Wildlife Society Bulletin 41(3):489–498; 2017; DOI: 10.1002/wsb.799

Original Article

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

DAVID WOLFSON,[1] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA*

JOHN FIEBERG, *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA*

JEFFREY S. LAWRENCE, *Minnesota Department of Natural Resources, Wetland Wildlife Populations and Research Group, 102 23rd Street, Bemidji, MN 56601, USA*

THOMAS R. COOPER, *U.S. Fish and Wildlife Service, Migratory Bird Management, 5600 American Boulevard West, Suite 960, Bloomington, MN 55437, USA*

DAVID E. ANDERSEN, *U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, 200 Hodson Hall, 1980 Folwell Avenue, St. Paul, MN 55108, USA*

ABSTRACT 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, USA, 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 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 determine whether the populations overlap on their breeding areas and autumn staging grounds. We captured and attached Global Positioning System–Global System for Mobile Communications transmitters to 50 cranes in the zone between the historical breeding-range boundaries of the 2 populations. Movements of 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.
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KEY WORDS *Antigone canadensis*, Minnesota, range overlap, sandhill crane, satellite telemetry.

Sandhill cranes (*Antigone canadensis*) are long-lived birds with delayed sexual maturity and lowest recruitment rates of any avian species hunted in North America, making accurate knowledge of distribution critical for well-informed harvest management (Tacha et al. 1989, Drewien et al. 1995). Sandhill cranes (hereafter, cranes) in North America are designated into 6 migratory and 2 nonmigratory populations for management purposes based on their geographic distributions (Tacha et al. 1994). Minnesota, USA, 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, 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,

Received: 11 April 2017; Accepted: 30 April 2017
Published: 3 September 2017

[1]*E-mail: wolfs064@umn.edu*

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). Harvest strategies for these 2 breeding populations differ; therefore, 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 to 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%/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, Canada, 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 and Tennessee, USA, in 2011 and 2013, respectively, 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, USA, and northern Mexico before migrating north during the spring to breed throughout central and western Canada, Alaska, USA, eastern Siberia, Russia, 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 to 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, Canada (Walkinshaw 1973, Lewis 1977).

