PROCEEDINGS OF THE

THIRTEENTH NORTH AMERICAN CRANE WORKSHOP

14-17 April 2014
Lafayette, Louisiana

FRONTISPIECE. Gary Krapu, Research Wildlife Biologist Emeritus, USGS Northern Prairie Wildlife Research Center, received the L. H. WALKINSHAW CRANE CONSERVATION AWARD in recognition of his career-long work to better understand the needs of sandhill cranes in the Platte River ecosystem; initiate a comprehensive, long-term research program to guide conservation and management of the Mid-continental Population of sandhill cranes; and for collaborative research efforts with biologists of other nations to guide international conservation of cranes. The Award was presented by Jane Austin, President of the North American Crane Working Group, on 17 April 2014. Gary received his M.S. and Ph.D. degrees in Animal Ecology from Iowa State University. He was employed as a Research Wildlife Biologist at Northern Prairie under the U.S. Fish and Wildlife Service and U.S. Geological Survey from 1968 until his retirement in 2011 and in emeritus status thereafter. While at Northern Prairie, he also conducted studies on waterfowl, including wetland habitat requirements, role of stored nutrients in waterfowl reproduction, brood habitat use and factors influencing duckling survival, waterfowl nutrition, and staging ecology of white-fronted geese. He continues to conduct research on sandhill cranes at Northern Prairie, primarily studying population dynamics of the Mid-continent Population and the geographic distribution and ecology of sandhill cranes breeding in Russia and western Alaska. (Photo by Glenn Olsen)

Front cover: Whooping crane family at nest, Jefferson Davis Parish, Louisiana, April 2016, by Eva Szyszkoski, Louisiana Department of Wildlife and Fisheries.

Back cover: Scenes from the Thirteenth Workshop in Lafayette, Louisiana, by Barry Hartup, Glenn Olsen, Tommy Michot, Eva Szyszkoski, Richard Urbanek, and Sara Zimorski.

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PREFACE

The North American Crane Working Group (NACWG) is an organization of professional biologists, aviculturists, land managers, non-professional crane enthusiasts, and others interested in and dedicated to the conservation of cranes and crane habitats in North America. Our group meets approximately every 3 years to exchange information pertaining to sandhill cranes and whooping cranes and occasionally reports about some of the other cranes species. Our meeting in Lafayette, Louisiana, 14-17 April 2014, celebrated the return of whooping cranes to Louisiana for the first time in 60 years. The workshop was organized by Sammy King and Gay Gomez, and we thank them for their efforts. The field trips to see the release site for the whooping cranes, as well as learning about Louisiana's crawfish and rice industry, were enlightening and enjoyable. The NACWG Board of Directors consisted of President Jane Austin, Vice-President Richard Urbanek, Treasurer Daryl Henderson, Felipe Chavez-Ramirez, David Aborn, Barry Hartup, and Sammy King. The scientific program consisted of 39 scientific talks and 13 posters. The papers in this volume include some of those presented at the workshop as well as others submitted later. Papers submitted for publication in the Proceedings are peer-reviewed according to scientific journal standards. We thank the following referees for their contribution to the quality of this volume:

Nicholas J. Aebischer, Jeb A. Barzen, Andrew W. Cantrell, Michael D. Culbreth, Martin J. Folk, Matthew A. Hayes, Scott G. Hereford, Jerome J. Howard, Anne E. Lacy, Julia A. Langenberg, and Sara E. Zimorski.

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David A. Aborn, Editor
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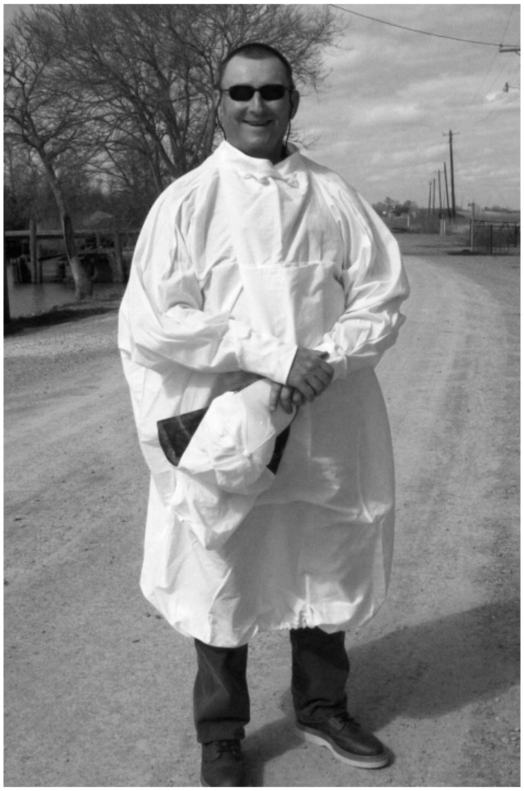

THOMAS J. "TOM" HESS, JR.
1950-2014

A native of Delaware, Tom Hess first encountered southwest Louisiana's marshes as a student at Rockefeller State Wildlife Refuge in Grand Chenier, Louisiana. Realizing he had found the place of his dreams, Tom, an avid waterfowl hunter and fisherman, vowed to return to the region. In 1972 he began work as a biologist assistant for the Louisiana Department of Wildlife and Fisheries (LDWF) at Rockefeller Refuge. He held a B.S. in Wildlife Management from Louisiana Polytechnic University (Louisiana Tech) and later earned an M.S. in Wildlife Management from Louisiana State University. Tom spent the first several years of his career as general manager and wetland manager of Little Pecan Island hunting lodge and preserve, a privately owned and managed tract of coastal fresh marsh near Grand Chenier, Louisiana. He spent the rest of his career as a biologist at Rockefeller Refuge, rising to the position of refuge manager, which he held until his death in March 2014. During his long career with LDWF, Tom worked with wetland management and endangered species. He contributed to the recovery of the state's brown pelicans and bald eagles and was an ardent supporter of the Louisiana whooping crane reintroduction. His enthusiasm for Louisiana's wetlands, waterfowl, and other wildlife was infectious; he worked well with landowners and other stakeholders and mentored many students and young staff members with his own inimitable blend of leadership, optimism, experience, and humor. In 2011 the Louisiana Wildlife Federation named him Professional Conservationist of the Year largely for his work with the whooping crane reintroduction. Indicative of Tom's passion for the Louisiana whooping cranes was his request that memorial donations be made to the Louisiana Wildlife and Fisheries Foundation, specifically to support the reintroduction project.

Gay Gomez, Lake Charles, Louisiana

SCOTT M. MELVIN
1953-2014

Scott Melvin earned a B.S. in Wildlife Management at the University of Maine in 1975. Scott's life-long love of cranes began when he followed with his graduate work at the University of Wisconsin. His M.S. at Steven's Point and his Ph.D. at Madison on the migration, habitat use, and nesting ecology of sandhill cranes pioneered the use of leg-band attachment of radiotransmitters and innovative tracking techniques for cranes. He returned to New England to work with the Maine Department of Inland Fisheries and Wildlife, where he was Assistant Leader of the Endangered and Nongame Wildlife Project, and the Massachusetts Division of Fisheries and Wildlife, where he worked for almost 30 years. He spent his free time documenting the first successful nesting of sandhill cranes in Maine in 2000 and Massachusetts in 2007.

As Senior Zoologist for Massachusetts Wildlife's Natural Heritage and Endangered Species Program, Scott oversaw research and conservation efforts for a variety of species ranging from turtles to grassland birds, but he is best known for his leadership in the recovery of the piping plover. Through conservation partnerships forged under Scott Melvin's tenure, the piping plover had a fourfold increase in numbers, with over 660 estimated nesting pairs in Massachusetts by 2014. While most of his time was spent as an agency biologist, he also enjoyed teaching over the years at the University of Maine, Harvard University, and the University of Massachusetts, where he also was advisor to many graduate students. While well known for his piping plover conservation efforts, cranes remained his first love, and he asked that memorial donations go to the International Crane Foundation.

Alison Whitlock, Petersham, Massachusetts, and Boston Globe (Photo by Bill Byrne)

TERRY J. KOHLER
1934-2016

Terry Kohler was a philanthropist, aviator, and pillar in conservation. In their corporate jet, Terry and his wife Mary transported eggs of trumpeter swans from Alaska and whooping crane eggs from northern Canada for hatching, rearing, and releases into Wisconsin. The Kohlers were leading supporters of the International Crane Foundation (ICF) for many years. They flew many cranes and eggs between ICF and the Patuxent Wildlife Research Center in Maryland and from these captive breeding centers to release sites in Florida, Idaho, Louisiana, and Wisconsin. Almost every one of the hundreds of reintroduced whooping cranes was transported in one of their planes. They supported hundreds of hours of flights to monitor both sandhill and whooping cranes east of the Mississippi River. Terry was an avid supporter of the ultralight aircraft-led migration technique used in reintroduction of the eastern migratory whooping crane population. Kohler aircraft flew biologists on hundreds of flights tracking the migration of released birds, translocating birds back to Wisconsin when needed, and surveying nests. The Kohlers recently became the major supporter of work in Texas to ensure the welfare of the natural population of whooping cranes on their wintering grounds.

The Kohlers flew around the world to deliver hatching eggs of Siberian cranes from ICF to a release project in Russia and visited the three areas of Russia where Siberian cranes nested. This flight was apparently the first passage of a private American aircraft across Russia. In 2009, Terry and Mary Kohler were awarded the Charles Lindbergh Award, which "is given annually to individuals whose work over many years has made significant contributions toward the Lindbergh's concept of balancing technology and nature."

Wildlife conservation, whooping cranes, and those of us lucky enough to work with Terry have lost a wonderful and generous supporter and friend. We will always remember and be forever grateful for the contributions made by Terry Kohler.

George Archibald, Baraboo, Wisconsin

USE OF SCIENTIFIC NAMES IN PROCEEDINGS OF THE THIRTEENTH NORTH AMERICAN CRANE WORKSHOP

Following publication of the *HBW* (Handbook of the Birds of the World) and *BirdLife International Illustrated Checklist of the Birds of the World* (del Hoyo et al. 2014), BirdLife International proposed modification of the scientific and common names for several crane species as well as for many other waterbirds. Four crane species (sarus, brolga, white-naped, and sandhill cranes) were removed from the genus *Grus* and placed in a new genus *Antigone*. The American Ornithologists' Union followed suit in its update to the checklist of North American birds (Chesser et al. 2016) by adopting the same changes. In these Proceedings, the editors of the North American Crane Working Group have chosen to retain the use of *Grus* for these species until further evidence is available to support the reclassification. We endorse the conclusions in Krajewski et al. (2010), the latest published research on this subject. Krajewski (personal communication, 2016) considers this reclassification to be premature. Crane phylogeny can only be confirmed when DNA data from nuclear genomes and more individuals of each species have been analyzed. Without such supporting evidence, it is recommended that the stability of taxon names that have been in use for many decades be maintained.

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CONTENTS

HABITAT SELECTION BY BREEDING SANDHILL CRANES IN CENTRAL WISCONSIN

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Abstract: We used compositional analysis to describe habitat use for a dense population of breeding sandhill cranes (*Grus canadensis tabida*) in central Wisconsin at 2 spatial scales: selection of home range within a study area and selection of habitats within the home range. Habitat use and home range size were estimated from radio-telemetry data from 12 breeding sandhill crane pairs. Research in Wisconsin that was performed on the landscape level suggests that breeding cranes depend on wetlands and do not select upland habitats. Evaluating habitat selection at different spatial levels, such as during different stages of the breeding season, can better illustrate the hierarchical nature of selection by breeding sandhill cranes. In establishing home ranges, breeding cranes selected wetland habitat over all other land-use categories. Within home ranges, breeding cranes still selected wetland habitat above all other habitat types; however, row crops and tall grass were also important. During daylight hours, habitats that were used consisted primarily of wetland (38.7% ± 4.5 [mean ± 1 SE]), row crop (24.3% ± 5.7), and short crop (14.0% ± 4.6). Home range size as well as the selection of habitat type was not constant during the breeding season. On average, home range size during the post-fledging stage was 3 times greater than pre-fledging stage. Wetlands were used daily (97.4% of all days) throughout the breeding season but for a greater percentage of each day when chicks were small than when large. Wetland accounted for 50.1% of all locations during the pre-fledging stage and for 30.6% of all locations during the post-fledging stage. The knowledge that breeding cranes require emergent wetlands at all spatial and temporal scales, but that the presence of both upland and wetland habitat within a home range is important, provides a greater refinement to the understanding of habitat needs of breeding sandhill cranes in Wisconsin.

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Key words: compositional analysis, greater sandhill crane, *Grus canadensis tabida*, radio-telemetry, seasonal habitat shifts.

Resource selection studies are common in wildlife research because determining which resources are selected provides basic information about the ecology of animals and how they meet their needs for survival (Manly et al. 2004). Resource selection studies have become an important tool in conservation biology and wildlife management (Leopold 1933, Pulliam and Dunning 1997, Garshelis 2000). Though frequently conducted, resource selection studies often produce contradictory results. A common problem of these studies is unclear definitions of basic terms (Jones 2001). Hall et al. (1997) reviewed 50 recent articles to compare how these studies defined habitat terms such as "use" and "availability" and found only 18% followed standard terminology.

Defining the appropriate geographical and temporal scales is another common problem with many resource selection studies. Resource selection can be categorized at a hierarchical order of spatial scale from geographic range (first order), to individual home range (second order), to habitats within the home range (third order), and to selection of certain items within a habitat (fourth order) (Johnson 1980). The criteria for selection of specific resources may be different at each level (Johnson 1980, Alldredge et al. 1998). If selection within the home range, for example, is the only geographical scale evaluated, the results may not indicate the actual criteria for the animal's choice of habitats if it is only selecting among individual food items within a field. Likewise, if temporal scale is not defined, results may also be inconclusive because changes in habitat composition may be related to some, but not all, portions of the annual cycle (Schooley 1994, Arthur et al. 1996).

Habitats are the resources and conditions present in an area that are needed by an organism to survive (Krausman 1999). In our study, habitat use is defined as an animal's use of the physical and biological resources in a habitat (Krausman 1999). Different habitat uses include foraging, sleeping (roosting), social interaction, and nesting. We define habitat availability as the accessibility of physical and biological components in a habitat (Krausman 1999). Habitat selection refers to the hierarchical process of behavioral responses (Jones 2001) that results in habitats being used disproportionately to their availability (Johnson 1980,

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Manly et al. 2004).

Several methods have been used to analyze habitat selection (Alldredge and Ratti 1986, 1992; Alldredge et al. 1998; McClean et al. 1998; Alldredge and Griswold 2006). Results produced by these methods are variable and are affected by several components of the study not necessarily tied to selection (Alldredge and Ratti 1986). We selected compositional analysis (Aebischer et al. 1993) as the most appropriate method to analyze habitat selection by breeding greater sandhill cranes (*Grus canadensis tabida*) because of the high variability in habitat use between home ranges and the potential for non-independence of radio-telemetry points. This method of analysis also addresses some of the shortcomings of other resource selection functions such as solving the problem of non-independence of proportions by using their log ratios (Aitchison 2003) and addresses the problem of defining habitat availability by conducting the analysis on several geographical scales. Finally, we did not correct for bias in habitat selection created by territorial species, which violates the assumption of independence between individuals. Since sandhill crane territories are maintained over multiple years (Hayes 2015), habitat selection that we measured should be relatively unbiased.

The eastern population of greater sandhill cranes that breed in central Wisconsin is an ideal study subject for resource selection analysis because of its accessibility and high density of individuals. Once categorized as rare (U.S. Fish and Wildlife Service 1966), this population is now abundant throughout much of its historic range (Lacy et al. 2015). There has been a gradual decline in the growth rate of the population (Meine and Archibald 1996) in the Central Sands region of Wisconsin, an area with the state's greatest density of birds (Su et al. 2004). Individual cranes primarily enter the breeding population through replacement of mates on existing territories (Hayes 2015), further evidence that most potential breeding territories are occupied.

Several components are necessary for sandhill crane breeding success. Though sandhill cranes are commonly seen using upland habitats during summer, the most important component of a breeding crane territory is thought to be a secure nest site associated with water (Armbruster 1987, Safina 1993). Research in Wisconsin supports this result and suggests that on a landscape level, breeding crane distribution is linked to wetland type and distribution (Su 2003). Su (2003) also found a clear spatial separation between territorial pairs and non-breeding flocks, indicating social status may be another factor affecting habitat selection in cranes (Hayes 2015). Pairs tend to stay close to the wetland while non-breeding flocks forage farther from wetland areas (Su 2003). Yet sandhill cranes have increased most dramatically in agricultural areas (Lacy et al. 2015), which suggests that upland habitats may also be important for territorial cranes in summer.

Walkinshaw (1949) found that most sandhill crane territories consist of areas used for nesting, roosting, and feeding and that the size of each area varies with time and crane density. Austin et al. (2007) suggested that water depth influenced daily nest survival for migratory sandhill cranes nesting at Grays Lake National Wildlife Refuge, Idaho. Nesbitt and Williams (1990) also observed that territory size of non-migrating, territorial Florida sandhill cranes (*Grus canadensis pratensis*) changed during the year, but they also found that whereas upland pastures were used more than predicted by their availability, wetland sites were not. Although breeding cranes return to the same location each year (Walkinshaw 1949), territorial boundaries are somewhat dynamic and may change based on the needs of the pair or based on availability of critical habitat components within the home range. The roles of wetland and upland habitats, as well as the role of spatial and temporal variation in these habitats, are thus not completely defined and suggest the importance of including these elements in developing the most accurate understanding of resource needs for sandhill cranes.

Evaluating selection at 2 different spatial levels within the same study population can better illustrate the hierarchical nature of habitat selection by breeding sandhill cranes while deemphasizing the difficulty of defining availability (Miller et al. 1999). Considering temporal variation in habitat selection also broadens the scope at which the needs of these pairs can be assessed. The objective of our study was to analyze habitat selection of breeding sandhill cranes in central Wisconsin using radio-telemetry and land cover data. Habitat selection was evaluated at 2 geographical scales: home range within a study area and habitats within a home range (Johnson 1980). We tested the null hypotheses that the selection of habitats at both of these scales was not different from random. We also evaluated temporal variation in selection of habitats within the home range by accounting for the influence of different stages of breeding season. Temporally, 2 null hypotheses were tested: 1) home range size did not vary during the breeding season, and 2) selection of habitats during the different stages of the breeding season was random.

STUDY AREA

The study area is located at the intersection of Marquette, Columbia, and Adams counties in central Wisconsin (Figure 1). Our study area was 7,531 ha and consisted of a heterogeneous landscape of wetlands, row crops, grassland, forest, and low-density residential areas. The wetlands in this area are predominantly palustrine with flow-through hydrology (Cowardin et al. 1979).

METHODS

Capture and Banding

Breeding pairs included in our study were captured on territory in the fall seasons of 1997, 1999, and 2000. We tracked these birds for the breeding season during the year following capture. We used alpha-chloralose, an oral tranquilizer, to sedate family groups for capture after baiting them with corn (Bishop 1991, Hayes et al. 2003). Each individual was marked with a U.S. Geological Survey (USGS) Bird Banding Laboratory band, a 7.62-cm-high numbered band, and a unique combination of 2.54-cm-high color bands (Dickerson and Hayes 2014). Advanced Telemetry Systems (ATS, Isanti, MN) radio transmitters (Series A3500 Model) were attached to the 2.54-cm color bands. Each bird was uniquely marked through transmitter frequency, color combination of plastic bands, or the USGS band number.

Classification of Habitats

Habitat boundaries were digitized in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA) using 1-meter-resolution aerial photographs taken in spring 2000 (Figure 2). For a concurrent study conducted by the International Crane Foundation (ICF), land-use changes were recorded every week each year to follow the progression of the crops throughout the growing season (ICF, unpublished data). For our analysis, we used land-use classifications from the middle of June of each year of the study to reflect the primary land-use for the season.

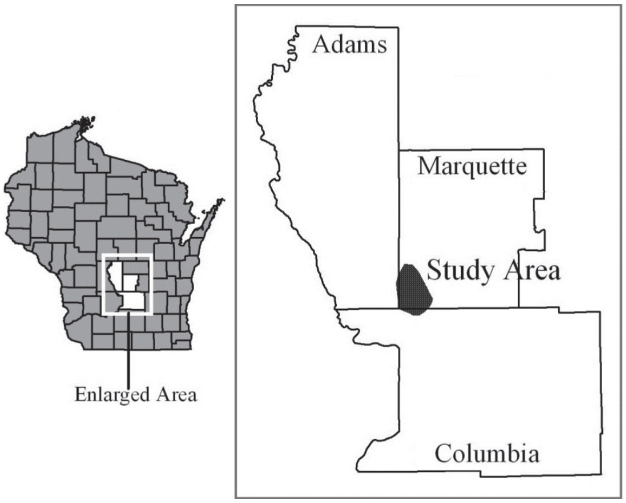

Figure 1. Breeding sandhill crane study area located within Adams, Columbia, and Marquette counties in the Central Sands Region of Wisconsin, 1997-2001.

We grouped 32 existing land-use classifications into 8 categories based on vegetation structure and hydrology: developed (DEV), vegetable crop (VC), row crop (RC), short crop (SC), tall grass (TG), upland forest (UFOR), wetland forest (WFOR), and wetland (WET). Developed included areas dominated by man-made features such as residential areas, ditches, roads, and Lake Mason. VC included crops such as beets, carrots, onions, peas, and potatoes. RC included corn, soybeans, wheat, oats, rye, and unidentified agriculture. SC included mowed grass, grazed grass, mint, and alfalfa. TG included grass, grass with less than 50% shrubs, fallow fields, and planted trees. UFOR included either hardwood, mixed hardwood pine, or pine forests. WFOR included any wetland area with tree cover, including grazed areas. The WET land use classification included emergent wet meadow wetland areas plus open water that was shallow enough for wading by cranes.

Radio-telemetry

Individual birds outfitted with radio transmitters were located using either a handheld or roof-mounted, 4-element Yagi antenna (ATS) with a portable receiver. Each individual was tracked once per week from sunrise to sunset, March-October. Location, behavior, and habitat data were recorded at 1.5-2-hour intervals. When bird locations were not visually confirmed, 3 compass bearings were recorded and then triangulated (White and Garrott 1990) on USGS 7.5-minute topographical

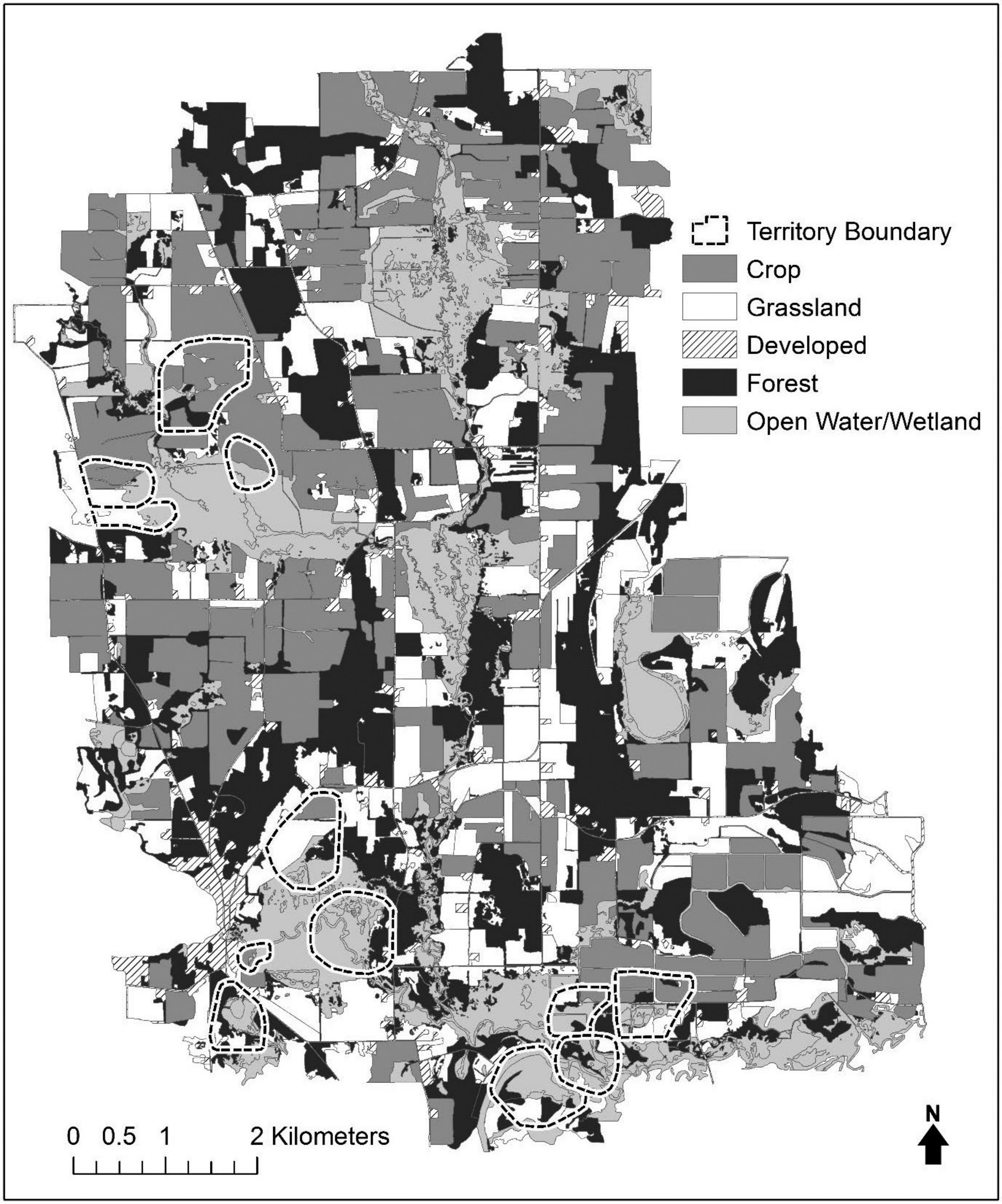

Figure 2. Distribution of general land use categories across the study area and within 12 territories of breeding sandhill cranes in the central Wisconsin study area during 1998, 2000, and 2001.

quadrangle maps. All locations were converted to the Wisconsin Transverse Mercator (WTM) coordinate system by plotting locations on quadrangles within an Access (Microsoft Corporation, Redmond, WA) database. These telemetry points were used to estimate home range size and to represent habitat use in the analysis of habitat selection within the home range.

Visual locations were plotted directly onto topographical maps using aerial photos as reference and were accurate to 0.5 ha. Triangulations with error polygons >3.5 ha were not used. Locations with only 2 bearings (termed bi-angulation here) had no error polygon. Error polygons >3.5 ha were excluded because this number represents over half the area of the average land-use polygon in the study area. The proportions of locations using bi-angulations were noted for each estimate.

Home range was calculated by the fixed kernel method, using least squares cross validation to select the smoothing parameter (Seaman and Powell 1996, Seaman et al. 1999). Calculations were made with the animal movement extension (Hoodge and Eichenlaub 1997) of ArcView 3.2 (Environmental Systems Research Institute 1992-1999). The home ranges estimated habitat use for home range selection within the study area and availability in the analysis of selection of habitats within the home range.

Habitat availability in the analysis of home range within the study area was defined by connecting the outermost points of the 12 individual home ranges. Location data from 36 additional color-marked breeding pairs in our study area were also included to construct the final habitat availability polygon. These additional pairs were part of an unrelated study and were entered into a Microsoft Access database similar to the radio-telemetry database. Adding these pairs increased the sample size sufficiently to enable us to measure availability, which better represented the population within our study area.

Roost-to-roost tracking (following a bird from its dawn roost to its evening roost for 1 diurnal day of tracking) allowed us to describe daily rhythms of habitat use. We could examine whether habitats were used in a clumped fashion such as when a food source becomes temporarily available and is used for several days before being abandoned or on a uniform basis such as habitats that are utilized each day. We examined frequencies of daily use of each habitat component for all pairs using pair days (the total number of days of observation for each pair combined) as our sample size. The days that a bird was not tracked for a full day and where the roost location was missed were excluded from this analysis.

Statistical Analysis

To compare home range size of breeding cranes during different stages of the annual breeding cycle we used a 1-way analysis of variance (ANOVA). *A posteriori* comparisons of means were made with Bonferroni's test (Sokal and Rohlf 2011). Breeding stages were combined if there was no significant change in size of the home range ($\alpha = 0.05$).

We used compositional analysis (Aebischer et al. 1993) to evaluate habitat selection of radio-tracked breeding sandhill cranes. This resource selection analysis method addressed 3 of the 4 common difficulties with habitat selection studies. To overcome the problem of non-independent bird locations, the individual was the sample unit. Since all birds in the study were members of a breeding pair and territories did not overlap, their territorial behavior minimizes overlap of used habitats. Proportions were log-transformed to rectify non-independence of use and availability ratios. This method tested between-group differences by referencing within-group and between-animal variation (DeHaan 1999).

Analysis of habitat selection within the study area was carried out on the 8 habitat categories described above. The analysis of habitat selection within the home range was carried out on the 6 habitat types available to all birds (DEV, UFOR, RC, SC, TG, WET). A value of 0.0001 was substituted for habitats with no use. We used Systat 9.0 (SPSS Inc., Chicago, IL) and command files available from the Game & Wildlife Conservation Trust (Fordingbridge, Hampshire, UK; Aebischer et al. 1993) to test the hypothesis that habitat use was proportional to availability. First, we tested if the use of habitats was non-random. To do so, we calculated the differences between the log-ratio transformations of the used and available proportions for each habitat using wetland as the denominator, then tested whether the average differences were jointly equal to zero using multivariate analysis of variance (MANOVA) (Aebischer et al. 1993). The level of rejection for a null hypothesis was $\alpha = 0.05$.

The second step in the analysis was to rank the habitat categories based on selection. Following Aebischer et al. (1993), we generated matrices of the means and standard errors of all possible log-ratio differences between telemetry locations (use) and habitat composition (availability). The sign of each value from the mean matrix was extracted and placed in a simplified ranking matrix that provided an indication of relative selection. A triple sign represented significant deviation from random at $P < 0.05$. Habitat categories were then ranked based on the number of positive signs compared to all other habitat types in the pair-wise comparison matrix. For 8 habitat categories, the rankings ranged from 0 to 7 with 0 being the least selected and 7 being the most selected.

Analysis of habitat selection was evaluated at 2 geographical levels: home range within the study area and habitats within the home range (Johnson 1980). Habitat use was also evaluated during the different stages of the breeding season. The breeding season was divided into 4 stages: 1) pre-nesting, 2) nesting (i.e., nest construction, egg laying, or incubation), 3) pre-fledged chick, and 4) post-fledged chick or pairs with no chick. Dates for these 4 reproductive stages were different for each pair and based on visual observations and movement patterns.

RESULTS

Radio-telemetry Error

For all 3 years of the study, the proportions of observations confirmed visually were similar and represented one-fourth to one-third of the sightings (Table 1). The percent of observations used in the analysis that were bi-angulations varied from 1.7 to 17.3%. All bird locations were checked against recorded land-use as well as with habitat observations made at the time of data collection. Errors in plotting the location of the point were corrected. In most cases, 2-azimuth bi-angulations in 1998 followed or preceded triangulated locations and birds had not moved significantly. Most error polygons were less than half the size of the average field polygon in the study area.

Table 1. Percentage of sightings (grouped by degree of potential error in the source data) used to estimate habitat use by sandhill cranes in central Wisconsin where a visual confirmation had the minimum error (0.5 ha) and 2-azimuth bi-angulations had undefined error.

Year	Visual confirmation	Error Polygon <3.5 ha.	Error Polygon >3.5 ha	Bi-angulation
1998	36.2	44.7	1.8	17.3
2000	34.4	56.1	7.4	2.1
2001	26.0	62.7	9.6	1.7

Habitat Use and Availability

The composition of habitats within the study area remained relatively constant during all 3 years of the study: UFOR (23.2% ± 0.03 [± 1 SE]), RC (25.0% ± 0.57), and WET (17.9% ± 0.00, Table 2). The mean home range size for breeding sandhill cranes over the entire season was 284.7 ha ± 59.7 ($n = 12$) and ranged from 24.9 to 794.0 ha (Table 3).

Home range size differed among the 4 temporal stages of the annual breeding season ($F_{3,\ 51} = 5.55$, $P = 0.002$). Home range sizes for pre-nesting, nesting, and chick stages did not differ, so these 3 stages were combined into 1 category, defined as pre-fledging (Bonferroni adjustment). On average, home range size during the post-fledging stage was 3 times greater than during the pre-fledging stage. Of the 12 individuals sampled, only 1 had a home range that was smaller during post-fledging.

Habitat composition during the entire breeding season was variable between individual home ranges (Table 2). Major habitats available to breeding sandhill cranes within their home ranges (habitat composition of the home range), March-October, were WET (35.6%

Table 2. Land-use composition of the study area, home range, and telemetry locations as defined for 12 breeding, radio-tracked sandhill cranes and 36 color-marked territorial pairs during 1998, 2000, and 2001 in central Wisconsin. Home range composition represents the average percentage of habitats within the 12 radio-tracked individuals' home ranges. Telemetry locations represent the used proportion in the compositional analysis of habitat use.

Land-use category	Study area composition (%)		Home range composition (%)		Telemetry locations (%)	
	Mean	SE	Mean	SE	Mean	SE
Developed	6.15	0.01	4.44	0.8	2.35	0.7
Upland forest	23.23	0.03	12.52	2.6	5.99	2.1
Vegetable crop	1.14	0.27	3.36	1.5	2.02	1.0
Row crop	25.02	0.57	21.31	3.8	24.29	5.7
Short crop	9.56	1.07	9.43	2.5	13.96	4.6
Tall grass	10.89	0.21	6.50	1.6	4.63	1.9
Forested wetland	6.15	0	6.79	2.1	8.07	3.8
Wetland	17.87	0	35.64	3.2	38.70	4.5

Table 3. Fixed kernel home range estimates (95%) calculated for the entire season (Mar-Oct), pre-fledge, and post-fledge/no chick seasons for 12 radio-tracked breeding sandhill cranes in central Wisconsin tracked during 1998, 2000, and 2001. The length of each stage in the breeding season was defined based on the reproductive cycle of each crane.

Identification frequency	Area (ha)		
	Entire season (Mar-Oct)	Pre-fledge	Post-fledge/ no chick
148.053	132.5	108.6	124.7
148.054	114.0	29.1	130.6
148.082	331.8	243.6	333.5
148.115	93.2	86.4	101.6
148.135	318.2	147.7	539.3
148.152	195.4	111.1	217.7
148.213	241.8	53.5	569.4
148.333	794.0	180.3	904.7
148.354	330.4	195.8	570.4
148.373	458.9	148.3	451.5
148.880	380.7	197.7	509.0
149.011	24.9	28.0	16.6
Mean ± SE	284.7 ± 59.7	127.5 ± 20.2	372.4 ± 75.8

± 3.2), RC (21.3% ± 3.8), and UFOR (12.5% ± 2.6). During daylight hours, habitats that were used consisted primarily of WET (38.7% ± 4.5), RC (24.3% ± 5.7), and SC (14.0% ± 4.6). On average, major habitats available in a home range during the pre-fledging stage were WET (43.0% ± 4.5) and RC (19.7% ± 5.2) (Table 4). Habitats used within the home range during the pre-fledging stage consisted primarily of WET (50.1% ± 4.9) and RC (20.8% ± 6.2). The composition of home range habitats during post-fledging was WET (30.3% ± 2.3), RC (24.6% ± 3.5), UFOR (12.5% ± 1.9), and SC (11.1% ± 2.8) (Table 4). On average, habitats used were WET (30.6% ± 3.2), RC (26.3% ± 5.1), and SC (20.5% ± 5.4).

With roost-to-roost tracking we could also measure absolute frequencies of habitat use within each day. Wetlands were used in 97.4% of the days on which we observed pairs ($n = 469$ pair-days), uplands (all habitats except WET and WFOR) were used in 83.6% of observed days, and 15.8% was unknown land-use (Table 5). Row crops and SC, whose relative importance is defined below, were used 60.8% and 32.6%, respectively. The total exceeds 100% as a tracked individual used multiple land uses in 1 day.

Habitat Selection

Selection of home ranges within the study area was not random ($\lambda = 0.072$, $F_{7,12} = 9.18$, $P = 0.013$). A ranking matrix (Table 6) ordered the habitat types in the sequence WET>RC>SC>DEV>TG>UFOR>WFOR. Wetland was used significantly more than any other habitat. There was no detectible difference in use of the 6 other habitats, implying that the order of their assigned ranks was not distinguishable ($P > 0.05$).

Analysis for habitat selection within home ranges

Table 5. Absolute frequency of daily use for wetland, upland, and unknown land use categories by 12 breeding sandhill cranes over the entire season (Mar-Oct) in central Wisconsin during 1998, 2000, and 2001. The total exceeds 100% as tracked individuals used multiple land use categories in 1 day ($n = 493$ pair-days).

Land-use category	Frequency of use (%)
Wetland	97.4
Upland	83.6
Row crop	60.8
Short crop	32.6
Unknown	15.8

Table 4. Mean composition of habitats and habitat use within the home ranges of 12 radio-tracked breeding sandhill cranes during the pre-fledged chick season and the post-fledged/no chick season in central Wisconsin during 1998, 2000, and 2001.

Land-use category	Pre-fledged chick season				Post-fledged/no chick season			
	Home range composition (%)		Telemetry locations (%)		Home range composition (%)		Telemetry locations (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Developed	3.5	1.1	2.0	0.9	5.4	1.3	3.1	1.0
Upland forest	8.8	1.7	6.2	2.1	12.5	1.9	6.1	2.0
Row crop	19.7	5.2	20.8	6.2	24.6	3.5	26.3	5.1
Short crop	6.2	2.4	6.2	2.4	11.1	2.8	20.5	5.4
Tall grass	6.9	1.9	4.6	2.0	6.2	1.6	4.6	1.8
Wetland	43.0	4.5	50.1	4.9	30.3	2.3	30.6	3.2

Table 6. Simplified ranking matrix for 12 breeding sandhill cranes over the entire season (Mar-Oct) based on comparing proportional habitat use within the home range with the proportions of total available habitat type in the entire study area, central Wisconsin, during 1998, 2000, and 2001. The disproportionate use of a habitat to its availability indicates an animal's preference or avoidance of that habitat. Each mean element in the matrix was replaced by its sign; a triple sign represents significant deviation from random at *P* < 0.05.

Habitat type	Habitat type								Rank
	DEV	UFOR	VC	RC	SC	TG	FW	WET	
Developed (DEV)		+	+	−	−	+	+	− − −	4
Upland forest (UFOR)	−		+	−	−	−	+	− − −	2
Vegetable crop (VC)	−	−		−	−	−	−	− − −	0
Row crop (RC)	+	+	+		+	+	+	− − −	6
Short crop (SC)	+	+	+	−		+	+	− − −	5
Tall grass (TG)	−	+	+	−	−		+	− − −	3
Forested wetland (FW)	−	−	+	−	−	−		− − −	1
Wetland (WET)	+++	+++	+++	+++	+++	+++	+++		7

was carried out on 6 habitat types available to all birds. Vegetable crop and WFOR were not considered because they did not occur in 50% and 25% of the home ranges, respectively. Both of these habitat categories also did not have a significant relationship with other categories and they were at the bottom of the ranking matrix. Habitat use within the fixed kernel home range was not random ($\lambda = 0.073$, $F_{7,12} = 15.22$, $P = 0.002$). At this scale, WET was ranked highest and was selected over all habitats ($P < 0.05$), and RC was ranked second highest and significantly different from the remaining rankings ($P < 0.05$).

Analysis of change in seasonal habitat selection was carried out on the same 6 habitat categories as the analysis of habitat selection within the home range over the entire breeding season (March-October). Habitat use within the kernel home range during the pre-fledging stage did not differ from random ($\lambda= 0.416$, $F_{5,12} = 1.97$, $P = 0.201$), whereas habitat use during the post-fledging stage approached significance ($\lambda= 0.2695$, $F_{5,12} = 3.79$, $P = 0.056$, Table 7). A ranking matrix was not created for the pre-fledge stage since overall the test for habitat use was not significant. We did explore the ranking matrix in the post-fledging stage and sequenced the habitat types as SC > WET > RC > TG > UFOR > DEV. The top 3 habitats, SC, WET, and RC were used more than the lowest 2 habitats, UFOR and DEV. There was no detectible difference in the use of the top 3 habitats, implying that the order of their assigned ranks was indistinguishable.

DISCUSSION

Central Wisconsin has one of the highest densities of breeding sandhill cranes in North America (Barzen et al. 2016), and this population is likely saturated with breeding birds (Hayes 2015). Individuals lost from breeding pairs are quickly replaced with adults from

Table 7. Simplified ranking matrix for habitat selection of 12 sandhill cranes during the post-fledged/no chick seasons based on comparing proportions of radio locations of each of the 12 radio-tracked sandhill cranes in each habitat type with the proportion of each habitat available within the animal's home range, central Wisconsin, 1998, 2000, and 2001. Each mean element in the matrix was replaced by its sign; a triple sign represents a significant deviation from random at *P* < 0.05.

Habitat type	Habitat type						Rank
	DEV	UFOR	RC	SC	TG	WET	
Developed (DEV)		−	− − −	− − −	−	− − −	0
Upland forest (UFOR)	+		− − −	−	−	− − −	1
Row crop (RC)	+++	+++		−	+	−	3
Short crop (SC)	+++	+	+		+	+	5
Tall grass (TG)	+	+	−	−		−	2
Wetland (WET)	+++	+++	+	−	+		4

local, non-breeding flocks without missing a breeding season (Hayes and Barzen 2006, Hayes 2015). Some nests are located as close as 11 meters apart and nest density of this population was 5.25 nests/km^2 of wetlands at the time of this study (Barzen et al. 2016). Thus most viable breeding territories were occupied, leaving little room for new territory establishment (Hayes 2015) and our habitat use estimates were not likely biased by the presence of unused, high-quality habitat.

In our study, the selection of habitats within the study area was not random. Breeding sandhill cranes selected wetland habitats over all other land-use categories, and upland habitat did not appear to influence the distribution of breeding pairs. These results support previous and current studies that concluded wetlands are the most important component of a breeding crane's territory (Safina 1993, Su 2003, Lacy et al. 2015). Unlike other studies, however, the analysis of habitat selection within the home range suggested that breeding cranes selected wetland habitat over all other habitat types but also selected row crops at this finer geographic scale. Daily use of wetland habitats within home ranges, however, suggests the importance of wetlands to breeding cranes even when upland habitats are also used and preferentially selected.

Though the importance of upland habitats for sandhill cranes is often mentioned (Melvin 1978, Armbruster 1987, Su 2003, Austin et al. 2007), before this study, selection for upland habitats has been quantitatively documented only in Florida for non-migratory breeding cranes and wetlands were used in proportion to their availability (Nesbitt and Williams 1990). On a daily basis, uplands were not used as regularly as were wetlands but they were still used with a high daily frequency (83.6%).

Breeding sandhill cranes are territorial (Walkinshaw 1949, Nesbitt and Williams 1990, Hayes 2015) and are behaviorally restricted by other territorial pairs to remain within their home range. Within the home range, however, territorial use (i.e., home range size) can vary throughout the breeding season and may change based on the needs of the pair. In our study the size of the home range during the pre-fledging stage was 3 times smaller than in the post-fledging stage/no chick stage (Table 3), and habitat use as shown in the telemetry data varied between these stages as well (Table 4). The mobility of family groups, as determined by the presence and developmental stage of the chick, and which changes over time, thus serves as an important modifier to habitat availability. During the pre-fledging stage, breeding pairs showed no selection for certain habitats, presumably because chicks were limited by how far they could travel between night roost areas and daytime foraging areas. Chick mortality is high during this pre-fledge stage (Littlefield et al. 2001; ICF, unpublished data). Post-fledging breeding cranes showed more selection for specific habitats since chicks could travel farther from the wetland and thus habitats no longer needed to be contiguous. The seasonal effect that Nesbitt and Williams (1990) demonstrated compared year-round resident pairs with pairs that left their territories after the breeding season, and so is not comparable to our results. Selection of habitats at the temporal scale that we examined was still weaker than selection over the entire breeding season.

This study supports the hypothesis that breeding sandhill cranes are dependent on wetlands as well as uplands that are adjacent to nesting and roosting habitat. Though the distribution of wetlands can limit the growth and expansion of the sandhill crane population in the Midwest, crane populations are likely to do best where they find an intermixing of wetland and upland habitat that is contiguous within 1 territory. Suitable upland habitat, in turn, appears to require low vegetation structure as upland forested areas ranked low in our selection matrices.

Breeding cranes return to the same home range (territory) over many years (Walkinshaw 1949, Hayes 2015). When breeding habitats are saturated with cranes, territory boundaries are restricted through behavioral interactions with adjacent breeding pairs who compete for similar resources. In areas where wetlands are adjacent to agriculture, land-use of uplands can vary widely year to year while territory boundaries remain relatively constant. The boundaries of a home range do not vary with the changing land-use because pairs need wetland for nesting (Hoffman 1983, Baker et al. 1995, Hayes 2015) and roosting (Iverson et al. 1987). This requirement constrains the extent to which selection for certain habitats can occur within a home range until birds can become more mobile and visit habitats that are not directly adjacent to the breeding wetland.

The longevity of territories makes selection for upland areas within the study area difficult to demonstrate under high-density nesting conditions. If upland habitats change greatly (e.g., switching from low crop to tall grass or shrub after an agricultural field is abandoned), breeding birds may show site fidelity to territories because there are no other open territories but reproductive productivity may decline as the quality of upland habitats decline (ICF, unpublished data). Though breeding productivity may change as the habitat converts from optimal to sub-optimal conditions (Cody 1985), bird use of the area may persist (Brown 1969, Brown and Orians 1970). This behavior results in significant lags between habitat change and crane habitat use in response to that change when the only alternative to maintaining the now sub-optimal territory is to join the non-territorial flock in which there is no opportunity to breed (Hayes and Barzen 2006). Several examples of this situation have occurred in this study area during the past 10 years (Hayes 2015).

Our data support Su's (2003) hypothesis that, though non-breeding cranes have greater mobility and show strong preference for specific upland habitats, they avoid upland habitats close to wetlands containing territorial birds. This segregation of resources is subtle but important to the manner in which 2 different social classes of cranes allocate resources among themselves within the same landscape.

With the knowledge that breeding cranes require emergent wet meadow wetlands (Hoffman 1983, Baker et al. 1995), we have a better understanding of the relationship between breeding cranes and their habitat requirements within both spatial and temporal scales. The results from our habitat selection analysis may help managers predict where and how crane-human interactions, such as crop damage, may occur in the future. In addition, a dependence on wetlands makes crane populations vulnerable to loss of wetland habitat, particularly where wetlands exist in agricultural-dominated landscapes. Since there is a lag effect between habitat loss and population response, it is important to monitor areas even where sandhill cranes are currently thriving.

