al. 2008). Future research that combines behavioral observations with movement data will allow further exploration of the interplay between breeding success, social interactions, and the role of habitat quality and density-dependence in determining landscape-level population dynamics.

Figure 1. A visualization of the workflow process for behavioral segmentation of sandhill crane (*Antigone canadensis*) trajectories. Box A shows the Global-Positioning System track of an individual crane on the landscape prior to demarking behavioral states (i.e., roaming and settled). The distance of each location to the centroid (D2C) of all points in the trajectory is then calculated, producing a time-series of D2C values (shown in Box C, post-segmentation). We then applied the Lavielle method to this time-series to find the optimal number of segments (K). This method finds, for any value of K, the segmentation that best matches the original trajectory in terms of a contrast function (in our case, the contrast function measured the mean within each segment) (Box B). We then chose the value of K for which there was a clear "break" in the decrease of the contrast function (in this case, 2). Using the chosen value of K, segments were assigned movement behavioral states (Box C). Behavioral states are visualized in Box D (blue=settled, orange=roaming).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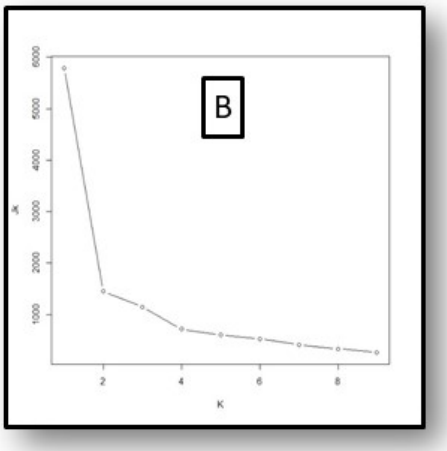
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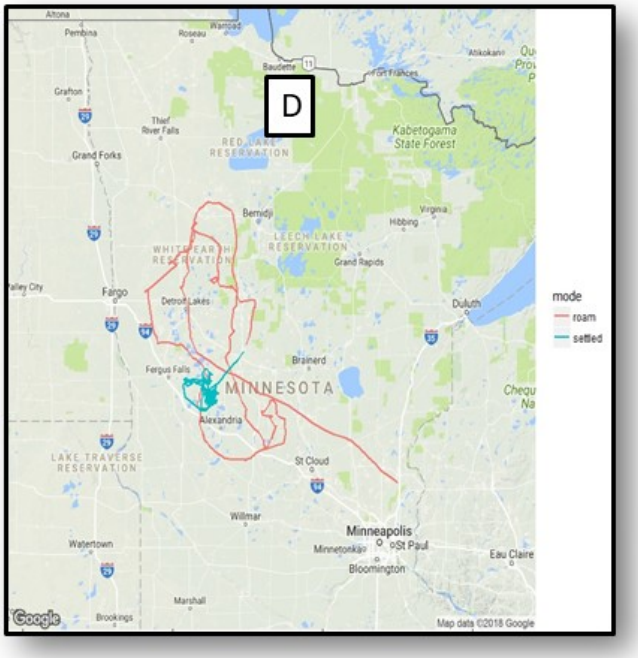
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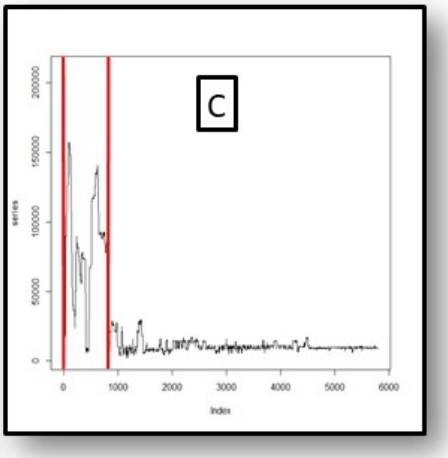
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Figure 2. Average 'Distance-to-Centroid' values for adult and juvenile sandhill cranes (*Antigone canadensis*) in Minnesota, USA for each month between 1 April and 1 September, 2016-2017. Error bars depict 95% confidence intervals.