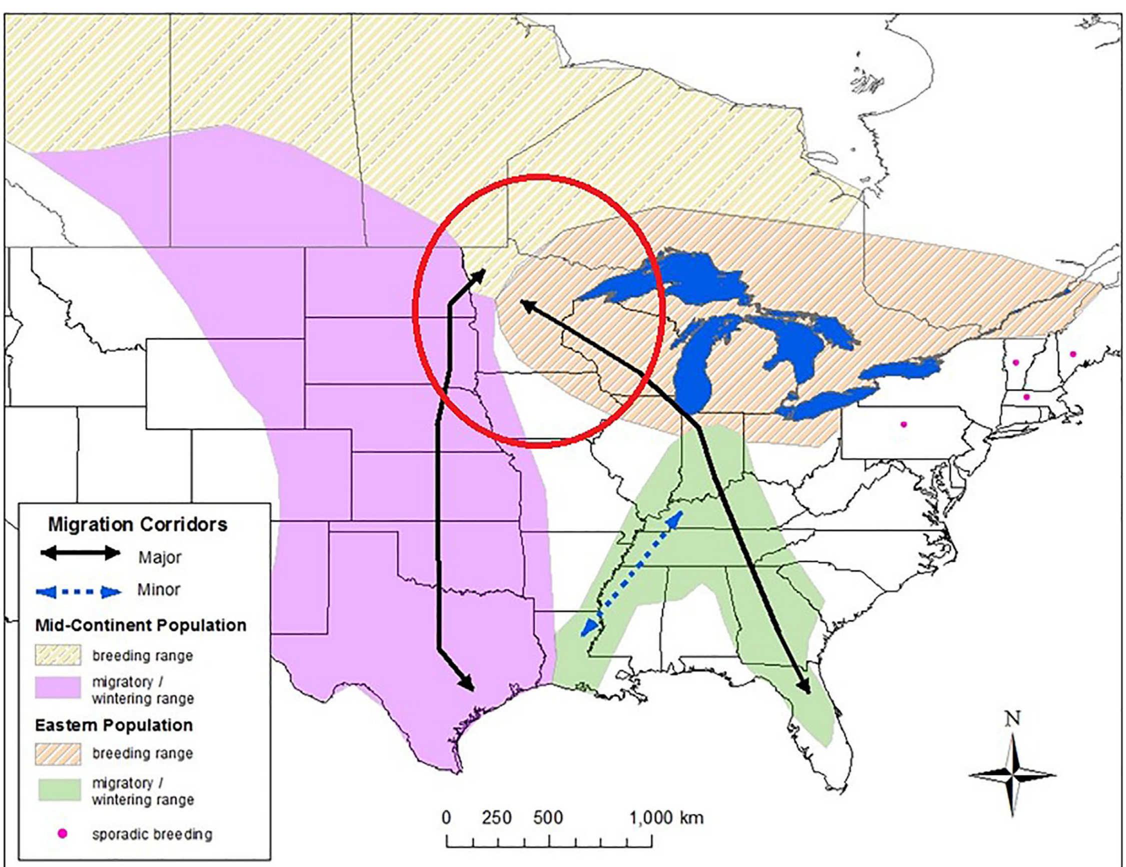

Figure 1. Primary breeding and migratory–wintering ranges for Mid-Continent and Eastern Populations of sandhill cranes in North America. Black arrows indicate the predominant migration routes for each population. Pink dots indicate sporadic breeding records of Eastern Population sandhill cranes in the northeastern United States. The red circle represents a potential convergence zone between the breeding ranges of the 2 populations.

However, the EP has recently expanded its breeding distribution throughout the Great Lakes region and northeastern United States and Quebec, Canada, and the wintering distribution has expanded north and west into Georgia, Alabama, Tennessee, Kentucky, and Indiana, USA (Melvin 2002, Sauer et al. 2014, Lacy et al. 2015, Fronczak et al. 2017).

Our goal 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 objectives were to 1) ascertain population affiliation of Global Positioning System–tagged cranes based on migratory pathways and wintering areas, and 2) determine whether EP and MCP cranes breeding in Minnesota overlap in breeding or autumn 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.

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 historical boundaries of breeding ranges of MCP and EP cranes in Minnesota (Fig. 2). We also captured 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 was 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. The landscape 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).

METHODS

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, USA). In 2014, we located crane nests by soliciting information from land managers and the general public. We also searched potential nesting areas on the ground from 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 (Bell Helicopter, Fort Worth, TX, USA) 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 m of throw (Olight, Smyrna, GA, USA) 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 hr after dusk until 2 hr before dawn. We avoided capture attempts on dates within a week of a full moon to decrease the likelihood of cranes flushing under conditions of relatively high levels of ambient light.

To increase efficacy of locating adult cranes on their roosts while night-lighting, we captured prefledged hatch-year cranes (colts) by hand during the day and marked these individuals with 6.7-g glue-on very-high-frequency radio-transmitters (Advanced Telemetry Systems [ATS], Isanti, MN, USA). 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 middorsal region using waterproof, nontoxic, quick-drying eyelash adhesive (Andrea Lashgrip Eyelash Adhesive; Ardell, Los Angeles, CA, USA; Spalding et al. 2001, Fox 2011). We tracked radiomarked 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 (~50–60 days old).

In October–November 2015, we captured and marked cranes using rocket nets near a staging area at Sherburne National Wildlife Refuge (Wheeler and Lewis 1972). We assembled a 13.1 × 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 daytime loafing later in the morning and 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, USA) 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 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, flanged halves—one half bonded to the transmitter and the other half engraved with a unique alpha-numeric code (Haggie Engraving, Crumpton, MD, USA). 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