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HIGH NEST DENSITY OF SANDHILL CRANES IN CENTRAL WISCONSIN

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Abstract: We conducted aerial surveys to determine nest locations of greater sandhill cranes (*Grus canadensis tabida*) in central Wisconsin, 2001-2003. Helicopter flights covered 8.90 km^2 of wetlands in each year, and we found 41 nests in 2001, 50 nests in 2002, and 48 nests in 2003 from 11 wetlands. Our best estimate of nest density ($n = 14$) included wetlands containing 5 or more nests and averaged 5.25 ± 0.36 (1 SE) nests/km^2 of wetland. Maximum nest density of larger wetlands in any 1 year was 7.80 nests/km^2. As some nests had likely failed by the time we completed our surveys, our measure of nest density likely under-estimated the total number of territories in each wetland. Minimum distances between nests averaged 222 ± 70 m (range 33-666 m) among all wetlands and 151 ± 41 m (range 33-571 m) for wetlands with 5 or more nests. Nest locations differed from a random distribution ($P < 0.05$) and were clustered within wetlands and within years. Nest locations were found more than expected in the wetland habitat type (Jacob's Index $D = 0.72$ in 2001, 0.66 in 2002 and 0.76 in 2003) and less than expected in open water, open shrub, and closed shrub. No nests were found in wetland forests. Crane nests also tended to occur on the outside margins of the wetlands. Nest density in central Wisconsin was greater than any previous estimate for any other crane population yet recorded and likely represents a breeding population at carrying capacity as well as a species that utilizes both upland and wetland habitats together.

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Key words: carrying capacity, eastern population, *Grus canadensis tabida*, habitat selection, territoriality.

Throughout North America, many populations of sandhill cranes (*Grus canadensis*) have recovered from population nadirs of the early 20th century (Meine and Archibald 1996). The Eastern Population (EP) of greater sandhill cranes (*G. c. tabida*) in Wisconsin was thought to have declined to as low as 25 breeding pairs (Henika 1936) and was lamented by Leopold (1966) as being on the brink of extirpation. Low densities of isolated breeding pairs occurred in very large, isolated wetlands (Henika 1936, Meine 2004), and this early description of nesting habitat has persisted. It was not until the 1970s that biologists began to describe a recovering sandhill crane population in Wisconsin (Hunt and Gluesing 1976, Howard 1977, Bennett 1978). Since then, the EP in Wisconsin has increased dramatically (Harris and Knoop 1987, Windsor 1990, Dietzman and Swengel 1994, Su et al. 2004, Lacy et al. 2015). Now, a different question arises: What is the limit of crane nesting territories that a wetland can hold?

Current studies suggest that sandhill cranes are strongly wetland dependent during their breeding season, utilizing wetlands both to place their nests and to roost at night while often foraging in uplands during the day (Walkinshaw 1973*a*, Melvin 1978, Hoffman 1983, Herr and Queen 1993, Su 2003, Miller and Barzen 2016). In turn, nest and fledging success of sandhill cranes has depended upon hydrologic characteristics and land management activities (e.g., predator control, prescribed burning, grazing, row-cropping) that occur in wetlands (Littlefield and Paullin 1990, Austin et al. 2007, Ivey and Dugger 2008) or adjacent uplands. Finally, sandhill cranes are large territorial birds that utilize the same territory perennially (Walkinshaw 1965, Drewien 1973, Hayes 2015) and this behavior might further constrain how many nesting crane pairs can utilize any single wetland (Brown 1969, Brown and Orians 1970, Maher and Lott 2000). Territorial cranes exclude non-territorial cranes from nesting areas of wetlands but not from night roosting areas of the same wetlands (Su 2003).

Measuring nest densities in populations that may be at or near carrying capacity (Hayes 2015) helps to elucidate maximum nest densities and formulate hypotheses on factors that limit the abundance of nests in any 1 wetland. Specifically, our objectives here were to: 1) describe nesting density of sandhill cranes in central Wisconsin, 2) explore environmental correlates

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with nest density, and 3) compare sandhill crane nest density in our population with other crane populations.

STUDY AREA

Our study area was located near Briggsville, Wisconsin, where Marquette, Columbia, and Adams counties meet (Figure 1). The study area for our long-term research project was 98 km^2 and located in areas created by recessional moraines and inter-moraine low areas (Martin 1965, Devaul and Green 1971). Farmland (about 60%) mixes with scattered wetlands (about 20%) predominantly in the low areas, and patches of forest (about 20%) occur mostly on the moraines. This study area is known for its high number of territorial and non-territorial cranes (Harris and Knoop 1987, Dietzman and Swengel 1994, Su 2003, Hayes 2015).

Our study focused only on a subset of wetlands within this larger long-term study area. Among 3 years we surveyed 24 wetlands totaling 20 km^2 but only 11 wetlands were surveyed consistently in all 3 years (Figure 1). Except where noted, we restricted our analysis to these 11 wetlands.

METHODS

Aerial Nest Surveys

Crane nest searches occurred 2-3 May 2001, 25-26 April 2002, and 23-24 April 2003. A team consisting

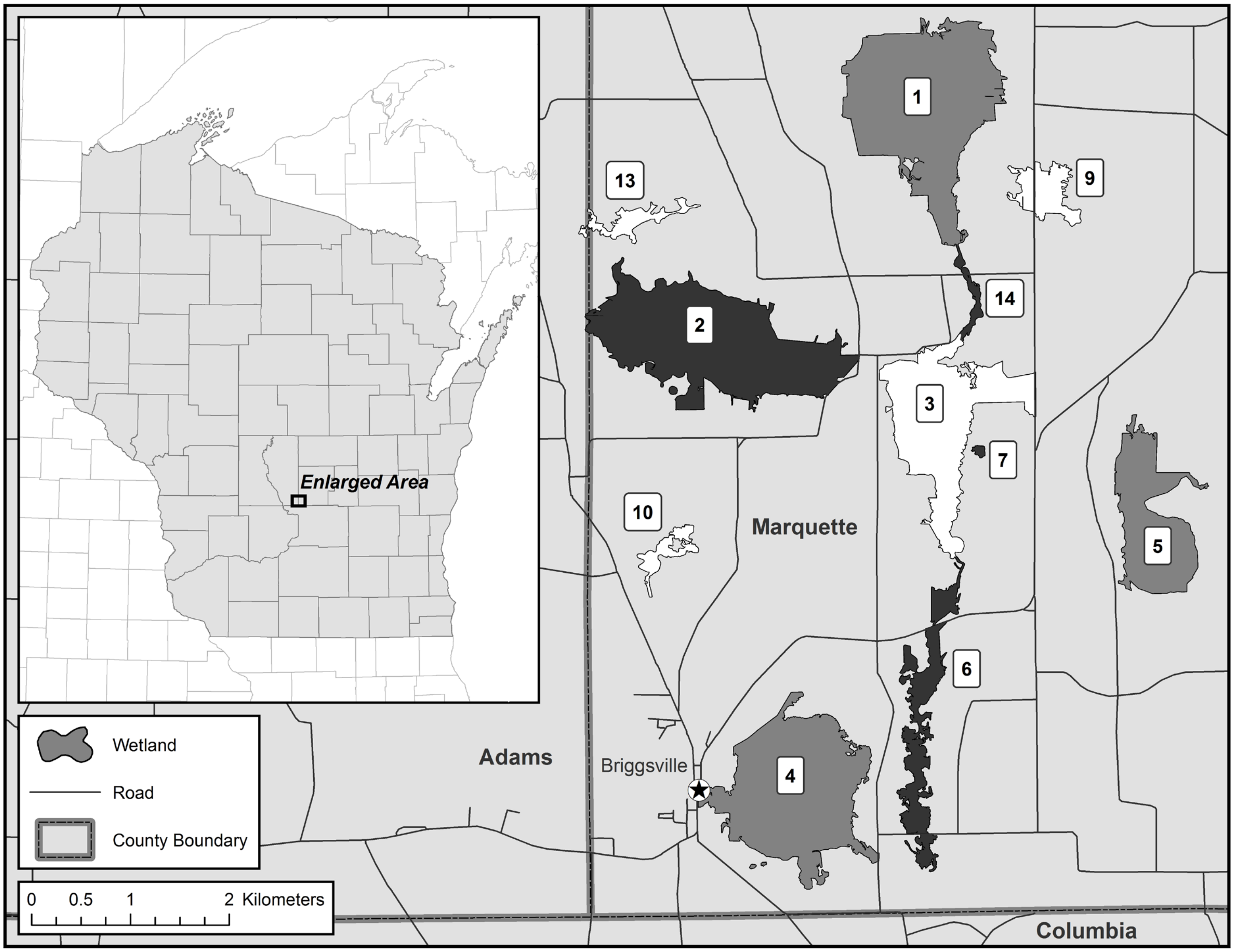

Figure 1. Locations of 11 wetlands surveyed for sandhill crane nest locations near Briggsville, Wisconsin, 2001-2003. Numbers denote wetland identifiers used throughout the text.

of pilot, videographer, mission coordinator, and 4 observers flew in a Bell 206 helicopter at an altitude of 175 m above the ground with transects spaced 100 m apart and running lengthwise over all wetlands. Flight speeds were 10 km/hr while nest searching. Once a nest was spotted, we took video images of each nest to verify whether it was active and to record habitat composition surrounding the nest. Only data for nests containing 1 or 2 whole eggs and having an adult flushing from, or guarding, a nest were presented here. Nests destroyed by predators prior to our flight were seen but were not included. GPS coordinates of nests were plotted on the air-photos with 1-m resolution.

Calculation of Nest Density

Even though sandhill crane territories in Wisconsin usually include both upland and wetland habitats (Miller and Barzen 2016), most nest sites occur in wetlands alone (Bennett 1978, Miller and Barzen 2016). We calculated nest density by dividing the number of nests found in each wetland complex by the area (km^2) of the wetland surveyed. Upland habitats were not included in these estimates even if they were located within territories.

Statistical Analysis of Spatial Patterns for Nest Locations

We used the G-test analysis in R (R Development Core Team 2014) to compare point-to-point nearest neighbor distances from nest locations to random points (Mohan and Tobias 2015), resulting in a complete partial randomness process (Kaluzny et al. 1996). Each location of a crane nest was considered as 1 point. Each wetland was defined as a specific region with the boundary being the outline of the entire wetland area. We did 100 simulations for each data set (where more than 5 nests were found) for each wetland and plotted simulation envelopes to compare $\hat{g}$ values of the crane data. These envelopes gave 98% confidence intervals ($\alpha = 0.02$) of $\hat{g}$ values for the crane data. This test qualitatively indicates whether the distribution pattern of the crane nest locations in wetlands conforms to random, regular, or clustered distributions (Mohan and Tobias 2015) and quantitatively tests whether distributions differ significantly from the random model. Levels of significance were set at $P < 0.05$.

Once the patterns of spatial distribution for nests were described, we quantitatively explored 2 factors that may have created the distribution of nests found. First, we examined nest site selection to see if nest distribution was influenced by the distribution of habitat types found within the wetlands. Wetland habitat types were interpreted from a geo-registered 1995 aerial photo with 1-m resolution and were digitized. Habitat types considered were: 1) open water or ditches (wetland areas containing no vegetation or only submerged aquatic macrophytes), 2) wetland (inundated areas dominated by emergent, non-woody wetland vegetation), 3) wetland shrub open (inundated areas where wetland shrubs had a dominant cover but emergent vegetation could still be seen between patches of shrub), 4) wetland shrub closed (inundated areas where only wetland shrubs could be seen in the aerial photo, and 5) wetland forest (inundated areas containing closed tree canopy). Once digitized, habitat types were verified through ground surveys. Although in each year the area covered by water varied slightly due to variation in the water budget, we assumed that the wetland boundaries and wetland habitat types did not change over the period of this study because dominant wetland vegetation is mostly composed of perennial species (Fassett 1940). The habitat type that each nest was located in was determined by estimating the dominant habitat type within a 5-m radius of each located nest.

Habitat selection was quantified with Jacob's Index: $D = (r - p)/(r + p - 2rp)$, where r was the proportion of a given habitat class that each nest was located in and p was the proportion of this habitat available within the studied wetlands. Following the definition of Aarts et al. (2008), we refer to habitats receiving more usage than expected by availability (taking into account accessibility) as "preferred" and areas receiving less as "avoided." A Jacob's Index value of 1 indicated complete preference and −1 indicated complete avoidance (Jacobs 1974).

Second, territorial behavior of sandhill cranes (Hayes 2015) suggests that nest locations within a territory, replicated over 3 years, might well be clumped. We used 2 GIS techniques to examine this behavioral influence on nest distribution. We overlaid nest locations from all 3-year surveys on classified digital land cover maps. Linear distance between nests in each wetland was measured to compare how close nests were likely to be located to each other in different wetlands but within the same year and how consistent nest location was between years. Closest nests for each wetland within a year was a simple calculation of linear distance between nest locations for each wetland.

To calculate the frequency of nests located near other nests for each wetland and within each year, we used a spatial consistency index (SCI) to measure the spatial consistency pattern of nest locations in a wetland where SCI = $1/M \sum (n_t . w_t)$. Here:

M = mean number of nests found in a wetland over the years of this study.

t = consecutive years: 3, 2 (if the study was longer than 4 years, T, T-1, T-2, … 2. T = total years of surveys in a wetland).

n_t = number of nest locations found in t consecutive years on approximately the same site. We analyzed the spatial consistency of the nest locations at 2 different proximity scales, (within) 50-m and 150-m radius.

w_t = weighted index for consecutive year t, $w_t = t/T$.

SCI values were regressed against nest density for the same wetland using least squared regression (Sokal and Rohlf 1981) to see if SCI increased as nest density increased.

RESULTS

Nest Density

The 11 wetlands surveyed in 2001-2003 varied in size from 0.006 km^2 to 2.05 km^2, collectively totaling 8.90 km^2, and were situated close to each other (Figure 1). In total, we counted 65 nests in 2001, 74 nests in 2002, and 63 nests in 2003 in the 24 wetlands of the area, but we considered 42 nests located in 2001, 51 nests located in 2002, and 48 nests located in 2003 that were found in the same 11 wetlands surveyed in all 3 years (Table 1). Only wetland 14 had no nests located in it during any of the 3 years of the study.

Nest density was calculated for each wetland complex and varied by the size of wetland in which cranes nested as well as from year to year (Table 1). Overall mean density (± 1 SE) of the 3 years was 11.55 ± 5.22 nests/km^2 of wetland and ranged from 2.40 to 103.1 nests/km^2 for all wetlands. Compared to all 11 wetlands, nest density in wetlands 1-5, in years that contained 5 or more nests, averaged 5.25 ± 0.36 nests/km^2 and reflected a more precise measure of density. Maximum nest density found in wetlands 1-5 for any of the 3 years was 7.80 nests/km^2 when 16 nests were located in wetland 2 (2.05 km^2), the largest wetland of the 11 that we studied.

Spatial Patterns of Nests

The distribution of nests in all 11 wetlands, surveyed for all 3 years combined, was clustered (Figure 2). Only wetlands 1-5 contained a sufficient number of nests to test further. Within each of these 5 wetlands, distributions of nests differed significantly from random when all 3 years were combined and for each year when data from all 5 wetlands were combined (Table 2). Nest distribution for each of the 5 wetlands in each of 3 years, however, did not differ from random. Still,

Table 1. Number and density of sandhill crane nests observed in wetland habitat from 11 surveyed wetlands near Briggsville, Wisconsin, 2001-2003.

Wetland ID[a]	Area (km^2)	2001		2002		2003		Mean nests/km^2	SE
		Nests/km^2	No. nests	Nests/km^2	No. nests	Nests/km^2	No. nests		
14	0.006	0	0	0	0	0	0	0	0
7	0.009	0	0	103.10	1	103.10	1	68.73	34.36
10	0.103	9.50	1	28.40	3	28.40	3	22.10	6.30
13	0.123	8.10	1	0.00	0	8.10	1	5.40	2.70
9	0.231	4.30	1	0.00	0	8.60	2	4.30	2.48
6	0.473	0.00	0	3.80	2	0.00	0	1.27	1.26
5	0.877	2.28	2	6.80	6	5.70	5	4.93	1.36
3	1.256	4.70	6	3.98	5	5.40	7	4.69	0.41
4	1.754	5.10	9	6.20	11	4.00	7	5.10	0.64
2	2.047	7.80	16	4.90	10	6.30	13	6.33	0.84
1	2.015	2.40	5	5.80	12	4.40	9	4.20	0.99
Total	8.895	4.02	41	14.82	50	15.82	48	11.55	5.22

[a] See Figure 1 for wetland locations.

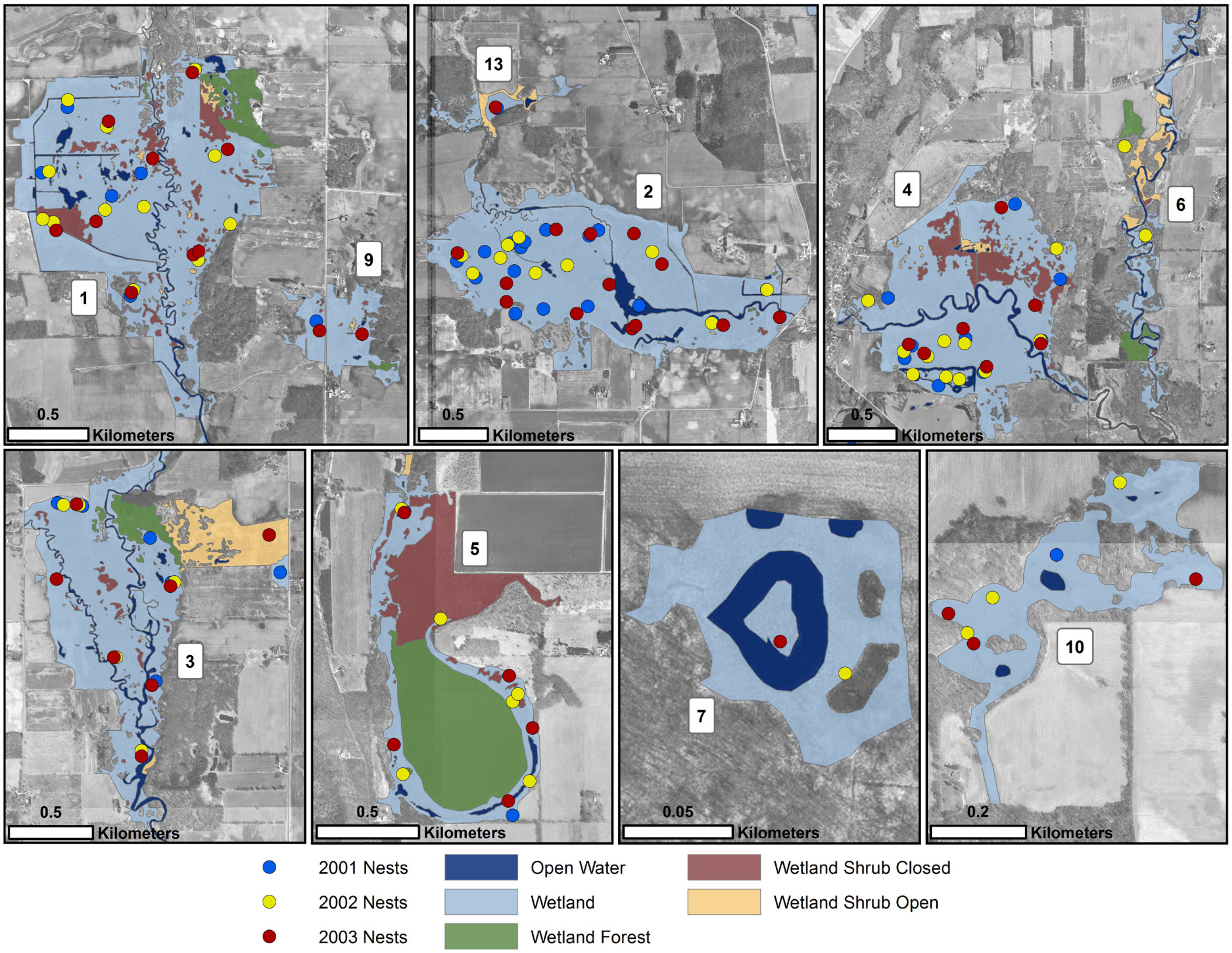

Figure 2. Habitat types and sandhill crane nest locations for each of the 11 wetlands surveyed near Briggsville, Wisconsin, 2001-2003. Nest locations vary by color for each of the 3 years studied while habitat types are denoted by color but did not change in each of the 3 years. Note that the spatial scale depicted was the same for all wetlands except wetlands 7 and 10.

qualitative evidence of patterning was seen for some of the 5 wetlands in each year. Spatial point pattern analysis for these 5 individual wetlands also showed greater variation in spatial distribution of nests at different spatial scales among some years. For example, during 2001, the nest distribution pattern in wetland 2 was clustered at small scale and was regular at a large scale whereas the reverse was true for wetland 1. Spatial patterning in wetlands 3-5 varied among years.

Given the non-random distribution of nests, what factors influenced this distribution? First, Jacob's Index described extensive preference for nests to be located in wetlands and avoidance of open water, open shrub, and closed shrub habitat types. No nests were located in forested wetland areas (Table 3). Not all wetlands contained all habitat types, but both the wetland habitat type (76% of all wetlands) and open water habitat type (6.46% of all wetlands) did occur in all wetlands (Table 4).

Yet even for the larger wetlands of this study (wetlands 1-5), clumping of nests occurred even within wetland habitat types. Some of the nests from different territorial pairs were separated by as little as 33 m (Table 5), and the mean minimum distance between nests among all 11 wetlands was 222 ± 70 m while among the 5 largest wetlands (wetlands 1-5) the mean minimum distance between nests was 151 ± 41 m. Among all 24 wetlands surveyed, the minimum distance between 2 active nests was 11 m. Wetland 2, the largest of 11

Table 2. G-test results[a] for 5 wetlands near Briggsville, Wisconsin, 2001-2003. Pattern is the qualitative description of nest distribution (random, cluster or regular[b]) while distance denotes the scale at which that pattern occurs. It is possible to have 2 patterns of nest distribution occur in the same wetland but at different spatial scales.

Wetland ID	2001		2002		2003		All years combined
	Pattern	Distance[c]	Pattern	Distance	Pattern	Distance	
1	regular cluster	<100 >100	regular		random cluster	<120 >120	cluster
2	cluster regular	<150 >150	cluster regular	<100 >100	very close to random		cluster
3	regular		random		regular		cluster
4	very close to random		cluster regular	<300 >300	very close to random		cluster
5	regular		cluster regular	<180 >180	regular to random		cluster
All wetlands combined	cluster		cluster		cluster		cluster

[a] All tests for each wetland, within a year, did not differ significantly from random. When data were combined by year or by wetland, nest locations significantly differed from random and were clustered in their distribution.

[b] A regular pattern describes nest locations that are equidistant from each other.

[c] Units of distance are measured in meters.

wetlands studied, had the lowest minimum distance between nests (61 m).

Maximum SCI values ranged from 0 to 1 and a low number would reflect a random distribution of nests while a high number would reflect a clumped distribution among years. We expected to find a clumped distribution of nests because territories are shaped to include both wetlands and uplands, so the wetland portion, where nests would be located, is relatively smaller. We compared each individual nest with a radius of 50 m and 150 m to see how likely it was to have another nest located within the chosen radius in different years. When using a 50-m radius, the mean SCI was 0.27 (Table 6). This increased to a mean of 0.51 when a 150-m radius was used. When SCI using a 150-m radius was compared to nest density using regression, however, there was no relationship (H_0: Slope = 0, $F = 2.18$, $P = 0.19$).

DISCUSSION

Interpreting Nest Density

Nest densities for the 11 wetlands in the Briggsville area varied from 2.3 to 103.1 nests/km^2, with smaller wetlands having a larger range in density estimates than larger wetlands (Table 1). The smallest wetland containing a nest was 0.9 ha which, when compared to mean territory size of 285 ha for 12 cranes in this area (Miller and Barzen 2016), suggests that, though wetlands may be important for nest location and night roosting (Su 2003), wetlands can comprise a small portion of the overall territory composition of sandhill cranes. Thus, a few nests in small wetlands can skew nest density estimates upward because our estimate of density is based on the number of nests found per unit area of wetland habitat only. A more biologically meaningful measure of density would include the number of territorial pairs per region that encompasses all territories within the study area (which includes upland components of territories if they exist). This estimate, however, cannot be procured without having individually marked birds because home ranges of non-territorial and territorial cranes in summer overlap, especially in wetlands (Su 2003, Hayes 2015). Though several studies have estimated the number of territorial crane pairs in summer (e.g., Hoffman 1983, Austin et al. 2007, Ivey and Dugger 2008), they did not estimate territory size per pair because they did not have enough marked

Table 3. Values for Jacob's Index, $D = (r-p)/(r+p-2rp)$, to measure selection (range –1 to 1) within each habitat type for all 11 wetlands combined, within each year surveyed, near Briggsville, Wisconsin, 2001-2003. The number of nests found refers to the dominant habitat type within a 5-m radius of the nest location.

Habitat type	Number of nests found			*r*			*p*[a]	Jacob's index (*D*)		
	2001	2002	2003	2001	2002	-.07	2001-2003	2001	2002	2003
Open water	1	0	1	0.02	0	0.02	0.06	−0.47	−1	−0.53
Wetland	39	47	46	0.95	0.94	0.96	0.76	0.72	0.66	0.76
Wetland forest	0	0	0	0	0	0	0.07	−1	−1	−1
Shrub closed	1	3	0	0.02	0.06	0	0.07	−0.50	−0.08	−1
Shrub open	0	0	1	0	0	0.02	0.04	−1	−1	−0.30
Total	41	50	48							

[a] The proportion of habitat types was assumed constant for the 3 years of the study.

birds to observe, especially using the same nesting wetlands.

Our estimate of nest density was most accurate and precise when we used the number of nests per area of wetland habitat in larger wetlands that contained at least 5 nests. With larger wetlands our estimate of nest density averaged 5.25 ± 0.36 nests/km^2. The highest density we encountered was in wetland 2, where 16 nests were found in 2001 (7.80 nests/km^2). Our surveys, conducted late in the initial nesting phase of the population (International Crane Foundation [ICF], unpublished data), likely missed some nests that had been lost during incubation before we searched, so we likely under-estimated nest density.

In Wisconsin the highest density of cranes in summer is concentrated in the central sand counties of which our study area is a part (Harris and Knoop 1987, Dietzman and Swengel 1994, Su et al. 2004). For the entire EP, Wisconsin hosts approximately two-thirds of the birds in summer (Lacy et al. 2015). Our estimate of crane nesting density likely reflects a maximum for the population.

Compared to historical densities, the density of breeding cranes in Wisconsin has recovered rapidly to a saturation point early in the 21st century (Su et al. 2004). The change in nesting density occurred primarily in the 1970s within our study area. For example, only 1 breeding territory occurred in wetland 4 (Figure 2) during 1973 (G. Archibald, personal communication) and 2 territories in 1976 (Bennett 1978; A. Bennett, personal communication), but in 2002, 11 nests were found (Table 1). As of 2015, this density has not changed (ICF, unpublished data).

Early studies on sandhill crane nesting habitat reported a preference for large open wetlands with shallow water and emergent plants (Walkinshaw 1973*b*), far from human

Table 4. Area (km^2) and percentage of area (%) of habitat types for each wetland studied near Briggsville, Wisconsin, 2001-2003.

Wetland ID	Open water		Wetland		Wetland forest		Shrub closed		Shrub open		Total (100%)
	Area	%	Area	%	Area	%	Area	%	Area	%	Area
1	0.118	5.8	1.624	80.6	0.099	4.9	0.157	7.8	0.018	0.9	2.015
2	0.128	6.2	1.911	93.4	0.003	0.1	0.005	0.2	0.001	0.0	2.047
3	0.094	7.5	0.879	70.0	0.067	5.4	0.025	2.0	0.192	15.2	1.256
4	0.107	6.1	1.429	81.5			0.198	11.3	0.020	1.1	1.753
5	0.016	1.8	0.258	29.4	0.364	41.5	0.237	27.0	0.003	0.4	0.877
6	0.084	17.8	0.248	52.5	0.062	13.0	0.005	1.1	0.074	15.6	0.473
7	0.002	23.5	0.007	76.5							0.009
9	0.002	1.1	0.218	94.0	0.006	2.7	0.004	1.6	0.002	0.7	0.231
10	0.003	2.5	0.101	97.5							0.103
13	0.008	6.3	0.085	68.7			0.000	0.3	0.030	24.7	0.123
14	0.017	29.6	0.041	70.4							0.058
Total	0.578	6.5	6.800	76.0	0.601	6.7	0.629	7.0	0.339	3.8	8.946

Table 5. Distances between the 2 closest nests within 11 surveyed wetlands near Briggsville, Wisconsin, 2001-2003. Only wetlands containing 2 or more nests are listed.

Wetland ID	Area (km^2)	Shortest distance (m)			
		2001	2002	2003	Mean
1	2.02	231	70	39	113
2	2.05	53	98	33	61
4	1.75	105	97	131	111
3	1.26	147	93	279	173
5	0.88	571	45	280	299
6	0.47	NA[a]	666	NA	666
9	0.23	NA	NA	267	267
10	0.10	NA	92	85	89
All wetlands			Mean		222
			SE		70
Wetlands 1-5			Mean		151
			SE		41

[a] NA = Not applicable, fewer than 2 nests were found that year.

Table 6. Proportion of adjacent nests that were located within a 50-m or 100-m radius of an individual nest (Spatial Consistency Index [SCI]) near Briggsville, Wisconsin, 2001-2003. Only wetlands containing at least 2 sandhill crane nests from within 1 year were used (see Figure 2).

Wetland ID	SCI	
	50 m	150 m
10	0.21	0.86
9	0.00	0.00
6	0.00	0.00
5	0.32	0.86
3	0.63	0.63
4	0.38	0.70
2	0.23	0.42
1	0.40	0.63
Mean	0.27	0.51

disturbance (Drewien 1973, Gluesing 1974). In contrast, sandhill cranes in our study nested in a broad range of wetland sizes (Table 1), as well as in wetlands with divergent habitat types and proportions (Table 4). Sandhill cranes have now occupied a wide variety of wetland-based territories as the population density has increased.

Environmental and Behavioral Influences on Nest Density

Wetlands at all spatial scales form an important component of habitat for territorial sandhill cranes in Wisconsin (Su 2003), and territorial sandhill cranes utilize both upland and wetland components of their territory on a daily basis during summer (Miller and Barzen 2016) as do non-territorial cranes (Su 2003, Hayes 2015). The strong preference for emergent vegetation in open wetlands (the wetland habitat type) for nest locations occurred in Wisconsin and taller vegetation such as trees and shrubs were avoided, as was open water. Similar results were found for greater sandhill cranes in northern Minnesota (Provost et al. 1992, Herr and Queen 1993). Structure of wetland vegetation also influenced nest success in Oregon (Littlefield and Paullin 1990, Ivey and Dugger 2008) as did hydrologic conditions (Austin et al. 2007, Ivey and Dugger 2008), so the preferred habitat likely links strongly with reproductive potential. Where wetlands contained substantial portions of non-preferred habitat, nest locations appeared to be strongly influenced by the distribution of habitat types (Table 4, Figure 2). Wetlands 4 and 5 presented the most striking examples of the influence that vegetation type may have on the distribution of nests.

In addition to habitat selection other behavioral responses by cranes may influence the distribution of crane nests. High SCI values for nest sites being located within 150 m of other nests in our study area (Table 6) suggest other factors may be important. Three conditions for cranes exhibiting a high SCI value in a wetland were met in our study area: 1) pairs returned to the same territory year after year (Hayes 2015), 2) cranes selected the same features for nest sites, presumably the most suitable sites available for nests, each year (Table 3), and 3) habitat features (quality) changed slowly among years (ICF, unpublished data).

Conditions for a high SCI existed in other studies as well. Sandhill cranes have demonstrated strong fidelity for using the same breeding territory each year (Drewien 1973, Walkinshaw 1973*b*, 1989). Walkinshaw (1973*b*, 1989) documented 8 pairs of greater sandhill cranes returning to the same territories and nesting in similar places each year (a few even used old nests) at 3 locations over a period of 13-28 years in Michigan.

Our high SCI values may also have been influenced by the need of sandhill cranes to have both wetland and upland habitats in their territory (Su 2003, Miller and Barzen 2016). Home range size when chicks were flightless was smaller than after chicks attained flight (Miller and Barzen 2016). Flightless chicks must walk between wetland sites and upland sites on a daily basis, which would make nesting toward the outer edge of wetlands advantageous because paths of 1 family group would not cross territories of another family when moving between wetland and upland. Evidence of nesting toward the perimeter of wetlands, independent of habitat patterns, can be seen in the larger wetlands 2, 3, and 4. Though nest distribution in wetland 5 was also strongly orientated toward the wetland perimeter, this likely was due to the distribution of wetland forest (an avoided habitat type).

Littlefield (1976) detected a negative correlation between population density and size of territory among cranes species. Both Maher and Lott (2000) as well as Adams (2001) reviewed studies on territoriality in a variety of taxa and concluded that territory size reflected pressure from adjacent territorial animals, aggressiveness of territorial holders, food abundance, and habitat quality.

With the marked increase in nesting density over the past 40 years, territory size has decreased in Briggsville. Currently, crane territories spatially, but not temporally, overlap one another in our study area (ICF, unpublished data). Now, minimum distance between nests averages 151 m in large wetlands and, when using a radius of 150 m, the SCI for nesting cranes is above 50%, meaning that a majority of nests can be found within 150 m of each other. In general, the territory provides necessary resources for survival and reproductive needs of the territorial birds (Maher and Lott 2000). Presumably, these resources are finite and, at some point become limiting to the population (Adams 2001), especially since non-territorial sandhill cranes do not reproduce (Hayes 2015). Further research is needed to understand the relationships among territoriality, resource characteristics, and breeding success.

Comparison to Other Populations and Species

Maximum densities of territorial greater sandhill cranes have varied across their geographic range in North America (Table 7). In the EP, the Upper Peninsula of Michigan reported the lowest density of 0.43 territories/km^2 (Urbanek and Bookhout 1992) while the Prairie Population had the lowest density of nests (0.25 nests/km^2) reported in northwestern Minnesota (Provost et al. 1992). In contrast, the density of territories in southern Michigan was as high as 4.04 territories/km^2 (Hoffman 1983) and maximum nest density in Wisconsin (7.80 nests/km^2) was almost twice that of Michigan. Density of territorial birds in the Rocky Mountain Population at Grays Lake was comparable to our average (Austin et al. 2007) and higher than that of greater sandhill cranes in the Central Valley Population nesting in Oregon.

Other crane species have experienced strong population recovery after reaching nadirs in the 20th century and may now be approaching or at carrying capacity as well. Though the autecology of other crane species differs from sandhill cranes, the carrying capacity for most species is as yet unknown and maximum nest densities among different species may provide clues regarding the importance of nesting habitat types. The non-migratory population of the red-crowned crane (*G. japonensis*) in Hokkaido, Japan, for example, has reached a maximum density of 1.46 territories/km^2 of wetland (called 'moor' in Masatomi et al. 2007) in the Lake Furen region. Red-crowned cranes are likely more wetland dependent (Masatomi et al. 2007) than are sandhill cranes (Miller and Barzen 2016) and might require more wetland habitat in each territory as a result. Mean distances between nests was 1.72 km at Lake Furen as opposed to a mean of 0.151 km for large wetlands in our study. Likewise, the mean home range size for 13 pairs of whooping cranes (*G. americana*), another species likely more dependent on wetlands than sandhill cranes, was 4.1 km^2 per pair (Kuyt 1993) or 0.24 pairs/km^2. This population of whooping cranes is likely not yet at carrying capacity.

In contrast, the highest density of Eurasian cranes (*G. grus*) in Germany was measured in the Mecklenberg-Western Pomarania region at 39 nesting pairs/100 km^2 (Mewes and Rauch 2012) while Sundar (2009), who used a similar measure for Indian sarus cranes (*G. antigone antigone*), found 0.91 territorial pairs/km^2 (91 pairs/100 km^2). Both Eurasian cranes (Mewes and Rauch 2012) and sarus cranes (Sundar 2009) utilize upland and wetland habitats as do sandhill cranes. Density estimates for both of these species included upland and wetland habitats in their estimates, but the total areas of territories were not clearly defined so they are difficult to compare to our estimate. We believe it likely that the more wetland-dependent a species is, the lower will be the maximum nest density per area of wetland.

Rosenzweig (1991) hypothesized that habitat selection would erode for a single species under a high population density. By studying single species and species co-existing with other closely related

Table 7. Annual maximum nest density measured in crane populations worldwide. This measurement takes the number of nests (not counting renests) or the number of territorial (sometimes called 'breeding') pairs and divides this by the area of habitat in which nests were found. For most species listed, this habitat is wetland habitat even though territories occur in both upland and wetland environs.

Population	Sub-population	Year	Wetland size (km^2)	Max. no. nests	Max. no. territorial pairs	Nest density (nests/km^2)[a]	Territory density (pairs/km^2)[a]	Reference
Sandhill crane								
Eastern	Central Wis.	2001-2003	8.1	40.3		5.25		This study
Eastern	Central Wis.	2001	2.1	16		7.80[b]		This study
Eastern	Seney NWR[c], Mich.	1987	116.0		50		0.43[d]	Urbanek and Bookhout 1992
Eastern	Waterloo Township, Mich.	1982	8.2		33		3.0 (4.04)[e]	Hoffman 1983
Rocky Mountain	Grays Lake NWR, Id.	1998-2000	52.6	228	256	4.33	4.87	Austin et al. 2007
Central Valley	Sycan Marsh, Oreg.	1982-1984	93.0		126		1.35	Stern et al. 1987
Central Valley	Malheur NWR, Oreg.	1977	122.0		236		1.93	Littlefield 1995
Central Valley	Malheur NWR, Oreg.	1991	122.0[f]		245		2.01	Ivey and Dugger 2008
Prairie	Roseau River WMA[g], Minn.	1989-1991	111.4	28	51	0.25	0.46	Provost et al. 1992[h]
Whooping crane								
Aransas-Wood Buffalo	Wood Buffalo National Park	1991			13		0.24[i]	Kuyt 1993
Red-crowned crane								
Non-migratory	Hokkaido, Japan	2002	327.3		290		0.88[j]	Masatomi et al. 2007
Non-migratory	Hokkaido, Japan	2002	47.9		70		1.46[k]	Masatomi et al. 2007

[a] Density is per km^2 of wetland unless indicated otherwise.

[b] Includes 16 nests found on 1 day in 1 wetland and represents the maximum estimate found.

[c] NWR = National Wildlife Refuge.

[d] Study area consisted of both upland and wetland areas but was approximately two-thirds wetlands.

[e] Hoffman reported 3.0 pairs/km^2, but the 33 pairs he surveyed in 1982 on 8.16 km^2 of non-forested wetlands = 4.04 pairs/km^2.

[f] No wetland area was given in Ivey and Dugger (2008), so estimate of wetland area from Littlefield (1995) for the same wetland area was used.

[g] WMA = Wildlife Management Area.

[h] Study area consisted of both upland and wetlands but was 85% wetlands.

[i] Kuyt (1993) listed mean size of home ranges for 13 nesting pairs in the core breeding area as 4.1 km^2. The reciprocal of this is 0.25 home ranges/km^2, the equivalent of the number of indicated pairs per km^2.

[j] Total number of breeding (territorial) pairs/area of wetlands from all 7 regions studied.

[k] Number of breeding (territorial) pairs/area at the most densely populated wetland region (Lake Furen).

species, Holmes (1961) and Diamond (1978) illustrated that species typically widen their niches under lack of inter-specific competition and increasing intra-specific competition. Under the theory of Ideal Free Distribution, high-quality habitats (territories here) will be occupied before low-quality habitats (Fretwell 1972) and, with territorial species, once all available territories are filled, some sexually mature birds will be unable to breed because they cannot find appropriate territories (Brown 1969). Sandhill cranes have populations of sexually mature, non-territorial cranes that co-mingle with territorial cranes (Su 2003, Hayes 2015) and nest in the highest known density of any crane species. Within our study area the rate of mate switching is high and reproductive rates are depressed for 2-3 years following mate switches (Hayes 2015). This feedback may provide 1 mechanism that drives density-dependent population dynamics (e.g., Sibly et al. 2005). Crane species that are more wetland dependent may be constrained further by habitat requirements and may, therefore, have lower maximum nest densities than do crane species that establish territories in more upland areas as well as wetlands. If our hypothesis is correct, more research is needed to understand this important parameter of population change.

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DIFFERENTIAL DETECTION OF TERRITORIAL AND NON-TERRITORIAL GREATER SANDHILL CRANES IN SUMMER

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Abstract: Abundance estimates allow wildlife managers to make informed management decisions, but differential detectability of individuals can lead to biased estimates of abundance. Our objective was to quantify detectability for non-territorial and territorial sandhill cranes (*Grus canadensis tabida*) during summer. We hypothesized that territorial sandhill cranes would be detected more often than non-territorial cranes. In 2009, 3 wetland areas were surveyed 2 days per week during the nesting season near Briggsville, Wisconsin. We created capture histories for color-marked territorial ($n = 52$) and color-marked non-territorial cranes ($n = 23$) and used the Huggins closed capture model in program MARK to estimate detection probability and abundance for each group. *A priori* models were developed that explained daily crane detection over the sampling period using distance from road, territorial status, observation event, and time of season as variables. The best approximating model included the variables territorial status and observation event (AIC_c weight = 0.92). Probability of detection was higher for territorial (0.11, 95% CI = 0.08-0.14) than for non-territorial (0.03, 95% CI = 0.01-0.07) sandhill cranes. In subsequent observation events, detection probability almost doubled to 0.18 (95% CI = 0.17-0.20) for territorial cranes, and almost tripled to 0.11 (95% CI = 0.09-0.14) for non-territorial cranes. Potential reasons for differential detection during subsequent observations include differing degrees of movement by birds and/or an observer effect in which the ability to observe birds or the perception by technicians of birds increased over time.

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Key words: *Grus canadensis tabida*, population size, sandhill crane, territorial status, Wisconsin.

Populations of greater sandhill cranes (*Grus canadensis tabida*) declined significantly in the early twentieth century (Henika 1936, Johnsgard 1983) but have recently recovered (Kruse et al. 2013). Currently, the eastern population (EP) of greater sandhill cranes is monitored by counts of all individual cranes seen during migration, and the raw counts are thought to serve as an index of true abundance (Kruse et al. 2010). Raw counts have been scrutinized by researchers because they do not account for changes in detection probability through time (Lancia et al. 2005, Giudice et al. 2013). Methods that attempt to account for detection probability, however, may be biased due to heterogeneous detection probabilities between individuals or groups within a species (Link 2003). A difference in movement patterns between territorial and non-territorial cranes in summer or between family groups and non-family groups in winter for example, may cause differences in detection probability which could make a population estimate less representative of true abundance. The U.S. Fish and Wildlife Service has recognized the disadvantages of raw counts and emphasized identifying reliable means of counting and monitoring the EP of greater sandhill cranes during migration (Kruse et al. 2010) and the remnant population of whooping cranes (*Grus americana*) in winter (Butler et al. 2013).

Detection probabilities are used to calculate more precise population estimates for many wildlife species (Butler et al. 2013). Social characteristics of a population, however, might influence detection probabilities differentially. To understand the application of detection probabilities for sandhill crane populations, we examined a well-studied population where social characteristics were known and could potentially influence detection probabilities. During the breeding season, sandhill cranes separate into 2 sympatric social groups: territorial and non-territorial birds (Walkinshaw 1973, Su 2003, Hayes and Barzen 2006). Territorial cranes are adults which actively and repeatedly exclude conspecifics from a finite area (Bennett and Bennett 1992) and these cranes have consistently nested in, and defended, the same territory

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over multiple summers (Hayes and Barzen 2006, Hayes 2015). Conversely, non-territorial cranes do not defend a territory and include subadult cranes, adult cranes that are capable of breeding but do not have territories, and adult cranes incapable of breeding (Hayes and Barzen 2006).

Movements of territorial cranes also differ from non-territorial cranes during the breeding season (Su 2003, Hayes and Barzen 2006). Non-territorial cranes have larger home ranges and travel farther from roost sites each day than do territorial cranes, which must remain within a specific area to exclude other cranes (Su 2003, Hayes 2015, Miller and Barzen 2016). During the breeding season, when not incubating, territorial cranes are most often observed in pairs or families while non-territorial cranes congregate in groups that vary from single birds to many individuals, sometimes exceeding 100 individuals (Miller 2002, Su 2003). The difference in movement and grouping patterns between these 2 social groups may affect detection rates and consequently affect abundance estimates from survey data.

Quantifying detection probabilities for each social group may help improve estimates for both population abundance and relative abundance of territorial and non-territorial groups. Relative abundance of these groups is meaningful because individuals within each group do not provide the same reproductive contribution to the population (Mills 2007). If part of the crane population is not able to contribute to recruitment due to lack of a nesting territory within suitable habitat, population dynamics and the population's response to pressure due to the hunting of cranes can be affected (Watson and Jenkins 1968, Mills 2007). Population fluctuations may be more affected by the amount of suitable habitat than by the number of adult cranes in the population (Watson and Jenkins 1968, Lande 1987, Fryxell 2001). Ecologically, the relative size of each social group also may influence social dynamics between groups (Nesbitt and Wenner 1987, Nesbitt et al. 2001, Hayes 2015).

Our objective was to estimate detection probabilities for 2 social groups of sandhill cranes, territorial and non-territorial, as a part of a larger effort to quantify the abundance of both social groups on a breeding area in Briggsville, Wisconsin. We are aware of only 1 other published estimate of detection probability for a crane species. Strobel and Butler (2014) estimated detection probability (± 1 SE) of 0.558 ± 0.031 within 500 m of aerial transects for whooping cranes. We hypothesized that territorial and non-territorial cranes would have different probabilities of detection because of different movement patterns (Su 2003, Hayes 2015, Miller and Barzen 2016). We also evaluated the effect of site size, distance to road, time of season, and observer bias on detection of cranes.

METHODS

Study Area

The study area was located near Briggsville, Wisconsin (43°36′N, 89°36′W), in an unincorporated township at the junction of Adams, Columbia, and Marquette counties, Wisconsin. The 6,600-ha site included 3 large wetland areas (100-200 ha) that were dominated by wetland species of sedge (predominantly *Carex* spp.). These wetlands maintained relatively constant water levels through groundwater inflow while wetland discharge was primarily from channelized outflow through streams that bisected each wetland (Barzen et al. 2016). In addition to larger wetlands, numerous smaller wetlands (<10 ha) were also present (Su 2003) and tended to be perched wetlands (Mitsch and Gosselink 2000). Wetland areas were surrounded by agricultural fields composed mainly of corn, alfalfa, and soybeans. Residential homes, grasslands, and forest were the other predominant types of land use in our study area (Su 2003).

Survey Methods

Sandhill cranes used in our analysis were previously color-marked (prior to 2009) by the International Crane Foundation. Cranes were captured as flightless chicks by chasing chicks until they hid (Hoffman 1985) or by baiting family groups after chicks could fly using corn treated with the sedative alpha-chloralose (Hayes et al. 2003, Hartup et al. 2014). Non-territorial cranes were color-marked when they were chicks in family groups during 2008 or before and then observed in 2009 as non-territorial cranes. Territorial sandhill cranes were either captured as territorial adults in 2008 or earlier or as chicks in a family group before 2008 and becoming territorial by 2009. Once restrained, a Bird Banding Laboratory (U.S. Geological Survey) metal leg band, a 7.62-cm plastic leg band displaying a unique, field-visible number, and 3 colored, 2.54-cm plastic leg bands indicating a unique identification code were attached (Dickerson and Hayes 2014).

