Research Article

Distribution and Migration Chronology of Eastern Population Sandhill Cranes

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ABSTRACT The Eastern Population (EP) of greater sandhill cranes (*Antigone canadensis tabida*; cranes) is expanding in size and geographic range. Little information exists regarding the geographic extent of breeding, migration, and wintering ranges, migration chronology, or use of staging areas for cranes in the EP. To obtain these data, we attached solar global positioning system (GPS) platform transmitting terminals (PTTs) to 42 sandhill cranes and monitored daily locations from December 2009 through August 2014. On average, tagged cranes settled in summer areas during late-March in Minnesota (7%), Wisconsin (29%), Michigan, USA (21%), and Ontario, Canada (38%) and arrived at their winter terminus beginning mid-December in Indiana (15%), Kentucky (3%), Tennessee (45%), Georgia (5%), and Florida (32%). Cranes initiated spring migration beginning mid-February to their respective summer areas on routes similar to those used during fall migration. Twenty-five marked cranes returned to the same summer area after a second spring migration, of which 19 (76%) settled <3 km from the estimated mean center of the summer area of the previous year. During the 2010–2012 United States Fish and Wildlife Service (USFWS) Cooperative Fall Abundance Survey for cranes in the EP, we estimated that approximately 29–31% of cranes that summered in both Wisconsin and the Lower Peninsula of Michigan were not in areas included in the survey. The information we collected on crane movements provides insight into distribution and migration chronology that will aid in assessment of the current USFWS fall survey. In addition, information on specific use sites can assist state and federal managers to identify and protect key staging and winter areas particularly during current and future recreational harvest seasons.

KEY WORDS *Antigone canadensis tabida*, distribution, Eastern Population, migration chronology, sandhill crane, satellite telemetry.

At the turn of the 20th century, the Eastern Population (EP) of greater sandhill cranes (*Antigone canadensis tabida*; cranes) was nearly extirpated from its historical breeding range because of habitat alteration and unregulated hunting (Walkinshaw and Wing 1955, Lumsden 1971, Hunt et al. 1976). Following protection from unregulated hunting after passage of the Migratory Bird Treaty Act of 1916 (i.e., closure of hunting in 1918) and in response to conservation efforts by state and federal agencies and non-government organizations, cranes in the EP increased in number and expanded their breeding range (Tacha et al. 1994, Amundson and Johnson 2011). However, an increase in population size has also been accompanied by management issues related to crop depredation, public pressure to allow recreational harvest, and enhancing non-consumptive wildlife opportunities (Van Horn et al. 2010). Similar to other crane populations, basic biological and annual life cycle information are needed to better manage cranes in the EP, especially information relating to spatial distribution of the population, current migration patterns, potential overlap with neighboring migratory and non-migratory populations, and identification of important use areas throughout their annual life cycle (Case and Sanders 2009).

In 2009, the Migratory Shore and Upland Game Bird Task Force under the direction of the Association of Fish and Wildlife Agencies identified priority information needs that were specific to developing a better monitoring program to reflect current distributions and migration patterns of cranes in the EP. This effort identified documenting the geographic extent of breeding, migration, and wintering ranges as essential information needs so that appropriate changes to the spatial-temporal design of the current United States Fish and Wildlife Service (USFWS) Cooperative Fall Abundance Survey (hereafter, USFWS fall survey) could be implemented (Case and Sanders 2009). The USFWS fall survey is a long-term survey established in 1979 that consists of efforts by volunteers and state and federal agencies from the Atlantic

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and Mississippi flyways (i.e., MN, WI, MI, IN, OH, PA, TN, GA, and FL). The main goal of the survey is to provide an estimate of the size and trend of the cranes in the EP and is focused on counting cranes that concentrate in Indiana, Michigan, and Wisconsin during fall migration. The survey was initially designed to begin the last week of October when cranes are concentrated in these states (Van Horn et al. 2010). The initial 1979 survey counted 14,385 cranes and has increased to 83,479 in 2014 with a recent 3-year average of 78,532 cranes for 2012–2014 (Kruse and Dubovsky 2015).

To address crane priority information needs, we combined and analyzed data from 2 concurrent ecology studies for cranes in the EP. One study focused on crane ecology on Manitoulin Island, Ontario (Hanna et al. 2014) and the other focused on crane migration ecology (Fronczak 2014); both studies used global positioning system (GPS) satellite platform transmitting terminals (PTTs). Specifically, we monitored cranes from 2009 to 2014 and identified current crane staging areas, travel routes, and migration chronology; identified current summer and wintering areas and durations of stay; and determined the proportion of cranes that occurred within the areas surveyed during the USFWS fall survey.

STUDY AREA

Our study area included the breeding and wintering grounds and migration corridors of cranes in the EP as determined by GPS locations of PTT-marked cranes and consisted of states and provinces within the Canadian Shield, Great Lakes, Mississippi Valley, and Southeast geographic regions of North America (Fig. 1). These areas include boreal softwoods, prairie hardwoods, eastern tall grass prairie, central hardwoods, and southeastern coastal plains. We captured and marked cranes throughout spring and fall migration and winter at 7 sites within the known EP range (Tacha et al. 1994) during 2009–2012.

We conducted the majority of our trapping at the Jasper-Pulaski Fish and Wildlife Area (FWA), northwest Indiana (41.2°N, −86.9°W) and the Hiwassee Wildlife Refuge (WR), southeast Tennessee (35.4°N, −85.0°W); both are considered major staging areas for cranes in the EP (Fronczak 2014). In addition to these 3 primary sites, we also trapped and placed satellite transmitters on cranes at Goose Pond Fish and Wildlife Area, Indiana (39.0°N, −87.2°W); Sherburne National Wildlife Refuge, Minnesota (45.5°N, −93.8°W); Crex Meadows Wildlife Area, Wisconsin (45.8°N, −92.6°W); and Hop-In Wildlife Refuge, Tennessee (33.3°N, −89.0°W). We also captured and marked cranes in the EP at a Canadian staging site at Manitoulin Island, Ontario, Canada (45.8°N, −82.2°W). Detailed area descriptions of trap locations have been described previously (Fronczak 2014, Hanna et al. 2014).