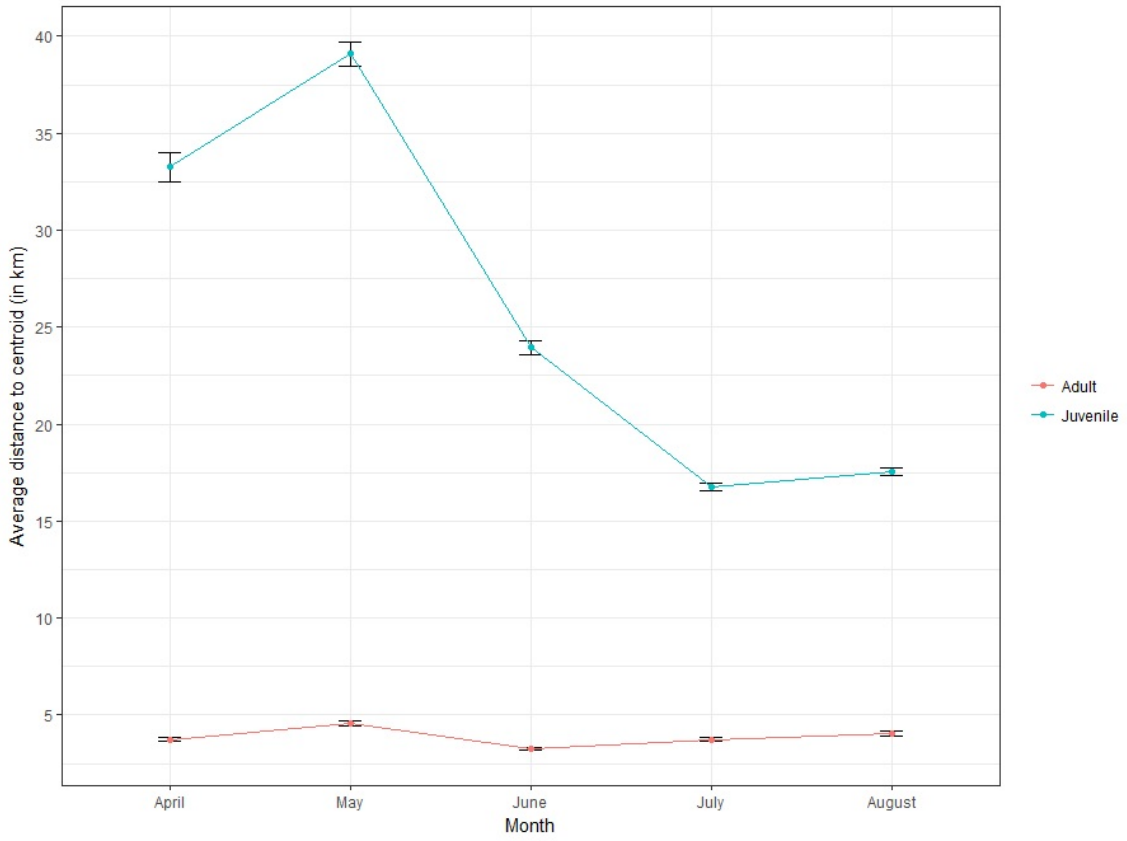


Figure 3. Assigned behavioral states of juvenile and adult sandhill cranes (*Antigone canadensis*) in Minnesota, USA, during the period 1 April-1 September 2016 and 2017. Light blue represents the roaming state and dark blue represents the settled state. Individual cranes are identified by a 2-digit alpha-numeric code.