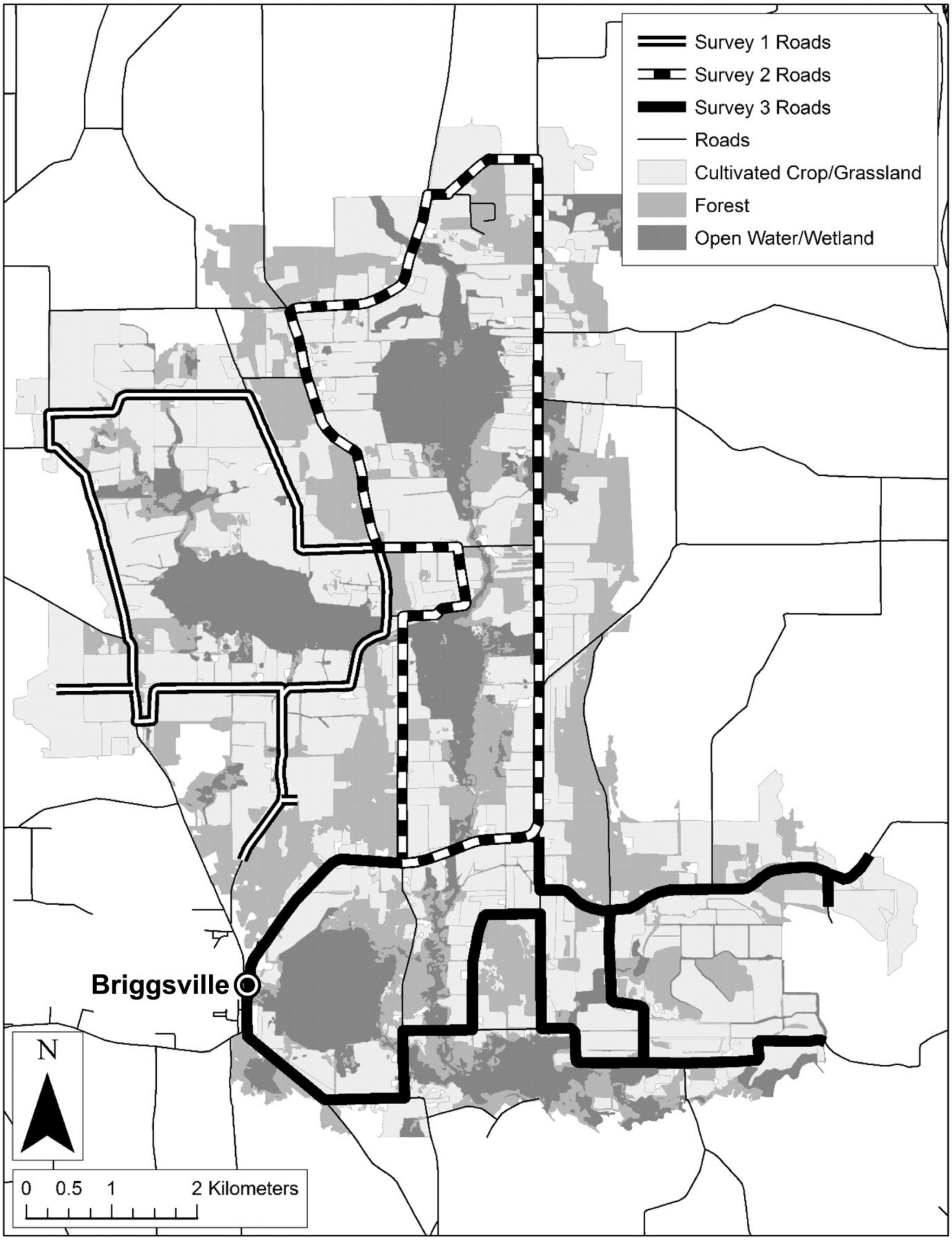

Figure 1. Three survey routes for sandhill crane observation from vehicles, near Briggsville, Wisconsin, 2009. Gray habitats were visible during the survey while white areas were not.

Sandhill cranes return to the Briggsville area to breed between late February and early March (Hayes and Barzen 2006). Surveys began on 3 April 2009 and ended on 16 June 2009. Each survey consisted of 3 routes (17.9 km, 21.8 km, and 24.5 km) on public roads, with each route circling 1 of the 3 primary wetland areas (Figure 1). Four technicians participated in observations during the field season. Technicians observed cranes on both sides of the road when vegetation or houses did not obstruct their view. Vegetation emergence and growth throughout the study did not affect the field of view. Each survey took approximately 1 hour to complete and circumnavigated 1 wetland complex. One survey day consisted of a technician driving the specified survey route 6 times during time periods that were stratified from a half hour before sunrise to a half hour after sunset. Each survey began at 1 of 6 randomly chosen starting points. In our analysis a "survey day" refers to all 6 surveys in 1 day and a "survey" will refer to 1 survey on any given day. Technicians observed cranes from a vehicle using binoculars (10×42) and spotting scopes (20-60× zoom), and recorded the color combinations of bands along with the locations of all banded cranes on printed aerial photos of the survey area. Technicians performed surveys twice a week at each wetland or route for a total of 67 survey days over 55 days of sampling (1 route was surveyed 1 extra time).

Data Analysis

We used the Huggins closed capture model (Huggins 1989) in Program MARK (version7.1, White and Burnham 1999) to explore differences in detection probabilities across the 2 social groups of sandhill cranes for color-marked birds only. The Huggins model also allowed us to model the effect of covariates on detection (Huggins 1989). Capture histories were created for each banded crane by treating each day as an observation event and pooling all 6 runs of a survey route. Thus, if a crane was sighted during any of the 6 runs in a day, it was coded as a 1, and if it was not seen at all it was coded as a 0. Only color-marked sandhill cranes that were confidently identified were included in our analysis. Only 5% of observed, color-marked birds were excluded.

Territorial cranes were identified as a pair of cranes occupying the same breeding and foraging area daily and displaying territorial behavior, such as low bows or ruffle bows directed at a conspecific near consistent boundaries (Tacha 1988), or nesting behavior such as incubation, nest building or nest exchange. Further, cranes were considered territorial in 2009 if they were classified as territorial during the 2008 breeding season and returned in the 2009 season paired with the same individual on the same territory location. We used this criterion so that territorial status could be used early in the season at the beginning of observations (3 April). Territoriality otherwise would take days to weeks to determine because the definition requires a series of observations. We identified the territorial status of all banded cranes and used this as a covariate in our analysis (Territorial status, Table 1). Non-territorial cranes neither defended a consistent area nor displayed repeated aggressive behavior toward conspecifics at a

Table 1. Detection models fit to sandhill observation data from 67 surveys along 3 routes, Briggsville, Wisconsin, 3 April-16 June 2009.

Model	K[a]	AIC_c[b]	ΔAIC_c[c]	AICc weight[d]	Model likelihood
Territorial status + observation event	4	3358.7	0	0.92	1
Time of Season + territorial status + observation event	12	3363.7	4.97	0.08	0.0831
Time of season + observation event	6	3388.0	29.33	0	0
Observation event	2	3390.9	32.18	0	0
Territorial status	2	3394.2	35.49	0	0
Time of season + territorial status	6	3397.9	39.26	0	0
Distance	2	3428.5	69.80	0	0
Null	1	3441.3	82.59	0	0
Time of season	3	3441.6	82.95	0	0

[a] Number of parameters.
[b] Akaike's Information Criterion corrected for small sample size.
[c] Difference in AIC_c relative to minimum AIC_c.
[d] Akaike weight.

specific location, and were most likely found in groups of 3 or more (Su 2003). We used observation histories of banded individuals to separate observations into first observation and subsequent observations, meaning any observation after the first observation (Observation event). This separation tested for the effect of independence for abundance estimates, which has been documented in other studies (Riddle et al. 2010). We would expect that if detection probabilities during initial and subsequent observations were independent and unbiased the probability of detection would not increase after the initial observation. At least 2 outcomes would explain a rejection of this hypothesis for independence: First if an observer learned to better identify cranes after an initial observation (this would be analogous to a trap response in traditional mark-recapture models), there would be an increase in detection probability after the first sighting. Second, if crane movements were non-random we would also expect detection probabilities between first and subsequent observations to be different.

We used ArcGIS software (Environmental Systems Research Institute, Inc., Redlands, CA) to determine the distance from the survey road to an observed crane for each sighting. The average distance of the crane from survey road over the entire 55 days of data collection was used in the analysis (Distance). We split observations into 3 intervals, each spanning 18-19 survey days to test the effect of time of season on detection probability (Time of season). This corresponded to the dates 3-25 April, 26 April-22 May, and 24 May-16 June.

Finally, we tested 9 *a priori* models containing 4 covariates (Territorial status, Observation event, Distance, and Time of Season) because we hypothesized that each covariate could affect detection probability. We also tested a null model. Akaike's Information Criterion (AIC; Burnham and Anderson 2002) was used for model selection. Due to the relatively small sample size of cranes in conjunction with variables (K) in several models (i.e., $n/K < 40$), we used AIC corrected for small sample size (AIC$_c$) for model selection (Burnham and Anderson 2002). We drew primary inference from models within 2 units of AIC$_{cmin}$, although models within 4-7 units may have limited empirical support (Burnham and Anderson 2002).

RESULTS

In 2009 we observed 52 uniquely banded territorial sandhill cranes and 23 uniquely banded non-territorial sandhill cranes. The model including territorial status + observation event best explained detection probability for sandhill cranes and had an Akaike weight of 0.92 (Table 1). The second best model included territorial status, observation event, and time of season. This model, however, was 4.97 Δ AIC$_c$ units from the first, providing little model support (Burnham and Anderson 2002). All other models were noncompetitive.

We calculated detection probabilities for both social groups of cranes as well as for first and subsequent observation events within the social group. The detection probability (± 1 SE) upon first observation for territorial sandhill cranes (= 0.11 ± 0.01, 95% CI: 0.08-0.14) was 3 times greater than for non-territorial sandhill cranes (= 0.03 ± 0.01, 95% CI: 0.01-0.07). In addition, detection probabilities for both social groups increased after the initial observation. Territorial sandhill cranes were 1.5 times more likely to be detected after an initial observation (= 0.1 ± 0.018, 95% CI: 0.17-0.20), and non-territorial cranes were more than 3 times more likely to be detected after an initial sighting (= 0.11 ± 0.01, 95% CI: 0.09-0.14).

For territorial sandhill cranes the population estimate (± 1 SE) derived from the best model was 52.1 ± 0.35 individuals (95% CI: 52.0-54.3) and for non-territorial cranes, it was 27.5 ± 4.8 individuals (95% CI: 23.8-47.9).

DISCUSSION

Although detection probabilities of cranes per day were low, the number of surveys conducted was sufficient to detect ≥ 99% of territorial cranes and 85% of non-territorial cranes. Of the models we prepared *a priori*, overwhelming support for the models containing territorial status suggested that territorial and non-territorial cranes are detected at different rates on the breeding grounds. Using either initial observations or subsequent observations, territorial cranes were more likely to be detected on any given day than non-territorial cranes. We speculated that the greater detection rate for territorial cranes was because of their restricted movement patterns on the breeding grounds as compared to the broader home ranges of non-territorial cranes. Home range size for territorial sandhill cranes in the Briggsville area varied over the breeding season with a mean of 284.7 ± 59.7 ha (n = 12, Miller and Barzen 2016). In the same population, home range sizes for non-territorial cranes decreased with age but were still over 22 times larger than territorial home ranges (Hayes and Barzen 2016). Restricted movement of territorial cranes may cause them to be present more often within the survey area and more available for observation.

The use of individual observation histories in the Huggins model revealed that detection probabilities for both social groups increased between initial and subsequent observation events. The Huggins closed capture model identified both territorial status and observation event as contributing to detection probability. Territorial cranes were 1.5 times more likely to be observed after the initial sighting, and non-territorial cranes were more than 3 times more likely to be observed after the initial sighting. Aspects of sandhill crane or observer behavior (or both combined) could account for an increase in detection probability after an initial observation. For instance, observers may learn where to look for sandhill cranes over time, or sandhill cranes may begin to use the same fields over time to improve social interaction or foraging efficiency. The effect of observer bias on abundance estimates has been documented in other studies (Riddle et al. 2010). Even when following standard methods for surveys, unforeseen biases in detection can affect survey results (Giudice et al. 2013). Environmental variables and heterogeneity between individuals being surveyed have been identified as important variables to consider when conducting detection probability studies (Conn et al. 2006, Giudice et al. 2013). Non-random sandhill crane behavior, as an example of individual heterogeneity, can also be important. With home ranges of non-territorial cranes covering 28-197 km^2 (Hayes and Barzen 2016), environmental conditions that modify habitat use can quickly skew sandhill crane behavior to increase repeated observations in a small area when resources such as food, for example, become available that can attract foraging cranes. Our survey applied many conventional methods designed to decrease survey bias, such as random starting points and observer training, but our results still show linkage between initial and subsequent observation events, so detection bias was possible. We also recognize that factors not identified by our analysis may affect detection probability of sandhill cranes.

Managers should take detection probability into consideration when deciding on survey methods to monitor sandhill crane species (Conway and Simon 2003). Our study found that territorial sandhill cranes during the breeding season had a substantially higher detection probability than did non-territorial sandhill cranes. Fewer surveys, therefore, may be needed to estimate population sizes for territorial than for non-territorial sandhill cranes. Spring census techniques that use volunteers to record unison-calling cranes (Voss 1977), illustrate examples of survey techniques (Harris and Knoop 1987, Dietzman and Swengel 1994) that may effectively detect territorial versus non-territorial cranes and can benefit from these results. Accurate census of most sandhill crane populations is difficult, so survey methods that incorporate detection probability estimates are valuable to wildlife managers who wish to monitor these cranes. Currently, an index of the EP of sandhill cranes is taken during fall migration (Kruse et al. 2010).

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TIMING OF FAMILY DISSOCIATION DOES NOT AFFECT LONG-TERM SURVIVAL ESTIMATES OF SANDHILL CRANE CHICKS

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Abstract: Sandhill crane (*Grus canadensis*) chicks depend on their parents beyond fledging, but timing of chick separation from their parents has rarely been quantified and reported. We color-banded and radio-tagged sandhill crane chicks on known natal territories in south-central Wisconsin and monitored family groups to determine age of chick independence. Using a Cormack-Jolly-Seber open population model in program MARK, we estimated survival for chicks that dissociated from their parents prior to fall migration, over winter (including migration), and following spring migration. Of 96 chicks with a known timing of dissociation from their parents, 11 (12%) became independent from their parents in the fall before migration during their hatch year, 76 (79%) became independent over winter, and 9 (9%) returned from spring migration with their parents and then became independent. Mean age (± 1 SE) at independence varied from 146 ± 7 days (fall) to 248 ± 14 days (off breeding areas) to 335 ± 11 days (spring). Season of chick dissociation did not affect whether a chick was philopatric or dispersive in its first year. Lifetime survival estimates were high (92%) and did not generally differ based on marking scheme (radio-tagged vs. color-banded), sex (male or female), or timing of dissociation (fall, off breeding areas, or spring). Chicks that did not migrate with their parents likely learned migratory routes and behaviors from conspecifics. More research on interactions between parents, their offspring, and other conspecifics off breeding areas (winter and migratory stopover areas) could provide insight into dissociation patterns and the mechanism of separation.

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Key words: Chick dissociation, estimated survival, *Grus canadensis*, independence, philopatry, sandhill crane.

Three main phases of the dispersal process (departure, transience, and settlement) have been described in animals (Bowler and Benton 2005, Clobert et al. 2009). During the departure phase, individuals separate from their parents and begin the process of living independently. The length of time that offspring are dependent on parents can affect population growth over time. While prolonged dependence increases offspring survival, it can also limit the number of breeding attempts for a breeding individual or pair in a given season (Verhulst et al. 1997). In species with cooperative breeding systems such as scrub jays (*Aphelocoma coerulescens*), however, prolonged dependence can increase subsequent breeding success (McGowan and Woolfenden 1990).

Duration and degree of an offspring's post-fledging dependence on its parents vary widely among avian species. Post-fledging family associations persist approximately as long as the nestling period in most passerines (Skutch 1976) while long-lived avian species often require double the nestling period or longer (Warren et al. 1993, McIntyre and Collopy 2006, Jonker et al. 2011). For example, exhibiting a brief post-fledging dependence, glaucous gull chicks (*Larus hyperboreus*) take 45-50 days to fledge but are dependent on their parents for only 5-10 days after fledging (Gaston et al. 2009). In contrast, Bewick's swan (*Cygnus columbianus bewickii*) cygnets that remained near their parents during a second and third winter benefited during aggressive interactions with other, unrelated swans (Scott 1980). Prolonged associations between parents and offspring are expected to increase offspring survival without impinging extensive cost to parents (Guo et al. 2010).

Precise stimuli for family dissociation are not well known. Departure behavior may be proximately driven by interactions among family groups as parents seek to balance fledged offspring survival with maintaining resources for the next breeding attempt. The end of the post-fledging period may also result from an offspring's innate decision to disperse (Weise and Meyer 1979; Bustamante 1994, 1995) or a response to a reduction in feeding by the parents (Holleback 1974, Guo et al. 2010, Vergara et al. 2010). Additionally, parents may actively chase offspring from their natal territory prior to the subsequent breeding season (Holleback 1974, Kamata and Tomioka 1991, Nesbitt et al. 2002).

Social hierarchies among brood mates in the same

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clutch may also be important drivers of departure. Dominant nest mates tend to explore away from natal locations and obtain open breeding sites while subordinate individuals remain near the natal site, losing potential breeding opportunities (Ellsworth and Belthoff 1999). Alternatively, dominant individuals may force subordinate nest mates to disperse from natal locations before they are socially or physiologically prepared (Ekman et al. 2002), thereby increasing their risk of mortality. Forced departure of subordinates by dominants has been observed at high population densities (Chitty 1967, Krebs 1978).

Cranes (Gruidae) are long-lived avian species where family groups (a territorial breeding pair and 1 or 2 offspring produced in a given year) remain together for many months (depending on the species) after chicks fledge at 70-110 days (Walkinshaw 1973). The extensive length of the post-fledging period is thought to be the result of the prolonged learning required by juvenile cranes. While crane chicks learn an array of foraging behaviors and food preferences from their parents, parental provisioning to offspring declines following chick fledging but does not cease (International Crane Foundation [ICF], unpublished data). Chicks also learn how to avoid predators and socialize with other cranes from their parents. Most importantly, crane chicks learn migratory routes from their parents and those that are not taught these routes and habits beforehand are typically sedentary (Nesbitt and Carpenter 1993) or show sporadic, non-traditional movements that do not resemble regular migration (Nagendren 1992, Hayes et al. 2007).

Though cranes are well-studied (Meine and Archibald 1996), the process of crane family group dissociation is poorly understood. Family group dissociation in non-migratory (Nesbitt et al. 2002) and migratory (Tacha 1988) sandhill cranes (*Grus canadensis*) occurred quickly even though parents separated from their chicks less than a month prior to nest initiation. In non-migratory red-crowned cranes (*G. japonensis*) (Kamata 1994, Kamata and Tomioka 1991) and in migratory Eurasian cranes (*G. grus*) (Alonso et al. 1984, 2004), familial dissociation was prolonged over a 1 to 3-month period during the winter and non-breeding season but was completed before the next breeding season. Proximate triggers of familial bond dissociation in cranes are unknown, but may result from chick voice and plumage maturation (Klenova et al. 2010), which often coincides with seasonal hormonal changes of breeding adults in preparation for the next nesting attempt (Tacha 1988, Kamata 1994). In red-crowned cranes, parental feeding behavior toward chicks changed from provisioning to displacement (by pecking and harassment) or abandonment of the young by parents on winter and non-breeding areas (Kamata 1994, Kamata and Tomioka 1991).

The goal of this study was to investigate the timing of chick dissociation from their parents in a migratory population of sandhill cranes breeding in south-central Wisconsin. If sandhill crane offspring benefit from prolonged association with their parents (e.g., learning foraging techniques, survival skills, and migratory routes), then chicks should remain with their parents at least until after their first fall migration. We expected chicks that dissociated from their parents in the spring after returning from migration to show higher levels of philopatry as second-year birds than those that dissociated during the previous fall or winter as hatch-year birds. We hypothesized that a chick that returned with its parents to its natal area and was then forced from the territory by its parents would benefit from remaining near its natal area to obtain resources and protection from predators. We also hypothesized that any offspring that dissociated from their parents before fall migration would have lower estimated survival than those that dissociated either over winter or post-migration in spring. We did not expect any difference in estimated survival between chicks that dissociated over winter or post-spring migration because chicks in both of these age groups have learned necessary survival skills and the southward migratory route from their parents, which should equally enhance survival probability. Moreover, we expected more chicks would dissociate from their parents over winter than post-spring migration because a chick's association with its parents through spring may increase energetic cost to the parents, as they prepare for the next nesting event, with minimal benefit to the chick, which is nearly adult size and will likely not breed during their second-year (Radke and Radke 1986).

STUDY AREA

Colored leg bands were deployed on sandhill crane chicks near Briggsville, Wisconsin (43°36′N, 89°36′W; Figure 1). This has been the site of a long-term study on sandhill crane breeding ecology and habitat selection by the ICF since 1991 (Hayes et al. 2003, Su 2003,

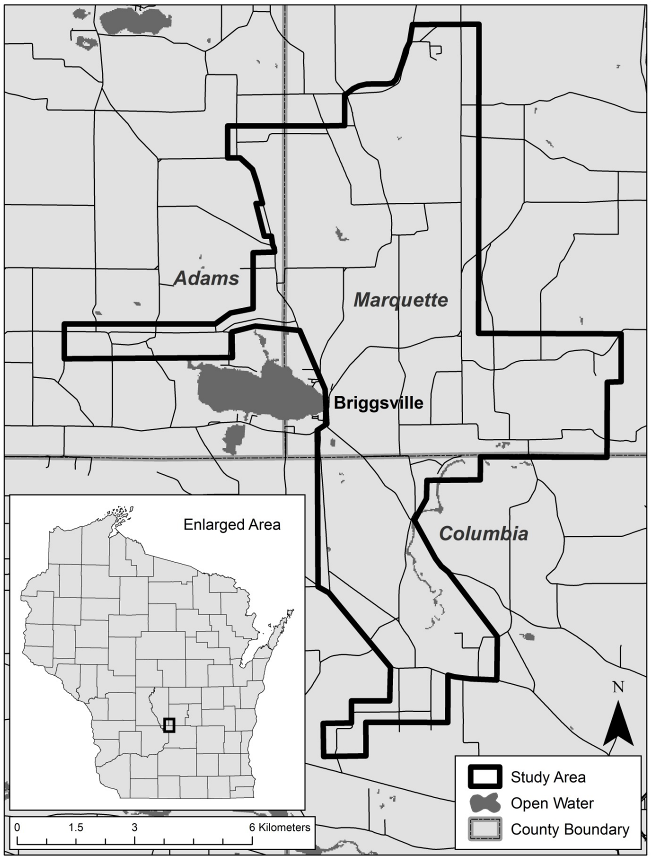

Figure 1. Map of the study area (delineated by the black line) near Briggsville, Wisconsin. This is the site of the long-term sandhill crane research project for the International Crane Foundation, 1991-2012.

Hayes 2015). The study area is primarily an agriculture-dominated landscape intermixed with small woodlots or forest patches, grasslands, flow-through wetlands, and dispersed human residences (see Su 2003). During summer, this study area contains a high density of territorial pairs that breed (Su et al. 2004) and flocks of non-territorial birds that do not breed (Hayes and Barzen 2006, Hayes 2015).

METHODS

Capture and Banding

Sandhill cranes were captured 1991-2012 using multiple methods. Flightless chicks (35-70 days of age) were pursued on foot until they hid and could be procured (Hoffman 1983). Volant adults and chicks (older than 70 days) were captured by using alpha-chloralose (Bishop 1991), an oral tranquilizer (Fisher Scientific Company, Fairlawn, NJ; and Biosynth Ag, Switzerland) according to the methodology described in Hayes et al. (2003), or leg snares (Hereford et al. 2001).

A captured crane was classified as a chick by the absence of red skin on the crown (Lewis 1979). For flightless chicks, age was further classified into the approximate number of weeks using growth criteria (Hayes 2015). Blood samples were collected from 198 of 204 (97%) chicks banded 1996-2012. Sex was determined from blood using molecular techniques (Griffiths et al. 1998, Duan and Fuerst 2001); otherwise, sex was determined through morphological or behavioral characteristics, i.e., males are larger than females (Nesbitt et al. 1992; ICF, unpublished data), and mature males and females have different pitches to their voices and exhibit different postures during unison call (Archibald 1976). Chicks for which this information was unavailable were considered of "unknown" sex.

Each crane received a size 9 rivet Bird Banding Laboratory (U.S. Geological Survey) band and a unique combination of colored plastic leg bands to allow re-sightings in the field using binoculars or spotting scope (Dickerson and Hayes 2014). Additionally, randomly chosen adults and chicks received leg band-mounted transmitters or backpack harness transmitters to allow identification and provide non-biased locations at any time (Miller and Barzen 2016, Hayes and Barzen 2016).

Behavioral Observations

Re-sightings of colored leg bands and radio telemetry were used to determine the last date when family groups were still intact, the first date when parents were observed without their fledged offspring, and the first date when fledged offspring were observed without their parents. Hatch date was estimated in 1 of 2 ways. If a chick was banded while flightless, its hatch date was calculated by subtracting its approximate age in days at capture from the date of capture. Fledged chicks are more difficult to age because morphological growth slows near the time of fledging while weight continues to increase (Ricklefs et al. 1986). For chicks banded post-fledging (*n* = 67), a mean hatch date was calculated from chicks caught while flightless in that same year. For post-fledged chicks with banded parents (*n* = 18), we then verified this estimate using previous sightings of the family that had occurred while the chick was flightless. From these dates, an approximate maximum age (days) of independence for each chick was obtained by subtracting the date when the family unit was last observed intact from the first date when either the chick was observed independent of the parents or the parents were observed without the chick.

Following dispersal, observations within the study area were regularly monitored from March through November annually. Outside Wisconsin, monitoring was more sporadic in some locations (e.g., Georgia and Florida), but regular from other locations (e.g., Hiwassee Wildlife Refuge in Tennessee since 2000 and Jasper-Pulaski State Wildlife Area in Indiana since 2009). Re-sightings outside breeding areas were sent to the ICF or Bird Banding Laboratory by other researchers or the general public, often by dedicated volunteers, after observing a banded bird. Re-sightings reported by non-ICF personnel were only accepted as high confidence in accuracy when they were accompanied by a digital photograph or if all of the bands were reported exactly as they were placed on the bird at the time of capture. All re-sighting and telemetry data were stored in a Microsoft Access or on-line Mapfeeder database.

Statistical Analyses

A deviation from normality was verified using a Q-Q plot in R. We used non-parametric tests for statistical analyses on all data that were not normally distributed. A Mann-Whitney U test (Sokal and Rohlf 2001) was used to determine if males and females differed in the approximate ages when chicks dissociated from their parents and if there was a difference in age for chicks that dissociated from their parents prior to fall migration as a result of capture compared to those that were not directly related to capture. Mean values are ± 1 SE. All data sets were tested for normality using a Shapiro-Wilk test (Shapiro and Wilk 1965), and significance was set at $P \leq 0.05$.

Chicks were considered philopatric if they were observed within the study area during pre- or post-nesting periods (Feb-Aug) following their hatch or dispersive if not seen in the study area during this period but seen alive elsewhere. Any point within the study area was within a distance 10 times the diameter of an average territory (Shields 1982). We did not consider birds seen in the study area only during September-November as philopatric because birds nesting outside the study area often stage (Melvin and Temple 1982) within our study area during this time (ICF, unpublished data). We evaluated radio-tagged and color-banded birds for philopatric or dispersive behaviors based on our detection method using a Fisher's exact test (Sokal and Rohlf 2001).

For birds with a known season of dissociation from their parents, long-term (lifetime) survival (φ) and encounter (ρ) rates were estimated using a Cormack-Jolly-Seber open population model (Cormack 1964, Jolly 1965, Seber 1965) in Program MARK (White and Burnham 1999). Because radio-tagged birds have increased detectability, especially on areas outside of breeding areas that were monitored, we separated radio-tagged birds ($n = 32$) from non-radio-tagged birds ($n = 57$) and ran each set separately in Program MARK. Each set of birds was further grouped based on sex or timing of familial dissociation (i.e., pre-fall migration, off breeding areas, post-spring migration). Program MARK was run 3 times for both radio-tagged and non-radio-tagged groups, allowing survival and encounter rates to vary by: 1) time, sex, and the interaction between time and sex, 2) time, season of familial dissociation, and the interaction between time and season, and 3) time, combined sex and season, and the interaction between time, sex and season. Model fit was evaluated by AIC_c and any model ≤ 2 AIC_c from the theoretically best model was considered valid (Burnham and Anderson 2002).

RESULTS

We banded 234 chicks (95 M: 123 F: 16 U) on 71 territories 1991-2012. Of these chicks, 90% had at least 1 banded parent and hatched on local territories in the study area. The remaining 10% had unbanded parents, but were banded as flightless chicks on their natal territory, so were known to be local. Of all chicks, 44 (19%) died or disappeared during their hatch year; 11 died and 18 disappeared prior to fledging while 9 died and 6 disappeared post-fledging. Of the remaining 190 chicks that were observed alive until their first fall migration, 14 (7.9%) were never observed after their first fall migration. This left 176 chicks (75%; 70 M: 97 F: 9 U) that survived their first migration and were observed at least once after reaching independence. Five of 176 birds had unbanded parents, so timing of dissociation could not be accurately determined. For the remaining 171 chicks with at least 1 banded parent, dissociation timing was unknown for 75 chicks (44%;

29 M: 41 F: 5 U) because neither the chicks nor their parents were observed prior to the parents' nesting season following their hatch year.

Remaining were 96 (56%; 39 M: 53 F: 4 U) chicks with a known timing of dissociation. Eleven of these birds (12%) dissociated from their parents prior to fall migration. This dissociation occurred approximately 3 weeks after being last observed with their parents (Table 1). Two of these chicks had radio transmitters and were never recorded in the same vicinity as their parents following dissociation. Seven of 11 chicks that dissociated in fall were members of 2-chick broods. The mean age of chicks that departed from their parents before fall migration was similar for males (n = 6; 143 ± 10 days, range = 116-170 days) and females (n = 5; 150 ± 11 days, range = 140-191 days; Mann-Whitney U = 16.5, P = 0.86). Six of the 11 pre-fall migration departures (3 M: 3 F) were likely caused by capture and subsequent asynchronous release of the family group because we never observed the chicks reunited with their parents following capture. Mean age when chicks dissociated from their parents was lower for dissociations resulting from capture (126 ± 4 days, range = 116-134 days, n = 6) compared to those that were not capture-caused (157 ± 5 days, range = 140-170, n = 5; Mann-Whitney U = 25, P = 0.01).

Because this population is migratory, the age of chicks that dissociated from their parents during winter or migration was difficult to quantify. Eight of 96 chicks (8.3%) were observed on wintering grounds without their parents (Table 1). Five of these chicks (2 M: 3 F) had radio transmitters, as did 1 parent of each chick, when observed apart. Each parent varied in the distance from its chick, ranging from being in different flocks (i.e., 1 km apart) to residing in different states (i.e., hundreds of km apart). An additional 68 of 96 chicks (71%) were observed with their parents before fall migration but parents and chicks were not observed together prior to the subsequent nesting season. These separations likely occurred off breeding areas, although there was no confirmation from observations in these areas. Twenty-three (8 M: 15 F) of these 68 chicks had active radio transmitters when they returned the following spring. Each chick's frequency was not detected when its parents were observed in the spring, reducing the likelihood that the chick had returned with its parents and then flown outside of our range of detection.

Nine of 96 chicks (9.4%), 2 of which had active radio transmitters, returned to the breeding grounds with their parents in the spring as second-year birds. Similar to chicks that dissociated from their parents in the fall, these birds dissociated from their parents approximately 3 weeks later. Mean age at familial dissociation post-migration in the spring did not differ between males (mean = 334 ± 18 days, range = 307-385 days, n = 4) and females (mean = 344 ± 14 days, range = 304-378 days; Mann-Whitney U = 10.5, P = 1.00, n = 5).

Overall, the season of family dissociation did not affect whether a bird was classified as philopatric or dispersive during their first year (Table 2). For each dissociation timing group, 50% of chicks were philopatric and 50% of chicks were dispersive in their first year. For chicks that separated from their parents away from breeding areas, second-year males tended to be more philopatric while second-year females tended to be more dispersive.

When sex and time were allowed to vary, 4 models were considered valid for radio-tagged birds and 3 models for non-radio-tagged birds (see Hayes 2015:81). For both radio-tagged and non-radio-tagged birds, estimated annual survival (φ) was consistent

Table 1. Summary of timing and age (days) when sandhill crane chicks dissociated from their parents in the population breeding near Briggsville, Wisconsin, 1991-2012.

Age at dispersion	n	Sex ratio (M:F:U)	Age (days) when last dependent			Age (days) when independent		
			Mean	SE	Range	Mean	SE	Range
Pre-fall migration	11	6:5:0	123	7	73-176	146	7	116-191
Off breeding areas[a] (known)	8	3:4:1	169[b]	9	136-207	248	14	198-295
Off breeding areas[a] (likely)	68	26:40:2	163[b]	3	51-201	unknown		
Post-spring migration	9	4:5:0	316	7	301-365	335	11	304-385

[a] Includes fall migration, winter, and spring migration.

[b] Age (days) = When chick was last observed with parents on breeding grounds before fall migration.

Table 2. Number of second-year birds showing philopatric or dispersive dispersal patterns in relation to timing of dissociation from their parents in the population breeding near Briggsville, Wisconsin, 1991-2012.

Dissociation timing	Second-year dispersal pattern				Total
	Philopatric		Dispersive		
	n	Sex ratio	*n*	Sex ratio	
Fall	4	3 M: 1 F	4	2 M: 2 F	8
Off breeding areas[a]	35	18 M:17 F	34	6 M: 25 F:3 U	69
Spring	4	2 M: 2 F	4	2 M: 2 F	8

[a] Includes fall migration, winter, and spring migration.

(approximately 92%) among data sets, even when φ varied by sex. Estimates of encounter rate (ρ) were more variable and tended to be higher for radio-tagged birds compared to non-radio-tagged birds (Hayes 2015:82).

When the season of dissociation (fall, off breeding areas, or spring) and time were allowed to vary in the mark-recapture models, estimates of φ and ρ were more consistent between radio-tagged and non-radio-tagged birds. For radio-tagged birds, 2 models were considered valid with ρ always varying based on season of dissociation and φ remaining constant or varying based on season (mean = 92%; Hayes 2015:83). For the model estimates when φ varied based on season, estimated survival was lower for radio-tagged chicks that dispersed during fall and highest for chicks that dispersed in spring. For non-radio-tagged birds, there was 1 best model with both φ and ρ remaining constant (Hayes 2015:84).

When radio-tagged and non-radio-tagged birds were grouped based on time and the combination of sex and season of dissociation from their parents, there was 1 best model for each data set. Estimates of φ remained constant and were identical (approximately 92%) for both data sets (Hayes 2015:85-86). Estimates of ρ were constant for radio-tagged birds (84%). Estimates of ρ were more variable for non-radio-tagged birds, with females encountered less than males and chicks dissociating in the fall (both males and females) encountered less than chicks that dissociated during the winter or spring (Hayes 2015:86).

DISCUSSION

Sandhill crane chicks likely dissociated from their parents and became independent at a continuum of ages, but we measured these separations at only 3 points in their life cycle: before their first fall migration, when they were off breeding areas, and after returning with their parents in the spring as second-year birds. Most chicks stayed with their parents through their first fall migration and the highest frequency of dissociations occurred off breeding areas followed by post-spring migration and then prior to fall migration. Overall survival rates of chicks were high and did not differ from each other, regardless of sex or season of dissociation from their parents. These observations show the flexibility of sandhill crane chicks to adapt to scenarios that diverge from the normal pattern of over-winter separation. There may not be an optimal dependence period for post-fledged sandhill cranes.

Season of dissociation from their parents did not affect philopatry rates during the first year. Chicks that dissociated from their parents in the fall were as likely to remain philopatric as those that dissociated off breeding areas or returned with their parents in spring. A chick's philopatric or dispersive behavior as second-year birds may be more reliant on social influence from conspecifics rather than their parents.

While encounter rates were highly variable among the sexes and seasons of dissociation (likely driven by dispersal rates), lifetime survival estimates were similar between chicks that dispersed from their parents before their first fall migration and those that dispersed over winter or the following spring. If sandhill crane chicks in this study are capable of living independently at 6 months of age or earlier, why do they remain with their parents for a longer time period? Sandhill crane chicks are dependent on their parents to learn migratory routes and behaviors (Nesbitt and Carpenter 1993). Because this study area is occupied by a dense breeding population of sandhill cranes during summer and large congregations in the fall, chicks that separated from their parents prior to their first fall migration likely joined pre-migratory aggregations and learned appropriate migration patterns and behaviors from conspecifics. For chicks from small and isolated populations (e.g., the northeastern U.S.), pre-migratory aggregations are not typically observed (D. Racine, personal communication). Separation from parents (either accidental or by choice) in these low-density areas could be fatal because there would not be as many conspecifics nearby to learn migration patterns. Familial dissociation patterns of sandhill cranes in the northeastern U.S. are currently unknown. Still, novel migrations can occur in at least adult cranes without learning (Hayes et al. 2007).

Hatch-year sandhill cranes (R. Urbanek, U.S. Fish and Wildlife Service, personal communication) and whooping cranes (*Grus americana*) (T. Stehn, U.S. Fish and Wildlife Service, personal communication) have been observed spending the entire first winter with their parents and then dissociating during spring migration or immediately after returning to breeding grounds. While it should be noted that our resolution of family dissociation off of breeding areas does not allow us to account for chicks that began spring migration with their parents and then dissociated before returning to their natal area, most pairs were re-sighted on breeding areas without a chick from the previous season present.

If migratory behavior was the main reason for a chick's dependence on its parents after it has already fledged, why are more chicks not observed on their natal areas with their parents in the spring? This behavior would reinforce migratory routes and behaviors without affecting long-term chick survival. Familial dissociation on non-breeding areas after the first fall migration may be related to costs to parents (e.g., provisioning and defending dependent chicks that are capable of living independently) versus the benefits to offspring (e.g., provisioned food and protection leading to increased survival). For example, Alonso et al. (2004) found that Eurasian crane families that defended winter territories had higher offspring survival than families that did not defend winter territories. These territories were costly to parents, however, because energy was used for territorial defense and offspring provisioning rather than in the pair's preparation for the next breeding attempt by building fat reserves (Krapu et al. 1985). Eurasian crane parents balanced this increased cost by leaving winter territories for breeding grounds earlier than their offspring, which migrated later (Alonso et al. 1984, 2004). Winter territoriality is known to occur in sandhill cranes (G. L. Ivey, ICF, personal communication); however, it is infrequent and the cause is unknown. Most sandhill cranes, regardless of reproductive status, form flocks during the non-breeding season (Tacha 1988, Krapu et al. 2011). While the exact cause of familial dissociation is unknown, this cost-benefit comparison could explain why sandhill crane parents remained with their chicks after teaching them the migratory route, but then dissociated from their chicks on wintering grounds (Kamata and Tomioka 1991, Kamata 1994) to focus on the next breeding attempt. Whether family group separation occurred through displacement behavior (by parents) or a reduced dependence by the chick as it ages, is unknown.

More research is needed on dissociation of sandhill crane families, especially on non-breeding areas during the winter. For example, pair members may or may not remain in close proximity during the non-breeding season (D. Aborn, University of Tennessee at Chattanooga, personal communication). Does the presence of a chick increase the chance that a pair will remain together during the winter? Are families that remain together throughout the non-breeding season more likely to return as a family unit in the spring? Does a chick home to its first wintering area in subsequent years? If a chick does home to a wintering area, does this affect wintering behavior and pair tenacity after it finds a mate? More intense behavioral observations during the non-breeding season would help address these currently unanswered questions.

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A REVIEW OF FALL SANDHILL CRANE MIGRATION THROUGH INDIANA

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Abstract: The Indiana Division of Fish and Wildlife conducts surveys from October to December to collect long-term data on greater sandhill cranes (*Grus canadensis tabida*). Results from these censuses contribute to a fall index of the Eastern Population, which informs wildlife management decisions and research priorities. Recent findings from the annual U. S. Fish and Wildlife Service Fall Sandhill Crane Migration Survey demonstrate a decline in the number of cranes observed at fall staging areas throughout Indiana since 1979. However, nationwide data exhibit a trend of population increase. I provide evidence to show that the apparent decline in the number of greater sandhill cranes migrating through Indiana does not indicate an actual decline in the Eastern Population but is a consequence of poor detection due to cranes migrating later each year. As a result, I suggest that survey periods be changed to later dates in the coming years to accommodate for this shift in migration chronology.

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Key words: climate change, greater sandhill crane, *Grus canadensis tabida*, Indiana, migration, migration delay.

During the 18th and 19th centuries, loss of wetland habitat through agricultural expansion and European settlement led to the rapid decline of greater sandhill cranes (*Grus canadensis tabida*) throughout North America (Meine and Archibald 1996, Van Horn et al. 2010). These threats, in combination with unregulated hunting, nearly drove the Eastern Population (EP) to extirpation. However, conservation measures throughout the 1900s, such as the Migratory Bird Treaty Act of 1918 and various pieces of legislation to protect wetlands (e.g., Clean Water Act of 1977, North American Wetlands Conservation Act of 1989), resulted in a resurgence of the population in recent years. Between 1966 and 2007, the North American Breeding Bird Survey showed a significant expansion of the EP in the upper Midwest with an average growth of 9.6% per year (Van Horn et al. 2010). Likewise, the Ontario Breeding Bird Atlas (BBA) documented a rise in the likelihood of detecting a breeding sandhill crane from 12% in the first BBA (1981-1985) to 33% in the second BBA (2001-2005) (Van Horn et al. 2010). The EP is now conservatively estimated at 80,000 to 100,000 cranes (Van Horn et al. 2010).

A similar history can be told of the EP sandhill cranes breeding in Indiana. Sandhill cranes were considered occasional summer residents nesting in northwest Indiana in the late 1800s (Castrale and Bergens 2000). Loss of wetlands through the early 1900s resulted in an absence of breeding cranes in Indiana for 53 years (Mumford and Keller 1984, Castrale and Bergens 2000). Not until 1982 was a nest reported again in northern Indiana and since then, the breeding population has steadily increased and expanded in range (Castrale and Bergens 2000). Records from the first Indiana BBA (1985-1990) report 7 blocks with confirmed breeding evidence in 4 counties in the northeastern corner of the state (Castrale et al. 1998). Twenty years later, the second BBA (2005-2011) lists 35 blocks with confirmed breeding evidence in 14 counties scattered throughout the north and reaching the western border in Newton County (USGS 2015). Castrale and Bergens (2000) suggest the westward expansion of nesting cranes was the result of a growing breeding population from nearby Michigan. Furthermore, recent reports suggest a southward expansion based on successful nesting at Wilbur Wright Fish and Wildlife Area (FWA) in Henry County and nesting attempts at Goose Pond FWA in Greene County (A. Kearns, Indiana Department of Natural Resources, personal communication).

It is evident that the protection of wetland habitat and the regulation of hunting have contributed to the recovery of sandhill cranes. However, as the population continues to increase and expand into areas of poor and declining habitat, human-wildlife conflicts will certainly increase. In addition, disease and other risks associated with living in a human-altered landscape will increase (Meine and Archibald 1996). Without periodic surveillance of the population, responsible management of sandhill cranes to address issues such as these would not be possible.

As a commitment to the U. S. Fish and Wildlife Service (USFWS), the Indiana Division of Fish and Wildlife (DFW) conducts surveys from October to November to collect long-term data on greater sandhill cranes. Results from these censuses contribute to a fall

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index of the EP, which informs wildlife management decisions and research priorities. This index is by no means a statistically accurate estimate of population size, but instead measures relative abundance to detect population trends (Van Horn et al. 2010). The Indiana DFW also conducts surveys at Jasper-Pulaski FWA from October to December to provide additional support in tracking the population. A large portion of the EP rests and refuels during the fall migratory season in the Kankakee River Valley in northwest Indiana, particularly, at or near Jasper-Pulaski FWA. With peak numbers reaching greater than 30,000 cranes in the past, counts at Jasper-Pulaski FWA provide a reliable proxy that contributes to the status of the EP.

Together, these surveys fulfill state monitoring requirements that inform management needs and assist in the early detection of threats to the population. Data from the 2015 USFWS fall sandhill crane survey and the fall crane surveys at Jasper-Pulaski FWA are discussed herein. Both surveys have been conducted for many decades (USFWS since 1979, Japer-Pulaski FWA since 1967) and provide long-term data to detect population trends.

METHODS

Statewide USFWS Fall Sandhill Crane Survey

The USFWS fall survey is a long-term survey established in 1979 which consists of efforts by volunteers and state and federal agencies from the Atlantic and Mississippi flyways (Wisconsin, Michigan, Indiana, Tennessee, Georgia, and Florida) (Fronczak 2014). The main goal of the survey is to provide an estimate of the size and trend of the EP cranes and is focused on counting cranes that concentrate in Indiana, Michigan, and Wisconsin during fall migration (Fronczak 2014). The survey was initially designed to begin the last week of October when cranes were concentrated in the 3 latter states (Van Horn et al. 2010). The initial survey conducted in 1979 counted 14,385 cranes and recent counts in 2014 have increased to 83,479 cranes with a 3-year average of 78,532 cranes for 2012-2014 (S. Kelly, USFWS, personal communication; Figure 1). Despite the significant rise in cranes observed during this period, the survey greatly underestimates the number of EP cranes. A study by Fronczak (2014) that tracked migrating cranes found that between 21% and 31% of tagged cranes were not in staging areas included in the USFWS survey. In an attempt to detect these cranes, a second period count in November was initiated in 2014. A larger portion of the EP cranes is expected to be associated with staging areas at this time (Fronczak 2014).

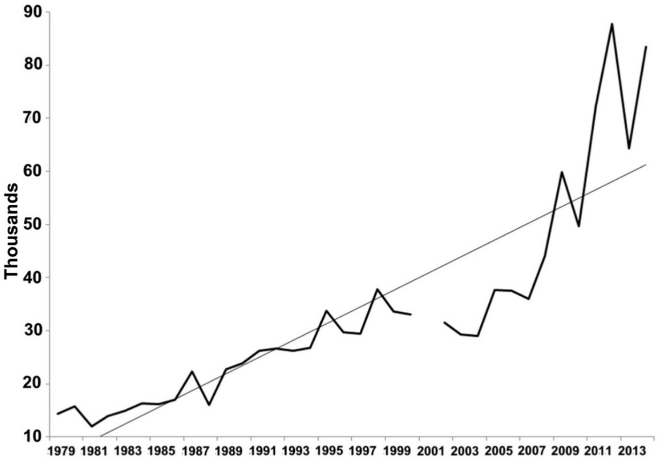

Figure 1. Number of sandhill cranes observed in the Eastern Population during the USFWS fall surveys from 1979 to 2014 (S. Kelly, USFWS, personal communication). No survey was conducted in 2001.