METHODS

Trapping

Cranes in the EP occur across broad geographic areas during summer and winter and exhibit variation in timing of migration across their range. To mark a representative sample of cranes in the EP, we used a strategy similar to that used by Krapu et al. (2011) in a comparable study of Mid-continent Population (MCP) cranes. We identified Jasper-Pulaski FWA and Hiwassee WR as the major staging areas used during migration by cranes in the EP, based on previous studies that described migratory routes (Walkinshaw 1960, Crete and Toepfer 1978), EP abundance surveys (e.g., Mississippi Flyway Cooperative Midwinter Survey [MWS], state surveys), and the subsequent behavior of cranes we marked in this study. For each stopover area, we selected trapping periods before, during, and after estimated peak abundance based on periodic surveys of cranes during fall migration (J. Bergens, Indiana Department of Natural Resources, unpublished data and R. Klippel, Tennessee Wildlife Resource Agency, unpublished data). We employed this capture protocol to mark a geographic, representative sample of cranes and to capture the temporal variation in crane movements through these stopover areas. In addition, we captured cranes on alternative breeding and staging areas, including Manitoulin Island, Ontario (Hanna et al. 2014), to include cranes from portions of their distribution that may not have been represented by cranes we trapped at major staging areas.

We used a rocket-propelled net assembly as the primary method to capture cranes. We identified potential trapping sites using the protocol developed for rocket netting cranes in the MCP by Krapu et al. (2011). Their protocol gave priority to daytime loafing sites with >20 cranes present in pasture or other open land-cover types and incorporated decoys. We modified their protocol by using bait instead of decoys. When cranes responded to bait for 2 consecutive days, we assembled a 13.1 × 19.7-m rocket-propelled net (Wheeler and Lewis 1972; D. A. Brandt, U.S. Geological Survey [USGS], Northern Prairie Wildlife Research Center, personal communication) at a potential capture location. We conducted trapping primarily in the morning because cranes consistently returned to baited sites after leaving nocturnal roosts. In addition to using a rocket-propelled net, we used a Coda NetLauncher (Coda Enterprises, Mesa, AZ, USA) to capture cranes in locations where using a rocket-propelled net was not feasible. We followed the standard Coda NetLauncher protocol developed for cranes by the Ohio Department of Natural Resources (D. E. Sherman, Ohio Department of Natural Resources, personal communication). We also used modified softcatch leghold traps (Victor no. 3, Oneida Victor, Euclid, OH, USA) as described by King et al. (1998).

We targeted adult female cranes because they are more likely than males to return to natal breeding grounds the following spring (Walkinshaw 1949, Drewien 1973). Sandhill cranes are perennially monogamous (Tacha et al. 1994), will re-mate after death or permanent separation (Nesbitt 1989, Hayes and Barzen 2006), and pair bonds will remain after departure from summer areas (Tacha et al. 1992, Hayes 2015). We assume little difference in migration behavior among cohorts in our sample because we targeted adult cranes. However, we acknowledge that we did not

Figure 1. Trapping locations by season where sandhill cranes were captured and marked with platform transmitting terminals. Gray shading denotes the geographic extent of movements of cranes during the annual cycle, 2009–2014.

know the breeding status of all of our marked cranes. We identified adult female cranes based on the physical and social characteristics described by Tacha (1998) as smaller body-sized cranes, with red skin on the crown of the head, more likely to be viewed following larger-bodied male cranes, and less likely to display agonistic behaviors. However, following capture, if we could not identify family groups, we selected a smaller-bodied, adult crane, that we presumed to be a female.

We affixed a 30-g, 3-solar-paneled GPS satellite PTT (North Star Science and Technology, Baltimore, MD, USA) to captured cranes via flanged leg bands. We selected tarsus-mounted PTTs because similar transmitters and attachment methods have been used extensively on cranes without apparent negative effects on survival or movements in comparison to backpack mounted transmitters (Melvin et al. 1983, Ellis et al. 2001, Krapu et al. 2011, Hayes 2015). We mounted PTTs on a 7.6-cm, 2-piece, color-coated polyvinyl chloride (PVC), alpha-numeric-coded engraved leg band (Haggie Engraving, Crumpton, MD, USA). Satellite PTTs incorporated 2 additional solar panels to increase the longevity of the transmitter compared with standard battery-powered or single solar-paneled transmitters. We reinforced the connection between the antenna and the transmitter housing as a precaution, because it is a weak point and a cause for loss of transmission (D. A. Brandt, personal communication). For cranes not marked with PTTs, we affixed a 7.6-cm, 1.5-wrapped, alpha-numeric-coded engraved, PVC tarsus auxiliary leg band above the distal tibio-tarsus joint. Flanged auxiliary markers and PTTs together weighed approximately 80 g ($\leq$2% of average body mass at capture) and were attached above the distal tibio-tarsus joint (Krapu et al. 2011). All birds marked received a standard USGS aluminum band.

For each PTT-marked crane, we drew blood from the vein below the tibio-tarsus and placed samples in a lysis buffer anticoagulant solution (Jones et al. 2005). Blood was subsequently analyzed by Avian Biotech International (Tallahassee, FL, USA) to determine sex. We did not collect blood samples from cranes at Manitoulin Island. When we captured >2 cranes/crew member at one time, we released cranes in excess of that number immediately without taking measurements or affixing markers to avoid detrimental effects (e.g., myopathy) of extended handling times. We released all cranes held for processing as a group within 30 minutes of being captured. We captured cranes under approval of the University of Minnesota Institutional Animal Care and Use Committee (protocol no. 1103A97333) and the University of Western Ontario Animal Use Protocol (protocol no. 2010–213).

We programmed most PTTs on 5- and 6-hour intervals to maximize the number of GPS locations per day, which afforded the ability to determine the status (i.e., sedentary locations or continuous movement) of marked cranes. We programmed other PTTs to collect GPS locations every 6 hours during migration and every 8 hours during non-migration periods in the summer and winter. Spatial location data were transmitted to satellites each 72-hour duty cycle through standard Doppler technology. Accuracy for GPS locations was classified into 4 quality levels: <26 m, 26–50 m, 51–75 m, and 76–100 m by the manufacturer's standards (K. LeSage, GeoTrak, personal communication).