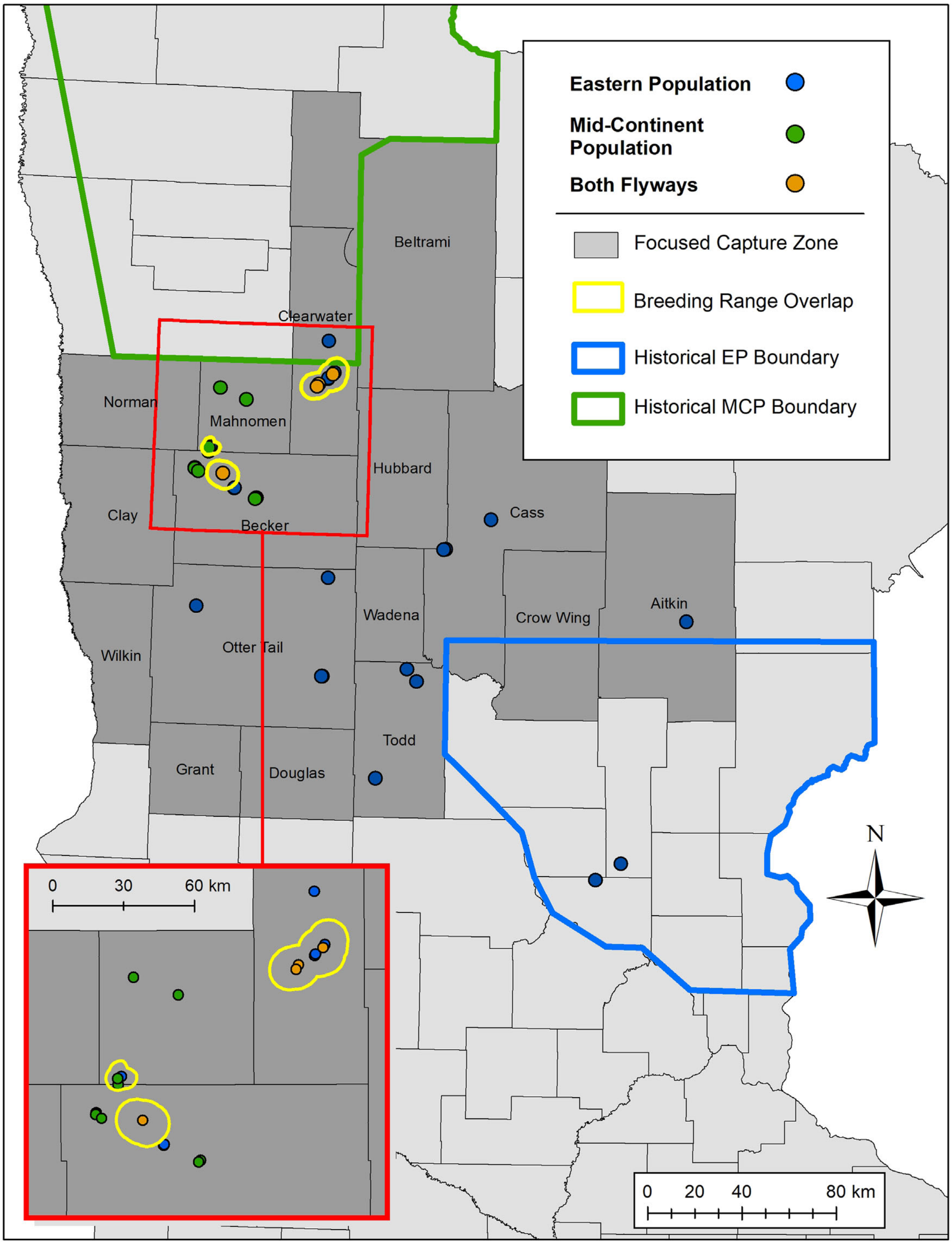

Figure 2. Capture locations of sandhill cranes during May–October 2014 and April–November 2015 in Minnesota, USA. Color of points represent population affiliation assigned based on migratory flyway (Central Flyway = Mid-Continent Population [MCP], Mississippi Flyway = Eastern Population [EP]), with MCP 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.

determine sex of captured cranes by DNA analysis (Avian Biotech, Tallahassee, FL, USA). We weighed all captured cranes and attached aluminum butt-end bands (size 8 or 9, U.S. Geological Survey Bird Banding Laboratory, Patuxent Wildlife Research Center, MD, USA) 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 per 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 autumn 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 autumn staging areas by first filtering telemetry locations for each period: 1 April–1 August for breeding, and 1 August–1 October for autumn 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 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 (v.3.2.2, R Development Core Team 2008). 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. Telemetry data and R code used to reproduce the analysis of autumn staging areas can be found at the Data Repository for the University of Minnesota (Wolfson et al. 2017).