To coincide with these changes, Indiana surveyors counted sandhill cranes during 2 survey periods (28 October-4 November and 9-13 November) in 2015. Surveyors were strongly encouraged to conduct the survey on the first day of each period, herein named target dates. If surveys were conducted on days other than the target dates, results were listed under the target date if the survey day fell within its respective survey period. Twenty-three surveyors were placed at 17 locations throughout the state; more locations concentrated in the north, thus maximizing the potential to detect most of the population as they are beginning their southward migration through Indiana. Surveyors were encouraged to conduct 1-hour long counts starting either 30 minutes before sunrise or 30 minutes before sunset in order to observe cranes leaving or entering their roosts. Surveyors then completed a standard form, indicating time, GPS location, weather conditions, number of cranes, methods, and habitat type found at the site. The length, timing, and methods used to conduct the counts were at the discretion of the surveyor, thus there was little consistency in protocol. The nature of this article is to ultimately report the number of cranes observed, without correlating count data to hours of effort, methodology, habitat type, and other variables.

Fall Sandhill Crane Counts at Jasper-Pulaski FWA

Greater sandhill cranes were counted once per week from 6 October to 6 December 2015 at Jasper-Pulaski FWA. In total, 11 surveys were conducted during this period. Four to 5 observers were stationed at the observation deck (41.14036°N, 86.92343°W) and counted cranes that left the nearby roost. On average, the survey lasted 2 to 3 hours in the morning.

RESULTS

Statewide USFWS Fall Sandhill Crane Survey

The first day of the USFWS sandhill crane survey was overcast with occasional rain. Most of Indiana encountered rain storms throughout the day, which were associated with Hurricane Patricia. Temperatures ranged from 1.7 to 12.8°C (35 to 55°F). A total of 8,593 cranes was detected (Table 1).

Weather conditions were calm and partly cloudy to sunny on the second target date of the USFWS survey. Temperatures varied between −1.7 and 11.1°C (29 and 52°F) depending on the time of day. Notable changes in crane numbers over the past year included Pigeon River FWA, which received nearly double the amount of cranes seen the previous year on the same target date. A total of 10,920 cranes was observed (Table 1).

Overall, Pigeon River FWA, private agricultural fields south of Kingsbury FWA, and Jasper-Pulaski FWA were major sites with cranes in 2015, and 1,635, 2,700, and 14,830 individuals were counted in those areas, respectively. A new site, the Northern Indiana Public Service Company (NIPSCO) power plant, had 4,150 cranes counted there and will be considered an important survey site in future counts. The total number of observed cranes in 2015 was 19,513 (Table 1).

Fall Sandhill Crane Counts at Jasper-Pulaski FWA

A steady rise in the number of cranes migrating through Jasper-Pulaski FWA was reported in October by property staff: 3,400 observed on 6 October, 5,000 on 13 October, 6,526 on 20 October, and 7,010 on 29 October. November censuses demonstrated alternating rise and fall of numbers with 8,890 observed on 5 November,

Table 1. Number of cranes observed at each location during 2 survey periods (28 October and 6 November target dates), Fall Sandhill Crane Survey, U.S. Fish and Wildlife Service, 2015. Counties are listed in order from north to south. N/A = no data available for 2014.

County	Location	28 Oct	9 Nov	Change from 2014
Elkhart	Lieber Preserve/Pipewort Pond	2	2	+4
Elkhart	Boot Lake	88	159	N/A
LaGrange/Steuben	Pigeon River FWA	287	1,348	+550
LaPorte	Kingsbury FWA	0	0[c]	−8
LaPorte	Farm fields south of Kingsbury FWA	1,200	1,500	+796
Kosciusko	Tri-County FWA	0	0	N/A
Kosciusko	Pisgah Marsh/Durham Lake	34	45	N/A
Jasper/Pulaski	Jasper-Pulaski FWA	7,010[a]	7,820[c]	+912
Jasper	NIPSCO power plant	1,516[b]	2,634[d]	N/A
Newton	Willow Slough FWA	6	3	+8
Henry	Blue River/Knightstown Reservoir	0	0	0
Johnson	Atterbury FWA	0	0	0
Franklin/ Union	Brookville Reservoir	0	0	0
Monroe	Monroe Reservoir	0	0	−5
Greene	Goose Pond FWA	0	88	+88
Jackson	Muscatatuck National Wildlife Refuge	0	0	−185
Jackson	Ewing Bottoms	0	0	0
	TOTAL	8,593	10,920	+2,297

[a] Surveyed 29 Oct.

[b] Surveyed 30 Oct.

[c] Surveyed 10 Nov.

[d] Surveyed 13 Nov.

7,820 on 10 November, 8,282 on 17 November, and 6,000 to 8,000 on 24 November. This was atypical, as in previous years, the number of observed cranes continuously rose until the peak count was reached. An accurate count could not be determined on 24 November because of foggy conditions. Larger totals were observed in the following weeks: 16,470 on 1 December, 17,235 on 8 December, and 18,330 on 16 December (Figure 2).

The last day of the count was 16 December, so it remains uncertain whether peak numbers were reached after this date. Because of this, 16 December will be treated in the analysis as the date when peak numbers were reached.

DISCUSSION

During the 2015 USFWS fall sandhill crane survey, most cranes were counted at properties in northern Indiana, suggesting that sandhill cranes were beginning their journey through the state. Eight of 10 northern properties received cranes, whereas 1 of 7 did in central and southern Indiana. Arrivals of cranes were also expected to be delayed given an unseasonably mild fall in 2015. Thus, numbers were expected to be lower than those of the previous year. The count of 2015 instead exceeded the previous year by 2,297 individuals. Elevated numbers of cranes likely derived from a new site (i.e., NIPSCO power plant) being added to the list of survey locations (Table 1). The NIPSCO power plant has recently provided a roosting site near Jasper-Pulaski FWA (a major stopover site) that is becoming more popular among cranes. Without the addition of the NIPSCO power plant site, altogether 15,363 cranes would have been observed in 2015, 1,853 cranes below that of the previous year. Increasing detection is a goal that is strived for each year to improve the precision of these surveys.

A single rise in crane numbers does not imply a consistent upward trend of the population. This can be determined by long-term data, which provide patterns of population changes over time. Figure 3 demonstrates the number of cranes observed in Indiana during the fall USFWS survey since 1979. Although the trend is negative, I do not conjecture that the EP is steadily declining. An opposing trend of population expansion is apparent in the multi-state data provided by the USFWS (Figure 1). Instead, the apparent overall decline may be the result of poor detection due to cranes migrating later each year.

A delay in migration is evident in survey data from Jasper-Pulaski FWA. Peak numbers were expected to occur during November (J. Bergens, Indiana Department of Natural Resources, personal communication), but instead were reached in early December in 2015 (Figure 2). This, I conjecture, is due to a late migration caused by unseasonably mild weather. Further evidence of a delayed migration is shown in Figure 4, which demonstrates that, on average, peak numbers of migrating cranes have been delayed by 1.17 days each year since 1976 (J. Bergens, Indiana Department of Natural Resources, unpublished data).

Fall migration times are shifting to later dates. This, in turn, may prevent surveyors from detecting cranes since more cranes are remaining in the summer breeding areas for a longer period of time instead of moving to staging areas where they could be counted during the surveys. Lacy et al. (2015) suggested that, during mild winters, cranes tend to initiate migration later and stage farther north. This likely explains the apparent decline

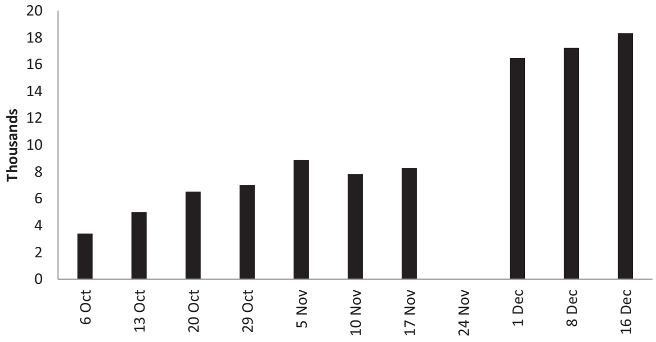

Figure 2. Number of sandhill cranes found during surveys conducted at Jasper-Pulaski FWA, Indiana, fall 2015. Fog prevented an accurate count on 24 November 2015.

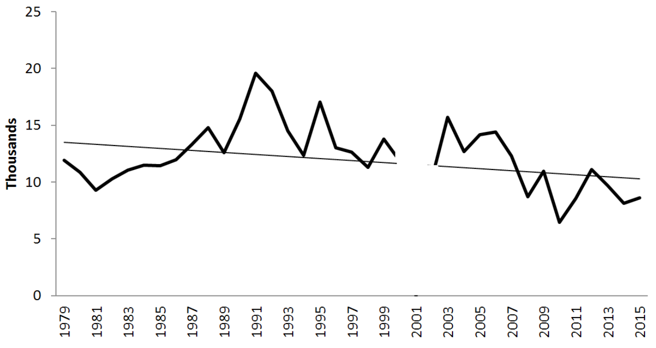

Figure 3. Number of sandhill cranes migrating through Indiana from 1979 to 2015 during the fall USFWS survey. No survey was conducted in 2001. Data from the second survey period in 2014 and 2015 are excluded.

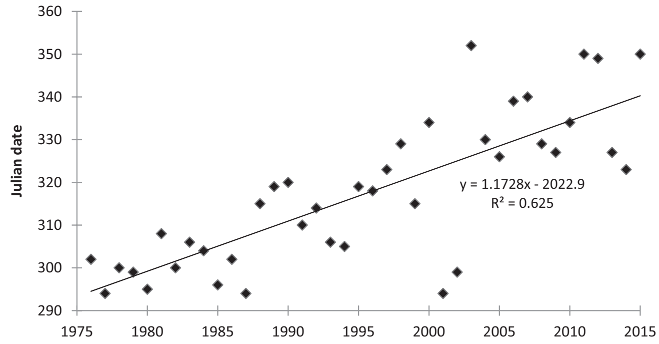

Figure 4. Julian dates of peak counts of sandhill cranes at Jasper-Pulaski FWA, Indiana, from 1976 to 2015 (J. Bergens, Indiana Department of Natural Resources, personal communication). Regression shows mean increase of 1.17 days per year since 1976. Julian dates of 290 to 360 = 17 October to 26 December in a normal calendar year.

in cranes detected during the USFWS fall survey since 1979. However, the USFWS survey has not altered the dates of its first target survey period. I suggest that survey periods be changed to later dates in the coming years to accommodate this shift in migration. When data from this year are added to the historical data and long-term changes in weather patterns are considered, I suspect that the data will show that there have been no drastic changes in the status of the EP of sandhill cranes. Rather, the data will show that the EP is expanding at a steady rate.

In addition, a 3-year roadside sandhill crane productivity study was concluded in 2015 within the Kankakee River Valley. Juveniles and adults were counted throughout private agricultural fields near Jasper-Pulaski FWA. Results from these surveys show that annual sandhill crane productivity averaged 9%, comparable to levels observed in the early 1980s within the same area (D. Fronczak, USFWS, personal communication). From the annual USFWS census data and the productivity survey, the EP of greater sandhill cranes appears stable.

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I thank all of the volunteers, DFW property managers, and USFWS staff that participated in this survey. With the coordinated efforts and dedicated hard work of our participants, these data were compiled swiftly and efficiently. Thank you J. Bergens and DFW staff who reported weekly on the status of the sandhill crane migration through Jasper-Pulaski FWA. Special thanks to D. Fronczak for inviting me to participate in the productivity survey and providing a summary of its results. Also, thanks to D. Fronczak and D. Slack for editing this report. Wildlife Diversity efforts were funded by State Wildlife Grants and the Indiana Nongame Fund through donations to the state income tax checkoff.

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WINTER AND MIGRATORY HABITAT USE OF SIX EASTERN GREATER SANDHILL CRANES

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Abstract: To better understand non-breeding ecology of sandhill cranes (*Grus canadensis tabida*), we harnessed 6 satellite GPS transmitters to adult cranes from 1 central Wisconsin breeding area. Using location data from these transmitters, we investigated non-breeding movements, including the routes and timing of migration. By combining satellite GPS data with a national land cover dataset, we also described habitat use on stopovers and wintering areas. Sandhill cranes tended to use larger home ranges on long stopovers (>3 days) than on short stopovers (3 days or less). The durations of northward migrations were longer and had more stopovers than southward migrations. We also documented a reverse migration pattern in 1 sandhill crane. There were differences in home range sizes of winter area and amount of time spent in the area (0.56-157 km^2, 29-101 days). Sandhill cranes departed from the breeding grounds, departed from wintering areas, and returned to the breeding grounds at about the same time each year, regardless of the distance migrated. Cranes departed from the breeding grounds in mid-November and returned in mid to late March. Non-breeding sandhill cranes seemed to select wetlands and row crop agriculture more often than grasslands, forested, or developed areas, but at varying rates in different wintering areas. Understanding winter and migratory habitat use and migration behaviors of sandhill cranes from different breeding areas can help us cranes in Wisconsin, as well as important use areas in the flyway.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:47-53

Key words: eastern population, greater sandhill crane, *Grus canadensis tabida*, habitat, migration, satellite telemetry, stopover, wintering grounds.

Productivity and survival of migratory cranes are influenced by behavior and use of habitat in each part of the annual cycle (Krapu et al. 1985). Understanding an individual's non-breeding movements and habitat use patterns can create a more complete picture of their life history. Habitat use and habitat quality on the wintering grounds influence an individual's body condition, which in turn influences migration patterns and subsequent survival and reproductive success (Strong and Sherry 2000, Ottosson et al. 2005).

Sandhill cranes (*Grus canadensis tabida*) in the eastern flyway have been extensively monitored on their breeding grounds, migratory stopovers, and wintering areas, but rarely have the same individual birds been studied throughout their entire annual cycle (Bennett and Bennett 1989, Littlefield 1995, Krapu et al. 2014). There have also been studies of cranes captured on stopover sites or wintering grounds and followed to their breeding areas, but few studies of wintering sandhill cranes from the same breeding areas (Nesbitt and Williams 1979, Krapu et al. 2011, Fronczak 2014). Researchers at the International Crane Foundation (ICF) have been studying sandhill cranes in a dense breeding population in central Wisconsin since 1990; in that time we have banded 607 sandhill cranes. Records of banded birds from this study area during the non-breeding season have mostly come from opportunistic sightings of cranes with colored leg bands by the general public. Very few individuals have been observed on multiple occasions during the non-breeding season, so there is no information about wintering locations or non-breeding habitat use for the majority of the sandhill cranes from the study area.

One way to gain more information about sandhill cranes over a large spatial scale during the non-breeding season is through the use of satellite telemetry. By fitting cranes with satellite transmitters, we were able to collect location data from multiple birds simultaneously as they were migrating and wintering in different states. The goals of this study were to describe stopover sites, wintering areas, migration routes, and migration timing of multiple non-breeding sandhill cranes from the same breeding population. This information can help us better understand population dynamics and identify important winter or stopover locations for sandhill cranes in the eastern flyway and the types of habitat important for cranes throughout the year.

METHODS

All cranes in this study were adult birds from a dense breeding population of sandhill cranes near

Briggsville, Wisconsin (43°36′N, 89°36′W). This area is mostly agriculture and wetland systems with limited development. Four male and 2 female sandhill cranes were captured within the study area with alpha-chloralose according to the methods outlined by Hartup et al. (2014). One bird was captured in October 2011, 3 in September of 2012, and 2 in September of 2014. The crane caught in 2011 developed exertional myopathy during capture, was rehabilitated in captivity for 14 days, and released. Each bird was fitted with a platform terminal transmitter (PTT) on a backpack harness as well as uniquely colored leg bands. Each transmitter recorded a location every hour of every day beginning when the transmitter was placed on the bird. These included locations recorded while the birds were roosting. Transmitters transmitted 189-1,033 days during the study, and 2 transmitters were still functioning as of July 2015. Locations were recorded using the Argos and GPS systems, and all points accurate to less than 100 m were used for this study (Argos 2014). Transmitters collected 3,995-18,970 locations per individual.

We defined stopovers as locations where cranes stayed at least 2 nights between their breeding area and wintering area. Short stopovers were defined as places cranes stayed for 3 days or less, and long stopovers were places cranes stayed for more than 3 days. Wintering areas were defined as the southern terminus of a bird's migration. Due to unequal sample sizes and unequal variance, we used a Welch's 2-sample *t*-test to analyze differences in home range sizes between short and long stopovers, number of stopovers made on migration, and duration of migrations. Distance migrated and timing of migration were compared using a linear model. All statistical analyses were done with the program R (R Core Team 2015).

We conducted all spatial analyses using ArcGIS 10.2 (ESRI 2013). To calculate length of migration, we computed the distance from the center point of a crane's breeding territory to the center point of its wintering area. To describe habitat characteristics of areas used by sandhill cranes, we used CropScape, a land cover dataset that covered the entire study area during the time period of this study and focused on agricultural habitats (USDA 2013). For habitat use analysis, we grouped land cover classes into 6 categories (developed, grassland, forested, row crop, wetland, and other). We delineated home ranges on stopovers and wintering areas using 95% minimum convex polygons (MCP) (Mohr 1947) using the ArcMap minimum bounding geometry tool (ESRI 2013). To describe habitat characteristics of areas available to cranes, we calculated the percent of each MCP home range composed of each habitat type. We then compared the habitat available within home ranges to the habitat of the locations of the bird, or the used areas, and calculated a preference index for each habitat category using methods outlined by Taft et al. (2008). We used 2-tailed 1-sample *t* tests to determine if preference indices for each habitat category were different from 1, or no preference.

RESULTS

Migration Patterns

These 6 sandhill cranes utilized a variety of migration routes and traveled to wintering areas in Indiana, Tennessee, Georgia, and Florida (Figure 1). The duration of southward migrations averaged 9.6 days and was shorter than northward migrations, which averaged 43.6 days ($P = 0.005$) (Table 1, Figure 2). On average, adult sandhill cranes left the breeding grounds on 21 November and arrived on their wintering areas 1 December. Cranes left their wintering areas around 4 February and arrived back on the breeding grounds on 19 March. Sandhill cranes also made more stopovers on northward migrations (mean = 4.1 stops) than on southward migrations (mean = 1.2 stops) ($P = 0.004$). Despite a wide range of distances migrated (304-1,774 km), these sandhill cranes did not demonstrate differences in the timing of departure from or arrival on the breeding grounds ($P > 0.05$) (Figure 3). Cranes wintering farther from the breeding grounds also did not leave wintering areas earlier than individuals wintering closer to the breeding grounds ($P > 0.05$).

Reverse Migration

In spring 2013 we documented a reverse migration, where a sandhill crane flew in the opposite direction to normal northward migration (Figure 4). The crane arrived at a staging area in northern Indiana on 14 March 2013 and in Sauk County Wisconsin on 18 March and then made a return flight to northern Indiana on 19 March, where it stayed until 28 March. The crane then flew north again and arrived on its breeding territory on 30 March, where it stayed for the rest of the breeding season.

Stopover Sites

On 19 migrations, the 6 sandhill cranes made 19

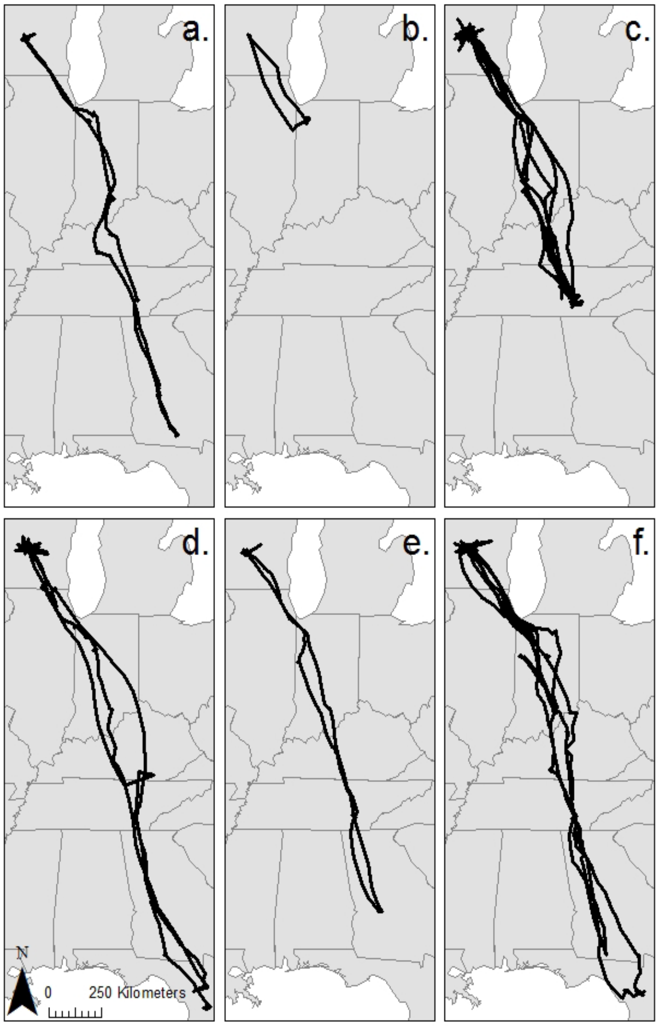

Figure 1. Migration routes used by each of the 6 sandhill cranes tracked in this study. All birds have breeding territories near Briggsville, Wisconsin. These migrations were made during a) fall 2014-spring 2015, b) fall 2011-spring 2012, c) fall 2012-spring 2015, d) fall 2012-fall 2013, e) fall 2014-spring 2015, and f) fall 2012-spring 2014.

short stopovers where they stayed for 3 days or less, and 30 long stopovers where they stayed for more than 3 days. Cranes used larger home ranges on long stopovers than on short stopovers (*P* = 0.001) (Figure 5). Mean 95% MCP home range size used by sandhill cranes was 35.4 km^2 during long stopovers and 8.6 km^2 during short stopovers. Cranes used stopover sites in Wisconsin, Indiana, Kentucky, Tennessee, and Georgia. However, 24 of the 49 stopovers were made in the state of Indiana. On average, stopover home ranges consisted mostly of agriculture, forested, and grassland areas; but the majority of used locations were in agriculture or wetlands (Table 2). Sandhill cranes on stopovers used wetland and agricultural areas proportionally more than these habitats were available in the stopover home range (mean preference index greater than 1, $P < 0.001$, $P = 0.02$). Cranes selected against grassland, forested, and developed areas within their home ranges ($P = 0.01$, $P = 0.006$, $P < 0.001$, respectively).

Wintering Areas

During 9 winters, the 6 sandhill cranes wintered in Indiana, Tennessee, Georgia, and Florida. One individual tracked over 3 winters spent all 3 winters at Hiwassee Wildlife Refuge in Tennessee. Another individual tracked for 2 winters, spent 1 winter in Georgia and the second winter in Florida. Cranes spent an average of 65 days on their wintering areas (29-101 days). Home range sizes averaged 48.7 km^2 and ranged from 0.6 to 157.0 km^2. Wintering areas were mostly forested, wetland, and agricultural areas, but more than half of crane locations were in wetlands (Table 3). Sandhill cranes selected for wetland areas and against forested, developed, and grassland areas within their home ranges ($P = 0.01$, $P = 0.006$, $P < 0.001$, $P = 0.02$, respectively). Agricultural areas were used proportionally to their availability within home ranges ($P = 0.14$).

Table 1. Duration, departure and arrival dates, and number of stopovers made during southward and northward migrations by 6 sandhill cranes from a breeding area near Briggsville, Wisconsin, 2011-2015.

	Southward migration (*n* = 10)		Northward migration (*n* = 9)	
	Mean	Range	Mean	Range
No. stops	1.2	0-2	4.1	0-7
Duration (days)	9.6	1-24	43.6	1-83
Departure date	21 Nov	12 Nov-28 Dec	4 Feb	26 Dec-10 Mar
Arrival date	1 Dec	23 Nov-5 Jan	19 Mar	11-30 Mar

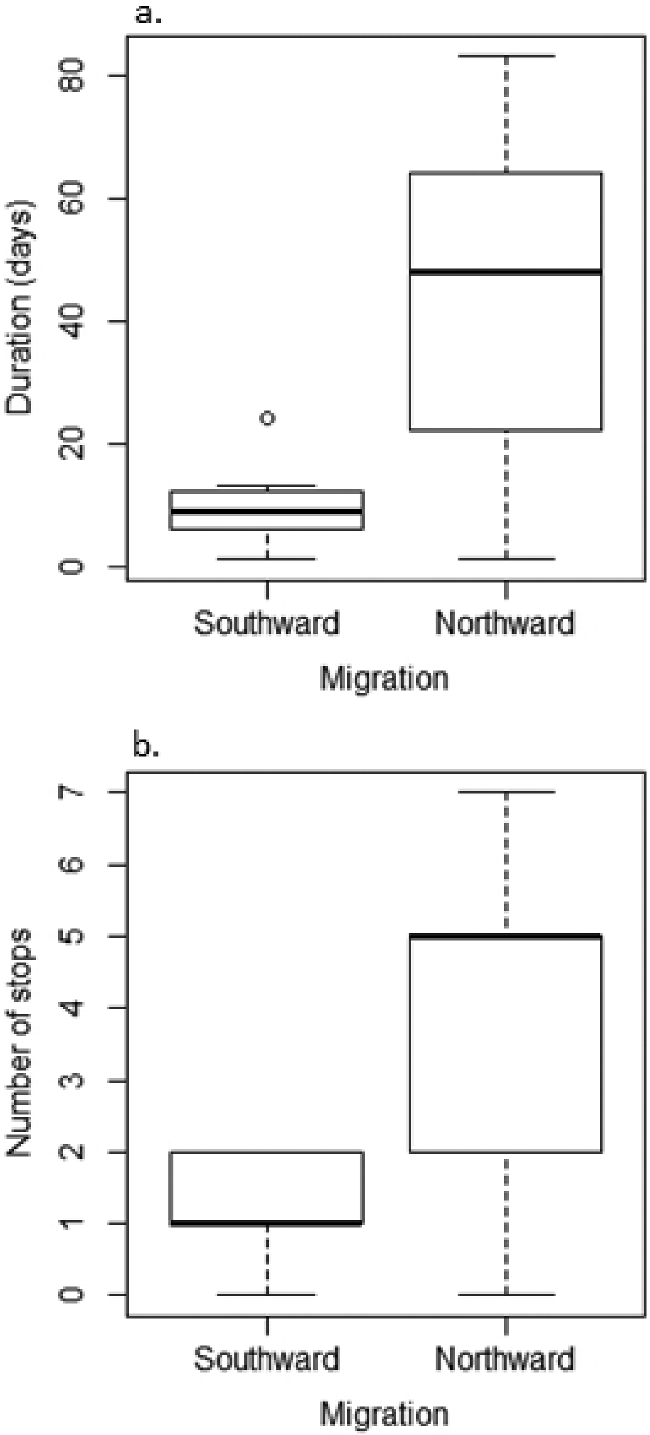

Figure 2. Migration duration (a) and number of stops (b) on southward and northward migrations made by 6 sandhill cranes from a breeding area near Briggsville, Wisconsin, 2011-2015. The duration of migration was measured by the number of days between when a bird began making large southward or northward movements and when it reached its southern or northern terminus. Stopovers were defined as when a crane would spend more than 2 nights in 1 location during migration.

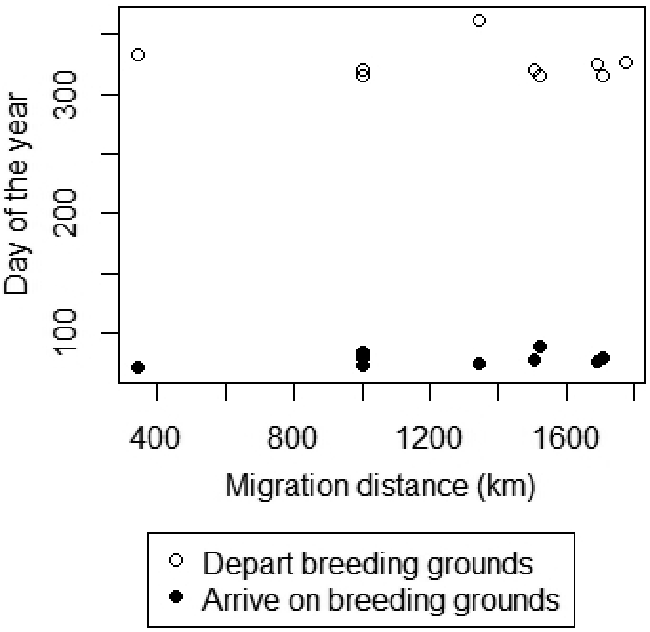

Figure 3. Timing of migration of 6 adult sandhill cranes migrating various distances from a breeding area near Briggsville, Wisconsin, 2011-2015.

DISCUSSION

Migration Patterns

Sandhill cranes from a dense breeding population in central Wisconsin migrated to wintering areas ranging from Indiana to Florida. While there were differences in the southern terminus of the migration route, there was considerable overlap in routes and stopover sites. Multiple birds tracked in this study used stopover sites at Jasper-Pulaski Fish and Wildlife Area in Indiana and Hiwassee Wildlife Refuge in Tennessee, both of which are known major stopover and wintering areas for sandhill cranes. These birds were very consistent in when they left the breeding grounds and when they returned. Departure dates from breeding grounds for birds from similar breeding areas were somewhat later than found by Fronczak (2014). This may be due to the fact that all of these birds were known breeding territorial adults that would benefit from spending the maximum time possible on the breeding grounds to defend and maintain their territory. For cranes migrating various distances, there were no differences in when birds left their wintering areas and began their northward migration. However, northward migrations

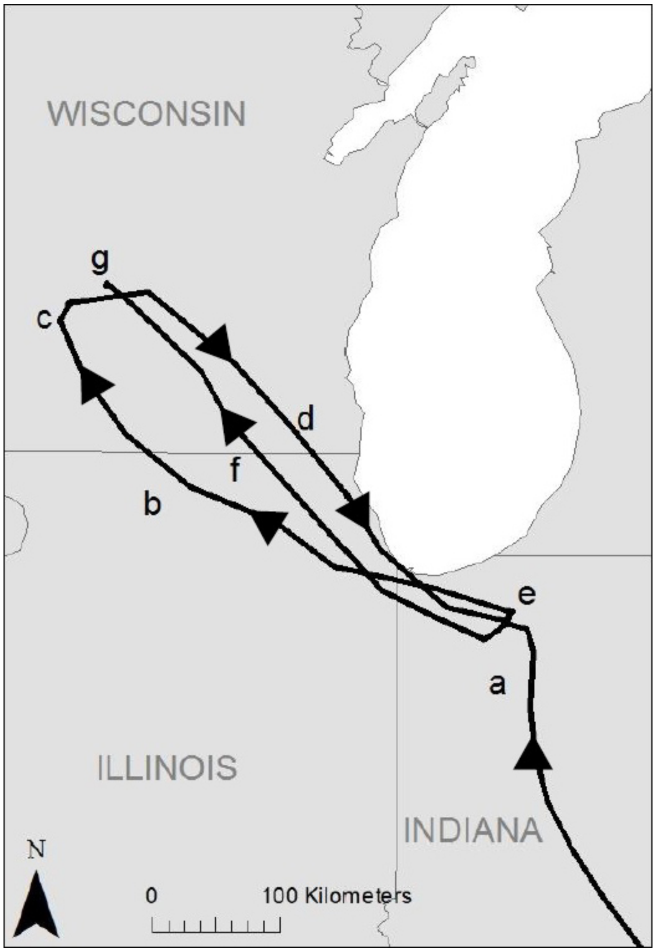

Figure 4. Example of a reverse migration exhibited by 1 sandhill crane during spring 2013. The bird traveled north to northern Indiana (a) where it stayed from 14 March until 16 March. On 17 March it flew north to Wisconsin (b), and stayed there on 18 March (c). On 19 March, it flew back to northern Indiana (d), and stayed there until 28 March (e). On 29 March, it flew to southern Wisconsin (f) and arrived on its breeding territory on 30 March.

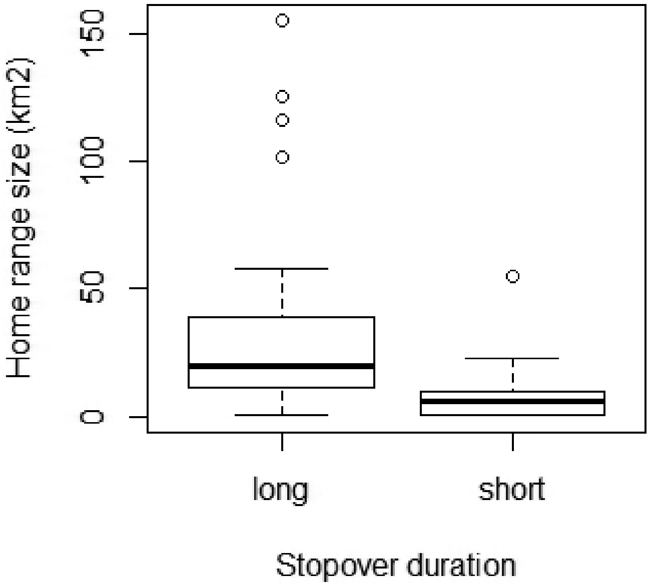

Figure 5. Home ranges (km²) of stopovers used for >3 days (long) or 3 days or less (short) by 6 sandhill cranes from a breeding area near Briggsville, Wisconsin, 2011-2015. Home ranges were calculated using a 95% minimum convex polygon around stopover locations.

were longer in duration and had more stopovers than southward migrations. It seems their strategy was to quickly migrate south, but move more slowly northward on the return trip, potentially dependent on appropriate weather conditions.

Reverse Migration

Reverse migrations have been documented in other species and are often attributed to severe weather events, poor body condition of the bird, inaccuracy in orientation of a bird, or as a search technique to refuel before crossing an ecological barrier (Åkesson et al. 1996, Komenda-Zehnder et al. 2002, D'Amico et al. 2014). In the case that we describe, of a sandhill crane arriving on the breeding grounds and returning to a staging area, the reverse migration was likely due to inclement weather. On 18 March 2013 in Briggsville, Wisconsin, the high temperature was 0°C (32°F) and snowing. The ground and water bodies were still frozen, making it difficult for cranes to forage, and potentially decreasing their security during nightly roosts. This could have potentially motivated a return flight to a staging area with above-freezing temperatures. When the crane arrived on its breeding territory on 30 March 2013, weather conditions were 10°C (50°F) and raining. Open water was available for roosting habitat, and foraging areas were open. These improved conditions likely prompted the crane to remain on its breeding territory.

Stopover Sites

Stopover sites used by these marked birds from 1 breeding population were similar to those used by sandhill cranes tagged on migration by Fronczak (2014) from a variety of breeding areas. There is significant overlap in staging areas used by cranes from throughout

Table 2. Habitat composition of stopovers used by 6 sandhill cranes from a breeding area near Briggsville, Wisconsin, 2011-2015. Home ranges were calculated using 95% minimum convex polygons.

	Agriculture		Wetland		Forested		Developed		Grassland	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Home range (%)	37.0	0.0-81.6	10.2	0.0-99.6	28.4	0.4-65.7	5.5	0.0-20.1	19.0	0.0-59.0
Bird locations (%)	40.1	0.0-97.8	35.7	0.0-100	10.2	0.0-75.8	0.8	0.0-15.8	13.1	0.0-64.9
Preference ratio	1.7	0.2-12.9	11.3	0.0-58.6	0.5	0.0-6.8	0.1	0.0-0.9	0.7	0.0-4.8

Table 3. Habitat composition of wintering areas used by 6 sandhill cranes from a breeding area near Briggsville, Wisconsin, 2011-2015. Home ranges were calculated using 95% minimum convex polygons.

	Agriculture		Wetland		Forested		Developed		Grassland	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Home range (%)	19.7	1.0-67.2	23.2	2.2-61.8	32.1	10.5-45.3	7.6	0.4-15.9	17.4	6.9-33.1
Bird locations (%)	14.9	0.0-51.8	59.1	3.6-89.5	11.9	0.2-46.8	4.4	0.0-37.2	9.7	2.6-19.1
Preference ratio	2.7	0.0-8.3	3.8	1.2-8.4	0.5	0.0-2.3	0.7	0.0-5.9	0.6	0.2-1.1

the breeding areas of the eastern population. Sandhill cranes also presumably used wetland habitats for roosting and agricultural habitats for foraging, which is consistent with stopover habitat use of sandhill cranes in the mid-continent population (Krapu et al. 2014). Due to the high use of some stopover sites by multiple sandhill cranes in our study as well as in other studies, and their consistent use of agricultural and wetland habitats on migration, land managers in the flyway could benefit cranes by planting crops (particularly corn) adjacent to wetland areas and leaving some forage in the fields (Iverson et al. 1987, Pearse et al. 2010).

Wintering Areas

We noticed large differences in wintering areas used by birds breeding in our study area. There were even differences for 1 individual bird in wintering areas used from 1 year to the next. However, this distribution of wintering areas is consistent with that used by sandhill cranes tracked by Fronczak (2014) from various breeding areas. Krapu et al. (2011) also reported that mid-continent population sandhill cranes from 1 breeding area used a variety of wintering areas which were also used by sandhill cranes from other breeding areas.

In these wintering areas, sandhill cranes preferred wetland habitat and selected against forested, developed, and grassland areas. They did not seem to prefer or avoid agricultural areas relative to their availability. This is different from the behavior exhibited on stopover sites, where birds also preferred agricultural habitats. This may be due to the higher energetic costs of migration, and cranes increasing fat reserves during migration to potentially offset low food availability when they reach the breeding grounds. Otherwise, wintering habitat use of these cranes was consistent with previous studies of wintering sandhill cranes in this and other populations (Bennett and Bennett 1989, Ballard and Thompson 2000, Krapu et al. 2014). Even though there were differences in locations used, sandhill cranes tracked in this study consistently used wetland habitats in their wintering areas. Some of the same areas used by cranes as stopover sites were used by other cranes as wintering areas, so these areas may be targeted for wetland management to benefit migrating and wintering sandhill cranes.

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HISTORIC AND RECENT WINTER SANDHILL CRANE DISTRIBUTION IN CALIFORNIA

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Abstract: Understanding the geographic distribution and long-term dynamics of winter foraging areas and night roost sites of sandhill cranes (*Grus canadensis*) is important to their conservation and management. We studied sandhill crane distribution in California's Central Valley from December 2012 through February 2013. We mapped observed flock and night roost locations. Flock locations occurred between Tehama County in the north and Kern County in the south. Flocks were concentrated in the northern Sacramento Valley, the Sacramento-San Joaquin Delta, the northern San Joaquin Valley south of Tracy to Mendota (including the lower Stanislaus and Tuolumne River floodplains and the Grasslands Region), and the southern San Joaquin Valley in the vicinity of Pixley in Tulare County. We also reviewed records of historic occurrences of cranes in California to interpret the importance of our flock and night roost locations. Although cranes wintered in the Los Angeles, San Diego, and San Francisco Bay metropolitan areas in the 19th and early 20th centuries, they no longer occur in significant numbers in these areas due to widespread habitat loss. Three additional areas which were used in the mid-20th century have apparently been abandoned or are being used only infrequently: the Red Bluff area (along the Sacramento River between Red Bluff and Anderson, Tehama County), the Goose Lake area (Kern County), and the Carrizo Plain (San Luis Obispo County). The primary cause of site abandonment at these sites is loss of suitable foraging habitat (small grain crops). With the exception of the Southern San Joaquin region, crane winter range has expanded in the Central Valley since the 1960s. Range expansion has principally been due to expansion of public wildlife refuges and private sanctuaries, plus improvements in their management (including reductions in hunting disturbance). To improve habitat conditions for cranes across their Central Valley wintering range, we recommend that management be focused on protection, enhancement, and creation of crane habitat complexes, each of which should contain 1 or more roost sites surrounded by sufficient well-managed foraging habitat. The following conservation strategies (listed in order of priority) should be implemented for each major crane wintering region: 1) protect existing, unprotected roost sites by fee-title acquisition or conservation easements (prioritize among sites according to their importance to greater sandhill cranes; *G. c. tabida*); 2) protect foraging landscapes around existing roosts, primarily through easements restricting development and crop types that are incompatible to cranes; 3) enhance food availability within those landscapes by improving foraging conditions on conservation lands and providing annual incentives for improvements on private lands; and 4) create additional protected roost sites toward the edge of their existing range where birds can access additional foraging areas.

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Key words: California, Central Valley, *Grus canadensis*, landscape units, Pacific Flyway, population status, sandhill crane, winter distribution.

California is an important wintering region for 3 migratory subspecies and 3 recognized populations of sandhill cranes (*Grus canadensis*), including greater sandhill cranes (*G. c. tabida*, hereafter, greaters) of the Central Valley (CVP; Pacific Flyway Council 1995) and Lower Colorado River Valley populations (LCRVP; Pacific Flyway Council 1997), lesser sandhill cranes (*G. c. canadensis*, hereafter, lessers) of the Pacific Flyway Population (PFP; Pacific Flyway Council 1983), and Canadian sandhill cranes (*G. c. rowani*, hereafter Canadians), which have not been designated as a population (Ivey et al. 2005). The CVP, PFP, and the Canadians winter in the Central Valley and the LCRVP winters in the vicinity of the south end of Salton Sea and along the lower Colorado River in California and Arizona. Greaters, which are listed as threatened in California (California Department of Fish and Wildlife [CDFW] 2013), are a priority for conservation actions, while lessers are considered a California Species of Conservation Concern (Littlefield 2008). Understanding the geographic distribution and dynamics of sandhill crane foraging areas and night roost sites is important to the conservation and management of their populations. By comparing past and current distributions we cannot only set current population status in an historic context, but can also better understand tolerances of the species to habitat alterations. This is useful for characterizing current threats and informing the development of conservation strategies.

Historic sandhill crane records in California suggest a much wider distribution than has been observed since the 1950s. Crane numbers were severely reduced by the early 20th century due to widespread habitat destruction concurrent with human settlement and, perhaps more importantly, unregulated hunting which continued until passage of the federal Migratory Bird Treaty Act in 1916 (Meine and Archibald 1996, Littlefield and Ivey 2002). For greaters, historic records collected outside the Central Valley include observations from the southern end of the Salton Sea, Imperial County in southeastern California (Abbott 1940), and from a bird collected along the Colorado River in 1857 or 1858 (Grinnell et al. 1918). Greaters still occur in these latter 2 areas and are members of the LCRVP. Greaters were formerly reported to be present in southwestern California during migration and occasionally in winter, as they were intermittently seen in Ventura and Los Angeles Counties; however, there is some uncertainty about these records because no specimens were collected (Willett 1933).

Within the Central Valley, crane flocks including both greaters and lessers were reported in the "Fresno District" (Fresno County) defined as the valley floor between Firebaugh and Wheatland on the west, and between Friant and Reedley on the east (Tyler 1913). Museum specimens of greaters were collected near Gridley, Butte County, in 1924, from the Butte Creek Basin, near Colusa, Colusa County, in 1923 and 1924, from 9.6 km west of Pennington, Sutter County, in 1936 (Grinnell and Miller 1944), from Los Banos, Merced County, in 1898 and 1909 (Mailliard 1921), and from Corcoran, Kings County, in 1918 (Swarth 1919).

Fossils of lessers were reported from Rancho La Brea in Los Angeles County (Miller 1912) and McKittrick in Kern County (Miller 1925). In addition, 1,000-5,000-year-old sandhill crane bones were found in Indian middens near Emeryville, Alameda County (Howard 1929). Historic records report that lessers ranged as far south as San Diego (Grinnell et al. 1918) along the southern California Coast and near Pasadena (Willet 1912). Museum specimens were collected from Mission San Rafael, Marin County, and Yerba Buena (now San Francisco), San Francisco County (Buturlin 1907), and in the San Francisco Bay area (Grinnell and Wythe 1927) in the 1840s, near Riverside in 1893 (Willett 1912), and near Newport, Orange County, about 1897 (Grinnell 1909). Specimens were also collected from Los Angeles County in 1904 (2 birds; Grinnell 1909) and 1918 (Wyman 1919), near Long Beach in 1912 (Willett 1912), and near Culver City in 1929 (Willett 1933). Lessers were also historically reported as moderately common near the Salton Sea, in the Imperial Valley, and also the Colorado River Valley (Abbott 1940, Grinnell and Miller 1944).

Museum specimens of lessers within the Central Valley include 2 without collection dates, 2 collected in 1897, and an additional 6 collected in 1909 from Merced County (Mailliard 1911, 1921), plus 1 collected in 1918 from Corcoran, Kings County (Swarth 1919). Flocks of lessers were reported in 1880-81 near Stockton, San Joaquin County; in 1884 near Marysville, Yuba County, and Gridley and Chico, Butte County; in 1914 near Lathrop, San Joaquin County; in 1918 near Los Banos (Grinnell et al. 1918); and in 1929 near Firebaugh and Mendota, Fresno County (McLean 1930).

There have only been a few studies and reports that provide specific information on sandhill crane distribution in the Central Valley since the 1960s. Their distribution in the Sacramento-San Joaquin Delta region (hereafter, Delta) was described in a report by Zeiner (1965). Distribution of lessers was studied by Pogson and Kincheloe (1981) and Littlefield and Thompson (1982). Studies of greaters were conducted throughout the Central Valley in the 1970s (Littlefield and Thompson 1979), mid-1980s (Pogson and Lindstedt 1991), and early 1990s (Littlefield 1992). Additionally, in 2005 the U.S. Fish and Wildlife Service (USFWS) developed a map depicting crane distribution in the Sacramento Valley (USFWS, unpublished data). More recently, an extensive study was conducted of sandhill crane distribution in the Delta region (Ivey et al. 2014). Our objective of this paper is to synthesize historic and current information to illustrate changes in crane distribution in the Central Valley of California to provide a comprehensive compilation of sandhill crane winter distribution patterns and to inform conservation planning for wintering cranes.