Data Analysis

We used GPS locations for cranes in the EP that completed full annual cycles beginning from the date of capture to describe distribution and migration chronology. For cranes that did not complete an annual cycle because of either signal loss or death, we used GPS data for any completed migration or duration of stay at a winter or summer terminus. When necessary, we incorporated Argos Doppler system locations as an alternative source of information to describe migration routes when GPS data locations were >5 days between signals because of environmental conditions that resulted in insufficient battery voltage and disrupted data transmission to satellites.

We retrieved data transmitted by PTTs from Collecte Localisation Satellites (CLS)-America (http://www.argos-system.org, Largo, MD, USA), which we decoded into a geographic information system shapefile format through satellite data decoder software (DSDCODE, version 4.d; North Star Science and Technologies). We filtered GPS locations using an adapted location filtering system based on the Douglas Argos-Filter Algorithm version 6.5 (Douglas et al. 2012, Pearse et al. 2015). We remained consistent with Krapu et al. (2011) and assigned attributes to GPS location records identifying 4 periods of the annual cycle (i.e., spring migration, summer area, fall migration, winter area) and classified summer and winter area locations as the terminus of migration based on a major departure from the previous location. We assigned fall and spring migration attributes to areas that we defined as a departure >15 km for >5 days from the summer or winter areas. We defined staging areas as locations where a crane stayed at a single geographic area for >5 consecutive days during migration. We considered areas where cranes stayed for a shorter duration (<5 days) during migration as stopover sites (Warnock 2010).

We estimated the proportion of marked cranes available for detection during the USFWS fall surveys by spatially matching survey locations to GPS locations of marked cranes during the same periods. Fall survey location descriptions ranged from general names of townships, nearest towns, or natural areas, to precise GPS coordinates. We determined that cranes were available during the fall survey if their GPS coordinates were located within the area described by the observer or if the GPS locations of cranes were <3 km from an observer's GPS location.

To assess philopatry to summer area, we compared centroids of locations during the period PTT-marked cranes occupied their summer range for consecutive summers. We calculated centroids of locations for each summer area with ArcGIS (version 9.2; ESRI, Redlands, CA, USA). We summarized the linear distance between these centroids between or among years for individual cranes and report an overall mean.

RESULTS

From 2009 through 2012, we captured 202 cranes: 194 using rocket-propelled nets, 7 with a Coda NetLauncher, and 1 with a softcatch leghold trap. We deployed 38 PTTs on 42 cranes (i.e., we recovered 4 PTTs and deployed them on a second crane). Of the 42 cranes, 25 (60%) were female, 6 (14%) were male, and 11 (26%) were undetermined sex because we did not draw a blood sample or the sexing analysis had inconclusive results. Seven cranes (17%) died, and 24 (57%) of the PTTs we deployed functioned >24 months. We monitored cranes between December 2009 and August 2014, which generated 103,882 GPS locations over 28,677 tracking days. The average number of GPS locations/day was 3.4 (range = 1.7–4.0) where 55% and 32% of the location quality levels were registered as <26 m and 26–50 m, respectively.

Summer Areas

Crane summer areas were dispersed across 3 states and 1 province of the Great Lakes region; 3 (7%) settled in Minnesota, 12 (29%) settled in Wisconsin, 9 (21%) settled in Michigan, and 16 (38%) settled in Ontario (Fig. 2A). Nine (21%) cranes that were marked on Manitoulin Island, Ontario remained on Manitoulin Island for the duration of the summer (Hanna et al. 2014). Cranes spent summers in east-central Minnesota (Benton and Sherburne counties), throughout Wisconsin (Brown, Crawford, Fond du Lac, Green Lake, Jefferson, Lincoln, Outagamie, Racine, Washburn, Waupaca, Waukesha, and Winnebago counties), on the Upper Peninsula (Chippewa and Mackinac counties) and the Lower Peninsula (Ingham, Jackson, Kent, and

Figure 2. Summer (A) and winter (B) area locations (black stars) for platform transmitting terminal-marked greater sandhill cranes, 2009–2014.

Muskegon counties) of Michigan, and the north shore of Lake Huron (Algoma District), Manitoulin Island (Manitoulin District), and east-central (Algoma, Cochrane, and Sudbury districts) Ontario.

Twenty-five cranes returned to their initial summer area after a second spring migration, of which 19 (76%) settled <3 km from the estimated mean center of the summer area of the previous year. For the 25 returning cranes, the average linear distance between summer area centroids between years was 1.55 km (SD = 2.18 km; range = 0.03–7.83 km). We were unable to assess summer area philopatry for 17 cranes because of PTT failure or death (Fronczak et al. 2015).

Fall Migration

Cranes migrated to their respective winter termini using migration corridors on either side of Lake Michigan (Fig. 3A). Cranes ($n = 14$, 33%) that summered in Minnesota and Wisconsin migrated through Wisconsin and primarily used staging areas along the Wisconsin River Valley (Iowa, Juneau, and Sauk counties) and areas surrounding Green Lake and Lake Poygon (Green Lake, Waushara, and Winnebago counties). All cranes summering west of Lake Michigan migrated to their winter termini through either the Kankakee River Valley (Jasper-Pulaski FWA; $n = 12$, 86%) or used routes through Illinois to southern Indiana staging areas ($n = 2$, 14%).

Cranes that summered on the North Channel of Lake Huron and Manitoulin Island, Ontario and the east side of Lake Michigan in Michigan ($n = 17$, 40%) migrated south through the central portion of southern Michigan and primarily staged in Barry, Calhoun, Eaton, Jackson, and Kalamazoo counties (south-central MI). Of the 17 cranes that staged in south-central Michigan, 8 departed south for routes through northeastern Indiana and western Ohio and 9 departed southwest to staging areas in Indiana.