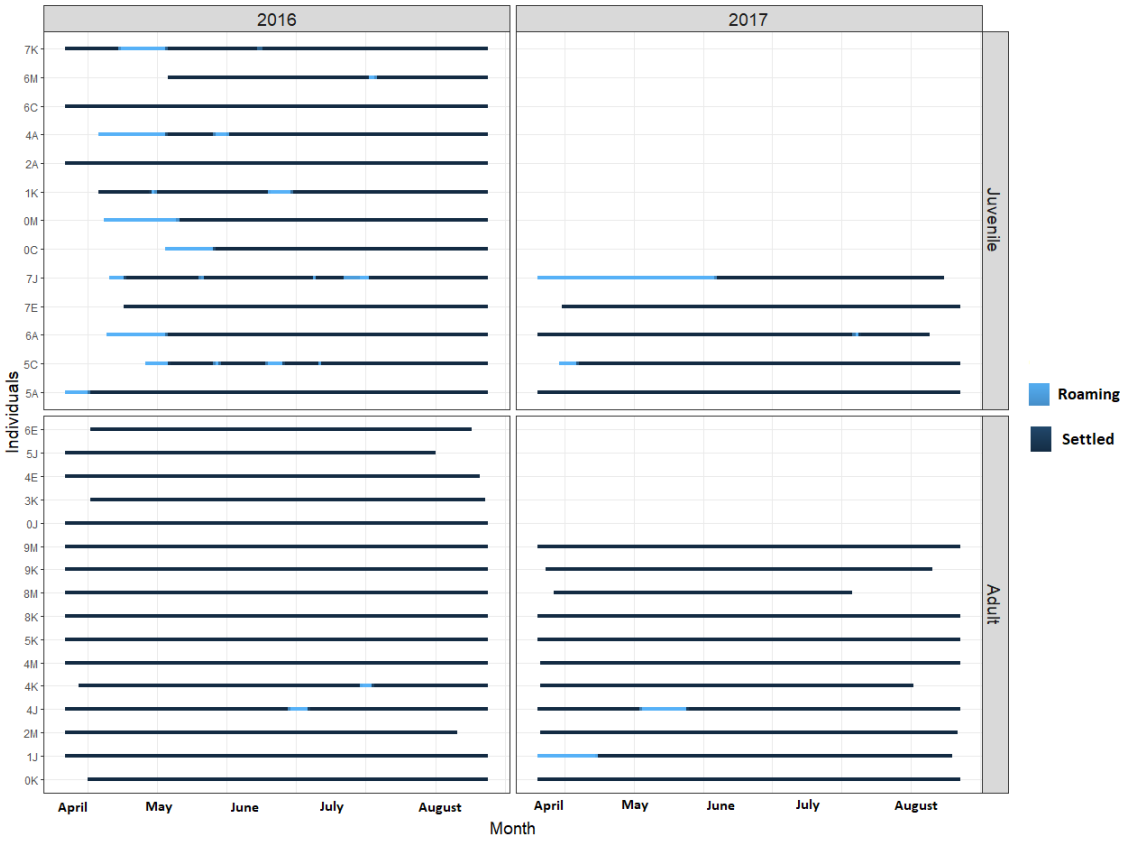


Figure 4. The distribution of animal-specific mean values for duration of time spent in a hull (left plot) and number of revisits per hull. Violin plots show the distribution of values for each group and the boxplots indicate the median (horizontal line), interquartile range (rectangular area), and the extent of values up to 1.5 times the interquartile range (thin lines extending above and below). Values are grouped by age class (adults in orange, juveniles in blue) and by behavioral state.