STUDY AREA

Our review of historic crane distribution during winter included all historic wintering sites in California, including the Central Valley, the San Francisco Bay region, the Los Angeles Basin, the San Diego region, and the Imperial Valley. Our field survey area encompassed major crane wintering regions in the Central Valley, approximately 700 km in length and 100 km wide (Figure 1). The major sandhill crane wintering

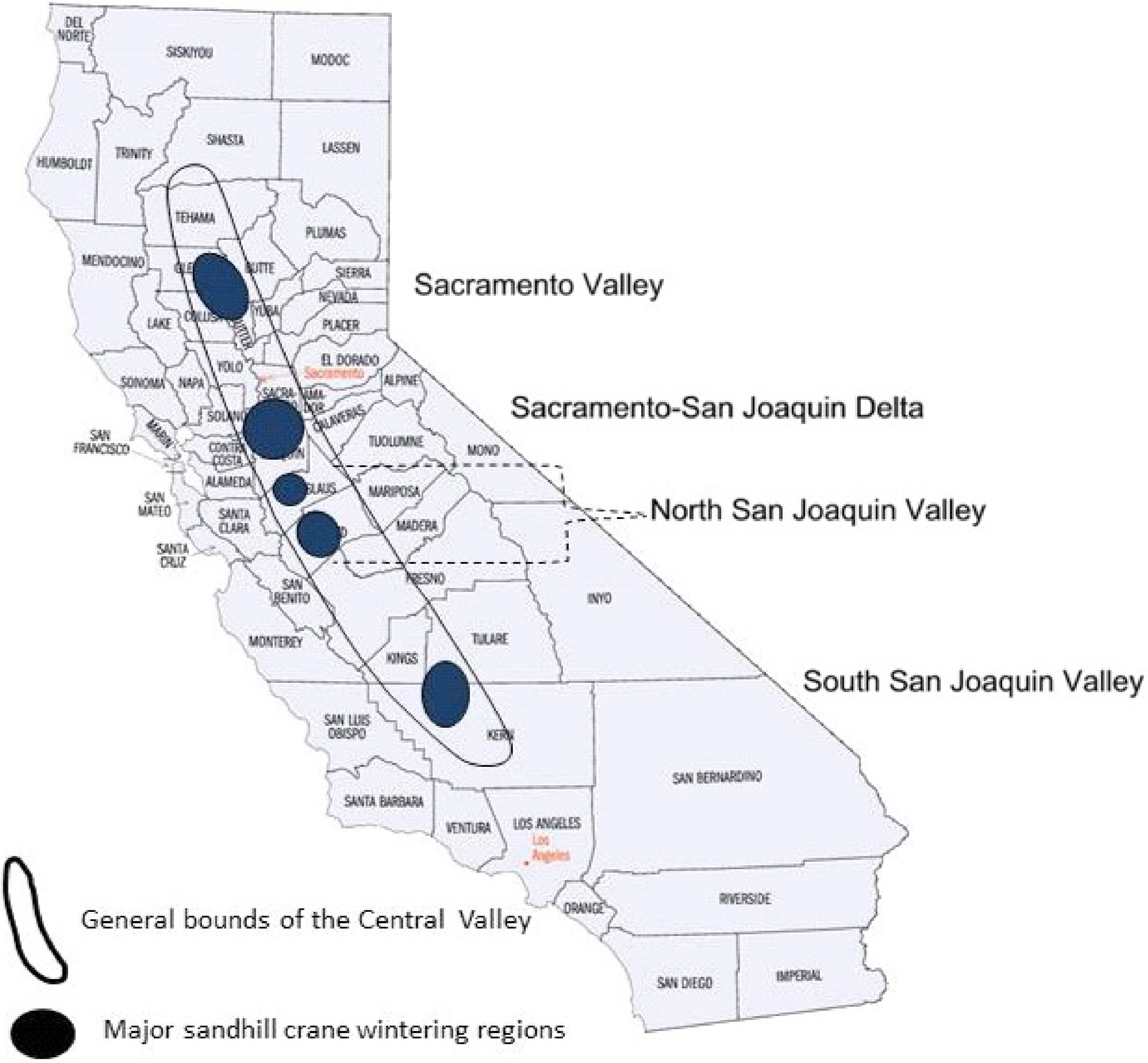

Figure 1. Central Valley of California study area with approximate locations of the Central Valley (black line) and major wintering areas of sandhill cranes.

areas in this study area include: the Sacramento Valley rice-growing region from Chico and Red Bluff, south to Williams and Marysville; the Sacramento-San Joaquin Delta (including the Cosumnes River Floodplain and the Delta region from Freeport south to Highway 4 west of Stockton); the North San Joaquin Valley south of Tracy to Mendota, including the lower Stanislaus and Tuolumne River floodplains, San Joaquin River National Wildlife Refuge (NWR) and the Grasslands Ecological Management Area (Merced County); and the South San Joaquin Valley south of Visalia to Bakersfield, especially around Pixley NWR. Additionally, sandhill cranes still occasionally use areas along the Sacramento River floodplain between Red Bluff and Anderson in Tehama County, the Mendota area in Fresno County, the eastern foothills of Merced and Stanislaus Counties, the Goose Lake area in Kern County, and Soda Lake on Carrizo Plain in San Luis Obispo County.

METHODS

Mapping Current Foraging and Roosting Sites

Sandhill crane winter foraging flock surveys were conducted from December 2012 through February 2013 on private lands in the Central Valley of California. Surveys were conducted by driving public roads and mapping flocks visible during daylight hours. Field work focused on identifying foraging sites during morning and evening foraging times, but we also recorded locations of roost sites. We used binoculars and spotting scopes to locate flocks and count flock sizes. In addition, we included 2012-13 reports of flocks on the ground from eBird (Sullivan et al. 2009) in our dataset. These locations and associated flock sizes were used to create a GIS layer using ArcGIS version 10.1 (Environmental Systems Resource Institute, Redlands, California). We focused our survey efforts on 5 Central Valley wintering regions to define the bounds of the sandhill crane winter ranges in these areas (Figure 1): 1) the Sacramento Valley between Marysville and Chico; 2) Sacramento-San Joaquin Delta; 3) lower Stanislaus-Tuolumne-San Joaquin rivers floodplains (San Joaquin River NWR area); 4) Grasslands Region; and 5) southern San Joaquin Valley (Pixley NWR area). We spent less survey effort in the Delta than in other regions, because sandhill crane winter range was recently defined there (Ivey et al. 2014). Flock and roost site locations were plotted using ArcGIS version 10.1. In addition to roost sites mapped in 2012-13, we also included roost sites identified during recent studies (Ivey and Herziger 2003, Shaskey 2012, Ivey et al. 2014).

Historic Sandhill Crane Habitat Use Patterns

We synthesized available geo-referenced historic flock location data in the Central Valley (none was obtained for the southern San Joaquin Valley). We examined changes in use of roost and foraging locations over time by summarizing available reports (since 1963) from agency files and publications and creating maps of the distribution of those sites using ArcGIS version 10.1 to illustrate changes. We also used mid-winter waterfowl survey data (USFWS 2014) and Audubon Christmas Bird Count (CBC) data (National Audubon Society 2010) to assess changes in crane numbers and distribution.

RESULTS

Current Sandhill Crane Distribution

We mapped 1,858 diurnal sandhill crane flock locations between 9 December 2012 and 3 March 2013. Observed flocks ranged between southern Tehama County in the north and northwest Kern County in the south. As expected, flocks were concentrated in the historically most used areas: the northern Sacramento Valley, the Delta, the northern San Joaquin Valley south of Tracy to Mendota (including the lower Stanislaus and Tuolumne River floodplains, San Joaquin River NWR and the Grasslands Region), and the southern San Joaquin Valley south of Visalia to Bakersfield (primarily Pixley NWR) (Figure 2). We spent less effort in surveys near Red Bluff and the Mendota area (2 mornings each), as we did not locate any sandhill crane flocks when we were there, and available data (eBird and birding sources) suggested sandhill crane use was sporadic at those 2 sites. We did not visit Carrizo Plain, as recent data suggest that sandhill crane use has become very limited in recent years, and we doubt that it will become

Figure 2. Distribution of sandhill crane foraging flocks mapped in December 2012 through February 2013 in the Central Valley of California.

an important sandhill crane area in the future because the area no longer provides grain fields.

From assembled reports, data, and personal communications with knowledgeable individuals, we mapped 121 roost sites that have been recorded since 2002 and classified them as either wetland (typically annually available during winter on the landscape) or cropland (often only temporarily available; Figure 3). These records are incomplete, especially in the Sacramento Valley, where there were numerous temporary roost sites that were used only when rice fields were flooded. Our surveys spanned 10 weeks in late winter and it is likely we missed many temporarily used roost sites.

Changes in Sandhill Crane Use Patterns in the Sacramento Valley Region

Since the mid-1980s study by Pogson and Lindstedt (1991), sandhill crane winter distribution has greatly expanded (Figure 4). The winter ranges depicted in Figure 4 should not be considered exact bounds of sandhill crane winter ranges, but rather generalized outside bounds of sandhill crane distribution, subject to the judgment of the individuals who drew them.

Occasional sandhill crane surveys in this region during the winter of 1981-82 revealed that most cranes were using areas surrounding Gray Lodge Wildlife Area and only 1 flock was ever observed west of the Sacramento River during that winter (G. Ivey, personal observation). The wintering region described by Pogson and Lindstedt (1988) showed sandhill cranes limited to 2 major areas in the mid-1980s, the Upper Butte Basin and the Butte Sink (Figure 4A). West of the Sacramento River, they reported “isolated records” of sandhill cranes. Sandhill cranes had expanded their range, toward Biggs and Riceton by 1993 (Littlefield 1993; Figure 4B). In 1994, the mid-winter survey recorded 69 sandhill cranes west of the Sacramento River, and since then, sandhill cranes have been regularly recorded there on those surveys; increasing to a peak of 2,259 in 2014 (USFWS 2014). By 2005, the winter range of sandhill cranes had expanded west of the Sacramento River, using areas west of Interstate 5 between Williams and Maxwell and around Delevan NWR (Sacramento NWR files, map dated 2005; Figure 4C). During our study, we found sandhill cranes had further expanded their use areas toward Live Oak and Sutter, around Colusa NWR, and toward Willows and Hamilton City (Figure 4D). Our foraging flock surveys documented the largest concentrations of sandhill cranes in the Willows-Bayliss-Hamilton City and the Rancho Llano Seco-Rancho Esquon areas.

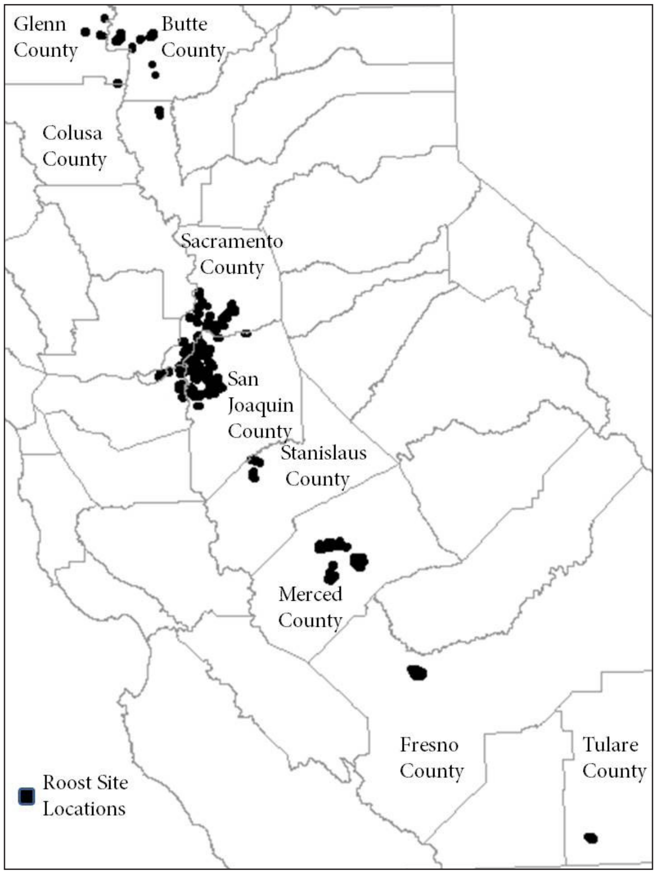

Figure 3. Sandhill crane roost site locations mapped in the Central Valley of California, 2002-2013.

East of the Sacramento River, some sites show reduced use by sandhill cranes, apparently due to conversion of former pastures and rice fields that had been used by foraging sandhill cranes to wetlands during the establishment of Upper Butte Basin Wildlife Area and Sacramento River NWR. Additionally, sandhill cranes were displaced by increased disturbance associated with waterfowl hunting programs and new duck clubs that were established in that area, causing cranes to shift to other use areas (J. Snowden, personal communication).

Changes in Sandhill Crane Distribution in the Delta Region

In the mid-1960s, the winter range of cranes in the Delta region was relatively small, and spanned

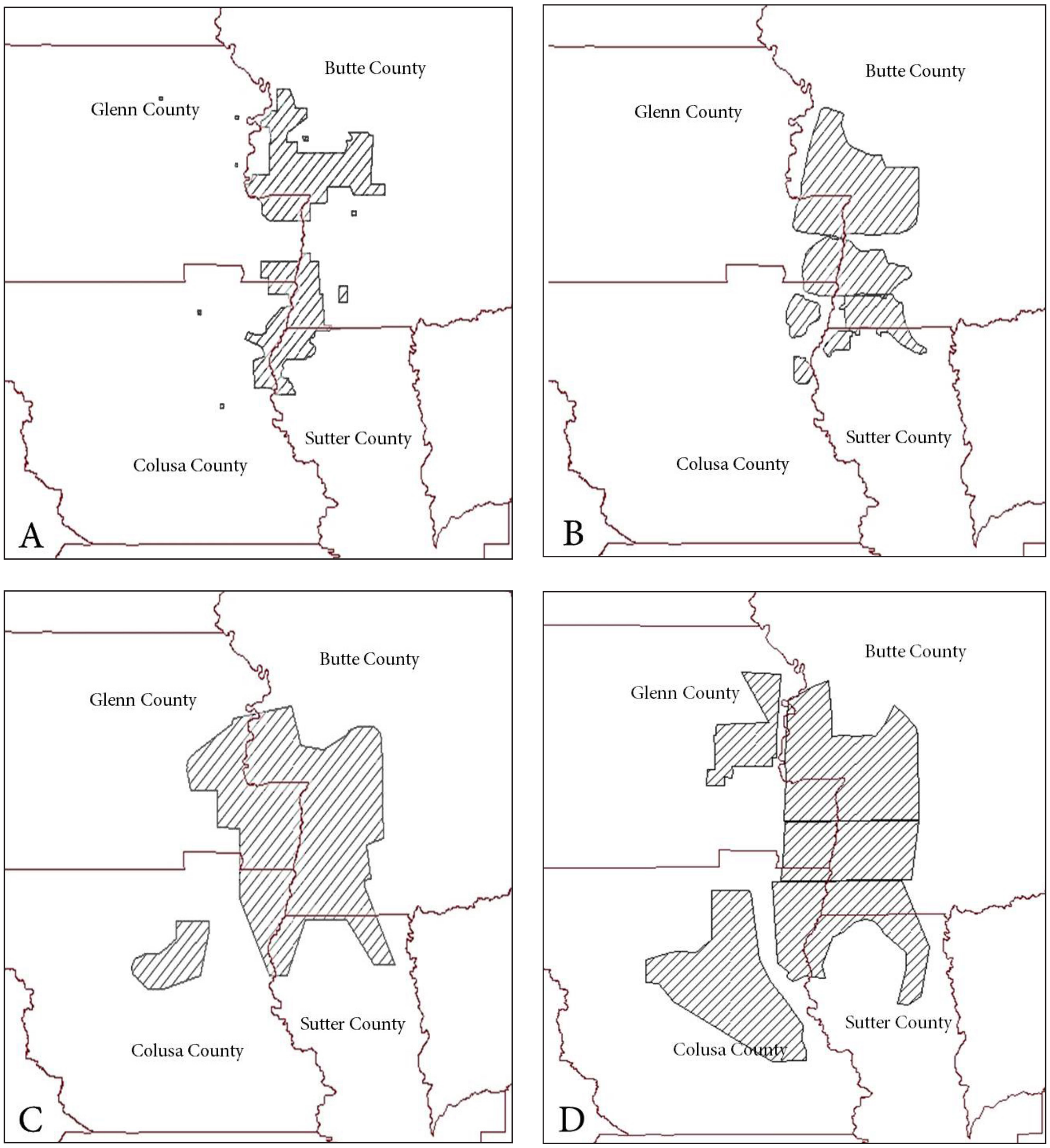

Figure 4. General distribution of wintering sandhill cranes in the Sacramento Valley of California over time; A = 1983-1984 (Pogson and Lindstedt 1988), B = 1991-1993 (Littlefield 1993), C = 2005 (Sacramento National Wildlife Refuge files), and D = 2012-13 (this study).

most of the area between the West Fork of the Mokelumne River at Staten Island and Interstate 5 to the south, including most of Terminous Tract, and all of Brack, Canal Ranch, and New Hope Tracts. Also included were areas west of Interstate 5, south of the Cosumnes River channel to about 3.2 km west of Galt, and south to the Mokelumne River channel, including the fields about 1.6 km south of Thornton (Zeiner 1965; Figure 5A), while the greatest concentration of cranes was centered on what is now the North Isenberg Sandhill Crane Reserve. Pogson and Lindstedt (1988) mapped Delta sandhill crane winter range, which included Tyler and Grand Island, and a few isolated locations south of Highway 12 (Figure 5B). They noted a couple of large roost sites on the Cosumnes River Floodplain, which are now within the Cosumnes River Preserve, 4 roost sites on Brack Tract, 1 on Canal Ranch, 3 on Staten Island, 3 on Tyler Island and 1 on Grand Island. These additional roost sites that Pogson and

Lindstedt (1988) identified likely allowed sandhill cranes to expand their wintering range.

An extensive study of the Delta region during 2006-2009 (Ivey et al. 2014) and our 2012-13 surveys documented a much broader winter range (Figure 5C), indicating that sandhill cranes have expanded their range north to Stone Lakes NWR and vicinity, east of Highway 99 on the Cosumnes River and Dry Creek floodplains, and further west and south in the Delta. This was likely due to an expanded number and distribution of roost sites, as Ivey et al. (2014) documented 69 roost sites, about half of which were in flooded croplands.

The establishment of protected areas providing roost sites since the mid-1980s, plus an apparent increase in farming practices using winter flooding as a management tool to facilitate stubble decomposition and reduce soil salts and weeds, has apparently contributed to this broader distribution of sandhill cranes in the Delta (Ivey et al. 2003). The El Dorado and Robin Bell gun clubs on Brack Tract were purchased in 1985 by CDFW to provide secure greater sandhill crane roosts on Brack Tract. Originally designated as Woodbridge Ecological Reserve, these 2 sites were renamed the Isenberg Sandhill Crane Reserve. Cosumnes River Preserve (CRP) was established in 1987 and has grown to over 20,000 ha, including the 3,700-ha Staten Island which was added in 2002. This preserve is managed under a broad partnership with The Nature Conservancy (TNC), Bureau of Land Management (BLM), CDFW, Sacramento County, California Department of Water Resources, Ducks Unlimited, and the California State Lands Commission. In 1994, the Stone Lakes NWR was established by USFWS. However, since early 1990s, approximately one-third of the winter range mapped in Figure 5C has been lost following conversion to orchards, vineyards, and in some cases, turf farms, blueberries, and more recently, solar farms (G. Ivey, personal observation). Such losses of foraging habitat may be contributing toward the winter range expansion we have documented.

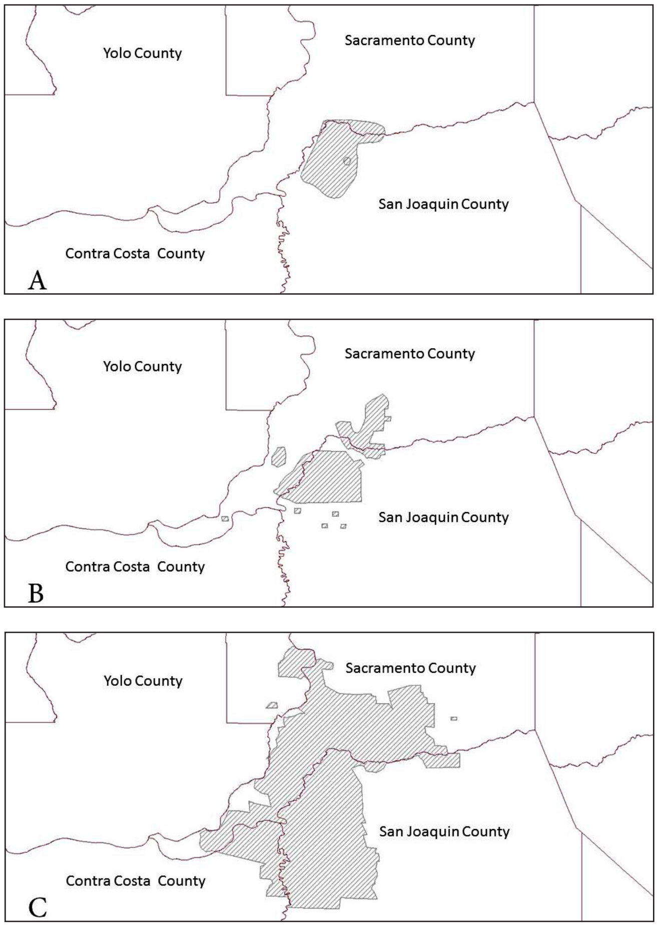

Figure 5. General distribution of wintering sandhill cranes in the Sacramento-San Joaquin Delta region of California. A = 1963-1965, B = 1983-1984, and C = 2006-2013.

Changes in the San Joaquin River NWR Region

In this region, the sandhill crane winter range, including 4 roost sites, was mapped by Pogson and Lindstedt (1988; Figure 6A). San Joaquin River NWR was established in 1997 and the USFWS subsequently acquired easements on several important properties, including large portions of the Faith and Mapes Ranches. As a result, sandhill crane winter range expanded (Figure 6B), likely because of increased security at roost sites and also the provisioning of a large roost site on the refuge, south of Highway 132 (White Lake). However, many of the croplands in this region have been converted to orchards and urban expansion from Salida and Modesto has reduced available habitat on the east side of this wintering area (G. Ivey, personal observation).

Changes in Sandhill Crane Use Patterns in the Grasslands Region

Historic maps of sandhill crane winter range for this region were not available. However, there has been significant expansion of conservation properties in the vicinity of the refuges here since the late 1970s. The Grasslands Wildlife Management Area (GWMA) is a

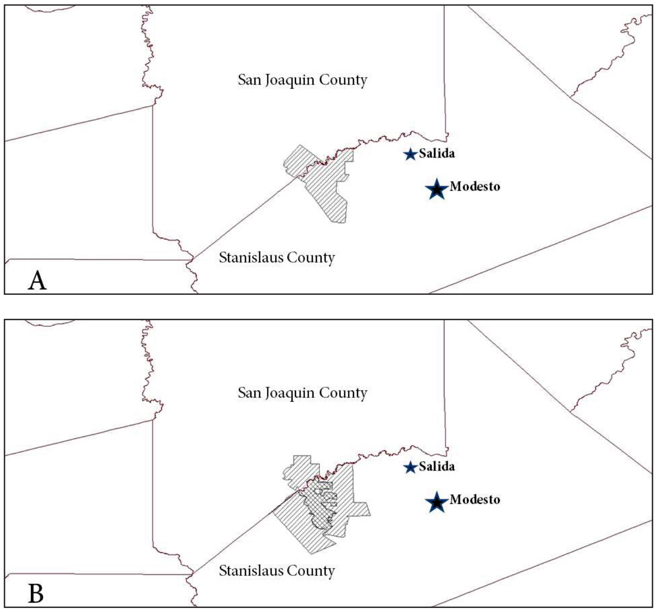

Figure 6. General distribution of wintering sandhill cranes in the San Joaquin River National Wildlife Refuge area of California. A = 1983-1984 (Pogson and Lindstedt 1988), and B = 2006-2013 (Ivey et al. 2014, this study; central cross-hatched area = San Joaquin River National Wildlife Refuge).

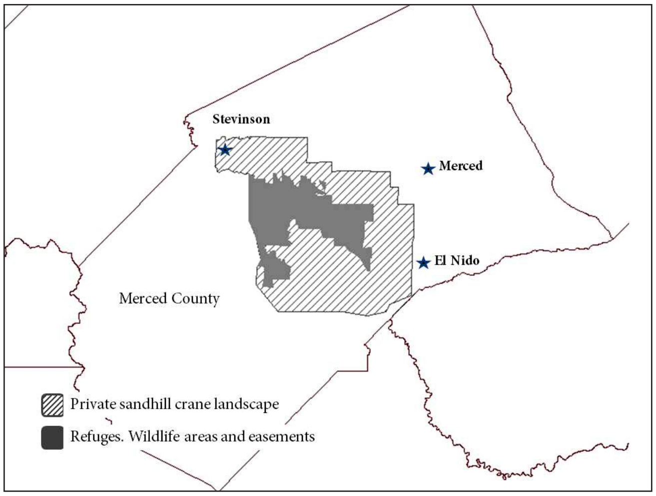

Figure 7. General distribution of wintering sandhill cranes in the Grasslands Region in 2013, Merced County, California.

USFWS block of conservation easements on private lands that was initiated in 1979, which currently encompasses over 32,000 ha. However, because much of the GWMA is comprised of duck hunting clubs, use by sandhill cranes on those properties is very limited. Areas within the GWMA that are east of Highway 165 are within the current sandhill crane winter range. Also, the Arena Plains Unit of the Merced NWR was established in 1992. Expansion of these conservation areas has provided additional secure sandhill crane roost sites. However, orchards are encroaching into this range around Stevinson, Merced, and El Nido (G. Ivey, personal observation). Figure 7 illustrates the current sandhill crane winter range in the Grasslands region, interpreted from our flock surveys and other recent data.

Changes in Sandhill Crane Use Patterns in the Southern San Joaquin Valley Region

Historic maps of sandhill crane winter range for this region were not available. Therefore, our 2013 flock surveys represent the first intensive surveys of the sandhill crane winter range in this region. Only 8 lessers were reported at Pixley NWR in 1969 (established in 1959) and a peak of 628 lessers was reported in 1970 at Goose Lake in Kern County (Littlefield and Thompson 1982). A 1979 aerial survey recorded 2,050 sandhill cranes at Goose Lake (Kern NWR, unpublished data), while Pogson and Kincheloe (1981) found 1,500 lessers there in 1981. Since those early investigations, sandhill crane numbers have apparently greatly increased at Pixley NWR and decreased at Goose Lake. Since 2000, numbers have reached peaks of over 9,400 roosting at Pixley NWR (Kern NWR, unpublished data). We found no sandhill cranes during our flock surveys in the Goose Lake area during January or February, 2013. However, flocks of 78 and 320 were observed there in October in 2013 and 2015, respectively (D. Hardt, personal observation). Our map of the current sandhill crane winter range is displayed in Figure 8. We note that orchards are also encroaching, primarily into the east side of this range, near the town of Pixley (G. Ivey, personal observation).

Areas of Former Importance

Carrizo Plain.–This site was formerly important primarily to lessers, as 3,200 were reported there in 1947 (Walkinshaw 1973) and an estimated 10,000-14,000 sandhill cranes were observed there in the 1960s (McCaskie 1967). More recently, this site has received little sandhill crane use. This reduced use has occurred since acquisition of Soda Lake by TNC and the BLM in 1988 and eventual designation of Carrizo Plain as a National Monument in 2001. CBC data provide an

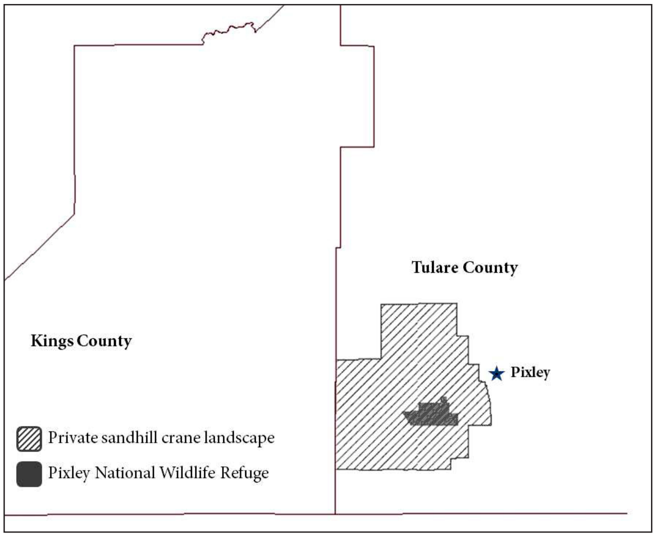

Figure 8. General distribution of wintering sandhill cranes in the Pixley National Wildlife Refuge Region in 2013, Tulare County, California.

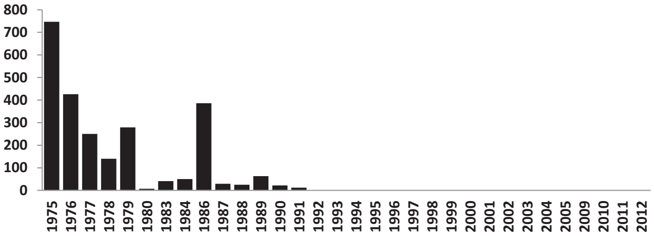

Figure 9. Numbers of sandhill cranes recorded on the Carrizo Plain Christmas Bird Count, California, 1970-2012.

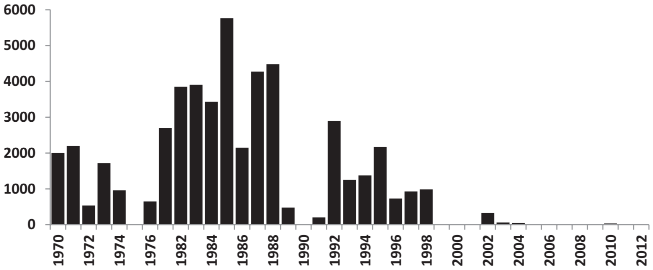

Figure 10. Numbers of sandhill cranes recorded on the Red Bluff Christmas Bird Count, California, 1975-2012.

assessment of the reduction in numbers at this site (Figure 9). The decline is probably due to the elimination of 16,000 ha of grain crops that were cultivated within the Monument prior to the acquisitions as well as the overall decline of cultivated grain fields in the valley and the foothills adjacent to the Monument (BLM 2010). It is not likely that this area will recover its former importance to cranes given that the Monument is now managed primarily for threatened and endangered arid upland wildlife species and because of the paucity of grain-farming elsewhere in the region.

Red Bluff.–This site is in the vicinity of Jellys Ferry, between Anderson and Red Bluff, along the Sacramento River. In 1970, 1,400 lessers were reported here (Littlefield and Thompson 1982). Another report states that up to 500 sandhill cranes were observed in this location in the 1970s and 1980s (Pogson and Kincheloe 1981), with birds roosting in the Table Mountain area and foraging north to the Anderson Bottoms and south to the Antelope Creek and Cond Ranch area (Littlefield 2008). However, sandhill crane use here has diminished since the early 1990s, for reasons unknown, as evidenced by CBC data which last recorded sandhill cranes in 1991 (Figure 10). Yet cranes have been reported here in more recent years (B. Deuel, personal communication; eBird data). Most recent sightings are relatively small flocks observed in late February or early March, during the period when sandhill cranes begin moving north, so the area apparently serves as a stop-over site for some spring migrants.

DISCUSSION

The Central Valley is the most important sandhill crane wintering area in the Pacific Flyway. Although this paper provides evidence for winter range expansion and an increasing population trend for sandhill cranes wintering in the valley, it is important to understand that cranes only use a small percentage of the available agricultural landscape. Given their strong fidelity to wintering sites (Ivey et al. 2015), continued loss of foraging habitats within their current range may reduce resources needed to support the size of the population. Therefore, it is important to focus activities on maintenance of suitable landscapes in this important sandhill crane wintering area.

The Sacramento Valley region is of particular importance to greaters (G. Ivey, unpublished data). In the early 1980s, undisturbed, secure night roost habitat was the significant limiting factor for sandhill cranes in that region (J. Snowden, personal communication), and we believe that this limitation contributed to the smaller winter sandhill crane landscape during that time. Legislation in 1991 (Connelly-Areias-Chandler Rice Straw Burning Reduction Act: AB 1378, Ch. 787, 1991) limited burning of rice stubble and resulted in greatly increasing the practice of flooding to decompose stubble (Miller et al. 2010). We believe this change allowed sandhill cranes to extend their winter range considerably in that region. Also, sandhill crane numbers have increased in the Sacramento Valley, as evidenced by the increasing trend of mid-winter survey numbers (USFWS, unpublished data), which likely has contributed to their range expansion there. However, even though there are extensive areas of flooded rice for sandhill cranes to choose from, most flooded rice fields are subject to disturbance from waterfowl hunting (Fleskes et al. 2005) and the majority are managed at water levels too deep to provide ideal roost site conditions (Shaskey 2012). It is likely that there is lower hunting pressure on private lands where we found concentrations of sandhill cranes during this study, leading to lower disturbance. Reduced disturbance due to hunting should allow more successful conservation of sandhill cranes in these areas.

Two necessary components of sandhill crane winter range include: 1) suitable, undisturbed roost sites, and 2) sufficient nearby foraging habitat (Ivey et al. 2014). A secure roost site is critical to sandhill crane wintering range because this dictates access to available foraging habitats. Without it, the birds will abandon those landscapes. Additionally, greaters in the CVP are very loyal to their wintering site, which makes them less adaptable to change compared to lessers (Ivey et al. 2015). Therefore, conservation of roost sites of greaters should be a priority. Because of energetic costs, foraging sites close to roost sites are more important to cranes than foraging sites more distant.

A suitable roost site and the associated foraging areas radiating out to a certain distance from the roost form a conceptual framework for thinking about “landscape units” as a basis for sandhill crane conservation (Ivey et al. 2015). The scale of effective conservation planning differs by subspecies. For greaters, focusing on a conservation radius within 5 km of a known roost was recommended. This radius encompassed 90% of the foraging flights made by greaters. For lessers, a conservation radius of 10 km was recommended (90% of their flights; Ivey et al. 2015). Ivey et al. (2015) recommended that management, mitigation, acquisition, easement, planning, and farm subsidy programs intended to benefit sandhill cranes will be most effective when applied at those scales, and that conservation and management of wintering habitats should include creating both new roost and feeding areas within these radii to ensure high chances of successful use. Developing new roost sites toward the edge of these crane landscape units will allow sandhill cranes access to additional agricultural fields and increase their winter range carrying capacity (Ivey et al. 2015).

In the Delta and San Joaquin Valley regions, most of the important roost sites are protected, as they occur on NWRs, state wildlife areas, and natural area preserves and conservation easement lands. In contrast, in the Sacramento Valley region, most existing roost sites currently occur on private lands where they are susceptible to conversion to unsuitable crops, incompatible farming practices (e.g., deep flooding), increased disturbance, and loss of irrigation water that prevents crop production and/or post-harvest flooding (i.e., due to drought). In addition, in all Central Valley sandhill crane wintering regions, their foraging areas are primarily on private lands (Littlefield 2002, Ivey and Herziger 2003, Shaskey 2012). These private lands are subject to loss from urbanization and conversion to incompatible crops, and also are not typically managed to optimize food availability to sandhill cranes. Habitat changes that occur on privately owned fields within the daily flight radius of a sandhill crane may change crane abundance at a roost, regardless of management actions at the roost site itself.

Existing wintering sites are threatened by habitat loss, which is occurring throughout the Central Valley. Habitat losses are primarily due to conversion of private lands to incompatible crop types (e.g., vineyards and orchards) as well as expanding urbanization (Littlefield 2002, Ivey et al. 2015). In the Delta, sea level rise may destroy significant areas of sandhill crane wintering habitat in the future, and generally the effects of climate change may limit future water supplies to critical sandhill crane roost sites throughout the valley. Other threats to sandhill crane habitat include development projects such as new water delivery systems and solar farms and the associated powerlines that serve them. Excessive disturbance (primarily from waterfowl hunting) can also reduce habitat availability to sandhill cranes. Additionally, some sandhill crane foraging habitat loss has occurred due to riparian forest and shrub plantings.

MANAGEMENT IMPLICATIONS

We recommend the following conservation strategies (listed in priority order) be implemented to maintain crane use in each major sandhill crane wintering region: 1) protect existing, unprotected roost sites by fee-title acquisition or conservation easements (prioritize by their importance to greaters); 2) protect foraging landscapes around existing roosts, primarily through easements restricting incompatible crop types and development; 3) enhance food availability within those landscapes by improving conditions on conservation lands and providing annual incentives for improvements on private lands; and 4) develop additional protected roost sites toward the edge of existing crane use areas to allow sandhill cranes to access additional foraging areas.

Prioritizing Among Wintering Sites

We recommend prioritizing conservation among winter regions based on the relative risk of habitat loss, the relative number of threatened greaters present, and the relative number of all sandhill cranes present.

Sandhill crane habitat loss is occurring throughout the Central Valley, primarily due to conversion to incompatible crop types (e.g., vineyards and orchards) as well as expanding urbanization, both of which pose a threat to these populations (Littlefield 2002). Conservation and management of wetlands and agricultural areas within Central Valley crane wintering regions is important. Although we are not aware of any detailed analyses of habitat loss for sandhill cranes, the Delta is certainly under the greatest threat due to pressures from expanding urban areas and is losing habitat to incompatible permanent crops faster than other regions (Central Valley Joint Venture 2006). Also, this region has the threat of sea level rise (which will likely eliminate many of the Delta Islands).

We recommend that conservation priority be geared toward the Delta because habitat loss is highest there and it supports the second highest number of greaters and the highest number of sandhills overall (Table 1). Secondly, the Sacramento Valley has the highest number of greaters and third highest number of sandhills overall. Therefore, we propose that the major wintering regions be considered in this priority for conservation focus: 1) the Delta, 2) the Sacramento Valley, 3) the Grasslands, 4) the Pixley NWR area, and 4) the San Joaquin River area. However, it would be good to work simultaneously in all 5 of these regions to maintain their value to wintering sandhill cranes and take advantage of conservation opportunities as they become available.

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Table 1. Peak numbers of greater sandhill cranes and all sandhill cranes counted during surveys of the wintering regions of the Central Valley of California, 1970-2014.

Sandhill crane wintering region	Highest estimate of greater sandhill cranes	Highest estimate of all sandhill cranes
Sacramento Valley	6,000 (1991-93)[a]	7,984 (2014)[b]
Sacramento-San Joaquin Delta	5,219 (1983-85)[c]	27,213 (2008)[d]
San Joaquin River NWR	298 (1971)[e]	4,383 (2012)[f]
Grasslands	110 (1971)[e]	15,275 (2010)[g]
Southern San Joaquin Valley	68 (1970)[e]	9,403 (2009)[h]

[a] Littlefield (2002).
[b] 2014 Mid-winter waterfowl survey (USFWS, unpublished data).
[c] Pogson and Lindstedt (1988).
[d] Ivey et al. (2014).
[e] Littlefield and Thompson (1979).
[f] 2012 Christmas Bird Count.
[g] San Luis NWR files (USFWS, unpublished data).
[h] Pixley NWR files (USFWS, unpublished data).

Guerena), Pixley NWR (S. Ludwig and N. Stanley), and the CDFW office in Sacramento (E. Burkett). W. Cook Jr. provided roost site locations for Los Banos Wildlife Area. Additional historic information was provided by B. Deuel, T. Keldsen, S. Shanks, J. Snowden, and M. Weaver. We thank the late W. Holt for providing information about sandhill crane distribution in the South Delta. Housing was graciously provided by D. McCullough, E. Deel, and San Luis and Stone Lakes NWRs. We also thank R. Kelsey, J. Langenberg, and L. Shaskey for improving this paper with their editorial comments.

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NESTING ACTIVITY BUDGETS AND ANTIPREDATOR BEHAVIORS OF MISSISSIPPI SANDHILL CRANES

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Abstract: We studied activity budgets and antipredator behaviors of Mississippi sandhill cranes (*Grus canadensis pulla*) to determine if parental behavior influenced nest outcomes. We used infrared motion-activated cameras to capture behavioral sequences from 21 nests over a 2-year period. Overall activity budgets were similar among crane pairs regardless of nest outcome. Specific activity patterns did predict nest outcomes; pairs at unsuccessful nests spent more time away from the nest and more time manipulating nest contents than successful pairs, while pairs at nests that were lost to predation cooperated poorly and started the nest a month later on average than successful nests. Wild-reared birds gave more agonistic displays toward potential threats than captive-reared birds, but both wild- and captive-reared birds successfully defended nests from potential predators. The results suggest that behavior patterns of nesting pairs can be used to predict likely nest outcome, and that birds differ in their ability to defend nests from predators. We suggest that training in antipredator behavior during captive rearing may increase behavioral competence and reduce losses to nest predators.

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Key words: behavior, captive breeding, *Grus canadensis pulla*, Mississippi sandhill crane, nest predators, reintroduction.

The Mississippi sandhill crane, *Grus canadensis pulla*, is a morphologically distinctive, non-migratory population of cranes inhabiting a small area of coastal Mississippi (Aldrich 1972). This population has been protected under the Endangered Species Act since 1973 (Gee and Hereford 1995) and has been the subject of a U.S. Fish and Wildlife Service reintroduction program since 1981, representing one of the largest and longest sustained reintroduction programs ever attempted (Ellis et al. 2000). Despite more than 30 years of supplementation with captive-reared cranes, the wild population on the Mississippi Sandhill Crane National Wildlife Refuge has remained stable at approximately 100 adult individuals over this time period.

While several factors may contribute to the limited success of reintroduction to date, including habitat area and quality (Ellis et al. 2000), low genetic diversity (Henkel et al. 2012), and predator pressure (Butler 2009), we also suspected that behavioral competence of nesting cranes may also be a serious impediment to successful breeding. Some breeding pairs on the refuge consistently produce chicks while others do not, and successful pairs frequently contain 1 member that was wild-reared or parent-reared in captivity. Most birds on the refuge were produced through costume-rearing in the captive breeding program, and a variety of behavioral problems are known to arise from altered social environment and learning opportunities during captive rearing (Curio 1998). Nesting birds must master a variety of behaviors critical to success, including cooperation with the mate during incubation, nest maintenance, and nest defense; data on how these behaviors may vary among birds on the refuge are currently lacking.

In this study we asked how behavior patterns differed across nesting pairs over a 2-year period, and how behaviors were related to nesting success. We first asked if the basic activity budgets of nesting pairs were similar regardless of the nest outcome. We then investigated the details of specific behavior patterns to determine if parental behaviors predicted whether a nest would be successful, unsuccessful, or suffer predation. Finally, we focused on antipredator defense behaviors and quantified the types of agonistic displays seen in the population, the frequency with which cranes performed them, and context in which they were given.

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METHODS

The study was conducted on the Mississippi Sandhill Crane National Wildlife Refuge, located 5 km north of Gautier in Jackson County, Mississippi. The refuge encompasses approximately 8,000 ha of pine savannah and flatwoods habitat, managed primarily to maintain high-quality wildlife habitat for Mississippi sandhill cranes (U.S. Fish and Wildlife Service 2007). The refuge currently supports approximately 100 adult cranes; typically, 20-30 nesting attempts occur annually.

We installed motion-sensitive infrared trail cameras (RM 45 Rapidfire, Reconyx Inc., Holman, WI) on 22 nests during 2009 and 11 nests in 2010. To avoid changing the visual horizon close to the nest, cameras were installed on existing landscape features such as small trees whenever possible. A few cameras were installed on steel fence posts that could be concealed by vegetation. Cameras were placed between 2 and 30 m of the nest with a clear field of view of the nest and surrounding area to reduce the triggering of photos by movements of vegetation in the field of view. Data were recorded on 4-gigabyte compact memory cards. Cameras were visited approximately once per week to change batteries or memory cards until the nest was abandoned.

We first developed a nesting ethogram that we used to calculate time budgets and event rates for each nest. We viewed images sequentially for each nest using Windows Photo Gallery in Windows 2007 (Microsoft Corporation, Redmond, WA) and classified behaviors into 1 of 5 states or 5 events (Table 1). States were defined as behaviors for which a duration could be calculated, and states were mutually exclusive. Events were defined as behaviors that could be tallied, and could occur within a state (e.g., an incubating crane could display alert behaviors without interrupting incubation). We calculated the duration of states using the time stamp on each image, and scored the state as occurring continuously until the crane changed to another state. Because we used black-and-white cameras placed at a distance from the nest, we were often unable to identify individuals by their band colors or numbers, and behavioral rates are presented for the pair as a whole. In pairs where 1 individual was unbanded or bore a transmitter, we were able to record the behavior of individual cranes, and these cases are reported as individual records.

Because a behavioral pattern or single incident may be more critical to nest outcome than the overall time budget, we developed additional behavioral measures to use in fitting models to predict nest outcomes. Since time spent off the nest for any reason may affect egg viability, we calculated total time spent off the nest as the sum of Near Nest and Absent. We calculated the mean duration of each of the behavioral states, and recorded the maximum duration of each state. Finally, we added the Julian date of nest initiation to the list of variables, since there is evidence that nests initiated later in the season may experience greater temperature stress and exposure to predation (Butler 2009).

We examined all images of predator and non-predator interactions in detail to identify the frequency of known threat and attack behaviors (Ellis et al. 1998)

Table 1. Behaviors included in ethogram of nesting cranes at the Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010.

Behavior	Definition
States[a]	
Incubate	Crane sits on the nest, otherwise inactive
Probe	Crane stands and manipulates nest or its contents with bill
Near nest	Crane is off the nest but within the camera’s field of view
Preen	Crane grooms feathers
Absent	Neither crane is within the field of view of the camera
Events[b]	
Alert	Crane changes posture to orient head to a stimulus
Exchange crane	One mate takes the place of the other on the nest
Predator interaction	Potential egg predator approaches within field of view of the nest
Non-predator interaction	Non-predator approaches within field of view of the nest
Adjust position	Crane stands briefly and resettles without manipulating nest contents

[a] Percent of total time observed.

[b] Rate per hour of observation.

and their relationship to the outcome of the interaction. The animals encountered were identified whenever possible; if they were not visible or if they were blurred on the image we classified them as unknown. We recorded unambiguous postural threats and movements and classified them into discrete behavioral classes as described in Ellis et al. (1998). Although we relied on still photos, we were able to use photographic sequences to distinguish between static postural threats and agonistic displays involving movement (e.g., wing-spread-hold vs. wing-spread-flap). All statistical analyses were performed in SYSTAT v.13 (SYSTAT Corporation, Redmond, CA). We used 1-way analysis of variance to determine if time budget components and event rates differed among successful, unsuccessful, and predated nests. We classified nests as successful if at least 1 egg hatched, unsuccessful if eggs failed to hatch but were not taken by predators, and predated if eggs were destroyed by predators. To identify behavioral variables that distinguished successful from unsuccessful nests, and successful from predated nests, we fitted models to the data using the expanded set of variables in the General Linear Models module in SYSTAT. The small number of nests available for analysis limited our ability to assess complex models. We first fitted single-variable models and used those with the lowest values of Akaike's Information Criterion (AIC) to further investigate a limited set of models with 2 or 3 variables.

RESULTS

We obtained 14 complete nesting records (cranes re-occupied the nest after camera installation and a definitive outcome was recorded) in 2009 and 7 in 2010. Cranes abandoned the nesting attempt shortly after camera installation in 4 cases, while in 8 others technical problems with cameras resulted in failure of recording before the fate of the nest could be determined. Of the 21 complete records, 3 nests were lost to flooding in 2009 and were excluded from analysis.

We analyzed over 330,000 images acquired over 7,160 hours of recording from all 33 nests at which cameras were installed; mean observation time for the 18 nests included in this study was 278 ± 47 hours (±1 SE). Of the 18 nests for which an outcome was definitively identified, 10 nests were successful, hatching at least 1 egg, while 3 were unsuccessful and 5 were predated. Not surprisingly, due to nest abandonment, unsuccessful and predated nests were observed for shorter periods of time overall (154 ± 69 hr and 175 ± 53 hr, respectively) than successful nests (367 ± 68 hr). However, this difference was not statistically significant ($F_{2,15} = 2.629$, $P = 0.105$).

None of the 5 states that made up overall time budgets for nesting cranes differed significantly among successful, unsuccessful, and predated nests (Table 2). Similarly, none of the 5 event rates calculated differed significantly among nests. The 2009 Ben Williams pair,

Table 2. Behavior related to nest outcome[a] of sandhill cranes at the Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010.