Cranes summering farther north in south-central Ontario and the eastern Upper Peninsula of Michigan ($n = 6$, 14%) used migration corridors on both the east and west side of Lake Michigan. These cranes traversed either west through the Upper Peninsula of Michigan to staging areas surrounding Lake Poygon, Wisconsin (Waushara and Winnebago counties) and then followed similar routes as cranes summering in eastern Wisconsin or traversed southwest from the staging area northwest of Lake Huron (Algoma District), crossing at the Straits of Mackinac, Michigan, to primarily use staging areas in south-central Michigan or northwestern Indiana.

As cranes continued south, 27 (64%) used the Kankakee River Valley (specifically, Jasper-Pulaski FWA) ≥1 year and 11 (26%) cranes bypassed the Kankakee River Valley ≥1 year during fall migration. These cranes left northern staging areas in late November to early December and made brief stops in Indiana, Illinois, and Ohio as they moved south to their winter termini (Fig. 3A).

Cranes that continued their migration south from Jasper-Pulaski FWA and the Kankakee River Valley moved either through western or central Indiana and then converged on similar routes through central Kentucky. Cranes that continued south from Kentucky ($n = 18$, 42%) moved through central Tennessee, used the Chickamauga Reservoir (specifically, Hiwassee WR) as a staging or stopover area prior to completing their migration. One crane that summered in Ontario migrated from south-central Indiana west through north-central Kentucky and eventually wintered at the Hop-In

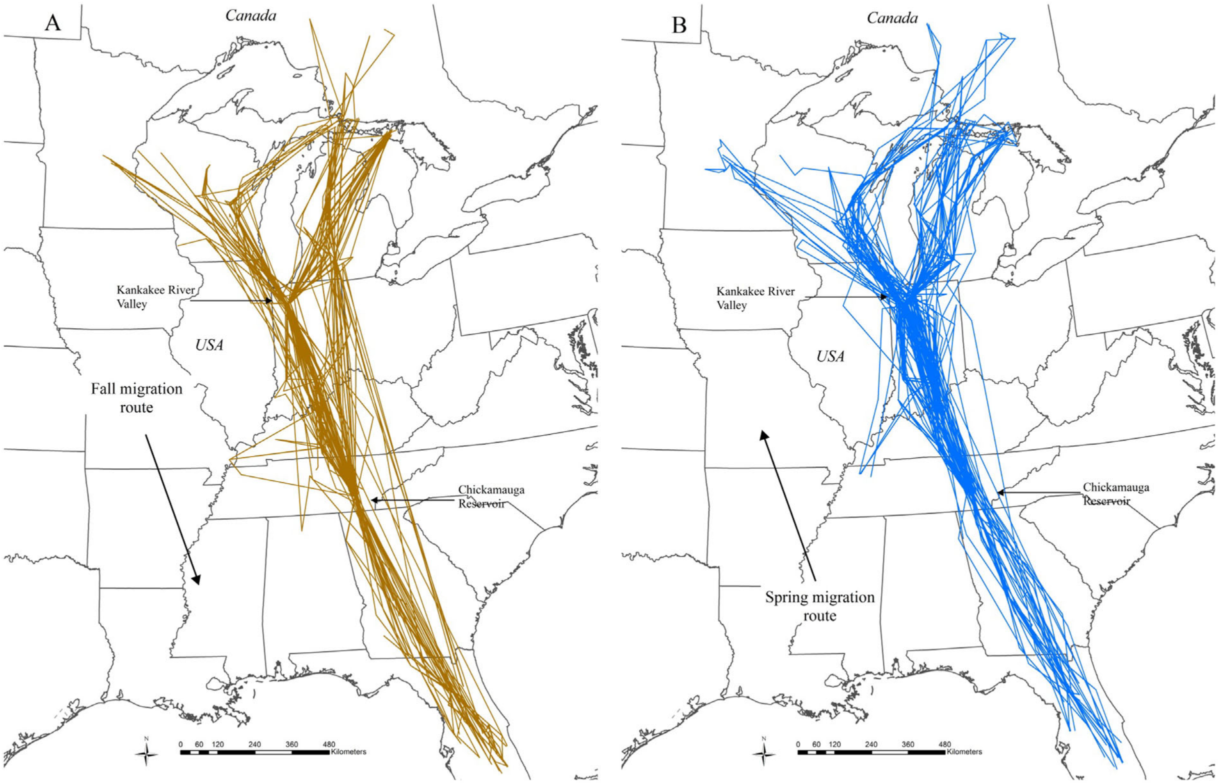

Figure 3. Fall (A) and spring (B) migration routes for platform transmitting terminal-marked greater sandhill cranes, 2010–2014.

WA (Obion County), Tennessee. Cranes that wintered in Georgia and Florida made multiple stops in a migration corridor through northeastern Alabama and west-central Georgia to their respective winter areas (Fig. 3A). There were 3 (7%) cranes that alternated their migration route around Lake Michigan to their respective winter termini at least once during the study.

Distribution of Winter Areas

The distribution of crane winter areas extended from Indiana to Florida (Fig. 2B). The majority of marked cranes ($n = 26$, 62%) wintered ≥ 1 year in southeastern Tennessee within the Hiwassee WR and surrounding Chickamauga Reservoir (Meigs, Rhea, and Hamilton counties), or in northwestern Tennessee (Obion County). South of Tennessee, 19 (45%) cranes wintered throughout the Florida Peninsula (Alachua, Brevard, Glades, Highlands, Lake, Levy, Marion, Okaloosa, Okeechobee, Osceola, Pasco, Polk, and Putnam counties) and 4 (10%) wintered in Georgia (Brooks, Crisp, Floyd, and Pulaski counties). North of Tennessee, 3 (7%) cranes wintered in Kentucky (Barren and Larue counties) and 12 (29%) wintered in Indiana (Greene, Jackson, Jasper, LaPorte, and Starke counties). Eleven (26%) cranes returned to the same winter area in subsequent winters and 31 (74%) wintered in ≥ 1 state at least once during the study period.