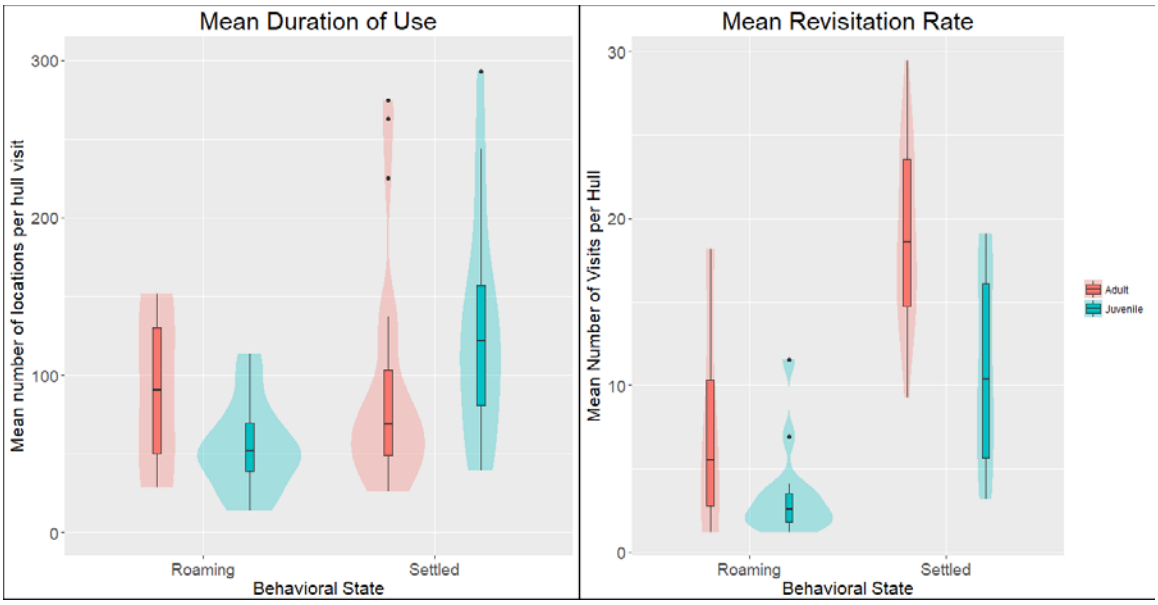
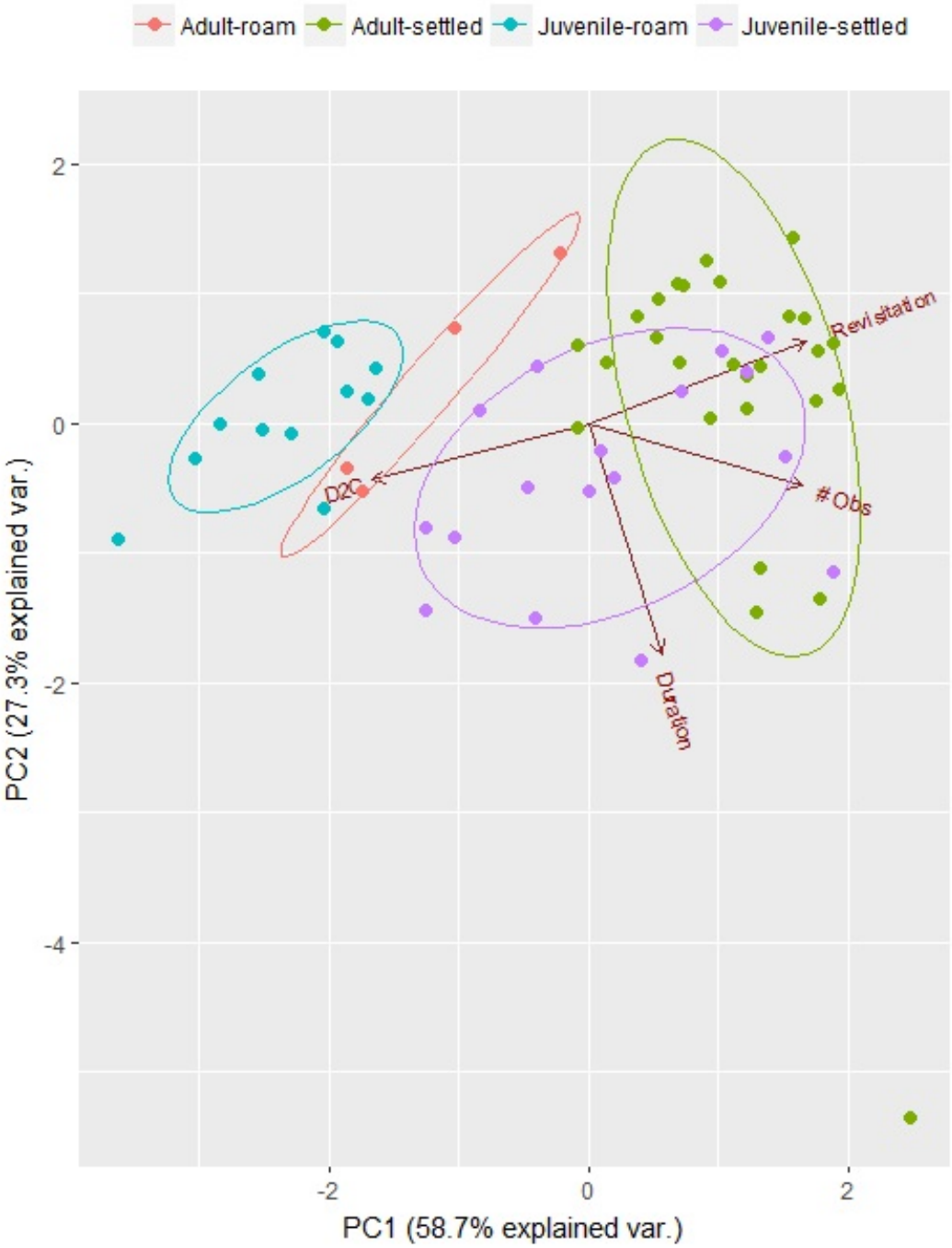