Behavior	Successful (n = 10)		Unsuccessful (n = 3)		Predated (n = 5)		$F_{2,15}$	P
	Mean	SE	Mean	SE	Mean	SE		
States[b]								
Incubate	92.1	3.0	93.0	2.8	82.7	9.2	0.999	0.392
Probe	4.0	2.6	1.3	0.6	1.9	0.94	0.312	0.737
Near nest	0.6	0.2	0.3	0.2	11.0	8.2	2.213	0.144
Preen	0.9	0.5	0.2	0.1	0.8	0.36	0.335	0.720
Absent	2.4	1.3	5.2	3.2	3.6	1.52	0.577	0.574
Events[c]								
Alert	1.29	0.7	0.15	0.06	7.69	7.04	1.626	0.230
Exchange crane	0.11	0.05	0.01	0.01	0.01	0.01	0.353	0.708
Predator interaction	0.01	0.01	0.01	0.02	0.00	0.00	0.450	0.656
Non-predator interaction	0.15	0.14	0.00	0.01	0.02	0.02	0.318	0.732
Adjust position	0.24	0.15	0.01	0.01	1.95	1.83	3.083	0.078

[a] Successful = Hatched at least 1 egg. Unsuccessful = eggs did not hatch but were not taken by predators. Predated = eggs destroyed by predators.

[b] Percent of total time observed.

[c] Rate per hour of observation.

whose nest was eventually predated, behaved very differently from all other pairs. In particular, this pair spent less time incubating and more time near the nest than other pairs and also had high rates of alert and adjust position. However, the behavior of this single pair was not sufficiently aberrant to produce significant differences between time budgets of predated and other nests (Table 2).

The best fit model predicting successful vs. unsuccessful nests included mean time off the nest and mean time probing the nest (Table 3). Three other models that received some support (δAIC = 2) included some combination of these variables and alert rate and maximum time preening. Pairs on unsuccessful nests averaged 63 minutes off the nest whenever they were not incubating, while those on successful nests averaged only about 9 minutes off the nest when not incubating (Figure 1). Pairs on unsuccessful nests spent an average of 3 minutes at a time probing the nest, while pairs on successful nests spent an average of only 2 minutes at a time probing the nest.

The best fit model predicting successful vs. predated nests included Julian date of initiation and rate at which cranes exchanged position on the nest (Table 3). One other model that received support (δAIC = 2) included Julian date, exchange rate, and percent of the total time spent off the nest. Predated nests were initiated nearly a month later on average (3 May) than successful nests (6 April) (Figure 2). Pairs on predated nests were also observed to exchange incubation duties at much lower rates than pairs on successful nests.

Descriptions of Nest Defense Behaviors

We counted 208 individual agonistic displays during the study (Table 4). The pre-attack droop wing display accounted for 75% of all agonistic displays and wing-spread-hold/wing-spread-flap displays accounted for another 13.5%. Run-flap, tertial elevation, and strut accounted for most of the remainder, and a single jump-rake display was also observed. The distribution of agonistic displays was uneven; 11 pairs used a recognizable threat display or aggressive behavior while 7 never displayed any agonistic behavior during the study. Eight pairs used the pre-attack droop wing display, and 6 of these exhibited at least 1 additional agonistic display.

We recorded 108 interactions between nesting

Table 3. Best-fit models distinguishing successful vs. unsuccessful and successful vs. predated sandhill crane nests[a], Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010.

Model	δAIC
Successful vs. unsuccessful nests	
Mean time off nest + mean time probing	0
Mean time off nest + max. time preening + alert rate	2
Mean time off nest + mean time probing + max. time preening	2
Mean time off nest + mean time probing + alert rate	2
Successful vs. predated nests	
Julian date + Exchange rate	0
Julian date + Exchange rate + percent of total time off nest	2

[a] Successful = Hatched at least 1 egg. Unsuccessful = eggs did not hatch but were not taken by predators. Predated = eggs destroyed by predators.

Table 4. Agonistic behaviors displayed by crane pairs at 18 nests at the Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010. Descriptions after Ellis et al. (1998).

Behavior	Description	Number of observations	Pairs exhibiting
Pre-attack droop wing	Crane advances with wings spread and primaries lowered to touch vegetation	156	8
Wing-spread-hold	Crane stands with wings lifted and held extended	20	6
Run-flap	Crane rushes at intruder while flapping wings	11	9
Wing-spread-flap	Crane stands with wings extended and flapping	8	3
Tertial elevation	Tertiary feathers are elevated over back	6	2
Strut	Crane turns sideways to intruder and walks in slow, measured steps	6	3
Jump-rake	Crane leaps into the air and slashes with talons	1	1

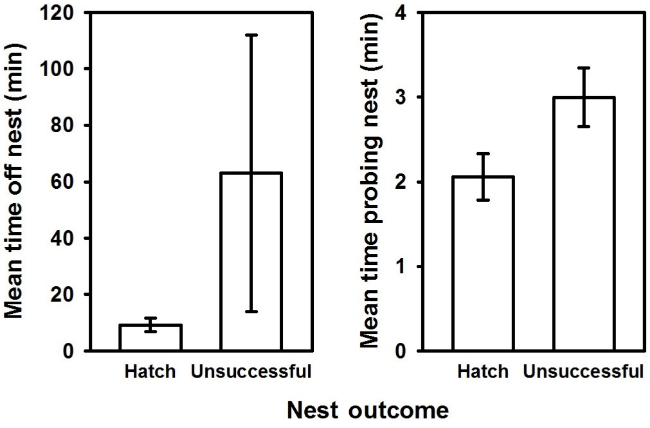

Figure 1: Parental behavior patterns distinguishing sandhill crane nests that produced chicks from nests that were unsuccessful but not predated, Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010. Histogram bars are mean ± SE.

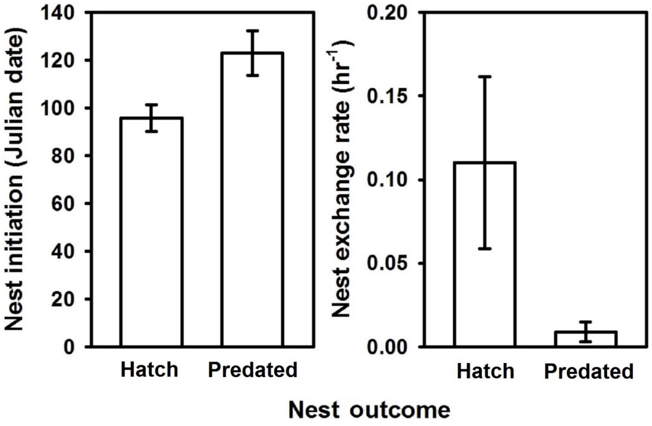

Figure 2: Parental behavior patterns distinguishing sandhill crane nests that produced chicks from nests that were lost to predation, Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010. Histogram bars are mean ± SE.

cranes and other animals; of these, 45 animals were identifiable while 63 were not visible in images. Three nests accounted for 78 of the 108 interactions, while the other 15 accounted for the remaining 30. Cranes encountered humans 8 times, and temporarily abandoned nests to avoid contact; in each case cranes returned to the nest within 4 hours after humans left the vicinity. Cranes encountered non-predatory animals 26 times and ignored them 24 times, giving agonistic displays in only 2 cases. One nesting pair encountered a second crane pair moving through their nest site, and 1 of the resident cranes displayed erect tertial feathers combined with a strut display until the transient pair moved away.

Interactions with known predators were often more complex and protracted than those with non-predators. Cranes at 5 nests interacted with visible predators in 10 instances: 2 owls (*Bubo virginianus*), 3 crows (*Corvus brachyrhynchos*), and 5 raccoons (*Procyon lotor*). Crows were easily intimidated by cranes simply approaching or displaying; crows left after a strut threat by 1 crane, a run-flap threat by another, and a wing-spread-flap threat by the third. One owl left after a single run-flap threat by the resident crane, but the other persistently attacked the single crane on the nest and was driven off after 22 minutes, during which the defending crane gave multiple pre-attack droop-wing and wing-spread-flap displays and knocked the owl into the surrounding pond during a jump-rake attack. Raccoons were both persistent and opportunistic; 1 nest was attacked on 3 different nights, during which the raccoon repeatedly approached the nest over periods ranging from 3 to 11 hours. The crane on this nest successfully defended on each of the 3 nights, displaying numerous pre-attack droop wing displays each time. However, raccoons destroyed 2 other nests with no effective defense from nesting cranes; at 1 the crane left the nest when the raccoon approached and at the other the crane stood nearby showing alarm but no defensive behavior. The successful defense was by an unbanded, presumably wild-reared crane, while the 2 ineffective defenders were both known costume-reared birds.

Cranes at 10 nests reacted in some way at least once to unidentified intruders. Cranes gave recognizable agonistic displays in all but 1 case, with the pre-attack droop wing displayed 43 times and the wing-spread-flap displayed on 13 occasions. Three nests accounted for 84% (53 of 63) of recorded events. In 2 of these 3 nests, 1 member of the pair was unbanded and wild-reared, and these individuals accounted for 68% of agonistic displays (21 of 31). At the third nest both members of the pair gave threats, but the female of the pair, a known costume-reared bird, accounted for a majority of agonistic displays.

DISCUSSION

Our data suggest that nesting Mississippi sandhill cranes have similar overall time budgets regardless of nest outcome. However, specific behavior patterns varied widely among nesting pairs and individual cranes, and some were predictive of nest outcomes.

The heterogeneity of behavior among members of this population may reflect their diverse origins; while most cranes in the study were costume-reared, some were parent-reared in captivity and still others were produced through natural reproduction on the refuge. The range of behaviors exhibited in this population may provide useful management indicators of prospective nest outcomes, while the diversity of rearing methods and learning opportunities experienced by cranes may allow rearing strategies that promote desirable reproductive outcomes to be identified and more widely implemented.

Detailed behavior patterns distinguished among nests that did not successfully hatch eggs or were predated and nests in which chicks successfully hatched. Cranes at unsuccessful nests spent extended periods of time away from the nest compared to those at successful nests, although it is not clear whether extended absences might have caused eggs to become inviable from insufficient incubation or might instead have resulted from a lack of cues from eggs that might promote attachment. Cranes at unsuccessful nests also spent significantly more time manipulating nest contents, perhaps in response to a lack of expected cues from eggs. The exact biological significance of these behavior patterns was not clear in this study, although they provide clear signs that a nest is likely to be unsuccessful, and that may be useful in managing crane populations.

The low rate of incubation switching among partners was strongly associated with nest predation. The failure of partners to cooperate in incubation may reflect poor attachment within the pair, and this might be a particular problem with young or inexperienced breeders. However, some pairs at predated nests are known to have nested in years prior to the study and were not completely naive. The cumulative stress of incubation for long periods without relief may predispose birds to leave the nest at critical times, and this interpretation is consistent with the inclusion of percent of total time off nest as a factor in the second-best supported model. The later start date of predated nests may be in part due to poorly attached pairs requiring extra time for bonding, or to re-nesting after an initial failure. Late-starting nests may be more vulnerable to predation due to higher predator activity rates or to vegetation growth providing more cover for predators later in the growing season. While the mechanisms underlying these patterns remain to be investigated, the combination of poor coordination among pair members and a late nesting date is a clear indicator of elevated predation risk.

Individuals and pairs varied greatly in their display repertoires and competence in defending nests, and the passivity of many birds to potential threats may be an important mechanism underlying poor nesting success in the refuge population. All pairs showed similar rates of alert behavior except for 1 hyper-vigilant pair, but few birds responded to potential danger with agonistic displays or attacks. Over a third of all pairs never made a threat display of any kind in response to any cue, and only 3 pairs accounted for a majority of threats directed at unknown cues. While it is possible that cues perceived by some pairs never indicated a danger requiring a response, observations of interactions with known predators suggest that some pairs did lack the ability to respond competently to threats in defense of the nest. The 2 instances in which cranes were present at the nest but took no action or left in response to egg predation by a raccoon clearly indicate that some birds lack the skills required to defend the nest. It is notable that these 2 pairs gave agonistic displays in other circumstances. Both gave pre-attack displays and run-flap or wing-spread-flap displays to perceived threats that were not captured on camera but failed to use them appropriately when confronted with a potential predator closely approaching the nest. This suggests that in some cases birds can perform appropriate defense behaviors but do not perform them in the proper context.

In contrast, other birds on the refuge did exhibit a large number of known agonistic displays and some employed them effectively in nest defense. Although our sample size is small, wild-reared birds appeared particularly aggressive toward unknown cues and persistent in nest defense. Competence was not limited to wild-reared birds, as costume-reared crane no. 337 was consistently aggressive to cues from perceived threats that were not visible on camera, and 1 member of a costume-reared pair mounted a sustained and effective defense against owl attack.

We suggest that competence in nest defense depends on social learning during development (Griffin 2004) and that the current refuge population has not had equal opportunity to learn appropriate displays or the context in which they must be given. The competence of wild-reared birds suggests that they likely observe the behavior of their parents during the pre-fledging period, learn which animals pose a threat, and learn how to use aggressive displays to deter them.

The fact that some costume-reared birds were highly competent suggests that these behaviors can be learned after fledging and release, but it is not clear whether naive birds must observe competent ones or gain their skills through trial and error, or how much experience may be required to become competent. It also seems likely that poor nest defense is a greater problem when confronting mammalian mesopredators than avian predators. Cranes effectively defended against crows and owls in all cases observed, and lost eggs only to raccoons during the study.

We propose that giving pre-fledging captive-bred chicks greater opportunity to learn common mammalian mesopredators, aggressive displays, and the context in which they are useful will help more birds learn skills required for nest defense after release. A pilot study to teach Mississippi sandhill cranes predator avoidance has been carried out with promising results (Heatley 2002), and although the methods developed in that study were not implemented in the rearing program, they provide a clear path to designing a program to condition nest defense behaviors. A number of captive breeding programs have used instruction in predator recognition and avoidance to improve survivability of released animals (Griffin et al. 2000), although cranes would require the modeling of appropriate aggressive behaviors rather than simple avoidance. Captive parent-reared chicks may be able to observe parental defensive behavior if their parents are themselves competent and are deliberately challenged by an appropriate mesopredator. Costume-reared chicks may benefit from having costumed personnel model threat displays in response to mammalian predators, perhaps adding realism to the relatively shapeless costume by utilizing wings from deceased birds or wings constructed to resemble them.

Some training programs for captive-bred animals have succeeded in teaching predator avoidance behavior using models such as stuffed predators or plush toys (McLean et al. 1999, Griffin and Evans 2003, Shier and Owings 2007) and this may provide a safe way to condition captive chicks without the risk of exposing them to actual danger. However, training programs will have to be carefully designed to promote learning of only appropriate cues and to avoid conditioning birds to irrelevant stimuli that are incidental to the training (e.g., specific movement patterns of models, unnatural noises, objects required to present stimuli). It is currently not known how many trials might be required to learn cues and responses, whether inanimate models would be effective, or whether cranes are capable of generalizing from 1 model to other mesopredators, so the complexity of a training system would have to be established through trial and error. This will present a significant challenge to current rearing methods, but improving viability of captive-reared birds after release would help advance the ultimate goal of creating a self-sustaining wild population.

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THE UTILITY OF CENSUS OR SURVEY FOR MONITORING WHOOPING CRANES IN WINTER

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Abstract: We discuss recent changes in the monitoring program for endangered whooping cranes (*Grus americana*) on their winter habitat in Texas. A 61-year annual census was replaced in the winter of 2011-2012 with a distance sampling procedure. Justification for the change was, in part, based on criticism of the previous methods of counting cranes and the assessment of crane mortality on the wintering grounds. We argue here that the arguments, methods, and analyses employed to discount the census procedure and mortality estimates were applied incorrectly or with flawed logic and assertions. We provide analysis and logical arguments to show that the census and mortality counts were scientifically valid estimates. The distance sampling protocol currently employed does not provide the accuracy needed to show small annual changes in population size, nor does it provide any estimate of winter mortality. Implications of the relative merit of census and mortality counts versus distance sampling surveys are discussed in the context of management of the whooping crane.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:75-84

Key words: causation, census, distance sampling, endangered species, *Grus americana*, population count, whooping crane.

The only naturally remaining endangered whooping crane (*Grus americana*) population has been monitored since 1938 on its sole winter habitat in and around the Aransas National Wildlife Refuge (hereafter Aransas) in Texas (CWS and USFWS 2007). The population, with a low of just 15-16 birds in 1941, has increased to an estimated 338 birds in 2015 (Butler and Harrel 2016). For 61 years (1950 to 2010) census flights were conducted annually by refuge biologists in order to track changes in abundance and guide progress toward recovery. The census was designed to count, as completely as possible, the total population of wintering cranes, estimate winter mortality, and document habitat use (Stehn and Taylor 2008). Beginning in the winter of 2011-2012, U. S. Fish and Wildlife Service (USFWS) personnel discarded the census protocol in favor of a distance sampling (Buckland et al. 1993) procedure as per the general recommendations for wildlife estimates of the National Wildlife Refuge System inventory and monitoring initiative. In doing so, they abandoned the notion of a population count and opted instead for a statistical estimate of crane abundance with confidence intervals. We are unaware of any criticism of the former census methods until the inventory and monitoring initiative was implemented.

The justification to shift whooping crane population monitoring to a sampling protocol from the census method centered around 3 perceived problems (Strobel et al. 2012; Butler et al. 2013, 2014*a*, 2014*b*). First, the census was stated to lack validity because it was possible to both miss individuals and double-count individuals (i.e., the census was not a complete count or enumeration). Second, the census method was perceived to be biased in the manner in which the aerial count was conducted. Third, estimates of mortality during the wintering period were claimed to be inaccurate and biased. All of these perceived shortcomings were alleged to invalidate the census method. We address each of these criticisms here. We present data analysis that demonstrates that the population census closely matched another key indicator of abundance, the nest count on the summer breeding grounds in Canada. In addition, we present methodological arguments and new analyses that refute the assertions that census and mortality estimates were invalid measures. Finally, we address the logic and validity of the criticisms leveled at the census method and the analyses that were used to make them.

METHODS

We compared the census results (population size) from 1966 to 2010 (n = 45) to nesting pair counts obtained by the Canadian Wildlife Service (CWS) on the breeding grounds in Wood Buffalo National Park, Canada, the following summer. Census methods are described in detail in Stehn and Taylor (2008). Nest count data from 1966 to 2005 can be found in the

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Canadian Wildlife Service and U.S. Fish and Wildlife Service international recovery plan for the whooping crane (2007), and from 2006 to 2010 in annual reports of the Canadian Wildlife Service, Prairie and Northern Wildlife Research Centre, Saskatoon, Canada.

Using linear regression, we estimated the relationship between the number of wintering adults and total nest count. We calculated a Durbin-Watson *D* statistic (Neter et al. 1985) to assess autocorrelation among regression residuals.

Mortality data and methods are described in detail in Stehn and Haralson-Strobel (2014). Mortality was assigned when 1 individual of a known group, usually a mated pair or pair with offspring, was determined missing after follow-up attempts failed to locate it. We compared total winter mortality estimates (hereafter referred to as Mortality) of whooping cranes from the winters of 1958-59 to 2010-11 to the number of census flights flown over the crane wintering period (n = 53). We did not include data from 1951 through 1957 because the total number of flights and whether data on mortality were obtained by aerial census or by ground search could not be determined from historical records of that period. Mortalities discovered by means other than aerial flights (e.g., ground reports) were excluded. Flights were conducted from October through April and often into May each wintering season. Number of flights computed using all flight data are referred to as Total Flights (TF). Occasional waterfowl survey flights with whooping crane observations made incidentally during the flight were excluded. Additional partitions of the TF data were analyzed: (1) TF-ZC – Total Flights minus flights where zero cranes (ZC) were found, (2) TF-NC – Total Flights minus flights in which there was no chance of detecting mortality (e.g., only a few subadult cranes and no family groups were present at Aransas), (3) TF-DM – Total Flights within the period from December through March (DM), and (4) FWS-DM – Total DM Flights published by Butler et al. (2014*a*). The number of December through March flights published by the USFWS differs slightly from our count. These additional partitions allowed us to exhaustively search for a relationship between the number of flights and Mortality with subsets of the TF data that could have been superior to the complete data set, and in the case of FWS-DM, to mimic the data set used by Butler et al. (2014*a*).

Using linear regression, we estimated the relationship between Mortality and the number of flights per winter and subsets of that variable described above. We also computed a ratio of total winter mortality by population size (MRatio) and performed the same set of regressions on this variable. In some analyses, we partitioned the data to analyze the periods 1982-83 to 2010-11 (n = 29) when data were collected by the same observer. Multiple regression and correlation analyses were performed on mortality, flight number variables, year, and population size in order to examine potential confounding variables that might affect the interpretation of Butler et al. (2014*a*) that the number of flights biased the mortality estimate. Data were analyzed with SAS (2008) PROC REG, and PROC CORR.

RESULTS

The number of nesting pairs located in the cranes' Canadian breeding grounds was highly associated with the previous winters' population census in Texas (r^2 = 0.94; $F_{1,44}$ = 674.69, $P \leq 0.001$) (Figure 1). A Durbin-Watson *D* statistic value of 2.03 indicated that there was no first-order auto-correlation among residuals of the regression analysis.

All linear regressions between mortality and the number of flights for the wintering periods 1958-1959 to 2010-2011 were significant (TF r^2 = 0.12, $F_{1,52}$ = 6.98, P = 0.011; TF-ZC r^2 = 0.12, $F_{1,52}$ = 6.70, P = 0.013; TF-NC r^2 = 0.11, $F_{1,52}$ = 6.31, P = 0.015; DM r^2 = 0.11,

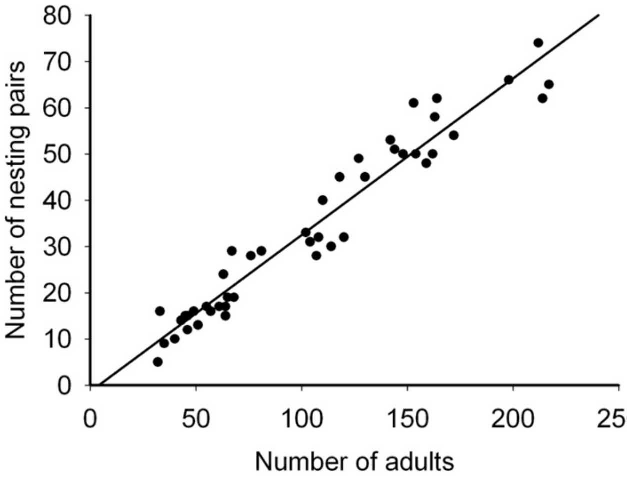

Figure 1. Plot and regression line of the yearly winter census of whooping cranes at Aransas National Wildlife Refuge, Texas, versus nesting pair counts in Wood Buffalo National Park, Canada, during the summer following the census, 1966-2010.

$F_{1,52} = 6.64$, $P = 0.013$; FWS-DM $r^2 = 0.08$, $F_{1,52} = 4.60$, $P = 0.037$). The number of mortalities declined with increasing number of flights. There were significant intercorrelations among the mortality estimate, number of flights, population size, and year (Table 1). Mortality decreased with number of flights, and increased with population size and year of study. The number of flights was inversely related to the population size and year of study, with correlation coefficients approximately twice the size of that of mortality with other variables. As the years of the study progressed and the population size increased, the number of flights declined. Substitution of the other Flight Number variables in Table 1 resulted in no material differences in the magnitudes or directions of correlations reported there.

Linear regression analysis of the ratio of mortalities to population size with the number of flights was not significant (MRatio $r^2 = 0.0$, $F_{1,52} = 0.09$, $P = 0.762$). Similar non-significant results were obtained on all measures of number of flights.

Multiple regression of the dependent variable Mortality with independent variables Total Flights (TF), Population Size, and Year was significant (Mortality $r^2 = 0.20$, $F_{3,52} = 3.97$, $P = 0.013$). The t-values and significance levels for independent variables were: TF $t = -0.28$, $P = 0.782$; Population Size $t = 1.79$, $P = 0.080$; Year $t = -1.25$, $P = 0.216$.

All linear regressions between Mortality and measures of the number of flights for the wintering periods 1982-83 to 2010-11 were non-significant (TF $r^2 = 0.08$, $F_{1,28} = 2.43$, $P = 0.130$; TF-ZC $r^2 = 0.07$, $F_{1,28} = 2.29$, $P = 0.142$; TF-NC $r^2 = 0.06$, $F_{1,28} = 1.91$, $P = 0.179$; TF-DM $r^2 = 0.11$, $F_{1,28} = 3.03$, $P = 0.093$; FWS-DM $r^2 = 0.08$, $F_{1,28} = 2.32$, $P = 0.139$). Total Flights decreased with population size (Pearson $r = -0.74$, $P \leq 0.001$) and with year (Pearson $r = -0.68$, $P \leq 0.001$).

Linear regression analysis, for the periods 1982-83 to 2010-11, of Total Flights with the ratio of mortalities to population size was not significant (MRatio $r^2 = 0.05$, $F_{1,28} = 1.32$, $P = 0.260$). Similar non-significant results were obtained on all measures of the number of flights.

Table 1. Pearson correlations (at $P <$ significance level) among relevant variables in the yearly census ($n = 53$) of whooping cranes, Aransas National Wildlife Refuge, Texas, winters 1958-59 to 2010-11.

	Mortality	Flights	Population size
Mortality			
Flights	−0.35 (0.01)		
Population size	0.41 (0.01)	−0.74 (0.001)	
Year	0.35 (0.01)	−0.68 (0.001)	0.96 (0.001)

DISCUSSION

Population Census versus Distance Sampling

Claims have been made that those conducting whooping crane censuses prior to and including winter 2010-11 assumed that they were doing a complete census (Strobel et al. 2012, Strobel and Butler 2014) and that these results are, therefore, not scientifically valid. However, Stehn and Taylor (2008) explicitly detailed the potential sources of error that may have influenced the population count's accuracy and, to our knowledge, no claim of a complete enumeration was ever made in any publication or official documentation of the whooping crane censuses. The USFWS has taken a strict definition of a census to be a complete count of all individuals in the population, as have other authors (Conroy and Carroll 2009). As such, they cite potential for errors in the census as reason to discount the method as flawed. However, censuses that are not complete enumerations are routinely performed to monitor animal abundance (e.g., Pugesek et al. 1995, Bibby et al. 2000, Ross and Reeve 2003), including for some species that are far more elusive, secretive, and difficult to observe in the wild than are wintering whooping cranes (e.g., Guschanski et al. 2009). Unfortunately, the USFWS chose to discount the validity of the population census by claiming that the most extreme definition of a population census is the only valid one.

In arguing that the distance sampling method is superior to the census method (Strobel et al. 2012; Butler et al. 2013, 2014*b*; Strobel and Butler 2014), the USFWS failed to recognize that a population census and a sample are 2 distinctly different methods with different data requirements (Gregory et al. 2004). A population census does not require unbiased sampling procedures to "estimate" the population because it is not a statistical sample and therefore does not require for its validity a rigorous set of procedures that are precisely repeated (Ross and Reeve 2003). Instead, the population census "counts" used a systematic and thorough aerial coverage of the wintering area to locate nearly all birds in the area with remarkably consistent search effort, area covered, and results from week to week.

Perhaps it would do well at this point to demystify the situation for the reader. We are considering here a search of a specified area of low-lying vegetation for a conspicuously colored white, red, and black bird standing upwards of 1.5 m tall. The animals are readily distinguished from their habitat, thus making them quite amenable to a census count procedure. There is simply no place for a whooping crane to "hide" from the census aircraft unless it leaves the census area, and whooping cranes rarely leave the census area (Stehn 1992). With a species this easily detected at long distances from the observer, we question the necessity of distance sampling. The USFWS provided no scientific evidence that the population census method was inaccurate and relied instead on a specious argument. The USFWS claimed as their proof that the census method was flawed is that they obtained a poor detectability of 0.558 in their attempts to analyze census data using distance sampling techniques (Strobel and Butler 2014). They then concluded that a census could not possibly be accurate with detectability so low that nearly half the birds were not seen during aerial flights. The low measure of detectability derived by Strobel and Butler (2014) is illogical. In fact, on the 4 census flights used by Strobel and Butler (2014) to calculate detectability, the census methodology reported finding 92.4% and 100% of the cranes estimated present on 2 of those flights (Stehn 2011). The other 2 flights occurred in early December with the migration still ongoing, so no comparison was made between the number of cranes seen and number estimated present. USFWS erred by attempting to derive detectability from census flights when detectability is clearly a measure derived from surveys. There is no reasonable way that the data from the census procedure could be analyzed or the procedure duplicated so that distance sampling estimates of detectability could be calculated. There are simply too many differences between survey and census methods.

It is important to note the differences in the way census flights were conducted versus survey flights utilized for distance sampling estimates. Chief among these differences was that in the census flights, at least twice as many transects were flown in the same area than on survey flights. On census flights, the single observer did not attempt to look into the sun to count birds, and transects were sometimes flown at an angle to the coast to improve the sun angle. In contrast, the survey flights used 2 observers looking out opposite sides of the aircraft, and although they attempted to count during mid-day as much as possible, given the winter sun and the time required to complete the survey, 1 of the 2 observers was undoubtedly hampered by sun glare the majority of the time. Survey results showed detectability, when compared to looking toward the sun, was 2.7 times greater when the sun was overhead, and 3.9 times greater when the sun was at the observer's back (Strobel and Butler 2014), demonstrating a significant advantage for the census methodology where the single observer always looked away from the sun. On census flights, the single observer would look down sun a distance of at least 1,000 meters. In full sunshine, cranes could be detected at a distance of over 1,600 meters (Stehn and Taylor 2008). Transects were usually a maximum of 500 meters apart, narrow enough to enable the observer to detect the same cranes on 2 adjacent transects, an essential practice needed to counter most of the ways to overlook cranes described by Stehn and Taylor (2008). Thus, each area of marsh was viewed at least twice. If there was uncertainty as to what was observed, the census pilot was directed to fly toward sightings and to circle them to verify group size and composition, and to sometimes make simulated landings close to the cranes to observe color bands to identify individual cranes. Also, whooping cranes seen in flight were followed to record the location to which they moved. In contrast, survey flights with transects spaced 1,000 meters apart only examined each area of marsh 1 time, with half of that area seen with the observer looking toward the sun or with the sun only partly overhead. In contrast to census flights, survey flights would not deviate from those lines to check on the identity of birds or determine, in cases of uncertainty, whether cranes were adult or juveniles.

These differences allowed the census flight to achieve, on average, a recount of 95.3% of the estimated number of whooping cranes present on subsequent census flights (Stehn and Taylor 2008), an indicator of detectability of 0.953 and not the 0.558 postulated by Strobel and Butler (2014). The 95.3% recount then provides an estimate of reliability of the census count that would be unattainable were detectability in the census counts actually 0.558.

With repeated census flights of the known wintering area, Stehn and Taylor (2008) concluded that 99% of the population was routinely identified at the wintering grounds. A few additional birds were added to the population total if they were still in migration or were wintering far outside the area flown and there was no reasonable chance they had been present in the area covered during the count. These birds were typically reported by the public and intensively monitored. In food shortage winters with the cranes moving more and spending considerable time on upland areas usually adjacent to their territories (Chavez-Ramirez and Slack 1999), and in winters where the number of census flights was below approximately 8, census accuracy was believed to drop several percentage points. However, by piecing information together from multiple flights on the location of territories and the makeup of the population (number of adults, subadults, and juveniles), we believe that the population estimate was 95-99% accurate.

The close correspondence of the census counts of the number of adults to the number of nesting pairs observed in the subsequent breeding season indicates that the counts were consistent and accurate and that winter territories as described by Bonds (2000) were delineated correctly. The non-significant autocorrelation among residuals indicates that error rates of population estimates were consistent irrespective of population size. In addition, mathematical analysis of changes in population size fit closely with expected values of a small population (Miller and Botkin 1974, Boyce and Miller 1985, Boyce 1987, Link et al. 2003). Only in 2 winters have mathematicians suggested inaccuracies in the counts, both in the 1940s before regular census flights were done.

There are some serious drawbacks to implementing the distance sampling procedure. Our experience conducting census flights tells us that it is necessary to look at all areas at least twice to minimize observer error, and to sometimes circle groups of cranes to detect birds directly under the plane. Using a high-wing aircraft such as a Cessna 172 or 210 creates a blind spot directly in front of the aircraft from the high instrument panel and aircraft engine. Once GPS flight tracking was implemented, experience showed that the most frequent reason for overlooking cranes on a census was that the aircraft flew directly over them. As a consequence, we do not believe that an important assumption of distance sampling has been met, namely, the assumption that 100% of individuals are counted at 0 distance from the transect line (Buckland et al. 1993). Our experience also tells us that the shortened 2-week time frame utilized for distance sampling flights, relative to previous census flights conducted throughout the winter, will likely result in missing late arrivals to the wintering grounds and other dynamics associated with estimating population size that we discuss here, nor will it monitor habitat use throughout the winter.

The census method had a system of detecting cranes outside the typical area flown. As sightings of cranes in unusual areas were reported by the public, the area covered on the census was expanded to include those areas. Nearby areas of unoccupied crane habitat were also occasionally flown to see if the known crane range had expanded. The distance sampling method has a more formal method of covering areas where crane use only occurs occasionally, but may spend substantial flight hours finding very few, if any, cranes. It also does not have the flexibility to respond to cranes being found in any unusual area for a relatively short period of time. For example, the survey protocol (Butler et al. 2014*b*) ignores cranes that may utilize farm fields between the Blackjack Peninsula and Austwell, an area used in multiple years, especially at the end of the fall migration.

Distance sampling does not delineate winter territories or record which pairs are bringing young to Aransas. This limits the ability to estimate an effective population size for whooping cranes to maintain genetic viability over the long-term, information needed to set de-listing criteria for species recovery (CWS and USFWS 2007). We maintain that the survey, as designed, has low utility. The survey protocol goal is to detect a change of 10-15% annual population decline over a 3- to 4- year period (Butler et al. 2014*b*). Conducting semi-annual sampling flights as they suggest (Butler et al. 2013) only exacerbates the situation. The detectability of cranes on USFWS survey flights is so low that 95% confidence intervals of estimates (i.e., ± 39 cranes out of an estimated population size of 329 in the 2015-16 winter) are too wide to be useful as a management tool. The crane population could be declining and the responsible managing agencies would be unaware in the short term of any threats. The Whooping Crane Recovery Team has suggested that the error rate of the abundance survey must be reduced to detect changes of 5% (The Aransas Project vs. B. Shaw et al., memorandum opinion and verdict of the court, 2013). The stated goal of the USFWS for the distance sampling is to be able to detect a 10% change in the population (Sikes 2013). However, in only 8 of the 30 winters between 1980-81 to 2010-11 has the change in population size been greater than 10%. Thus, using the current survey protocol, USFWS will, in a majority of the winters, not be able to detect and document with confidence if population size increased or decreased from the previous winter.

Although the distance sampling survey method is designed for less experienced personnel without knowledge of existing crane territories, it still requires experience identifying whooping cranes from the air (Butler et al. 2014*b*) as well as learning the technology used to record crane presence and location. Having a survey that can be used by less experienced personnel makes it workable, but does not make it better than a census done by an experienced observer. Although the survey requires fewer flights of shorter duration than doing periodic census flights, the survey is conducted during a 2-week period, usually in December, leaving biologists without any monitoring of crane habitat for much of the winter and spring. Crane arrivals of family groups have been documented to occur as late as 20 December (T. Stehn, unpublished data), therefore, some cranes could have arrived after the survey flights were completed in 2011-2016. USFWS contends that the increasing number of cranes and expanding winter range make it necessary to simply sample the population. However, we contend that 1 aircraft working over 2 days, or 2 aircraft working simultaneously could census a population of 600 or more whooping cranes.

Crane Mortality Estimate

Another critical drawback of the new whooping crane survey protocol is that it makes no estimate of winter mortality. We do not know of any mortality estimates made since the survey was initiated, despite Recovery Action 1.1.3 in the Recovery Plan stating the need to determine mortality (CWS and USFWS 2007). Whooping crane carcasses are found only incidentally at Aransas and are few in number compared to mortality estimates based on census methodology. Without these data the USFWS will not be able to relate changes in population size to environmental conditions, such as drought on the nesting grounds or reduced river inflows at Aransas. For example, without the critically important mortality estimates obtained on census flights, the connection between reduced inflows and increased whooping crane mortality would never have been proven in federal court (The Aransas Project vs. B. Shaw et al. 2011).

Collection of winter mortality data enabled researchers to examine the relationship between food abundance and mortality (Pugesek et al. 2013). Butler et al. (2014*a*) criticized the direct measures of food availability (Pugesek et al. 2008, 2013) on the main crane food source, blue crabs (*Callinectes sapidus*), calling it "precarious" to assume that food availability could be measured at 2 nearby locations on the winter habitat. Butler et al. (2014*a*) did not discuss several important facts, and as a consequence, mischaracterized the crab abundance results. There were initially 3 locations sampled, the third location far removed from the first 2 (Pugesek et al. 2008) in a 4-year intensive study. Data were collected monthly from September through mid-April. Statistical and experimental controls were employed to determine the best low-intensity sampling protocol that would accurately measure the abundance of blue crabs and minimize disturbance to the cranes (Pugesek et al. 2008). Once that protocol was developed and tested on the first 4 years of data, the sampling protocol was repeated for another 4 years and used to analyze the relationship between crane mortality and crab abundance published in Pugesek et al. (2013).

Instead of a direct measure of food availability, Butler et al. (2014*a*) chose instead to compare mortality indirectly to several drought indices that they called "surrogates". They claimed that the surrogates encapsulated food availability and several other variables. Butler et al. (2014*a*) provided us with no information as to the construct validity (Bollen 1989) of their "surrogate" measure. In fact, Butler et al. (2014*a*) provided no evidence to suggest that there was any relationship at all between drought indices and the list of variables that they were supposed to measure. Since low construct validity can be a major source of error that can bias the results of regression-based statistics (Bollen 1989, Pugesek and Tomer 1995, Pugesek 2003), we believe that a direct measure of food abundance is the superior approach for investigating relationships with mortality. The logistic regression analyses of Butler et al. (2014*a*) were also problematic in that their sample size of 59 was inadequate for this type of regression. Logistic regressions require large sample sizes with *n* exceeding 200 recommended (Demidenko 2007, Machin et al. 2011).

USFWS made critical errors in their review and criticism of mortality detected on previous census flights (Strobel et al. 2012; Butler et al. 2014*a*,*b*). Butler et al. (2014*a*) falsely claimed that mortality was assigned when it was likely that the whooping crane had simply moved to upland habitat or outside the census area. Thus, according to them, birds were mistakenly counted as dead when they moved to other habitat and the chances of detecting a move back to the original territory increased when more flights were conducted.

In making their claims, USFWS failed to acknowledge some basic elements of whooping crane behavior that were of critical importance in making mortality estimates. Color-banding and radio-telemetry data clearly show the territoriality of wintering whooping cranes (Stehn and Johnson 1987, Bonds 2000). Whooping crane adult pairs establish winter territories that they return to annually (Allen 1952). Offspring remain, with only rare exceptions, with their parents throughout their first winter.

Using the census method allowed delineation of the population into adult pairs, family groups and subadults. When 1 crane was first noted to be missing from a pair or family group, the territory and nearby surrounding areas were searched a minimum of 2 times per flight to make sure the crane was not being overlooked. When not located on 2 consecutive flights, it was declared as a mortality. It is important to note that if all members of a pair or family group were not found on a census flight, this was never recorded as mortality; only single birds were ever declared as mortalities.

There has been only 1 instance of a bird declared as "dead" that reappeared the following fall. This involved a color-banded subadult in the 1989-90 winter, not located in the latter part of the winter, and declared "dead", that was sighted the following winter. Twenty color-banded birds have been declared as mortalities that were never resighted (note that color bands were read during yearly censuses as described above) (T. Stehn, unpublished data).

There are no known examples of a single crane in a mated pair or family group that has split off and moved outside the wintering area as postulated by Butler et al. (2014*a*) when they created their hypothetical category of "lost"; this is an illogical category because pairs or family groups almost never separate during the winter. Individual cranes belonging to pairs or family groups do not move by themselves from territories to upland habitat; the group moves together synchronously out of the territory. Movements of groups from a territory have never been counted as mortalities. Mortality was recorded only when 1 member of a group disappeared from a territory. There are no data supporting the claim that "lost" cranes were simply overlooked due to what was claimed as faulty census techniques (Butler et al. 2014*a*).

A correlation was found between upland use and crane mortality (Butler et al. 2014*a*), but this does not disprove the validity of the mortality estimate. This result, although the product of an analysis with a substandard sample size, would be expected when one postulates that increased use of uplands can be caused by food shortages in the marsh that stresses the population and leads to increased mortality. Also, predation risk from bobcats (*Lynx rufus*) increases with increased use of uplands (Chavez-Ramirez 1996). We believe that correlation is not a result of overlooking cranes on census flights that had moved to uplands as postulated by Butler et al. (2014*a*), since upland areas were thoroughly searched, and also as pointed out previously that individuals from adult pairs and family groups do not wander off by themselves.

Subadults do not have winter territories and may utilize different parts of the winter crane range over time. Also, subadult groups are variable in size and composition over time (Bishop 1984), so having 1 bird absent from a subadult group is not an indication of mortality. As a result, it was more difficult to ascertain mortality in the subadult group and generally only occurred when individuals appeared injured or sick and could not be subsequently located. Since subadults comprised approximately one-third of the population (T. Stehn, unpublished data), the mortality data likely underestimated the true mortality rate.

USFWS criticism of reported mortality is mainly based on their claim of finding an inverse relationship between reported winter mortality and number of flights conducted. This led them to falsely conclude that cranes were simply being overlooked, had left their territories in search of resources elsewhere, or left the census area (Butler et al. 2014*a*). While we believe there is some justification for the *a posteriori* partitioning of the Total Flights data set into subsets that remove flights when no whooping cranes were observed or there was no chance of detecting mortality, we know of no justification for USFWS to partition data to flights between December and March. They offer no explanation as to why they omitted a portion of the flight data or why the flight data were analyzed against mortality data from the entire winter period and included mortality discovered by means unrelated to aerial flights. Mortality as observed during census flights can be detected during periods when cranes are still arriving or departing the wintering grounds and has been documented outside of the December-March time frame. As a consequence, we believe that their entire analysis is invalid and their criticism of detection of mortality on census flights is not justified on this basis alone.

As previously mentioned, sample sizes in logistic regressions published by Butler et al. (2014*a*) were probably only one-third of that necessary to provide stable results. Sampling variation is inversely related to sample size. Inadequate sample size insures greater instability (i.e., departures from reality) among regression coefficients. It is for this reason that we used simple linear regressions in analyses presented here.

Our analysis of the entire Total Flights data set and subsets also indicated significant relationships between number of flights and mortality. Both the population size and year of data collection were also positively related to mortality, a finding that is to be expected. The number of flights was higher during the 1950s because objectives during that time frame included defining the dates when cranes arrived and left the wintering area. The number of flights declined further during the winters of 1982-83 through 2010-11 due to difficulty finding certified contract aircraft, and budget shortages as flight costs increased considerably with more time needed per flight to cover an expanded crane range. A higher number of mortalities would be expected from a larger population, and since year is highly positively correlated to population size we found a significant relationship between mortality and year. Year is likely autocorrelated with mortality, with no causal relationship between the variables.

Our results demonstrate that the number of flights and mortality are also autocorrelated, with no causal relationship between the 2 variables. First, since the number of flights per year declined significantly through time and with increasing population size, the significant relationship found by us and USFWS between mortality and number of flights is likely an artifact (i.e., autocorrelation) of the relationship between mortality and population size. In other words, the low r^2 detected between mortality and number of flights resulted from the same relationships described above between mortality, population size and year (i.e., time). At the very least, we can conclude that there is room to doubt the functionality of a causal relationship between mortality and number of flights when there is a more plausible alternative explanation. Furthermore, our alternative explanation is more parsimonious compared with the theories advanced by the USFWS, whose premises are fraught with error as previously described here.

Second, we acknowledge that the multiple regression reported here has a sample size that is too small for a reliable result. Sample size in multivariate regression-based models should be at least 100 but preferably 200 or more (Kerlinger and Pedhazur 1973) and the number increases with the number of variables (Thorndike 1978). However, the multiple regression illustrates an important point. Our results on this data set showed that when all the suspect causal variables are included in the analysis, Total Flights had no effect on mortality. Only population size, just short of significance at the 0.05 level, appeared to have any relationship with mortality. Multiple regression chooses a solution using the variable that explains the most variance, followed by the next variable that can explain the most remaining variance, and so on. In our example, population size is obviously the most important variable. Once population size is accounted for, year and number of flights, both of which are significantly related to mortality in univariate analyses, explain insignificant amounts of variation in mortality. This result, although short of proof, concurs with our suspicion that the number of flights is unrelated to mortality.

Third, our analysis of the ratio of mortalities to population size converts mortality to a rate. The conversion has the effect of controlling the analysis for population size. Once this is done, we find no relationship between the mortality rate and the number of flights. Had number of flights been associated with mortality, independent of time and population size, mortality rate should also have been significantly related to number of flights. This finding provides further proof to support our alternative explanation, and removes the primary postulate made by Butler (2014*a*) to criticize census mortality estimates.

Finally, no relationship was observed between mortality or mortality rate and any measure of number of flights in the modern data from 1982-83 to 2010-11. These are the methods and data under criticism by USFWS.

The USFWS approach to the issue was unsound and did not follow basic principles of data analysis. Chief among them was that they did not address the impact of confounding variables (Hahn and Dogaksoy 2011). As a consequence, we believe that they promulgated a logical fallacy, *cum hoc*, *ergo propter hoc* "with this, therefore, because of this". They concluded that 1 thing caused another simply because event Y occurred with event X, therefore, event Y must have caused event X.

CONCLUSIONS

We believe that the criticisms leveled at the previous census methodology are unfounded. The accuracy and limitations of the current distance sampling methodology are, in our opinion, a less desirable approach to monitoring whooping cranes on their wintering grounds at Aransas. In addition, the attempt by the USFWS to discredit the previous census methodology has, unfortunately, left repercussions in its wake that can only be described as detrimental to professional biology's relationship with the public and, in particular, with elected policy makers (White 2015).

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SIZE DIFFERENCE IN WHOOPING CRANES REARED FOR TWO REINTRODUCTION METHODS

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Abstract: We investigated a possible size difference in whooping cranes (*Grus americana*) captive-reared for 2 reintroduction methods to establish a migratory population in eastern North America. Cranes reared for ultralight aircraft-led migration (UL) to Florida were significantly larger than cranes reared for direct autumn release (DAR) on the natal area in central Wisconsin. Mean tarsal length was 315.5 ± 0.98 (1 SE) and 308.1 ± 1.87 mm, respectively, for UL and DAR males and 296.9 ± 1.03 and 290.8 ± 2.60 mm, respectively, for UL and DAR females. Because of the different rearing schedules, eggs for the DAR method were generally laid later than eggs for UL. Eggs later in the laying sequence had lower weights and resulted in smaller birds, although this overall effect was small. Size difference did not appear related to genetic factors. Although survival to 5 years after release was not significantly related to size within groups of the same sex and release method, captive-rearing effects such as size on survival and behavior of released birds should be considered in assessment of reintroduction programs.

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Key words: direct autumn release, *Grus americana*, reintroduction methods, size, tarsus, ultralight-led migration, whooping crane.