Description of Spring Migration

Marked cranes used similar spring and fall migration routes (Fig. 3). Cranes that wintered in Florida and southern Georgia traversed central and western Georgia and northeastern Alabama and staged either within the Chickamauga Reservoir (i.e., Hiwassee WR; $n = 12$, 29%) or migrated directly to staging areas in north-central Tennessee, central Kentucky, and southern Indiana. Cranes that wintered in the Chickamauga Reservoir used multiple staging areas in Kentucky, concentrated in south-central Kentucky ($n = 17$, 40%; Barren and Metcalfe counties) and north-central Kentucky ($n = 25$, 60%; Hardin and Larue counties). Two cranes (5%) that wintered in northwestern Tennessee (Obion County) migrated to Indiana staging areas either through southern Indiana or through eastern Illinois.

Cranes migrating north from central Kentucky moved to southern Indiana staging areas in the White River Valley ($n = 27$, 64%; Jackson County) and west-central Indiana staging area at Goose Pond FWA and surrounding area ($n = 13$, 31%; Greene County). Most cranes ($n = 35$, 83%) used stopover sites at the Jasper-Pulaski FWA and throughout the Kankakee River Valley after departing southern Indiana, and from there, continued migration to their respective summer areas. Several cranes ($n = 10$, 24%) moved from southern Indiana staging areas and bypassed Jasper-Pulaski FWA and the Kankakee River Valley on to their summer areas.

Cranes that summered outside of Lower Peninsula Michigan and north and east of Lake Michigan ($n = 16$, 38%) followed a route through central Michigan continuing through either the Straits of Mackinaw or across Lake Huron (i.e., those summering on Manitoulin Island, Ontario). Cranes that summered outside of Wisconsin and north and west of Lake Michigan migrated either through central Wisconsin ($n = 3$, 7%) or through eastern Wisconsin, and continued through the

Table 1. Mean arrival date, length of stay, and departure date on summer areas for platform transmitting terminal-marked greater sandhill cranes in the Eastern Population, North America, 2010–2014.

	Arrival date			Length of stay (days)			Departure date		
Yr	n	$\bar{x}$	SD (days)	n	$\bar{x}$	SD (days)	n	$\bar{x}$	SD (days)
2010	7	22 Mar	14	7	194	34	16	6 Oct	22
2011	32	30 Mar	16	30	185	32	30	6 Oct	28
2012	33	20 Mar	11	26	196	36	27	5 Oct	30
2013	17	3 Apr	15	9	176	34	9	2 Oct	25
2014	8	6 Apr	16	3	192	36	3	11 Oct	31
All years	97	27 Mar	15	75	189	34	85	5 Oct	27

Upper Peninsula of Michigan ($n = 7$, 17%). Seven (17%) cranes that summered on the Upper Peninsula of Michigan, in north-central Ontario, and east of Lake Michigan (North Shore of Lake Huron and Manitoulin Island, Ontario) migrated west of Lake Michigan and through the Upper Peninsula of Michigan, at least once during the study period. There were 6 (14%) cranes that alternated their migration route around Lake Michigan to their respective summer area at least once during the study.

Chronology of Annual Movements

Cranes on average arrived at their summer areas on 27 March ($n = 97$; range = 22 Feb–3 May; Table 1) and stayed on summer areas 189 days ($n = 75$; SD = 34 days). Average departure from summer areas for staging areas was 5 October ($n = 85$; range = 10 Aug–28 Dec), and cranes traveled on average 59 days ($n = 79$, SD = 37 days; Table 2) from summer areas to winter termini. Average cumulative distance traveled between subsequent stops from summer to winter termini during fall migration was 237 km ($n = 433$, SD = 177 km). Cranes used an average of 6.1 stops ($n = 75$, SD = 2.8 stops) during fall migration; on average 1.8 ($n = 84$, SD = 1.0 stop) of these stops were at staging areas and 3.3 ($n = 89$, SD = 2.1 stops) were at stopover sites. We identified 43 fall staging areas and 136 fall stopover sites. Average number of days spent on individual staging areas was 35 ($n = 79$, SD = 22 days), where 34% and 18% of fall migration days were spent in the Kankakee River Valley and south-central Michigan, respectively (Appendix A).

Average arrival date of cranes at their winter areas was 11 December ($n = 86$, range = 21 Sep–27 Jan; Table 3) and they remained on winter areas an average of 67 days ($n = 85$, SD = 33 days). Average departure date of cranes from winter areas was 16 February ($n = 102$; range = 15 Jan–29 Mar) and cranes traveled on average 40 days ($n = 94$, SD = 18 days; Table 4) from winter areas to summer areas. Average distance traveled between sequential stops prior to reaching summer areas was approximately 195 km ($n = 652$, SD = 132 km). Cranes stopped on average 7.6 times ($n = 97$, SD = 3.1 stops) during spring migration; 4.6 ($n = 100$, SD = 2.7 stops) of these stops were at stopover sites and 2.1 ($n = 91$, SD = 1.0 stop) were at staging areas. We identified 43 spring staging areas and 172 spring stopover sites. Average number of days spent on staging areas during spring migration was 15 ($n = 91$, SD = 6 days), where 34% and 9% of the cumulative migration days were spent in the Kankakee River Valley, northwestern Indiana and the White River Valley, southern Indiana, respectively (Appendix B).

USFWS Fall Survey

Approximately 30%, 29%, and 31% of crane locations were outside of areas surveyed during the 2010, 2011, and 2012 USFWS fall surveys, respectively. Crane locations that were outside surveyed areas included northern and east-central Wisconsin and central and north-central Michigan (Fig. 4). However, these cranes eventually moved to staging areas that would have been covered by observers, after the fall survey period. All of the cranes that summered in Canada were present in surveyed locations during the survey period.

DISCUSSION

Summer Area Distribution

Summer areas used by marked cranes were widely distributed throughout Minnesota, Wisconsin, Michigan, and in the eastern portion of Ontario, Canada, and occurred within the previous estimated breeding range of cranes in the EP (Van Horn et al. 2010). Geographic distribution and migration routes that cranes used coincided with previously reported

Table 2. Average number of days, number of stops, and length of stay at staging areas (stop duration >5 days) from summer areas to winter termini for platform transmitting terminal-marked greater sandhill cranes in the Eastern Population, North America, 2010–2013.