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 F, 24 M) 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 for $\geq$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 Flyway (EP) for autumn and spring migrations in autumn of 2015 and spring of 2016, but switched to the Central Flyway (MCP) during the autumn of 2016. One crane used the Mississippi Flyway in the autumn 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, USA, 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 1 area in central Clearwater County. We identified 4 autumn-staging areas in northwestern Minnesota that were used by both EP and MCP cranes (Figs. 4 and 5). Of these, 3 were used in both 2015 and 2016, and 1 was used only in 2016 (Fig. 4). The northwestern Minnesota staging area that had the greatest use by EP cranes in both the autumn of 2015 and autumn 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 autumn staging, whereas 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 autumn 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, because of logistic constraints, we were unable to sample uniformly across this zone. Also,

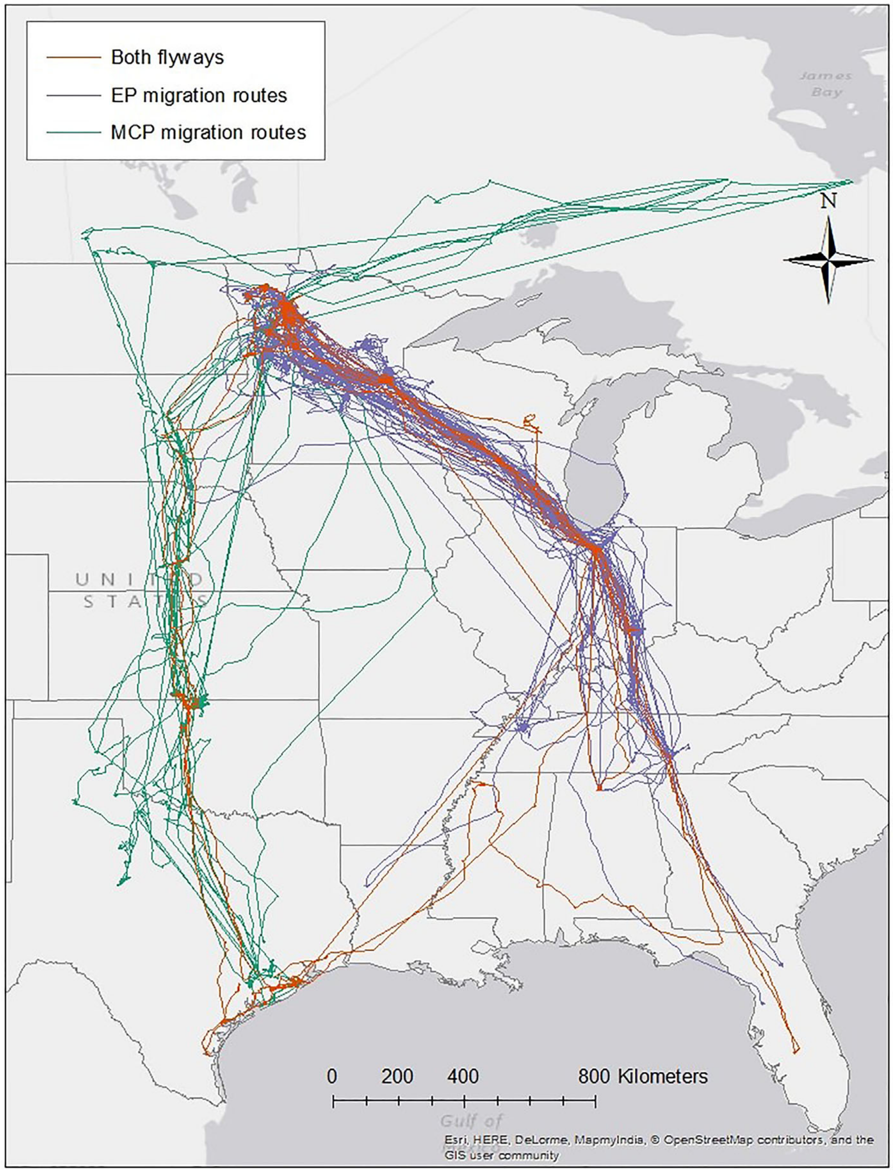

Figure 3. Migration routes of radiotagged sandhill cranes in 2014 ($n = 4$) and 2015 ($n = 36$). Color of lines represent population affiliation, assigned based on migratory flyway (Central Flyway = Mid-Continent Population [MCP], Mississippi Flyway = Eastern Population [EP]), with Mid-Continent Population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

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 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 autumn staging. Migratory cranes tend to move from their breeding territories to staging areas (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 autumn 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, where they would be vulnerable to harvest.