The whooping crane (*Grus americana*) is an endangered species occurring in a single natural remnant population which nests in and near Wood Buffalo National Park, Northwest Territories and Alberta, Canada, and winters on and near Aransas National Wildlife Refuge (NWR) on the Texas Gulf Coast (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2007). That population was reduced to 15-16 birds in 1942 and by winter 2010-11 had increased to 283 individuals (Stehn and Haralson-Strobel 2014). Recovery of the species may depend on establishment of additional populations. Attempted reintroductions that began in the Rocky Mountains in 1975 (Ellis et al. 1992) and central Florida in 1993 (Folk et al. 2010) were unsuccessful. A third reintroduction using captive-reared juveniles began in central Wisconsin in 2001. The initial reintroduction method consisted of training costume-reared juvenile whooping cranes to follow ultralight aircraft (UL) and then leading the cranes to winter release sites on the Florida Gulf Coast each year through 2010 (Lishman et al. 1997, Duff et al. 2001). A second method, direct autumn release (DAR), was used from 2005 to 2010 and consisted of releasing captive-reared birds in central Wisconsin in October of each year and allowing them to migrate unassisted. The DAR method was based on earlier studies by Horwich (1989), Urbanek and Bookhout (1992), and Ellis et al. (2001).

The 2 reintroduction methods have been associated with differences in survival and some behaviors after release (Urbanek et al. 2014). The effects of captive propagation on physical characteristics of released birds may also affect post-release success and should be evaluated. Our objective was to further investigate size difference between cranes of the 2 reintroduction methodologies and discern possible implications.

METHODS

Whooping crane juveniles for reintroduction by the UL method were hatched at Patuxent Wildlife Research Center (Patuxent), Laurel, Maryland, from eggs produced in captive propagation facilities at Patuxent; International Crane Foundation (ICF), Baraboo, Wisconsin; Calgary Zoo, Alberta; Audubon Center for Research of Endangered Species, New Orleans, Louisiana; San Antonio Zoo, Texas; and from eggs salvaged from nests on Necedah National Wildlife Refuge (NWR), Wisconsin. Chicks were reared with puppets and costumes to avoid imprinting and habituation to humans (Horwich 1989, Urbanek and Bookhout 1992).

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Chicks were initially trained to follow ultralight trike aircraft (Cosmos, Dijon, France) according to techniques developed by Operation Migration, Blackstock, Ontario (Lishman et al. 1997, Duff et al. 2001) at Patuxent and then transported to Necedah NWR at 35-65 days of age (12 June-15 July). Training continued at isolated facilities on the refuge until the UL migration began in October of each year. Cranes were led to isolated release facilities on Chassahowitzka NWR, Citrus County (HY2001-09) and St. Marks NWR, Wakulla County (HY2008-09), on the Florida Gulf Coast. These assisted migrations began 10-17 October and were completed 30 November-28 January. Cranes were provided food *ad libitum* and protection in a large open-topped pen at each site through the winter and then migrated unassisted northbound on spring migration in late March or early April (Urbanek et al. 2005, 2010).

Chicks for DAR were hatched at ICF from eggs of the captive propagation facilities and costume-reared. They were transferred to an isolated rearing facility on Necedah NWR at 17-57 days of age. Operation of this field facility was closed 18-30 October, and juveniles were moved for release near older whooping cranes elsewhere on the refuge. Juveniles migrated by following whooping cranes, sandhill cranes (*Grus canadensis*), as a group, or alone. In some of the latter cases, juveniles were retrieved and relocated to other areas containing cranes (Zimorski and Urbanek 2010). All cranes were equipped with individually color-coded leg bands and leg-mounted VHF (conventional [very high frequency]) radiotransmitters (Advanced Telemetry Systems, Isanti, MN) and some (3-8 each year) additionally with PTT (satellite [platform transmitter terminal]) transmitters (Microwave Telemetry, Columbia, MD; North Star Science and Technology, King George, VA; Telonics, Mesa, AZ). Cranes were tracked by a team of 2-4 trackers after release throughout their annual cycle and geographic range.

The first author (RPU) measured length of the left tarsometatarsus (tarsus) (Johnsgard 1983:240) of all cranes at 80-139 (mean = 112, UL) and 75-145 (mean = 101, DAR) days of age. Because ossification of the tarsus is complete by 10 weeks of age (Curro et al. 1996), this measure was representative of adult tarsal length and a stable index of bird size. To reduce handling time during banding, project protocol permitted a single linear measurement. Tarsal length was selected as the primary measure of size because it was the standard linear measurement with the highest correlation coefficient to other measurements (e.g., culmen and wing chord) in 6 species of cranes in previous work, and it was fixed at completion of growth, unlike weight, which varies seasonally by 30% each year (Swengel 1992).

We obtained sex identification from DNA blood tests (Griffiths et al. 1996), egg weights (with few exceptions within 1 day of laying), egg position in laying sequence, identities of dam and sire, and QG (Queller and Goodnight 1989) and AS (allele-sharing, Blouin et al. 1996) coefficients of inbreeding based on microsatellite DNA profiles (Jones et al. 2002) from captive propagation records.

Because size is sexually dimorphic in cranes, we performed analyses separately for each sex with program R (R Development Core Team 2010). We compared size between reintroduction methods with 2-sample *t*-tests corrected for unequal variance. We examined relationships between egg weight and sequence, and size with egg weight/sequence and inbreeding coefficients with linear regression. We examined effect of common parents on size with paired *t*-tests. We compared survival to 5 years after release within each group consisting of the same sex and method with 2-sample *t*-tests corrected for unequal variance.

RESULTS

Male whooping cranes averaged 20 mm longer in tarsal length than females. Mean tarsal length of males ($n = 113$) was 314.3 mm ± 0.91 (1 SE) and ranged from 289 to 336 mm; two-thirds (prominent data cluster) of males had a tarsal length of 306-324 mm. Mean tarsal length of females ($n = 97$) was 295.3 ± 1.05 mm and varied from 257 to 318 mm; two-thirds had a tarsal length of 285-305mm.

Mean tarsal length of males was 315.5 ± 0.98 and 308.1 ± 1.87 mm, respectively, for UL ($n = 94$) and DAR ($n = 19$). The difference of 7.4 mm was significant ($t = –3.53$, $\nu = 28.8$, $P = 0.001$). Mean tarsal length of females was 296.9 ± 1.03 and 290.8 ± 2.60 mm, respectively, for UL ($n = 71$) and DAR ($n = 26$). This difference of 6.1 mm was also significant ($t = –2.17$, df $= 33.2$, $P = 0.038$).

Tarsal length was correlated with weight within all groups: UL males ($R = 0.26$, $n = 81$, $P = 0.019$), DAR males ($R = 0.48$, $n = 19$, $P = 0.039$), UL females ($R = 0.30$, $n = 54$, $P = 0.029$), and DAR females ($R = 0.56$, $n = 26$, $P = 0.003$).

Egg weight and egg sequence data were available for 166 individuals. There was a highly significant relationship ($F_{1,164}$ = 20.08, $P < 0.001$), and 10.9% of variation in egg weight was explained by the egg sequence (slope = –2.721 ± 0.607). Egg weight decreased with the increase of sequence of the egg in the laying cycle. There was a tendency (t = 1.91, df = 73, P = 0.059) for eggs assigned to DAR (mean = 3.38 ± 0.24, n = 42) to be later eggs than those assigned to UL (mean = 2.84 ± 1.82, n = 159).

Tarsal length was significantly related to the residuals of the egg weight/egg sequence relationship ($F_{1,164}$ = 5.65, P = 0.019), but only 3.3% of variation was explained by these residuals (slope = 0.194 ± 0.082). Tarsal length was longer when the egg weight was larger than expected from its sequence.

Inbreeding data were available for 155 individuals. There was no effect of inbreeding coefficients AS ($F_{1,153}$ = 0.2753, P = 0.601) or QG ($F_{1,153}$= 0.0576, P = 0.811) on length of tarsus.

Of 29 known sires and 31 dams which contributed progeny to the reintroduction, 9 sires and 11 dams were parents of chicks in both UL and DAR. The UL juveniles were significantly larger than DAR juveniles originating from eggs laid by the same females (Table 1). The same relationship was discernable for male parents only for female chicks when 1 unusually large DAR female chick was removed from analysis.

There was no significant difference in tarsal length between birds surviving and not surviving from release to age 5 years: UL males (t = 0.77, df = 70, P = 0.444), DAR males (t = 1.41, df = 14, P = 0.181), UL females (t = –1.12, df = 53, P = 0.267), and DAR females (t = –1.07, df = 18, P = 0.300). Although not significant, mean survival for both reintroduction methods was greater for smaller than larger males and for larger than smaller females.

DISCUSSION

Tarsal length was significantly greater (2.4% for males and 2.1% for females) in UL than DAR juveniles. The range of tarsal length of whooping cranes is limited, i.e., about two-thirds of total project birds were within an 18-mm range for males and within a 20-mm range for females. Differences in tarsal length between the 2 reintroduction groups amounted to 42% and 31% of these ranges for males and females, respectively. A small linear difference in tarsal length corresponds to a much larger 3-dimensional difference in overall size, i.e., weight and volume, of the whooping crane. However, the relationship between a long bone measurement and weight is not generally very predictable for whooping cranes because weight is also related to many other factors such as nutritional condition and season.

Since additional time was needed to train birds to follow ultralight aircraft, eggs laid in the first half of the breeding season were usually assigned to the UL project. The earliest eggs laid at ICF were sometimes shipped to Patuxent for the UL project. However, most eggs at ICF, where laying phenology was later than at Patuxent because of the more northern latitude, were assigned to the DAR project. Because of the different rearing schedules for UL and DAR, DAR tended to receive later eggs. Eggs laid later in laying sequence have lower weights and result in smaller birds, although this overall effect was small.

No inbreeding effect was detected to account for difference in size between the 2 groups. Some of the chicks in both UL and DAR had common parents. The small sample size and unequal weighting (means of means) limited comparisons. Even so, UL chicks were still found to be significantly larger than DAR

Table 1. Mean difference in tarsal length of chicks of common whooping crane sires and dams reintroduced by ultralight-led migration (UL) and direct autumn release (DAR) techniques, eastern migratory whooping crane reintroduction, 2001-2010.

Parent	Sex of chicks	Parents (n)	Mean tarsal length difference (mm)	SE	t	P^a	df	UL chicks (n)	DAR chicks (n)
Sires	male	5	1.03	2.69	0.38	0.360	4	10	15
Sires	female	5	0.96	4.70	0.20	0.425	4	13	16
Sires[b]	female	4[b]	5.44	1.81	3.00	0.029*	3	12	15
Dams	male	7	3.35	1.24	2.70	0.018*	6	30	14
Dams	female	7	5.72	2.18	2.62	0.020*	6	18	19

[a] One-tailed test (UL > DAR). *Significant at $P = 0.05$.

[b] Excluding 1 outlier (unusually large DAR female with 318-mm tarsus)

chicks produced by the same dams. Genetics was not, therefore, responsible for the size difference.

Costume-rearing protocols, although generally similar for UL and DAR, had many subtle differences involved with facilities, staff, general health, feeding, and exercise regimes which may have contributed to the size difference in these 2 groups of birds. While later egg sequence explains some of the smaller size of DAR birds, interaction between food and exercise likely had greater effects.

The DAR cranes exhibited lower survival (65.7%) than UL cranes (85.1%) during their first year after release (Urbanek et al. 2014). This was to be expected because DAR juveniles were released to perform their first autumn migration unassisted. The UL birds were not released until after they had completed their first migration to Florida, and then they were gentle-released with intensive protection through their first winter. Direct or hard releases typically have lower survival than soft or gentle releases (Nagendran et al. 1996).

Size might affect survival. For example, larger size could reduce susceptibility to predation, especially of females. However, larger size of males might increase susceptibility to power line collision. Because of large differences in reintroduction protocols, including many confounding variables, the effects of size on post-release survival were only tested within groups of the same sex and method and found to be insignificant. However, effects of smaller size on behavior and survival of DAR cranes after release could not be directly tested. The use of later eggs and resulting smaller chicks may have post-release effects which remain to be identified and understood in order to fully evaluate and implement successful reintroduction programs.

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USE OF FRESHWATER PONDS BY WHOOPING CRANES DURING A DROUGHT PERIOD

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Whooping cranes (*Grus americana*) spend nearly half their annual cycle in coastal habitats within and around the Aransas National Wildlife Refuge Complex (ANWRC) located in the central portion of the Texas Coast. When drought conditions prevail in their winter range and salinities in the local bays exceed 23 parts per thousand (ppt), whooping cranes must seek alternate sources of dietary drinking water (Stehn 2008, Chavez-Ramirez and Wehtje 2012). They begin frequent (often daily) trips to freshwater sources in upland areas. These trips may result in extra energy expenditures that can impact their overall health and ability to store energy for spring migration (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2007). We opportunistically used game camera images obtained from a physiological research project (B. Hartup, unpublished data) to gain additional information on how whooping cranes used refuge-managed freshwater resources in relation to prevailing environmental conditions.

Game cameras were used during the winter from November through April 2012-2015 (referred to as winters 2012, 2013, and 2014) at 7 excavated freshwater pond sites along an 8.3-km transect of the Blackjack Peninsula (28.2094°N, 96.8532°W) within the ANWRC (Figure 1). Each site consisted of a pond (mean = 843 m^2) and a 5-20-m mowed border. Pond size varied with local rainfall and weather conditions; all ponds contained some water throughout the study.

Figure 1. Locations of excavated pond sites at the Aransas National Wildlife Refuge Complex, Blackjack Peninsula, Texas, 2012-2015. The 7 sites extend southwest to northeast from South Pipeline pond to Williams mill pond.

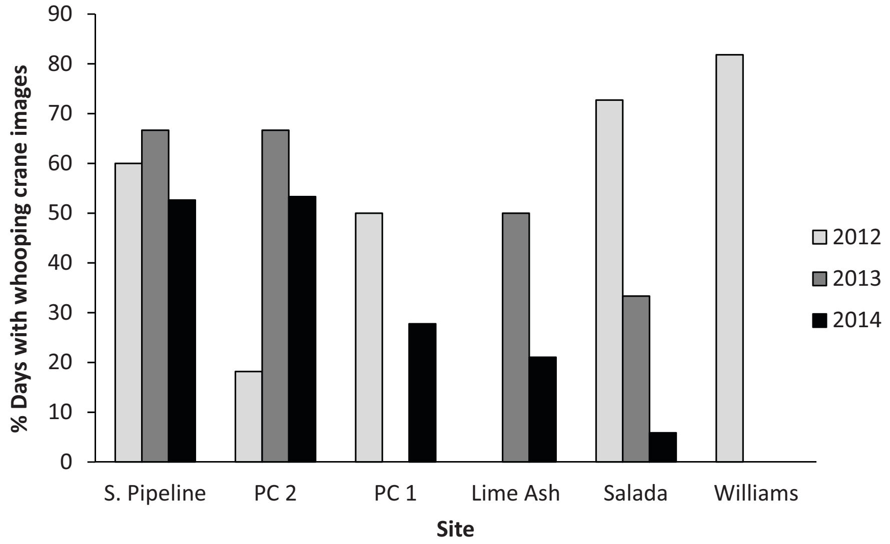

Figure 2. Percentage of days with at least 1 game camera image of a whooping crane by site and winters 2012-2014. Sites are listed from southwest to northeast along the Blackjack Peninsula, Aransas National Wildlife Refuge Complex, Texas. Salada = both Salada sites 1 and 2 (see Figure 1) combined. No bar indicates game cameras were not deployed due to lack of crane sign.

Whooping crane sign (droppings, footprints) and direct observation were criteria used to decide at which of the ponds to deploy cameras each year. Cameras were mounted on T-posts facing north approximately 1.5 m above the ground and positioned to capture the majority of the site in each image. Camera models and settings differed due to resource and personnel constraints for the physiological study, but resulting images were a minimum of 1.7 megapixels and captured using an infrared motion sensor or time lapse setting (every 5 min) between 0700 and 1700 hours. The total number of images available for analysis was 37,879 (2012 = 13,491, 2013 = 2,320, 2014 = 22,068).

We used the percentage of days in which at least 1 image contained a whooping crane to evaluate crane presence among all sites and years. To reduce the number

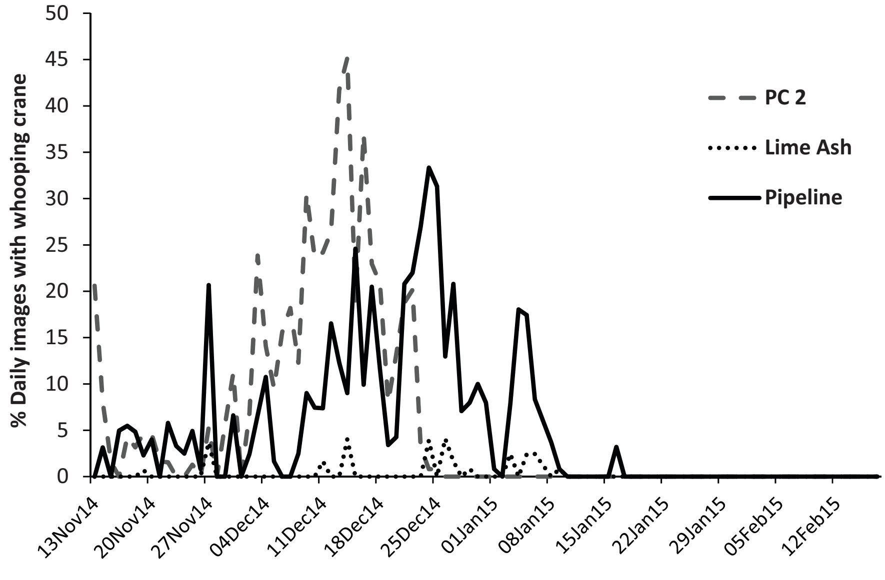

Figure 3. Percentage of daily game camera images containing at least 1 whooping crane at 3 sites during winter 2014. PC2 = Pump Canal 2. Graph terminated mid-February 2015 for clarity (no whooping crane use continued through April).

of images that were evaluated, and to support data needs for our other study, we used only data from every other week during the 3 winters, i.e., the dates of fecal sampling, for all 7 sites. In addition, for 3 of the 7 sites, we used all images for continuous monitoring in 2014. This approach appeared valid for estimating overall crane presence at the sites, i.e., there was no statistical difference in the proportions of days with a whooping crane based on either periodic or daily sampling at 3 sites during 2014. The continuous monitoring from the 3 sites in 2014, however, allowed us to compare the magnitude of daily site use by determining the proportion of images with at least 1 whooping crane each day for the entire winter. Finally, to summarize use by time of day, we recorded the time of each image containing at least 1 whooping crane for pond Pump Canal 2 (PC2) in 2014, and categorized them into 1 of 4 time periods (hr): early morning (0700-0900), late morning (0901-1200), early afternoon (1201-1500), and late afternoon (1501-1700).

Whooping crane use of freshwater pond sites varied greatly by year (Figure 2). Of the sites monitored, the furthest southwest site (South Pipeline) was used at least once a day more than 50% of days monitored in all 3 years. All other sites showed considerable year-to-year variation in whooping crane use. Figure 3 shows variable daily use of 2 southwest sites (South Pipeline and PC2) in 2014, with peak use observed in mid to late December (>30% of images per day contained whooping cranes), followed by rapid decline after significant rainfall events in late December and January. These sites were used regularly and for progressively greater periods in early winter compared to the Lime Ash site to the northwest, which was infrequently used and for only short periods in 2014. The lower usage at the beginning of the winter may have been a reflection of lower numbers of whooping cranes having completed fall migration in November and/or settling within range of the SW sites. The peak abundance of the Aransas-Wood Buffalo population at ANWRC is estimated to occur shortly after 1 December each year (Butler et al. 2014). During 2014, whooping cranes used the PC2 site least during early morning hours and most during late morning, with a decline in afternoon use toward sunset (Figure 4). Distinctive individuals or groups of cranes were observed at the pond for longer periods (up to 30 min), suggesting the site was also used for foraging, loafing, or perhaps socialization.

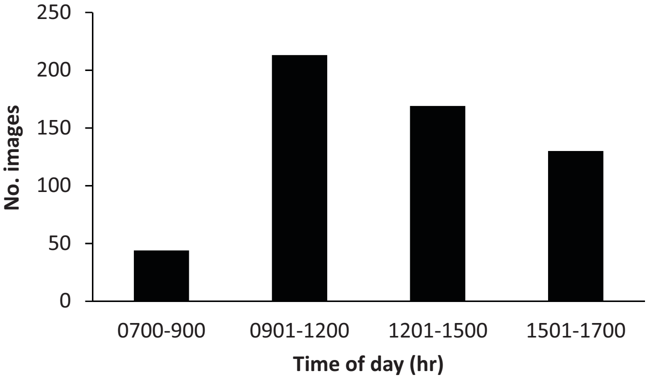

Figure 4. Number of game camera images with at least 1 whooping crane by time of day at Pump Canal 2 in winter 2014. Data were pooled over the period 13 November 2014 through 4 February 2015 and were based on review of 9,768 images.

Whooping cranes were documented drinking from ponds at all sites. Individuals, pairs, families, and even groups of birds as large as 11 were photographed. There were also several sightings of groups including multiple adult plumage birds and juveniles congregating in close proximity to each other. These anecdotal observations, as well as the substantial changes in the use of individual pond sites among years, suggest that ponds may be used opportunistically when fresher water is needed instead of habitually.

Seventeen of 18 months of the study occurred in conditions categorized as abnormally dry (8 months) or moderate drought (9 months) by the U.S. National Drought Mitigation Center for Aransas County, Texas (NDMC 2016). No drought condition existed by April 2015. Heavy rain in January 2015 appeared to signal the end of the multi-year drought. No cranes were observed in any images after 16 January 2015 through to the end of the study in April. Field observations from crane and habitat surveys conducted within coastal marsh habitat along the Gulf Intracoastal Waterway documented cranes drinking in shallow depressions within the marsh vegetation throughout January-March 2015 (E. Smith, personal observation). Salinity data collected in a separate study in coastal marsh ponds in late February, however, recorded salinities above 23 ppt and higher than bay waters (J. Wozniak, Texas Research Institute for Environmental Studies, personal communication). We believe rainfall pooling in depressions increasingly provided drinking water in marsh habitat and correlated with absence of crane use of managed freshwater sites prior to significant declines of bay and marsh pond salinities more favorable to whooping cranes.

MANAGEMENT IMPLICATIONS

While much further investigation is required, the use of game cameras allowed us to characterize some aspects of crane behavior around freshwater ponds during periods of drought. Whooping cranes utilized the ponds throughout the day, but use was greatest between 0900-1200 hours. Birds were rarely seen before 0900, suggesting that early morning or later afternoon may be optimal times to conduct potentially disruptive activity near the ponds or along this area of the Blackjack Peninsula. Ponds were used frequently throughout the drought, with most sites experiencing some use on at least 30% of the sample days. With drought increasing in length and severity associated with regional changes in climate, the mitigation effects of these communal spaces on whooping cranes may be worthy of further study. Standardized camera traps and weather measurements taken directly in the coastal marsh may provide a better correlation of the factors affecting crane behavior and physiology, particularly when the localized weather patterns in this area of coastal Texas may drive discrete habitat condition improvements within the wintering range of the whooping cranes.

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Key words: drought, freshwater, game camera, *Grus americana*, management, whooping crane.

PROTOCOL AND RESULTS FROM THE FIRST SEASON OF CAPTIVE-REARING WHOOPING CRANES FOR A NON-MIGRATORY RELEASE IN LOUISIANA

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The principal historic range of the whooping crane (*Grus americana*) consisted of the tall grass prairies and wetlands of southwest Louisiana, Texas, and parts of Mexico (Allen 1952). Whooping cranes migrated there from Illinois, Iowa, Minnesota, Dakotas, Manitoba, Saskatchewan, Alberta, and breeding grounds of the remnant flock in and near Wood Buffalo National Park, Canada.

Louisiana was unique in that both resident and migratory populations existed there in historic times. Whooping cranes used marshes and ridges of Louisiana's Chenier Plain and upland prairie terrace (Allen 1952, Gomez 1998). The resident non-migratory whooping cranes in Louisiana centered on the White Lake Marsh area and what is today the White Lake Wetlands Conservation Area (WLWCA). Thirteen whooping cranes, including 2 young of the year, were found there on a survey in 1939 (Lynch 1956). In 1940 a hurricane reduced numbers to 6. This was followed by the loss of 1 bird per year, until in 1947 a single bird remained, and on 11 March 1950 the last remaining wild Louisiana whooping crane was captured and brought into captivity (Barrett and Stehn 2010). The area, once in private corporate hands, is now owned and managed by the Louisiana Department of Wildlife and Fisheries. That organization, along with Louisiana State University, and the U.S. Geological Survey (USGS) Louisiana Cooperative Fish and Wildlife Unit are our partners in this venture. Plans were formulated in 2007 at in meeting in Lafayette, Louisiana, to initiate releases in this area.

USGS Patuxent Wildlife Research Center, Laurel, Maryland, has used the costume-rearing technique (Nagendran et al. 1996) for rearing whooping cranes for release in Florida (1993-2005) and in Wisconsin for the Eastern Migratory Population (2001-2015). The Eastern Migratory Population currently numbers 100+ whooping cranes migrating between Wisconsin and southeastern states. Releases into the Eastern Migratory Population in Wisconsin required most chicks to be costume-reared and trained to follow ultralight aircraft.

To begin the Louisiana releases in the winter of 2011, USGS Patuxent Wildlife Research Center hatched 12 whooping crane chicks in May and June 2010. All chicks were hand-reared by caregivers wearing complete white costumes and black boots. This is similar to techniques used to rear Mississippi sandhill cranes (*Grus canadensis pulla*) and whooping cranes for both the Florida non-migratory releases and the Whooping Crane Eastern Partnership releases in Wisconsin. Modifications were made in the earlier rearing protocols and medical care program. In addition, extensive behavioral observations were made starting in June and continuing through November 2010 on this group of cranes and compared to ultralight costume-rearing for the Wisconsin release.

Whooping cranes were released for the first time in Louisiana in the late winter of 2011. The reintroduction had the following objectives: 1) Establish a self-sustaining whooping crane population on and around WLWCA. A self-sustaining population is defined as 130 birds including 30 nesting pairs. 2) Maintain numbers for 10 years without restocking from captivity. 3) Raise and release 8 whooping crane colts during breeding season 2010. Move these whooping cranes to WLWCA in Louisiana in February 2011. 4) Monitor first-year survival and provide management remedies to increase survival if needed. 5) Release second and third cohorts of 8-14 birds each in 2012 and 2013.

All whooping crane chicks for this program were costume-reared at the USGS Patuxent Wildlife Research Center in Laurel, Maryland. In addition to Patuxent's own flock of whooping cranes, eggs came from various sources, including captive flocks at the Audubon Zoo and Species Survival Center, New Orleans, Louisiana; San Antonio Zoo, San Antonio, Texas; Calgary Zoo, Calgary, Alberta; International Crane Foundation, Baraboo, Wisconsin; and wild released whooping cranes in central Wisconsin that had abandoned their nests. All whooping crane eggs were naturally incubated for the first half to two-thirds of incubation under either whooping cranes or sandhill cranes at Patuxent and then transferred to artificial incubators and hatchers for the remaining incubation. After hatching, the whooping crane chicks were moved from the hatchery to an intensive care incubator for approximately 24 hours until they were considered strong enough to be in a pen. All indoor pens used in this study were 3×3 m and equipped with a heat lamp, brood model, food, and water bowls. Substrate was indoor carpeting for the first week, then hardwood shavings (Beta Chips, Northeastern Products Corp., Warrensburg, NY; mention of trade name does not imply U.S. Government endorsement).

For the first week, chicks learned to eat and drink with the help of costumed human caregivers. During this period all chicks received daily health examinations. This was the time of the most intense contact with costumed caregivers, but all chicks were housed next to pens containing adult whooping crane imprint models.

Chicks were initially taken for walks during the latter part of the first week, following the costumed caregiver who led them with a whooping crane puppet head. Late in week 1, at mean age of 6.4 days (range 4-9 days, *n* = 10), the chicks were taken for foraging trips with a costumed person. During week 2, feeding with the puppet head continued, if needed, to reinforce self-feeding. Walks and foraging with a costumed caregiver continued in week 2. Also in week 2, swimming to increase exercise and prevent leg deformities began, with each chick engaging in a minimum of 20 minutes of this activity daily.

During week 3, socialization with other chicks was initiated at a mean age of 15.5 days (range 8-22 days). Exposure to ponds and marshes during the foraging walks occurred at this time. Health examinations continued daily until day 10, then twice weekly. During weeks 3-5, foraging and walking trips continued until mean age of 46.1 days (range 39-57 days). Swimming continued to 20-25 days of age, then stopped. Socialization with other chicks began at an early age during the initial walks and continued through week 5. Formal socialization activities ended at mean age of 49.7 days (range 40-65 days) in 2010 when the chicks were considered socialized and housed as 1 group. Health examinations continued twice weekly and included vaccinations for eastern equine encephalitis and West Nile virus.

During week 6 and beyond, the chicks were moved to outdoor pens. At first these were dry pens, but later pens with small wetland ponds (10-m-diameter) were used. Whooping cranes were introduced to the ponds at mean age 53.2 days (range 48-59) in 2010. At first the chicks were only in the pond pens during the day and under supervision of a costumed caregiver, but eventually birds were left in the pens with ponds all day and night. The chicks were observed and monitored for social interactions using video cameras. Health examinations were conducted at weekly intervals until 60 days of age, then every 2 weeks thereafter.

Pre-shipment health examinations occurred in early January and included complete blood count, serum chemistries, radiographs, examination of feces for parasites, and testing for *Salmonella*, Inclusion Body Disease of Cranes, and Infectious Bursal-like Disease. Shipment was delayed 2 weeks because of adverse weather, but the whooping cranes were finally flown to Louisiana in mid-February for release in early March 2011.

During the period when the whooping crane chicks were being reared at Patuxent, chicks were randomly chosen for behavioral observations. The costume-rearing technique was originally established with whooping cranes introduced into a non-migratory flock in Florida (Nagendran et al. 1996) and is now used for the Louisiana reintroduction. The modifications to enable training with an ultralight aircraft (Operation Migration 2008) were developed by Patuxent personnel in consultation with Operation Migration, our partner in the ultralight aircraft-led reintroductions. From each release project, 6 chicks were randomly selected for observations. Five-minute focal observations were done at randomly selected times during daylight hours. No observations were made at night. All crane chicks were observed primarily by use of cameras, but secondarily by observers in costume and working from a distance so as not to influence the chick's behavior. Repeated measures analysis of variance was performed on the resulting data by using a Statistix 8 software package (Analytical Software, Tallahassee FL).

Whooping crane chick behavioral observations were divided into 2 categories: a locomotion category (Figure 1) and a behavior category (Figure 2). For example, a chick could be standing (locomotion category) and foraging (behavior category), walking and foraging, walking and vigilant, or walking and non-vigilant. Walking movement was observed 10.1 ± 1.1% (mean ± SE) of the time for Louisiana costume-reared birds and 7.3 ± 1.9% for ultralight-trained birds. Standing was observed 50.8 ± 3.5% for Louisiana crane chicks and 49.9 ± 7.3% for ultralight crane chicks. Running was only observed 0.3 ± 0.1% of the time for Louisiana chicks and 0.2 ± 0.2% for ultralight chicks. Hock-

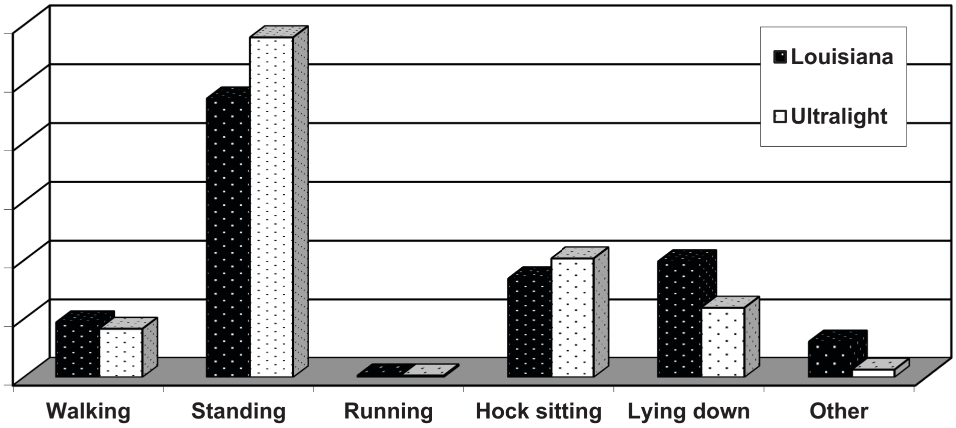

Figure 1. Observed movements (locomotion) of ultralight-trained, costumed-reared whooping cranes for release in Wisconsin (*n* = 6) and costume-reared whooping cranes for release in Louisiana (*n* = 6), at USGS Patuxent Wildlife Research Center, Laurel, Maryland, 2010. Only the "Other" category was significantly different at the *P* < 0.05 level.

sitting was observed 17.7 ± 2.5% for Louisiana chicks and 19.2 ± 4.3% for ultralight chicks. Lying down was observed 10.8 ± 2.3% of the time for Louisiana chicks and 13.0 ± 3.7% for ultralight chicks. Other types of movements were observed 6.1 ± 2.5% of the time for Louisiana chicks and 1.0 ± 0.6% for ultralight-trained chicks. Other movements included such activities as stretching wings, stretching legs, short flights, jumping and dancing. Louisiana ultralight chicks were out of view 9.4 ± 1.5% of the time.

For the behavior categories, we observed Louisiana chicks foraging 19.9 ± 2.9% of the time while ultralight chicks foraged 23.4 ± 5.1% of the time. Louisiana chicks were vigilant 2.7 ± 0.8% of the time, and ultralight chicks were vigilant 3.8 ± 0.8% of the time observed. Non-vigilant behavior was observed 24.5 ± 1.8% of the time for Louisiana chicks and 22.5 ± 3.3% of the time for ultralight chicks. Comfort behavior (e.g., preening, grooming, bathing) was observed 20.5 ± 2.6% of the time for Louisiana chicks and 23.1 ± 2.9% of the time for ultralight chicks. Sleeping was observed 3.4 ± 1.0% of the time for Louisiana chicks and 4.3 ± 1.1% of the

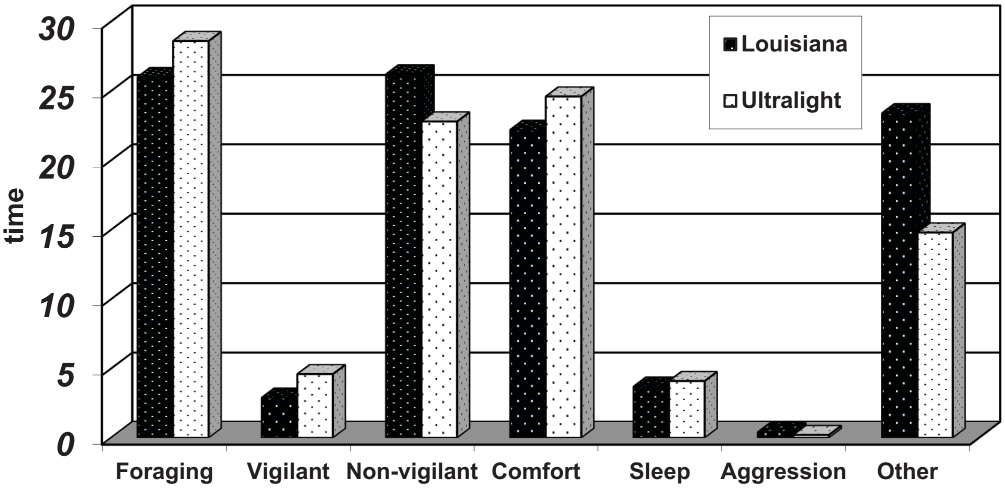

Figure 2. Behaviors observed in whooping cranes costume-reared and trained with ultralight aircraft for release in Wisconsin (*n* = 6) and whooping cranes costume-reared for release in Louisiana (*n* = 6), at USGS Patuxent Wildlife Research Center, Laurel, Maryland, 2010. Only the "Other" category was significantly different at the *P* < 0.05 level.

time for ultralight chicks. Delivering aggression was seen 0.4 ± 0.4% of the time and receiving aggression was seen 0.003 ± 0.003% of the time for Louisiana chicks. Delivering aggression was seen 0.2 ± 0.1% of the time and receiving aggression was seen 0.1 ± 0.1% of the time for ultralight chicks. Other types of behavior (e.g., eating pelleted food, pecking at brood models) was seen 21.5 ± 3.0% of the time for Louisiana chicks, but only 13.5 ± 1.4% of the time for ultralight chicks. We observed no statistical differences ($P > 0.05$) in any of the locomotion (movements, Figure 1) or behavior categories (Figure 2) when comparing whooping cranes trained with ultralight aircraft for release in Wisconsin and whooping cranes raised for release in Louisiana without ultralight training except in the category "other" for both the movement category and the behavior category. This was a large category and in the future we may consider including some of the behaviors grouped under this category as separate behaviors.

Time spent in active movements such as walking and running was similar for the 2 rearing methods (Figure 1). Time spent in survival behaviors such as being vigilant and foraging for food was also similar for the 2 rearing methods (Figure 2). The use of these observations helps confirm that the methods used for the Louisiana release of whooping cranes were producing chicks with similar behavioral patterns that had proved successful for survival in the Wisconsin releases. Ten chicks reared for release in Louisiana were successfully released there in early March 2011, while 1 chick was euthanized because of severe scoliosis and 1 chick remained in captivity for genetic reasons.

ACKNOWLEDGMENTS

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PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:94-97

Key words: behavior, costume-rearing, *Grus americana*, Louisiana, training, whooping crane.

PHOTOPERIOD AND NESTING PHENOLOGY OF WHOOPING CRANES AT TWO CAPTIVE SITES

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Increasing day length is considered to be a stimulus to breeding in many avian species in northern latitudes (Welty 1975). Crane species that breed in high latitudes include Siberian crane (*Leucogeranus leucogeranus*), lesser sandhill crane (*Grus canadensis canadensis*), hooded crane (*G. monacha*), and whooping crane (*G. americana*). The first captive breeding records for hooded and Siberian cranes were induced with the use of artificially extended photoperiods (Mirande et al. 1996). Most likely, cranes that breed in mid-latitudes also respond to increasing daylight. In 1 study, captive greater sandhill cranes (*G. c. tabida*) were stimulated to lay earlier than controls by using artificial lights to alter the photoperiod (Gee and Pendleton 1992).

The physiological response to light may be combined with an environmental or climate effect. Observations of breeding captive whooping cranes in Wisconsin and Maryland indicate that when temperature and humidity rise, breeding activity ceases, despite the continued use of artificial light to increase the photoperiod (Mirande et al. 1996). For Siberian cranes a temperature >21°C stops semen production (Einsweiler 1988).

Light intensity and the spectrum of the light are important. Morris (1967), studying poultry, found that >16 foot-candles (170 lux) was required in the cage area to detect a photoperiod effect on breeding. Quartz or metal halide lamps are recommended as providing a good light spectrum, and these lights are longer lasting and more energy efficient than traditional lamps. I examined the past light cycles and breeding season results from whooping crane pairs at U.S. Geological Survey (USGS) Patuxent Wildlife Research Center (Patuxent), Laurel, Maryland, and the International Crane Foundation (ICF), Baraboo, Wisconsin.

Patuxent staff used 3 different photoperiod regimens during 2002-2009: 1) in 2002-2007 there were 2 lights used to produce light of 170 lux in the crane pens, 2) in 2008-2009, only 1 photoperiod light was used for each pen, reducing the light by 50%, and 3) in some years during the period 2002-2009, some whooping cranes had no photoperiod lights. Photoperiod lights were first turned on between days 42 and 55 (11 and 24 February) (2002-2009, mean = day 48, 17 February), with the exception of 2006 when photoperiod lights were not turned on until day 75 (16 March) due to extensive pen damage from a late winter snowfall. For the years with 2 photoperiod lights per pen (2002-2005, 2007), the mean first lay date was day 93.6 ± 12.1 (3 April) with a range of mean first lay dates of days 81 to 121 (22 March to 1 May). When 1 light per pen was used (2008-2009), the mean first lay date increased to day 103 (13 April), with a range of days 94 to 116 (4 April to 26 April). When no photoperiod lights were used on some pens, the mean first lay date was day 109.3 ± 13.8 (19 April) with a range of days 94 to 129 (4 April to 9 May).

In the 1 year (2006) when the lights were turned on approximately 1 month late (16 March), the mean first lay date was day 108 (18 April) with a range of days 100 to 123 (10 April to 3 May), very similar to the effect seen with no lights. Starting the photoperiod 1 month late was essentially equivalent to having no photoperiod lights. However, the delayed first lay date was not persistent, as the next year (2007) 3 females that laid in both years had earlier first lay dates in 2007 of 3, 6, and 25 days. Photoperiod lights were first turned on in 2007 on day 53 (22 February). There were 4 pairs that did not lay eggs during 2002-2009 despite the photoperiod lights. Twelve pairs that did lay during this period are included in the results above.

Results from ICF were similar to the results from Patuxent. With photoperiod lights, the mean day of first lay was day 108.66 ± 2.39 (1 SE) (18 April), and without photoperiod lights the mean day of first lay was day 116.26 ± 2.34 (26 April), almost a week later. This difference was statistically significant ($P = 0.026$, $F = 5.16$, 1-way ANOVA). Neither the number of eggs laid ($P = 0.510$, $F = 0.44$) nor the length of the egg-laying season ($P = 0.243$, $F = 1.38$) was significantly different between years when photoperiod lights were used and when they were not used. There were highly significant differences for first egg lay dates and number of eggs laid by individual females (first egg lay date by female, $P < 0.001$, $F = 9.19$; number of eggs laid per year by female, $P = 0.011$, $F = 2.75$). The length of the egg-laying season did not vary significantly among the various female whooping cranes ($P = 0.171$, $F = 1.51$). The strength of the photoperiod lights in the ICF whooping crane pens was not known. First lay dates shifted from year to year but there was no significant pattern (Figure 1).

With 2 lights per pen at Patuxent, whooping cranes laid their first egg on average 10 days earlier than when 1 light was used and 16 days earlier than when no lights were used. At ICF the difference between lights on a pen and no lights was only 8 days in the first lay dates, but still this was statistically significant.

The conclusion from these data is that artificially increasing the day length at the captive centers helps to lengthen the breeding season by up to 2 weeks, which potentially results in more eggs from the captive pairs. However, raising cranes 1 year on a photoperiod date that is later than the norm (such as day 75, 16 March, in 2006) has no permanent effect on subsequent years when the photoperiod increase starts at the earlier February date. Therefore, there should also be no effect of the artificial photoperiod lights on the young birds produced from these pairs. Rather, when the offspring mature and begin breeding, they will respond to the light cycle encountered in their breeding area. There is also no effect of starting the breeding period earlier or later 1 year by using or not using photoperiod lights on the first lay date in subsequent years. That is, altering the lay date 1 year does not alter subsequent lay dates if the factor causing the alternative lay dates, such as artificial lighting, is removed.

What triggers the breeding season in non-migratory whooping cranes in Florida and in Louisiana, where the change in photoperiod is much smaller than that on the northern breeding grounds in Canada or at the more northerly captive breeding facilities? One might suspect rising temperature and/or humidity may play a role in triggering the onset of breeding activity. The whooping cranes in Florida, when they breed, are known to breed earlier than the whooping cranes in captivity in Wisconsin or Maryland.

Effects of Multiple Clutching

In the wild, whooping cranes lay 1 clutch of 2 eggs. The first lay date of whooping crane females in captivity is somewhat predictable. Each female starts laying on or about a certain date dependent on some external variables such as photoperiod as already discussed above, but also the health of the female, unusual disturbances (e.g., weather events such as a snow storm in late winter 2006), movement to a different pen, or a new mate. The 2 eggs in a clutch are normally laid about 2-4 days apart. One-egg clutches are possible.

Whooping cranes are indeterminate egg layers, as are all cranes (Mirande et al. 1996). If something happens to the first nest resulting in abandonment or loss of the eggs, whooping cranes are capable of renesting. In captivity, we remove eggs from a nest to stimulate cranes to lay additional eggs, which is called multiple clutching. Two techniques are used to increase reproduction. In the first the eggs are removed as laid. The second technique is to allow the female to complete the clutch of 2 eggs before removing both eggs. Kepler

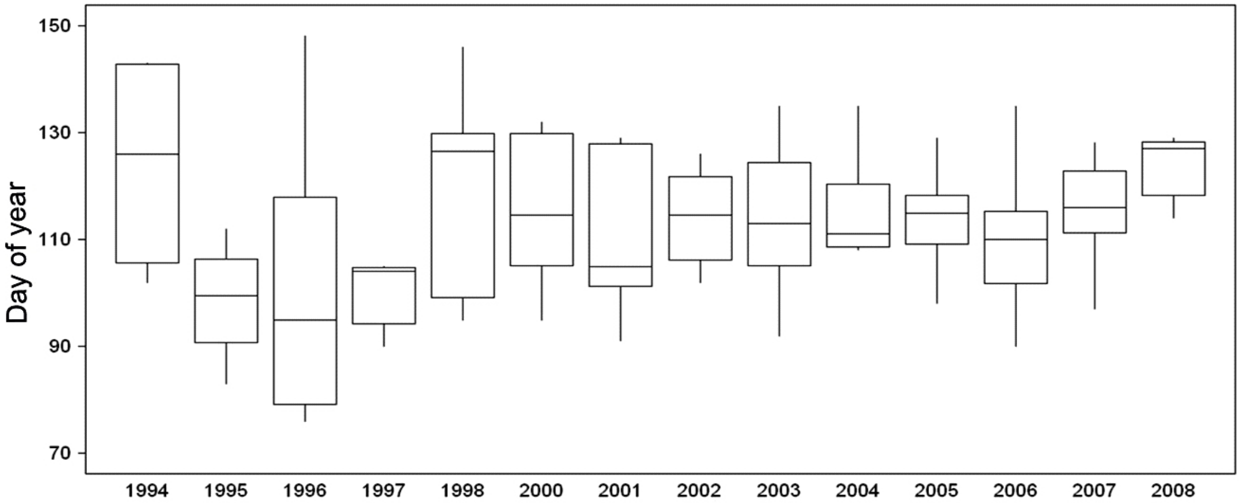

Figure 1. Mean first egg lay dates (median, quartiles, range) for whooping crane eggs (*n* = 82) laid at the International Crane Foundation, Baraboo, Wisconsin, 1994-2008.

(1978) found that for nesting whooping cranes, when each egg is removed shortly after being laid, there was an increased production (6.4 eggs per female) as compared to the technique of waiting for the clutch to be complete before removing the eggs (5.3 eggs per female).

Multiple clutching has a significant negative effect (*P* = 0.023, Hunt 1994) on the fledging rate. Eggs laid late in the breeding season in late clutches have a decreased probability of fledging. Hunt (1994) did not directly look at whooping crane data, but examined information from Siberian, Florida sandhill (*Grus canadensis pratensis*), white-naped (*G. vipio*), and red-crowned (*G. japonensis*) cranes. At Patuxent we have noted a decrease in egg size with later eggs when multiple clutching. There may also be an increase in medical problems in late-clutch chicks. We will be studying these effects of multiple clutching further.

There are also problems for the female that are associated with multiple clutching. Calcium depletion leading to uncalcified eggs or even to the collapse of the laying female is possible. Decreased hatchability, decreased growth rate, decreased survival, and decreased fertility have been reported for later eggs when multiple clutching (Koga 1976). Despite all the potential problems, the gain in production of live, healthy chicks far outweighs the problems encountered when multiple clutching. On the positive side, some studies (Koga 1955, 1961, 1976) have shown that multiple clutching may actually improve fertility.