	Total days			No. stops			Length of stay (days)		
Yr[a]	n	$\bar{x}$	SD (days)	n	$\bar{x}$	SD (stops)	n	$\bar{x}$	SD (days)
2010	16	54	32	16	5.9	1.9	17	42	23
2011	30	58	36	29	5.9	2.6	29	36	22
2012	25	61	41	22	6.3	3.6	23	29	19
2013	8	72	40	8	6.8	3.2	7	33	13
All years	79	59	37	75	6.1	2.8	79	35	22

[a] Summaries are unavailable for 2014.

Table 3. Mean arrival date, length of stay, and departure date on winter areas for platform transmitting terminal-marked greater sandhill cranes in the Eastern Population, North America, 2009–2014.

	Arrival date[a]			Length of stay (days)[a]			Departure date		
Yr	*n*	$\bar{x}$	SD (days)	*n*	$\bar{x}$	SD (days)	*n*	$\bar{x}$	SD (days)
2009–2010							6	16 Feb	6
2010–2011	24	10 Dec	13	26	66	17	35	18 Feb	9
2011–2012	31	14 Dec	28	31	65	32	34	15 Feb	15
2012–2013	22	6 Dec	34	20	74	49	19	19 Feb	22
2013–2014	8	14 Dec	20	7	63	29	8	14 Feb	17
All years	86	11 Dec	26	85	67	33	102	16 Feb	14

[a] Summaries unavailable for 2009–2010 winter locations.

geographic distributions (Walkinshaw 1949, Tacha et al. 1994) and migration routes (Walkinshaw 1960, Melvin and Temple 1982). However, at smaller spatial scales, some areas thought to support breeding cranes in the EP were not represented by our sample, including northwestern Wisconsin-northeastern Minnesota (Cutright et al. 2006, Minnesota Breeding Bird Atlas Project 2014) and eastern Ontario, including the eastern shore of Lake Huron and the southern peninsula of Ontario (Cadman et al. 2007). None of the cranes in our sample overlapped the summer range of cranes in the MCP identified by Krapu et al. (2011). Summer area locations of marked cranes were concentrated in east-central Wisconsin and the north shore of Lake Huron, Ontario, which support relatively high densities of breeding cranes (Cadman et al. 2007, Van Horn et al. 2010).

Cranes consistently returned to the same summer areas in subsequent years, similar to cranes in the Rocky Mountain Population (Drewien 1973) and MCP (Krapu et al. 2011). On average, cranes in the EP and MCP (Krapu et al. 2011) used subsequent summer areas within <10 km of one another; 65% of cranes in the EP used subsequent summer areas within 1 km of one another, compared to 38% for cranes in the MCP (Krapu et al. 2011). We observed 3 instances when individual cranes moved an average linear distance of 67.2 km (range = 25.1–98.9 km) among subsequent summer areas, and we speculate that these cranes may have been sub-adults (Bennett 1989, Nesbitt and Williams 1990, Hayes 2015). However, 2 of these cranes returned to the same summer area in subsequent years and the third crane died during the first summer.

Migration Routes and Chronology

Cranes followed migration routes similar to those identified in previous migration studies that used very high-frequency transmitters in south-central Minnesota (Crete and Toepfer 1978) and cranes marked with ARGOS Doppler PTTs on Manitoulin Island, Ontario, Canada (S. A. Petrie, Bird Studies Canada, unpublished data). Unlike those studies, we were able to provide more precise information, particularly about routes and locations where cranes stopped during migration. We also observed that 8 (19%) cranes with summer areas in the Upper Peninsula of Michigan, Manitoulin Island, Ontario, and east-central Ontario used migration routes west of Lake Michigan, instead of the more intuitive route through the Lower Peninsula of Michigan. Six of these cranes also alternated migration routes around Lake Michigan during sequential migration (i.e., fall and spring) and in subsequent years. Our study represents the first evidence of this behavior and use of both of these migration routes by individual cranes. We also documented cranes ($n = 8$, 19%) that summered on Manitoulin Island used migration routes over large bodies of water (Lake Huron and portions of Lake Michigan) similar to Krapu et al. (2011), who described cranes crossing the Bering Strait of Alaska and the Arctic Ocean to and from breeding grounds.

Recent observations of migratory cranes that wintered in Louisiana led to speculation that EP cranes are potentially using non-traditional migration corridors. King et al. (2010) monitored 2 PTT-marked cranes that wintered in central Louisiana and migrated north through the Mississippi Alluvial Valley toward summer areas within the EP summer distribution. One marked crane in their study used a migration route through west-central Illinois to southwestern Wisconsin, and then into the Upper Peninsula of Michigan, after which they were unable to receive additional location information from the transmitter. The other crane traveled a similar route used by some of the

Table 4. Average number of days, number of stops, and length of stay at staging areas (stop duration >5 days) from winter termini to summer areas for platform transmitting terminal-marked greater sandhill cranes in the Eastern Population, North America, 2010–2014.

	Total days			No. stops			Length of stay (days)		
Yr	*n*	$\bar{x}$	SD (days)	*n*	$\bar{x}$	SD (stops)	*n*	$\bar{x}$	SD (days)
2010	6	39	11	6	6.8	0.8	6	12	1
2011	33	42	16	34	8.4	3.0	33	14	4
2012	33	32	15	33	7.1	3.0	29	17	8
2013	16	41	22	17	7.1	4.0	15	17	7
2014	6	62	11	7	7.7	2.5	8	14	4
All years	94	39	18	97	7.6	3.1	91	15	6