Figure 5. Biplot of the first 2 principal components summarizing movement characteristics of sandhill cranes (*Antigone canadensis*) by age class and behavioral state. The vectors labeled D2C, # obs, Revisitation, and Duration depict loadings for PCA input variables 1) Distance-to-Centroid values, 2) number of locations in each age group by behavioral state category, 3) mean revisitation rate of hulls, and 4) mean duration of time spent in hulls, respectively. Ellipses represent the 68% (1 standard deviation) contour of each 'age class by behavioral state' category.


Adult-roam
Adult-settled
Juvenile-roam
Juvenile-settled
Revisitation
D2C
Obs
Duration
PC2 (27.3% explained var.)
PC1 (58.7% explained var.)
2
0
-2
-4
-2
0
2

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Appendix A. Sandhill cranes (*Antigone canadensis*) tracked via GPS telemetry in Minnesota, USA, during the period of 1 April-1 September 2016 and 2017. The number of days in each behavioral state is given as is the proportion of each crane's total time spent in each state.

Crane ID	Year	Age	Behavioral State	Days in State	Percent of Period in State
4J	2016	Adult	Roaming	8	5
4K	2016	Adult	Roaming	5	3
0J	2016	Adult	Settled	147	100
0K	2016	Adult	Settled	121	100
1J	2016	Adult	Settled	143	100
2M	2016	Adult	Settled	142	100
3K	2016	Adult	Settled	82	100
4E	2016	Adult	Settled	143	100
4J	2016	Adult	Settled	145	95
4K	2016	Adult	Settled	138	97
4M	2016	Adult	Settled	153	100
5J	2016	Adult	Settled	120	100
5K	2016	Adult	Settled	148	100
6E	2016	Adult	Settled	118	100
8K	2016	Adult	Settled	89	100
8M	2016	Adult	Settled	97	100
9K	2016	Adult	Settled	153	100
9M	2016	Adult	Settled	153	100
0C	2016	Juvenile	Roaming	18	17
0M	2016	Juvenile	Roaming	27	20
1K	2016	Juvenile	Roaming	11	8
4A	2016	Juvenile	Roaming	31	22
5A	2016	Juvenile	Roaming	8	5
5C	2016	Juvenile	Roaming	20	16
6A	2016	Juvenile	Roaming	21	16
6M	2016	Juvenile	Roaming	4	5
7J	2016	Juvenile	Roaming	14	12
7K	2016	Juvenile	Roaming	19	14
0C	2016	Juvenile	Settled	88	83
0M	2016	Juvenile	Settled	111	80