We identified 4 autumn staging areas in Minnesota where MCP and EP cranes co-occurred. However, each staging area received predominant use by one population and only brief visitations by cranes from the other population. These short visits correspond with an increase in relatively long-distance movements by cranes in the autumn, possibly to investigate staging areas that are optimal for foraging (Sparling and Krapu 1994). Two commonly used staging

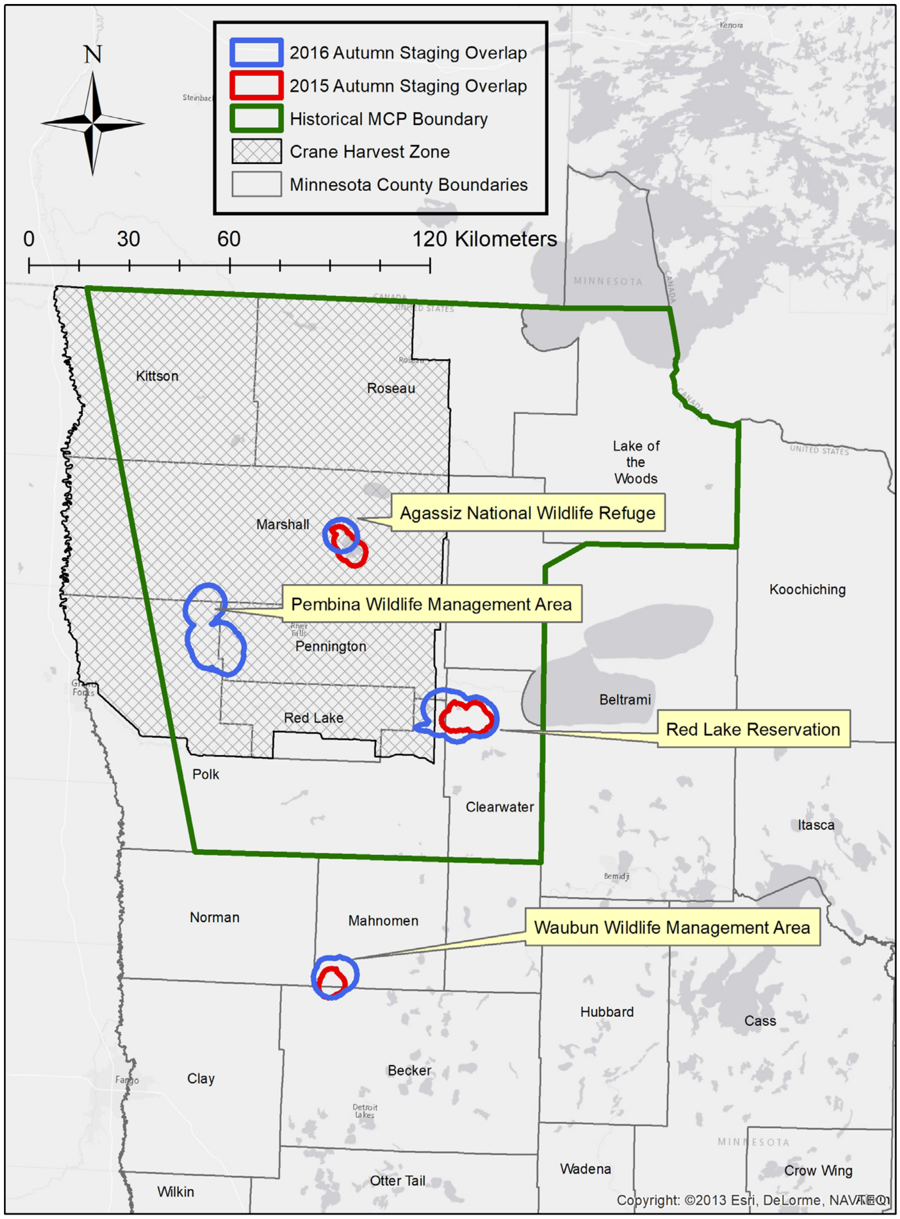

Figure 4. Areas of overlap between Eastern Population and Mid-Continent Population sandhill cranes in Minnesota, USA, during the autumn staging periods of 1 August–1 October 2015 and 2016. Red polygons represent overlap during 2015 and blue polygons represent overlap during 2016. The Northwest Goose 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.

areas (Agassiz National Wildlife Refuge and Pembina Wildlife Management Area) were within the Northwest Goose and Crane Zone, whereas another (Red Lake Reservation) was just outside the boundary. In addition to 2 EP cranes that used the Agassiz National Wildlife Refuge staging area for one 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 despite the presence of gene flow between them (Jones et al. 2005). 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