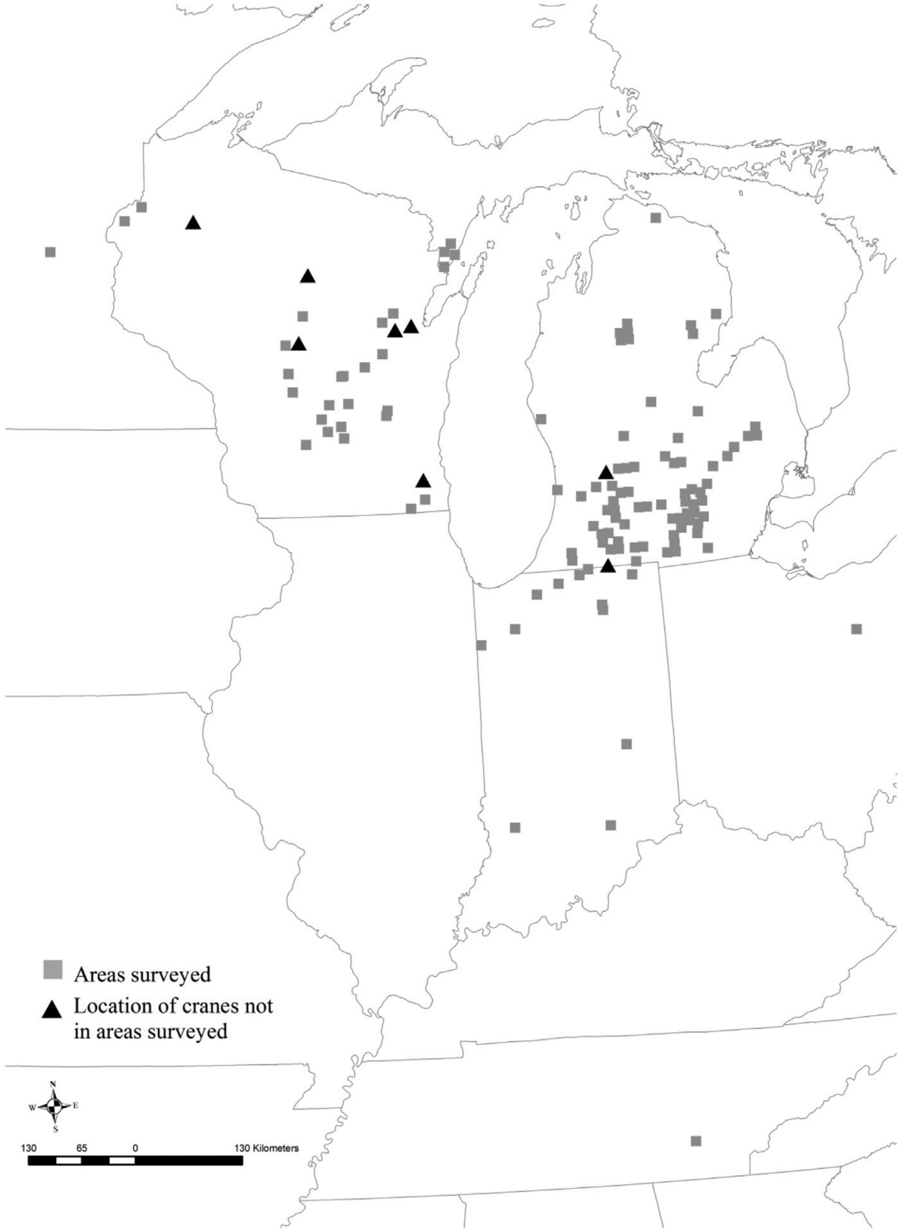

Figure 4. Locations of areas surveyed (gray squares) during the United States Fish and Wildlife Service Fall Eastern Population Sandhill Crane Survey; also shown are locations (black triangles) where platform transmitting terminal-marked sandhill cranes were not observed during the annual surveys, 2010–2012.

cranes in our sample through west-central Indiana (Goose Pond FWA), northwestern Indiana (Kankakee River Valley), east-central Wisconsin, and then through the Upper Peninsula of Michigan to a summer area in north-central Ontario.

A single PTT-marked crane in our sample from the Manitoulin Island, Ontario study site migrated west from the White River Valley, Indiana (Jackson County) and wintered at the Hop-In WR, Tennessee (Obion County). However, that crane did not return to Hop-In WR in the subsequent year. In anticipation of identifying a potential western migration corridor to Louisiana, we affixed 2 PTTs to cranes that wintered at Hop-In WR. However, only 1 returned to winter at the Hop-In WR and the other wintered in Florida the following year.

Cranes consistently used staging areas along migration routes, but made fewer stops for a longer duration during fall migration than during spring migration. Locations where cranes stopped during migration along the north shore of Lake Huron, Algoma District, Ontario; Lake Poygon, east-central Wisconsin; the Kankakee River Valley, northwestern Indiana; and counties in south-central Michigan were frequented more by cranes during fall migration (Fig. 3A; Appendix A). Cranes used Hardin County, north-central Kentucky; White River Valley (Ewing Bottoms, Jackson County), south-central Indiana; and the Kankakee River Valley, northwestern Indiana more frequently during spring than during fall migration (Fig. 3B; Appendix B). These areas support shallow-marsh roosting habitat, have an abundant food supply from agricultural production, and are more likely to be protected from human disturbances (i.e., hunting and sporting activities). The Kankakee River Valley located in northwestern Indiana was the most frequented of all staging areas during fall and spring migration, where cranes spent 34% of migration days.

Winter Area Distribution

Crane winter areas extended from Indiana to Florida, well north of the areas previously described by Tacha et al. (1994), who reported that cranes in the EP wintered mainly in southeastern Georgia and in Florida. Cranes wintered in Florida, Georgia, Tennessee, Kentucky, and Indiana with the Chickamauga Reservoir (specifically, Hiwassee WR), Tennessee having the highest proportion of use among all winter areas. The proportion of cranes that used the Chickamauga Reservoir Valley for the winters of 2009 and 2010 may be biased high because we trapped the majority of cranes ($n = 6$, 14%, 2009–2010; $n = 12$, 28%, 2010–2011) at the Hiwassee WR during December and January of those years. However, in 2010, MWS estimates for the Chickamauga Reservoir indicated a record number of wintering cranes ($n = 48{,}300$; J. R. Kelley, USFWS-Migratory Bird Management, personal communication), suggesting that a large portion of cranes in the EP likely used that area. Furthermore, many of the cranes we captured in other locations used the Chickamauga Reservoir during migration in years following their capture. The Chickamauga Reservoir is ideal for staging and wintering cranes. Agriculture crops (corn, soy beans, and winter wheat) are produced annually for wintering wildlife and adjacent sand bars and low water levels on Chickamauga Reservoir provided roosting habitat and sanctuary for sandhill cranes during the fall and winter months (R. Klippel, personal communication). Hunting for sandhill cranes is allowed throughout the reservoir; however, the Hiwassee WR is designated a non-hunting zone.