1K	2016	Juvenile	Settled	133	92
2A	2016	Juvenile	Settled	153	100
4A	2016	Juvenile	Settled	113	78
5A	2016	Juvenile	Settled	144	95
5C	2016	Juvenile	Settled	107	84
6A	2016	Juvenile	Settled	111	84
6C	2016	Juvenile	Settled	83	100
6M	2016	Juvenile	Settled	73	95
7E	2016	Juvenile	Settled	131	100
7J	2016	Juvenile	Settled	102	88
7K	2016	Juvenile	Settled	117	86
1J	2017	Adult	Roaming	22	19
4J	2017	Adult	Roaming	17	11
0K	2017	Adult	Settled	139	100
1J	2017	Adult	Settled	96	81
2M	2017	Adult	Settled	140	100
4J	2017	Adult	Settled	134	89
4K	2017	Adult	Settled	109	100
4M	2017	Adult	Settled	148	100
5K	2017	Adult	Settled	126	100
8K	2017	Adult	Settled	107	100
8M	2017	Adult	Settled	76	100
9K	2017	Adult	Settled	141	100
9M	2017	Adult	Settled	154	100
5C	2017	Juvenile	Roaming	7	5
6A	2017	Juvenile	Roaming	3	3
7J	2017	Juvenile	Roaming	63	50
5A	2017	Juvenile	Settled	154	100
5C	2017	Juvenile	Settled	126	95
6A	2017	Juvenile	Settled	112	97
7E	2017	Juvenile	Settled	145	100
7J	2017	Juvenile	Settled	62	50

Appendix B. Summary statistics of time-use metrics for sandhill cranes (*Antigone canadensis*) tracked via GPS telemetry in Minnesota, USA, over the period of 1 April-1 September 2016 and 2017. Values are animal-specific averages for cranes that exhibited at least some time in the state referenced in column 2.

		Duration of Stay in each Hull (Average number of locations per visit)			**Number of Revisits to each Hull**		
Age	State	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Adult	Roam	90	29	152	8	1	18
Adult	Settled	114	26	720	19	9	29
Juvenile	Roam	54	14	113	3	1	12
Juvenile	Settled	127	39	293	11	3	19

Appendix C. The first table presents the summary of principal component analysis with factor loadings for each of the 4 principal components. The input variables are 1) the distance between each Global-Positioning System (GPS) location and the centroid of all points for each sandhill crane (*Antigone canadensis*), 2) number of locations in each age group (adult or juvenile) by behavioral state category (settled or roaming), 3) mean revisitation rate of hulls, and 4) mean duration of time spent in hulls. The second table presents standard deviation, proportion of variance, and cumulative proportion of variance explained by each principal component. Each of the input variables were derived from the movement paths of sandhill cranes tracked via GPS telemetry in Minnesota, USA, during the period of 1 April-1 September 2016 and 2017.

Rotation (4 x 4)	PC[a]1	PC2	PC3	PC4
Number of points in movement phase	0.56	-0.24	0.68	-0.40
Mean distance-to-centroid value	-0.57	-0.22	0.65	0.45
Mean duration of visit (to a hull)	0.19	-0.89	-0.32	0.27
Mean revisitation rate (of hulls)	0.57	0.32	0.84	0.75

	PC1	PC2	PC3	PC4
Standard deviation	1.53	1.04	0.59	0.45
Proportion of Variance	0.59	0.27	0.09	0.05
Cumulative Proportion	0.59	0.86	0.95	1.00

[a] Principal component