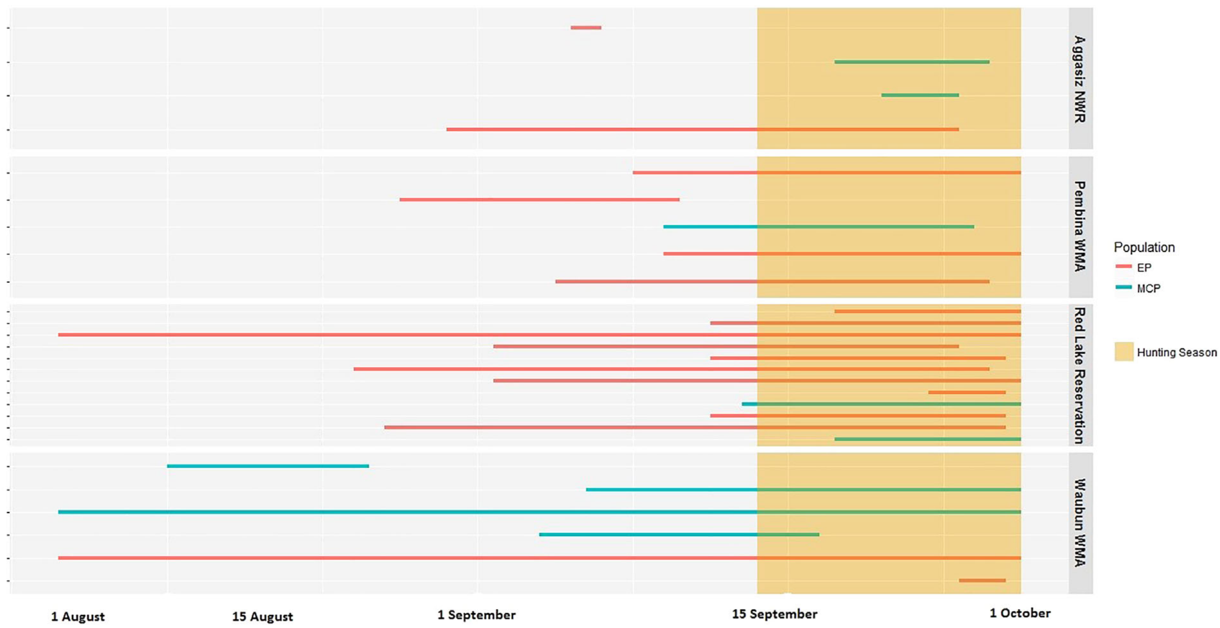

Figure 5. Temporal overlap between Eastern Population (EP) and Mid-Continent (MCP) sandhill cranes in Minnesota, USA, during the autumn staging period of 1 August–1 October 2015 and 2016. Orange lines represent use by EP cranes and green lines represent use by MCP cranes. The period of the autumn hunting 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 National Wildlife Refuge and Pembina Wildlife Management Area) 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 farther south of the NWGCZ.

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, U.S. Geological Survey, personal communication). However, Hayes (2015) reported that at breeding areas with high territory density such as central Wisconsin, USA, 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. Crane populations are defined in part by the migratory paths linking summer and winter ranges; 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.

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 autumn 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 autumn 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 midlatitudes into distinct populations (i.e., MCP or EP) may at some point no longer be useful as a management tool.

ACKNOWLEDGMENTS

We thank N. Cross, J. Dachenhaus, J. Fox, D. Fronczak, K. Kovach, G. Kramer, E. Ulrey, E. Wells, and S. Zudrow for assistance with fieldwork and many private landowners for granting access during our study. We thank W. Brininger, T. Buker, L. Domine, W. Ford, A. Hewitt, G. Knutsen, M. North, and H. Saloka for logistical support. Thanks to K. Barrett, G. Henderson, K. Larson, B. Liddell, M. Loss, E. North, J. Provost, T. Stursa, E. Thorson, and many more for information on crane locations. Thanks to B. Maas for piloting the helicopter surveys. We thank A. ArchMiller, B. Grisham, D. Johnson, S. Steiniger, and F. Thompson III for comments on previous drafts of this manuscript. Funding for this project was provided by the U.S. Fish and Wildlife Service and U.S. Geological Survey (Science Support Program) through Research Work Order No. 101 at the U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit; by the Minnesota Environmental and Natural Resources Trust Fund as recommended by the Legislative-Citizen Commission on Minnesota Resources (LCCMR); by the U.S. Fish and Wildlife Service Webless Migratory Game Bird Program; and by the Minnesota Department of Natural Resources. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government, the University of Minnesota, or the State of Minnesota.

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Associate Editor: Thompson.