Recent analysis of long-term Christmas Bird Count data indicated that cranes in the EP wintered at staging areas north of Georgia and Florida in recent decades (Amundson and Johnson 2011, Lacy et al. 2015). Lacy et al. (2015) suggested that climate and increased agriculture throughout the EP range may influence cranes to winter farther north. However, there has been no formal analysis to demonstrate that these factors are main contributors to a more northerly winter strategy. Thirty-one (74%) cranes in our sample that wintered north of Georgia and Florida used migration staging areas in Indiana, Kentucky, and Tennessee. Winter destinations for cranes varied among years, where 11 (26%) returned to the same winter area in subsequent winters. The remaining 31 (74%) cranes wintered in $\geq$1 state at least once during the study period, indicating a variation in migration strategy possibly influencing cranes to settle in a particular winter area.

Eight (19%) cranes used the Kankakee River Valley in northwestern Indiana as a winter area in $\geq$1 year. These cranes that wintered in the Kankakee River Valley used the Jasper-Pulaski FWA until all available roosting sites froze, then roosted within the Schahfer Generating Station property in Wheatfield, Indiana about 10 km north-northwest of Jasper-Pulaski FWA. The power station provided roosting areas that remained ice-free and the surrounding agricultural landscape provided waste grain throughout the winter (J. Bergens, personal communication). These cranes then used areas throughout the Kankakee River Valley in proximity to Jasper-Pulaski FWA as the winter progressed.

Additional winter locations outside of traditional areas are not well understood. Location data from King et al. (2010) suggested that cranes in the EP used winter areas in northern Louisiana and 3 cranes from our sample wintered at the Hop-In WR, Tennessee west of previously reported wintering areas for cranes in the EP. Observations during the MWS of cranes at the Wheeler NWR, Alabama, have steadily increased since 2003, with an average of 4,583 cranes (range = 293–12,032) and a peak count of 12,032 cranes in 2013. Furthermore, observations of cranes in Arkansas and Mississippi along the Mississippi Alluvial Valley are frequent during the MWS (J. R. Kelley, personal communication). These cranes likely are part of the EP and most likely used the Hop-In WR as a staging area.

MANAGEMENT IMPLICATIONS

Location and chronology data from our study can be used to adjust timing of hunting seasons to potentially avoid high harvest pressure on local breeding adults and focus harvest pressure on migrants. Location and chronology data can also be used to identify specific locality information for potential land conservation and opportunity for non-consumptive recreational activities (e.g., crane festivals and bird watching).

We estimated a proportion of cranes in the EP were located in areas not currently covered by the USFWS fall survey during the survey period. If the absence of these cranes in the USFWS fall survey area is similar through time, series of counts from surveys will likely provide a reasonable estimate of population trend. Alternatively, if the proportion of cranes not present in survey areas changes, it may be necessary to redesign the survey by moving the survey period later into the fall or early winter, when a larger portion of cranes are associated with known concentration areas. However, the effects of moving the survey period would need to be evaluated to avoid issues related to 1) comparability to previous surveys; and 2) cranes arriving on wintering areas in Florida where it is difficult to distinguish cranes in the EP from Florida non-migratory greater sandhill cranes (*A. c. pratensis*).

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APPENDIX A

Fall migration staging areas, average number of cranes using the staging areas, and percent of fall migration days at the staging area for platform transmitting terminal-marked sandhill cranes in the Eastern Population, North America, 2010–2013. Fall staging areas are areas that had ≥1% of the total fall migration days in that area.

State or Province	County or District	Location names	No. marked cranes ($\bar{x}$)	Days in staging area (%)
IN	LaPorte, Jasper, Pulaski, Starke	Kankakee River Valley	12	33.7
MI	Barry, Calhoun, Eaton, Jackson, Kalamazoo	South-central Michigan	9	17.9
WI	Waushara, Winnebago	Lake Poygon	4	5.9
WI	Columbia, Iowa, Juneau, Sauk	Wisconsin River Valley	2	4.4
ON	Algoma, Sudbury	North Shore of Lake Huron	3	4.1
WI	Wood		2	3.3
WI	Lincoln		1	2.6
TN	Meigs, Rhea	Chickamauga Reservoir	7	2.5
IN	Jackson	Ewing Bottoms	4	2.2
MI	Chippewa		2	2.0
MN	Sherburne	Sherburne National Wildlife Refuge	1	1.9
WI	Green Lake	Green Lake	1	1.5
MI	Bay		1	1.2
WI	Oconto		1	1.0

APPENDIX B

Spring migration staging areas, average number of cranes using the staging area, and the percent of spring migration days at the staging area for platform transmitting terminal-marked sandhill cranes in the Eastern Population, North America, 2010–2014. Spring staging areas in the table are areas that had ≥1% of the total spring migration days spent in that area.

State or Province	County or District	Location names	No. marked cranes ($\bar{x}$)	Days in staging area (%)
IN	LaPorte, Jasper, Pulaski, Starke	Kankakee River Valley	19	33.9
IN	Jackson	White River Valley	9	8.7
MI	Barry,Calhoun, Eaton, Jackson, Kalamazoo	South-central Michigan	5	6.6
KY	Hardin, Larue	Cecilia	8	6.4
IN	Greene	Goose Pond FWA	3	3.8
WI	Waushara, Winnebago	Lake Poygon	2	2.9
MI	Missaukee		2	2.4
KY	Barren, Metecalf	Barren River Valley Reservoir	4	2.3
MI	Cass		1	2.3
WI	Green Lake	Green Lake	2	2.1
IN	Morgan		1	2.0
MI	Oceana		2	1.9
ON	Algoma, Sudbury	North Shore of Lake Huron	4	1.7
TN	Meigs, Rhea	Chickamauga Reservoir	3	1.4
MI	Mason		1	1.1