One question that has been asked by members of the Whooping Crane Eastern Partnership is whether multiple clutching has any effect on shifting the date when the first egg is laid. Patuxent has been multiple clutching for many years. During this time there has been great variation in first lay dates (Figure 2). However, most of this variation is explained by the variation in photoperiod light intensity (see above section on photoperiod lights) and by weather factors, especially several recent years with heavy late winter snowfalls. If the years 2002-2005 and 2007 are examined when the photoperiod lights

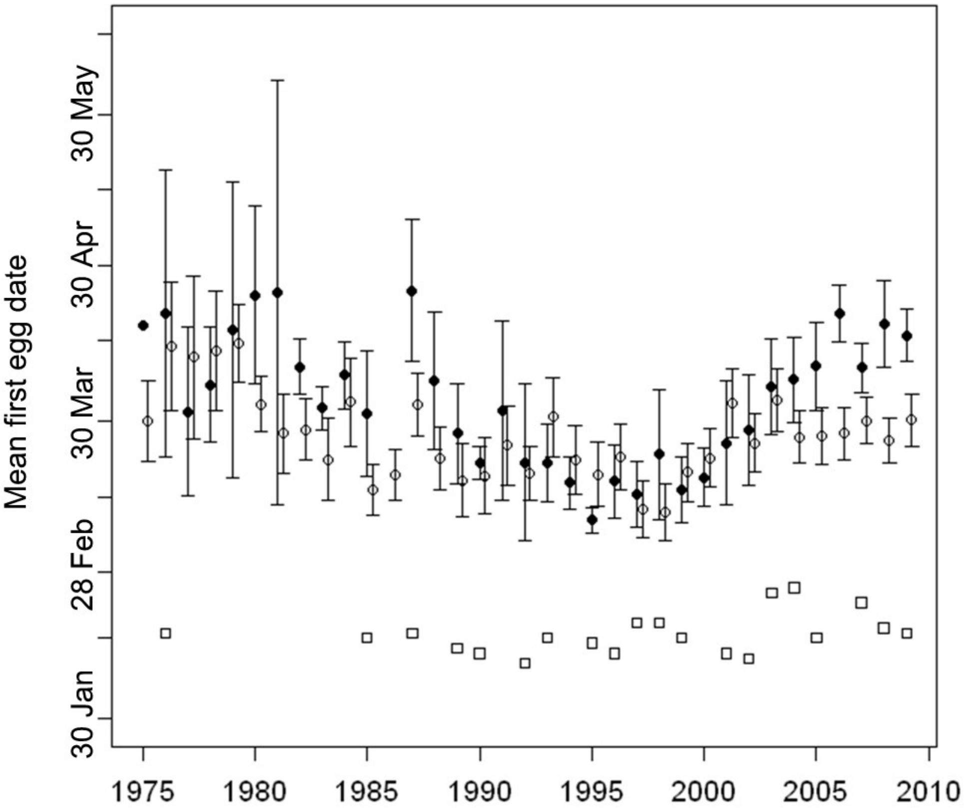

Figure 2. Mean first egg lay dates for whooping cranes and sandhill cranes at USGS Patuxent Wildlife Research Center, Laurel, Maryland. Filled circles are whooping cranes, open circles are greater sandhill cranes, and open squares are Florida sandhill cranes.

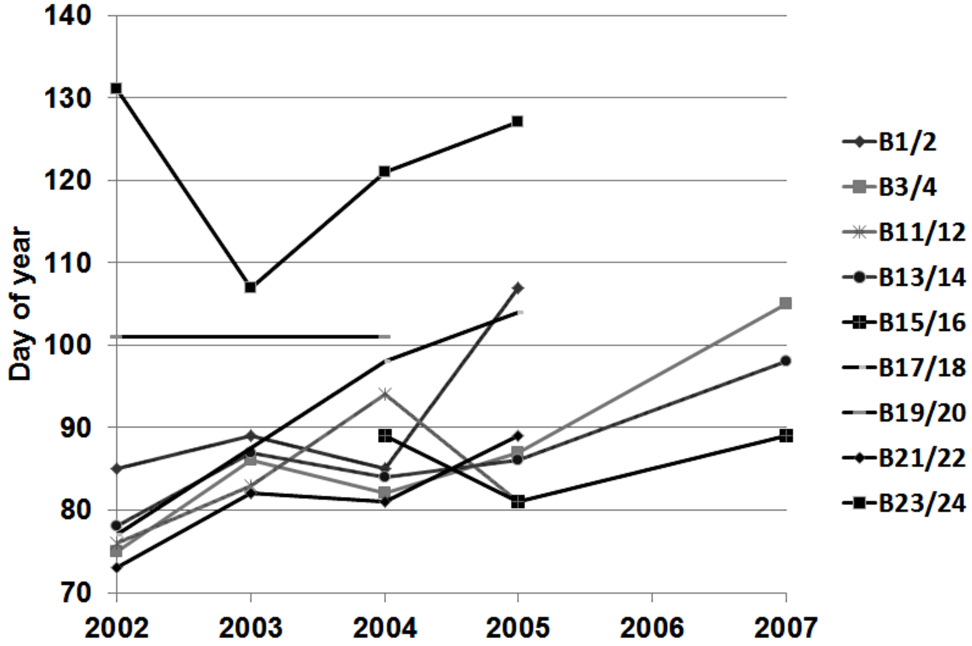

Figure 3. First egg lay dates for 9 whooping cranes at USGS Patuxent Wildlife Research Center, Laurel, Maryland, 2002-2007. All whooping cranes were multiple clutched and received photoperiod lights starting in mid-February and of the same intensity of 170 lux.

were kept at maximum brightness and there were no late winter snow storms, there still appears to be great variation in first lay dates (Figure 3). The mean change in the 7 whooping cranes showing later first lay dates was 14 days; the range was 1 to 27 days later. For the 2 cranes that had earlier lay dates, 1 was 1 day earlier and only laid twice in the 5-year period. The other crane showed no constant pattern, as 2003 was 24 days earlier than 2002, but 2007 was only 4 days earlier than the date in 2002. None of these shifts was statistically significant. When comparing recent first lay days with those over the entire history of captive breeding at Patuxent (Figure 2), we see that there is great variation from year to year and that current first lay dates are only now approaching those seen in the early years of the program, thus no conclusions regarding the effect of multiple clutching on first lay date can be formulated. More study of factors affecting first lay dates is warranted, especially the effects of weather, including temperature.

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Key words: crane, *Grus americana, Grus canadensis,* nesting, phenology, photoperiod, sandhill crane, whooping crane.

HEMATOLOGY RESULTS FROM EXPERIMENTAL EXPOSURE OF SANDHILL CRANES TO WEST NILE VIRUS

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West Nile virus (WNV), a Flavivirus, was introduced into New York City in 1999 (Centers for Disease Control 1999, Enserink 1999). In the past decade the virus has spread across the continental United States and southern Canada, resulting in large numbers of deaths among native bird species (Anderson et al. 1999, Calle et al. 2000). The U.S. Geological Survey (USGS) Patuxent Wildlife Research Center in Laurel, Maryland, is home to the world's largest collection of cranes. These cranes are used for research and for reintroduction programs. As of 20 October 2016, this collection included 77 of the highly endangered whooping cranes (*Grus americana*) used for reintroduction programs in Wisconsin and Louisiana.

The U.S. Fish and Wildlife Service was interested in protection of the endangered captive flock of whooping cranes through preventive vaccination, but with only approximately 500 of these birds in the world, including less than 150 in captivity, there was no possibility of doing safety and vaccination-challenge studies. Sandhill cranes (*G. canadensis*) were chosen as a suitable surrogate species for these needed vaccination-challenge studies. Similar use of sandhill cranes as surrogates for viral research of concern to whooping cranes has occurred with the Arbovirus that causes eastern equine encephalitis (Olsen et al. 1997, Olsen et al. 2005). A killed vaccine was used to produce immunity with eastern equine encephalitis (Olsen et al. 2005). No adverse reactions were encountered when vaccinating the cranes. No clinical signs of WNV disease were seen when the cranes were given the WNV challenge. Titer and necropsy results from the vaccination trials have been previously reported (Olsen et al. 2009), and a summary of the antibody titer results is presented in Table 1. We found a significant difference in titers between vaccinated and unvaccinated cranes at 14 days post-challenge ($P = 0.048$, $F = 5.44$) (Olsen et al. 2009). The objective of this paper is to summarize hematological responses to vaccination and challenge with WNV.

We selected adult sandhill cranes ($n = 12$) of mixed sexes that tested negative for previous exposure to WNV as measured by antibody titers. Seven of these cranes were vaccinated in the winter with 3 doses of 0.5-ml killed WNV vaccine (Fort Dodge Laboratories, Fort Dodge, IA; mention of commercial products does not imply U.S. Government endorsement) over a 4-week period at the USGS Patuxent Wildlife Research Center. Five sandhill cranes were injected with only sterile water (Table 1). Two months after completing the vaccinations, the sandhill cranes were shipped by commercial airline to the USGS National Wildlife Health Center, Madison, Wisconsin, where a BL-3 laboratory was available for the challenge phase of this study.

Following a 2-week adjustment period, the vaccinated ($n = 5$) and unvaccinated ($n = 5$) sandhill cranes were challenged by inoculating each with a 0.1-ml subcutaneous injection of a mosquito dose (5,000 plaque-forming units) of a WNV isolate from the original outbreak in New York State. Cranes designated as controls ($n = 2$) each received a 0.1-ml subcutaneous inoculation of sterile water. All cranes received health examinations, including taking 5.0-ml blood samples by jugular venipuncture for antibody titers and clinical pathology before, and at regularly scheduled intervals after inoculation with WNV. All cranes were humanely euthanized and necropsied at day 42 after challenge with the WNV.

Table 1. Titers of sandhill cranes inoculated with 1 mosquito dose (5,000 pfu [plaque-forming units]) of West Nile virus, USGS National Wildlife Health Center, Madison, Wisconsin, February 2002 (modified from Olsen et al. 2009).

Crane no.	Vaccinated	Challenged	Titers		
			Day 0	Day 14	Day 42
SC 003	Yes	No	<1:5	<1:5	<1:160[a]
SC 017	Yes	No	<1:5	<1:5	<1:10[a]
SC 001	Yes	Yes	<1:5	1:10240	1:10240
SC 028	Yes	Yes	<1:5	1:640	1:5120
SC 060	Yes	Yes	<1:5	1:2560	1:2560
SC 053	Yes	Yes	<1:5	1:10240	1:5120
SC 061	Yes	Yes	<1:5	1:20480	1:10240
SC 113	No	Yes	<1:5	1:320	1:2560
SC 004	No	Yes	<1:5	1:320	1:1280
SC 041	No	Yes	<1:5	1:1280	1:10240
SC 055	No	Yes	<1:5	1:640	1:2560
SC 065	No	Yes	<1:5	1:640	>1:2560

[a] Lowest titer tested.

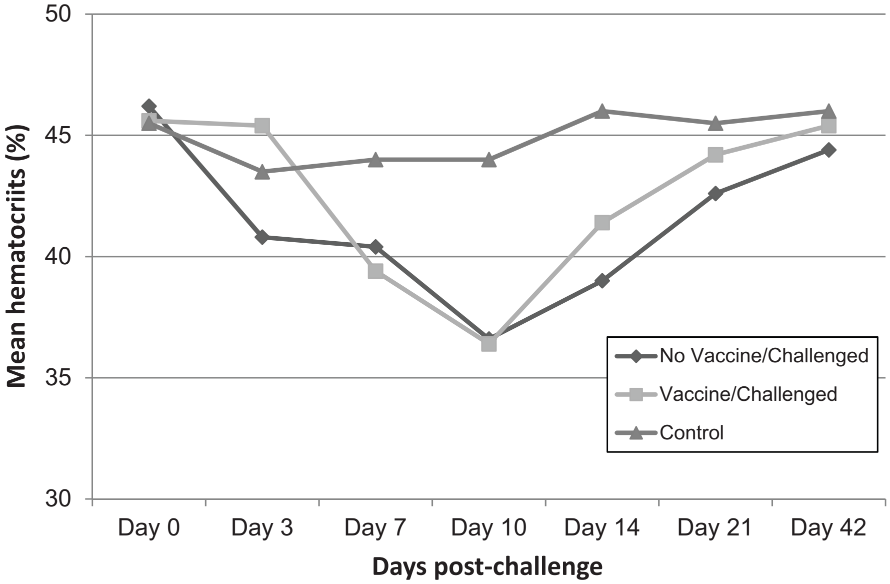

Figure 1. Mean hematocrits (%) of vaccinated/no challenge (control), vaccinated/challenged, and no vaccine/challenged sandhill cranes post challenge. Challenged whooping cranes were given 1 mosquito dose (5,000 pfu) of West Nile virus at the USGS National Wildlife Health Center, Madison, Wisconsin, February 2002.

Blood samples were collected by venipuncture of the right jugular vein (Dein 1984). Blood was placed in standard heparinized and plain blood tubes and blood smears made using the two coverslip method (Dein 1984). Blood smears were stained using Diff-Quick (American Scientific Products, mention of trade

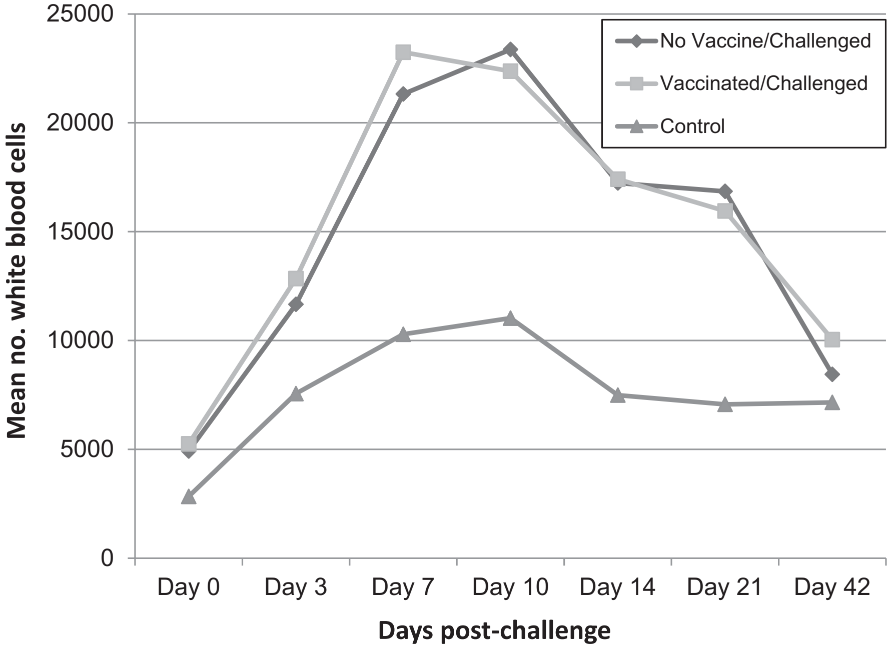

Figure 2. Mean white blood cell counts of vaccinated/no challenge (control), vaccinated/challenged, and no vaccine/challenged sandhill cranes. Sandhill cranes were challenged with 5,000 pfu of West Nile virus at the USGS National Wildlife Health Center, Madison, Wisconsin, February 2002.

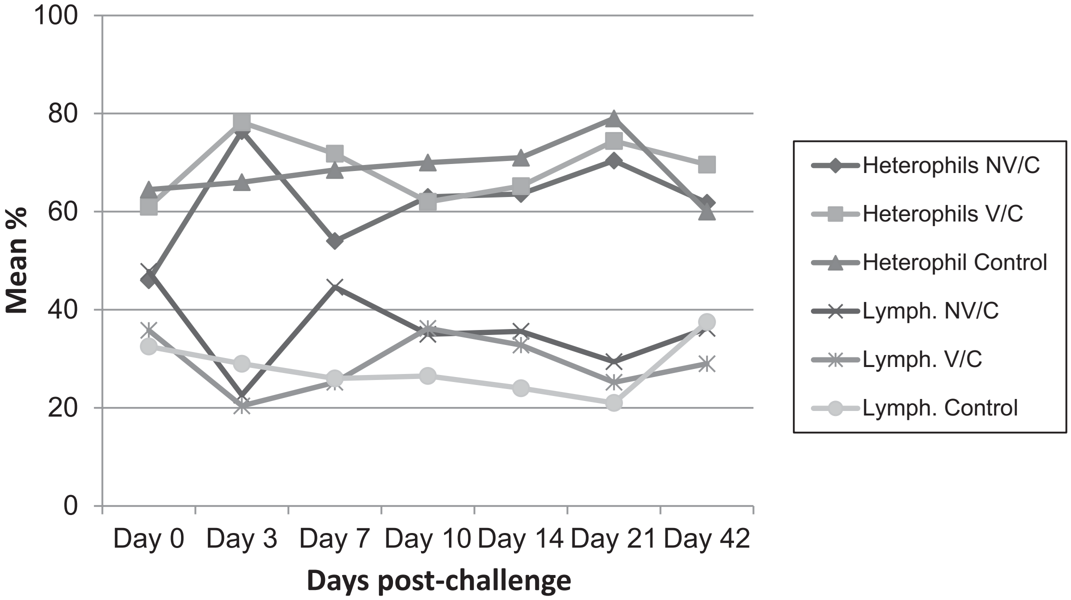

Figure 3. Mean percent heterophils and lymphocytes in vaccinated/no challenge (control), vaccinated/challenged (V/C), and no vaccine/challenged (NV/C) sandhill cranes. Sandhill cranes were injected (challenged) with 5,000 pfu of West Nile virus at the USGS National Wildlife Health Center, Madison, Wisconsin, February 2002.

name does not imply U.S. Government endorsement). Hematocrits were obtained by centrifuging a microhematocrit tube in a high speed centrifuge and reading the percent of red blood cells (Dein 1984). Total white blood cell counts were made by the Eosinophil Unopette Method (Dein 1984) (Becton-Dickinson, Test #5877) and then corrected for the percentage of heterophils and eosinophils in the differential count read from the blood smear (Dein 1984). This study was approved by the institutional animal care and use committees at the USGS Patuxent Wildlife Research Center and the USGS National Wildlife Health Center.

Between 1 and 2 weeks post-challenge, cranes exposed to the live WNV had lower hematocrits, whether or not they were previously vaccinated as compared to unchallenged controls (Figure 1). Mean white blood cell counts in all cranes given the live WNV challenge, whether vaccinated or not, were elevated as compared to the unchallenged controls ($n = 2$). The white blood cell count elevation lasted from day 3 to day 21 (Figure 2). Even though the white blood cell counts were elevated up to 2.5 times normal or control levels, there were no distinct shifts observed between heterophils and lymphocytes (Figure 3).

The most important findings were that vaccination of sandhill cranes with commercial killed equine WNV vaccine produced quickly elevating antibody titer levels when these previously vaccinated cranes were challenged by live WNV. Cranes with experimental infections with WNV had lowered hematocrits and elevated white blood cell counts as compared to control cranes not exposed to the virus housed under similar circumstances. This elevation in total white blood cell count occurred in both previously vaccinated cranes and unvaccinated cranes.

West Nile virus is a deadly virus for young cranes. In testing vaccines on adult sandhill cranes, we found that some blood parameters were altered by exposure to the virus. White blood cell counts were the most obvious and may be used as an indicator of WNV exposure in cranes, although this elevation in white blood cell counts is non-specific to WNV. Other hematology and serum chemistry results were studied and only hematocrit, percent heterophils, and percent lymphocytes were of interest, along with the already published information (Olsen et al. 2009) on titers encountered in experimental infections. Clinical pathology results showed challenged cranes, whether vaccinated or not, had a decrease in their hematocrits and an elevation of 2.5-fold in their white blood cell counts as compared to unchallenged control sandhill cranes. This is similar to a case report of a sandhill crane with an elevated white blood cell count found during a fatal WNV infection (Hansen et al. 2008). In this study no differences were apparent in the differential counts of heterophils and lymphocytes. Our work would suggest that a combination of white blood cell counts and antibody titers can be used to diagnose and assess the severity of WNV infections in cranes.

ACKNOWLEDGMENTS

I thank the staff of the USGS National Wildlife Health Center and especially K. Miller, V. Bochsler, L. Sileo, and D. Docherty for their help and the use of the BL-3 laboratory facilities used for the virus challenges. They were my co-authors on the paper published on challenge studies. I thank the crane crew of the USGS Patuxent Wildlife Research Center, especially B. Clauss, for help with the cranes and this project. This study was funded by grants from the Whooping Crane Conservation Association and the U.S. Fish and Wildlife Service, Region 3.

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PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:103-106

Key words: crane, Flavivirus, *Grus canadensis*, hematocrit, hematology, sandhill crane, West Nile virus, white blood cell count.

SERUM CHEMISTRY, BLOOD GAS, AND PHYSIOLOGICAL MEASURES OF SANDHILL CRANES SEDATED WITH ALPHA-CHLORALOSE

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Capture techniques that lessen handling stress may also lessen pathologic influences on physiologic measures, improving the validity of these measures for use in individual health assessment of free-ranging wildlife. Since 1990, the International Crane Foundation (ICF) has successfully used chemical immobilization with alpha-chloralose (AC; $C_6H_{11}Cl_3O_6$), a chloral derivative of glucose, to facilitate captures of sandhill cranes (*Grus canadensis tabida*) for ecological studies (Hayes et al. 2003). Although this chemical has been used orally for the immobilization of many species, the physiologic effects of AC are not well understood in cranes. The primary purpose of this study was to measure serum chemistry, venous blood gas, and physiological values in free-ranging sandhill cranes successfully immobilized using this technique.

Sandhill cranes were captured near Briggsville, Wisconsin (43°36′N, 89°36′W), between 1996 and 1999 as previously described (Langenberg et al. 1998, Hayes et al. 2003). Once at a nearby holding pen, each crane was banded, weighed, measured and blood samples were taken from the left or right medial metatarsal or right jugular veins. Starting in 1997, the cloacal temperature and minute heart and respiratory rates of each crane were determined prior to blood collection. Sampling occurred approximately 1 hour post-capture. Samples were analyzed for the concentrations of selected serum enzymes and electrolytes (glucose, aspartate aminotransferase [AST], alanine aminotransferase [ALT], alkaline phosphatase [AP], creatine kinase [CK], lactic dehydrogenase [LDH], cholesterol, total protein [TP], phosphorous [P], calcium [Ca], sodium [Na], potassium [K], chloride [Cl], bicarbonate [HCO_3], uric acid, and anion gap) by Marshfield Laboratories (Marshfield, WI). Blood samples were also analyzed for venous blood gas levels by using an i-STAT Portable Clinical Analyzer (i-STAT PCA; Sensor Devices Incorporated, Waukesha, WI). The EG7+ cartridges used with the i-STAT PCA provided tests for hydrogen ion concentration (pH), carbon dioxide tension (pCO_2), oxygen tension (pO_2), Na, K, ionized calcium (iCa), and hematocrit (PCV) measurement; in addition, the i-STAT provided HCO_3, total carbon dioxide (tCO_2), base excess (BE), oxygen saturation (sO_2), and hemoglobin (Hb) as calculated values based on the measurements. The i-STAT PCA has been validated for use in chickens for all analytes except K and BE (Steinmetz et al. 2007).

The mean and standard deviation (SD) for each serum chemistry, blood gas, and physiologic value were calculated for hatch-year juvenile and adult sandhill cranes. Age was determined through field markings (Lewis 1979). Sex of each bird was determined through relative size (Nesbitt et al. 1992), behavior (Archibald 1976), or through genetic analysis of blood samples (Griffiths et al. 1998). Individual cranes that were clinically abnormal at the time of sampling or had values that differed from the mean by more than 3 SD were omitted from the analyses. Reference ranges for all parameters represent the mean ± 2 SD. Results have been pooled by sex due to sampling of 8 unknown sex juveniles and a preliminary analysis that showed no sex differences among adults.

Samples were obtained from 23 juveniles (6 males, 9 females, 8 unknown; mean age = 135 days, range 118-175 days; estimated hatch date of May 1), and 47 adults (21 males, 26 females). Serum chemistry findings are based on data from 19 juveniles and 37 adults (Table 1). Venous blood gas analysis using the i-STAT PCA, as well as summary physiological measures, reflect data from 14 juveniles and 35 adults (Table 2).

Our results for electrolytes, cholesterol, TP, P, and Ca are similar to those of Ellis et al. (1996), and reference ranges for these values and glucose and uric acid are similar to those found by Olsen et al. (2001). Alkaline phosphatase levels were increased in juveniles compared to adults, and likely due to ongoing skeletal development described similarly by Olsen et al. (2001). Reference ranges for AST were similar in both age groups of this study, but higher than those reported by Olsen et al. (2001). Abnormal AST activities have been linked to vitamin E, selenium or methionine deficiencies, liver damage, pesticide and carbon tetrachloride intoxication and muscle damage (Ritchie et al. 1994). CK results produced very wide reference ranges for

Table 1. Laboratory serum chemistry results from adult and hatch-year greater sandhill cranes sedated with alpha-chloralose, near Briggsville, Wisconsin, 1996-1999.

	Adults					Hatch-year				
	Mean (n = 37)	SE	Min.	Max.	Reference range	Mean (n = 19)	SE	Min.	Max.	Reference range
Glucose (mg/dL)	237	5	172	312	174.6-299.5	257	6	210	308	206.5-307.8
AST (U/L)	269	11	158	466	139.7-398.1	294	15	182	423	160.2-426.8
ALT (U/L)	35	2.2	11	60	7.9-61.1	33	4.1	5	65	0-68.3
AP (U/L)	147	18	13	605	0-371.4	383	49	190	963	0-813
CK (U/L)	1440	203	84	5425	0-3914.7	1611	297	162	4689	0-4203.8
LDH (U/L)	370	26	202	853	55.1-684.6	456	44	171	931	76.43-835.6
Cholesterol (mg/dL)	142	4	93	195	93.0-190.9	142	7	65	199	79.4-205.2
TP (g/dL)	3.3	0.1	2.5	4.4	2.5-4.1	3.2	0.1	2.7	3.8	2.6-3.8
P (mg/dL)	1.9	0.1	1.0	4.7	0.3-3.6	4.9	0.3	3.3	7.1	2.6-7.3
Ca (mg/dL)	9.3	0.1	8.7	10	8.4-10	9.3	0.2	7.2	11	7.5-11
Na (mmol/L)	142	1	136	151	136-147	141	1	138	151	135.2-147.3
K (mmol/L)	3.9	0.1	2.1	6.8	2.2-5.6	4.3	0.2	2.4	7.1	2.4-6.3
Cl (mmol/L)	104	0.4	100	111	98.7-109	103	0.5	97	107	98.7-108
HCO_3 (mmol/L)	29	0.5	24	35	23-35.4	27	0.7	23	32	21-33.8
Uric Acid (mg/dL)	4.4	0.2	2.4	7.4	1.7-7.2	4.7	0.3	2.7	6.5	2.2-7.1
Anion Gap (mmol/L)	12	0.5	6	18	5.6-18.8	15	0.6	11	19	9.2-20.3

Table 2. Physiological and i-STAT PCA venous blood gas results from adult and hatch-year greater sandhill cranes sedated with alpha-chloralose, near Briggsville, Wisconsin, 1997-1999.

	Adults					Hatch-year				
	Mean (n = 35)	SE	Min.	Max.	Reference range	Mean (n = 14)	SE	Min.	Max.	Reference range
Cloacal temp (°C)	40.1	0.1	38.7	41.8	38.7-41.6	39.7[a]	0.2	38.7	41.3	38.2-41.3
Heart rate	142[b]	6	84	200	76-208	164[a]	18	80	280	34-294
Respiration rate	30	2	12	70	3-58	29[a]	2.6	18	52	9.6-48
pH	7.43[c]	0.02	7.23	7.52	7.29-7.56	7.40	0.03	7.24	7.48	7.26-7.54
pCO_2 mmHg)	39.6[c]	1.5	30.6	66.0	22.7-56.4	45.5	3.2	31.6	69.3	21.9-69.1
pO_2 (mmHg)	61	1.7	38	78	41-81	58.6	2.2	42	71	41.7-75.4
Na (mmol/L)	140	0.3	135	146	136-144	140	0.6	136	143	136-144
K (mmol/L)	4.2	0.1	3.4	5.1	3.3-5.1	4.3	0.1	3.8	4.8	3.6-4.9
iCa (mmol/L)	1.15	0.02	0.98	1.28	1.00-1.30	1.24	0.03	1.13	1.34	1.11-1.38
PCV (%)	38	0.6	32	48	31-46	34.8	1.0	29	42	27.4-42.2
Hb (g/dL)	13	0.2	11	16	11-16	12	0.3	10	14	9.5-14
BE (mmol/L)	1[c]	0.4	−2	6	−3-5	2.6	0.8	−1	11	−6.7-8.9
HCO_3 (mmol/L)	26[c]	0.4	21	30	21-30	27.3	0.9	23	36	20.4-34.2
tCO_2 (mmol/L)	27[c]	0.4	22	31	22-31	28.8	1.0	24	38	21.5-36.1
sO_2 (%)	90[c]	1.3	66	96	75-100	88.1	2.1	67	95	72.6-100

[a] n = 13; physiological measures not recorded for 1 hatch-year crane.
[b] n = 34; heart rate was not recorded for 1 adult crane.
[c] n = 32; smaller n for these parameters was due to i-STAT PCA system failures of single or multiple values for some samples.

both age groups and were much higher than results reported from captive populations. In healthy turkeys, CK has been reported to be very sensitive to stress and exercise (Lumeij 1987). Muscle damage, neuropathies, vitamin E or selenium deficiencies, and lead toxicity can be possible causes of CK increases. LDH is another enzyme that can be elevated with hemolysis, hepatic necrosis, and muscle damage, but its non-specificity limits its diagnostic value in birds. The hatch-year cranes' LDH values in this study were greater than adult birds and greater than all age groups reported by Olsen et al. (2001). We believe the variously elevated values of AST, CK, and LDH were attributable to muscular exertion experienced during the induction phase or initial sedative effects and 1-hour lag in blood sampling from alpha-chloralose capture. The mild elevations that we observed were subclinical and a byproduct of the capture technique. These changes are distinct from values determined using captive cranes that experience minimal exertion prior to blood sampling following physical capture and restraint. As shown elsewhere, exertional myopathy is a significant risk factor with the use of AC, yet morbidity and mortality rates with this method are comparable to or less than most other contemporary alternative capture techniques (Hartup et al. 2014).

Heart and respiration rates for sedated greater sandhill cranes are previously unpublished. The heart rate reference range for hatch-year birds has a higher upper limit than for adults. The reference range established in this study for cloacal temperature is broader than that reported by Ellis et al. (1996), but this would be expected given possible exertion and stress experienced by free-ranging birds with varied levels of sedation (Hayes et al. 2003).

With the exception of Na, K, PCV, and Hb, the venous blood gas parameters measured using the i-STAT PCA are previously unpublished for this species. Langenberg et al. (1998) reported preliminary results from a small number of cranes, but provided additional information on these parameters up to 8 hours following immobilization. Olsen's (2001) reports for PCV and Hb in captive greater sandhill cranes are consistent with those of this study, but Ellis et al. (1996) reported higher means for Na. Potassium and BE were found to be unreliably measured by the i-STAT PCA when compared to laboratory assays (Steinmetz et al. 2007). All the venous blood gas parameters are comparable between adult and hatch-year cranes with a high degree of overlap, except for iCa that was higher in the younger birds. Bone remodeling associated with normal juvenile growth may have been responsible for this difference.

Cranes in this study were clinically asymptomatic and the omission of individuals with any outlier values presumably selected for a healthy reference pool, but underlying disease states, like parasitic infection, were still probable. Other effects from age, sex, reproductive status, nutrition, disease, and environment can affect each bird's health status as reflected through its serum chemistry and physiology. Our findings extend the normative physiological reference data available for free-ranging sandhill cranes.

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PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:107-110

Key words: alpha-chloralose, blood gas, capture, clinical pathology, cranes, *Grus canadensis tabida*, physiology, serum chemistry.

AGE-SPECIFIC SURVIVAL OF GREATER SANDHILL CRANE COLTS IN NEVADA

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Abstract: We estimated daily survival rates and fledging success and evaluated factors influencing survival of greater sandhill crane (*Grus canadensis tabida*) chicks (i.e., colts) in northeastern Nevada. We monitored 101 colts during 2009-2010. We found survival was lower on Ruby Lake National Wildlife Refuge compared to private or state-owned lands. Colts located on the Refuge had essentially no prospect of fledging (1 ± 6% in 2009, <1 ± 3% in 2010), whereas colts located on private and state lands had higher and more variable probability of fledging (25 ± 13% in 2009, 15 ± 9% in 2010). Daily survival rates were lowest early in development and increased with age of colts. We did not detect an effect of weather or habitat use on survival. Our results support previous findings of predation as the primary cause of pre-fledging mortality in cranes. Our findings are inconsistent with sibling competition as a major source of mortality but support extrinsic factors as important determinants of survival. Our results suggest that management of predator populations may influence fledging of cranes in northeast Nevada.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:111

Key words: chick survival, fledging success, *Grus canadensis*, Nevada, sandhill crane.

WHOOPING CRANE DISTRIBUTION AND HABITAT USE: PAST, PRESENT, AND FUTURE?

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Abstract: Accurate determination of the historic range for a species can be important to the success of the species conservation and reintroduction efforts. The remnant wild population of the endangered whooping crane (*Grus americana*) historically had a wide distribution but is now limited to a small portion of that range. What can past and present whooping crane distributions tell us about the future? In addition to historic data compiled by R. P. Allen in 1952, we obtained 76 supplementary records and used geographic information systems to re-assess historic distribution and habitats of whooping cranes in their former breeding and wintering ranges. We extended the breeding, summering, and wintering ranges into several new areas. Whooping cranes historically were found in 9 biomes and many ecoregions, extending from the tundra and boreal forests of northwestern Canada to the Gulf Coast and xeric shrublands of interior Mexico. Based on crane life history, landscape, and wetland features of historic locations, we identified 4 features common to breeding and wintering areas: 1) high densities of wetlands or large wetland complexes; 2) shallow, open wetland systems with emergent vegetation; 3) subtle to rolling topography that provides an interspersion of wetland and low meadow or prairie habitats with relatively sparse cover of trees and shrubs; and 4) high productivity due to hydrological pulsing, periodic inflow of nutrients, or periodic disturbances. The new insights from this assessment, combined with site-specific studies of current habitat use by whooping cranes, should better inform future evaluations and selection of reintroduction sites.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:111

Key words: distribution, *Grus americana*, habitat, historic range, whooping crane.

BEHAVIORAL MOVEMENTS OF ARANSAS-WOOD BUFFALO WHOOPING CRANES: ANOMALIES OR INDICATIONS OF WAYS TO FURTHER ENHANCE SPECIES RECOVERY

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Abstract: Aransas-Wood Buffalo whooping cranes (*Grus americana*) usually summer and nest in and around Wood Buffalo National Park, winter at or near Aransas National Wildlife Refuge, and migrate between these sites during spring and fall each year. Since 2010 the Whooping Crane Tracking Partnership has monitored movements of 57 individual whooping cranes marked with transmitters that collect multiple GPS locations per day. The Whooping Crane Tracking Project and advancements in technology have provided an unprecedented opportunity to study this imperiled species in ways that to date have not been possible. Among other things, we have observed many behavioral movements that are well documented in the literature, but other movements have rarely or never been observed or reported. We have been able to document birds that summered in Saskatchewan, western Alberta, and eastern British Columbia, and even birds that spent weeks hundreds of km north of Wood Buffalo National Park. We have also observed migration paths that were well outside the range of the typical migration corridor and have documented birds wintering over 160 km, inland and along the Gulf Coast, from the Aransas National Wildlife Refuge. Here we present some behavioral movements observed to date that may provide additional insight into the recovery of the species.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:112

Key words: Aransas, *Grus americana*, movements, tracking, whooping crane, Wood Buffalo.

INFLUENCES ON NEST SUCCESS IN A REINTRODUCED POPULATION OF WHOOPING CRANES

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Abstract: Historical nesting areas of extirpated whooping cranes (*Grus americana*) included wetlands in divergent taiga, tallgrass prairie, and Gulf coast biomes. The wild migratory population breeds in taiga while, since 2001, the Whooping Crane Eastern Partnership has worked to reintroduce an Eastern Migratory Population (EMP) in the tallgrass biome. Compared with previous reintroductions, most aspects of the EMP reintroduction have been successful. Adult survival is high, and pairing, foraging, migratory, and copulatory behaviors appear normal. Reproductive rates, however, are unsustainable. Multiple hypotheses including attacks by blood-feeding black flies (*Simulium* spp.), slow maturation of breeding birds, inappropriate energy-storage patterns, mal-adaptations to wild situations, inappropriate habitat use, and predation all potentially explain low nest success and are not mutually exclusive. Abundance of avian-feeding black fly species was related to nest failure, but the relevant species were found in high numbers only in the Necedah area. In 2012, when black fly populations were suppressed, nest success increased to 45% although only 2 of 9 chicks fledged, further suggesting that multiple biological constraints were involved. In 2013, a second control year in which black fly populations were not suppressed, nest success was again low. Conservation actions include maintaining the core population near Necedah along with other potential actions such as facilitating dispersion to new habitats that have different wetland productivity levels, black fly populations, and predator communities. How birds use the varied landscapes they inhabit can help guide reintroduction efforts as the reintroduced birds respond to varied situations for the first time in more than a century.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:113

Key words: black flies, Eastern Migratory Population , *Grus americana*, nesting, whooping crane.

DETERMINING DIET COMPOSITION AND INGESTION RATE OF CRANES THROUGH FIELD MEASUREMENT

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Abstract: Determining diet composition and ingestion rates of food helps elucidate how a species utilizes its habitat. Yet determining diet and food intake rates can be difficult. With endangered species, foraging individuals cannot be sacrificed. Feces can often be hard to find in wetland species, and stable isotopes cannot completely overcome biases from differential digestion. Utilizing field measurements to determine diet composition and ingestion rates is an under-utilized technique and requires further assessment. We used vegetation community, food acquisition behavior (glean, probe, stab–associated with stalking, and jab), and food manipulation time to predict diet composition. At least 17 unique food items were identified in the diet of reintroduced whooping cranes (*Grus americana*) foraging in Wisconsin during summer. Our model was then tested with data independent of model creation and was over 90% correct. Ingestion rates were experimentally determined by baiting birds with a known number of food items. A regression, where the counted number of food items removed from the bait pile was used to predict the number of food items observed being consumed, explained over 80% of the variance. To increase knowledge on diet composition, our model provides a foundation and should be applied to broader habitats (e.g., Texas Gulf coast or Wood Buffalo National Park). These data may also be potentially predicted with accelerometers in 3 planes of motion and by precise locations superimposed on habitat maps so that diet information may be estimated remotely.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:114

Key words: diet, food intake, *Grus americana*, ingestion rates, model, whooping crane.

HABITAT USE AND MOVEMENT PATTERNS OF WHOOPING CRANES IN THE OIL SANDS MINING REGION

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Abstract: Aransas-Wood Buffalo whooping cranes (*Grus americana*) migrate through the oil sands region of North America twice annually. Other migratory waterbirds, e.g., ducks, frequently land on oil sands tailings ponds and are oiled. Whooping cranes are speculated to be threatened by oil sands during migration, but it is unknown if mining activities pose a risk. We characterized movement patterns and habitat use of whooping cranes in the oil sands region using data from 49 individually marked cranes which made 146 individual migrations to or from the breeding grounds. Of these, 48 migrations were by juveniles and 98 were by adults or subadults. A considerable proportion (41%) of marked cranes flew over the oil sands region at least once between spring 2010 and fall 2012 and a large proportion (63%) of these landed at least once during migration at a stopover location in the oil sands region. The duration of stopovers was short, in most cases either 1 or 2 nights. Stopover and flight locations were recorded in close proximity to tailings ponds during spring migration (2.51 km and 0.96 km, respectively) but were considerably farther from tailings ponds during fall migration (26.29 km and 24.75 km, respectively). Results from this study will be used to guide land use decisions and management actions to mitigate potential threats from oil sands mining to whooping cranes.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:115

Key words: Aransas-Wood Buffalo, *Grus americana*, migration, mining, oil sands, stopover, whooping crane.

CAPTURE AND DEPLOYING GPS PTTS ON ARANSAS-WOOD BUFFALO WHOOPING CRANES: LESSONS LEARNED WITH NEW TECHNIQUES AND TECHNOLOGIES

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Abstract: Research conducted by the Whooping Crane Tracking Partnership requires capture and marking of Aransas-Wood Buffalo whooping cranes (*Grus americana*) at their breeding and wintering grounds. Capture of pre-fledging whooping cranes at Wood Buffalo National Park had been successfully conducted by E. Kuyt. We emulated their methods with similar safety and efficiency. Adult whooping cranes from this population had never before been captured on the wintering grounds. In the first 2 winters (2009-2011) we captured 3 cranes. Starting in 2012, we developed a new methodology to effectively capture birds on the wintering grounds. This modified leg noose includes a remote trigger device and a retraction mechanism that cinches the noose and allows for variable resistance as the bird advances or retreats. During the ensuing 3 winters we successfully captured >30 birds with this technique. Overall, Platform Transmitter Terminals (PTTs) equipped with GPS receivers were attached to 31 pre-fledging whooping cranes in and around Wood Buffalo National Park and 26 birds (24 after hatch year, 2 hatch year) were marked on the wintering grounds in Texas through 2013. As of 1 January 2014, marked birds have provided >100,000 Doppler locations and >80,000 GPS locations. In inspection and preliminary use of data, we found communications between transmitters and satellites can be corrupted resulting in invalid locations. We developed algorithms that flag obvious and potential errors based upon several filters. Using this automated method, we found that approximately 1% of GPS locations are likely erroneous and should be removed before more detailed analyses are conducted.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:116

Key words: Aransas-Wood Buffalo, capture, GPS, *Grus americana*, leg noose, PTT, remote trigger, Tracking Partnership, whooping crane.

CAN HORMONE METABOLITES PREDICT THE TIMING OF REPRODUCTIVE BEHAVIORS IN THE CAPTIVE WHOOPING CRANE?

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Abstract: Cranes are known for their elaborate courtship behaviors. Whooping crane (*Grus americana*) reproductive behaviors are well documented, both in their native habitat and in captivity. However, little is known about the influence of hormones on these behaviors. Reproductive behavior is shown to be strongly influenced by reproductive hormones in a variety of species, so in this study we attempted to understand the relationship between hormone concentrations and reproductive behaviors observed in the whooping crane. In understanding this relationship we could better interpret how captive management practices affect cranes. Our study assessed reproductive output in 7 captive whooping crane pairs through non-invasive hormone monitoring and behavioral observations. We found that reproductively-active females produced higher estradiol concentrations and displayed more reproductive behaviors than females that failed to reproduce. Initial observations also revealed higher proportions of reproductive behaviors following detection of elevated reproductive hormone metabolites with a lag time of approximately 7 days. This pattern was especially strong directly before an egg-laying event. We explored this relationship further using mixed models and model selection in order to obtain statistical estimates of the lag time between hormone elevation and increased levels of reproductive behaviors. Understanding this relationship will not only increase our knowledge of reproductive biology within this species but could create another monitoring tool for crane hormones and behaviors.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:117

Key words: *Grus americana*, hormones, reproductive behaviors, whooping crane.

BREEDING DISTRIBUTION OF SANDHILL CRANES IN RUSSIA

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Abstract: Breeding distribution of the Mid-continent Population (MCP) of sandhill cranes (*Grus canadensis*) in Russia is poorly understood. Most published information has described the species breeding range in Russia being limited mostly to the Chukotka Autonomous Region and part of the Kamchatka Peninsula. We describe the historical and current breeding distribution of sandhill cranes in Russia with a primary focus on the 1,000-km range expansion in northern Yakutia over the past 60 years. We identify the current western limits of crane breeding in Russia based on results from our investigations. We also identify the Anadyr Lowlands, Chaun Depression, and Kolyma Region as the most important centers of sandhill crane breeding in Russia based upon settling patterns of a random sample of 133 PTT-tagged cranes tagged on the principal spring staging areas of the MCP in North America. Densities of sandhill cranes from across their breeding range in Russia are compared based on results from ground and aerial surveys. Possible factors contributing to the major range expansion of sandhill cranes in Russia starting in the mid-20th century include climate change and population growth.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:117

Key words: Breeding distribution, *Grus canadensis*, MCP, Mid-continent Population, PTT, Russia, sandhill crane.

A REVIEW OF PARENT-REARING WHOOPING CRANES AT PATUXENT WILDLIFE RESEARCH CENTER, 1988-2003.

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Abstract: Seventy-four whooping crane (*Grus americana*) juveniles were reared by captive whooping crane parents between 1988 and 2003 at Patuxent Wildlife Research Center. Fifty-two chicks (70%) survived to 1 October of their hatch year. Chicks were raised by their own parents or by foster parents using 4 different adoption methods to foster eggs or chicks. Eleven pairs raised chicks with rates of success for each pair varying from 0 to 100%. Forty-six parent-reared whooping cranes were released in central Florida as part of an attempt to establish a non-migratory flock and 6 were kept in captivity. Parent-rearing increased Patuxent's capacity to rear chicks for release.

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Key words: *Grus americana*, parent-rearing, Patuxent, whooping cranes.

PREDICTING OUTCOMES OF REINTRODUCTION STRATEGIES IN A DECISION-ANALYTIC SETTING

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Abstract: Thoughtful long-term planning of reintroductions to the Eastern Migratory Population of whooping cranes (*Grus americana*) is critical given the high-stakes nature of the reintroduction: it is an important element of the species' recovery plan but is costly in terms of money, time, and use of captive-bred propagules. As part of a 5-year planning process embarked upon by the Whooping Crane Eastern Partnership (WCEP), we took a decision-analytic approach to reintroduction planning. The authors served as analysts and facilitators for the WCEP Guidance Team, which has responsibility for the reintroduction. Through this process, decision objectives and alternatives were identified, and models were developed to predict objective outcomes under various alternatives. The most complex of these models predicted probability of population persistence based on a Bayesian Population Viability Analysis (BPVA). The BPVA was parameterized with empirical estimates from a Bayesian multi-state mark-recapture model, and with expert opinion. Expert opinion was necessary to allow for prediction of unobserved demographic processes, such as breeding success at novel release sites, which are key to evaluating alternative strategies. The BPVA also integrated model-based uncertainty, reflecting uncertainty about the cause of widespread nest failure in this population. The predictions made in the BPVA were integrated into the decision-analytic process, and decisions on a 5-year strategy will be forthcoming. However, it is important to see decision analysis in this case not as a process with a defined beginning and end, but as an ongoing process to support adaptation in the management of this population as uncertainties are resolved over time.

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Key words: Bayesian Population Viability Analysis, BPVA, Eastern Migratory Population, *Grus americana*, reintroduction, WCEP, whooping crane, Whooping Crane Eastern Partnership.

MOVEMENT STRATEGIES OF SUBADULT INDIVIDUALS ON WINTER HABITAT INFLUENCE WINTER RANGE EXPANSION OF A MIGRATORY BIRD

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Abstract: Habitat qualities encountered on wintering grounds by migratory birds have carry-over effects on population dynamics in the breeding season and may influence future winter range expansion. Furthermore, subadult individuals of many long-distance migratory birds often wander farther distances on wintering grounds than paired birds that defend winter territories, suggesting various habitat qualities are encountered by these individuals each winter. We developed a preliminary model for the endangered whooping crane (*Grus americana*) to investigate how 2 different movement strategies utilized by subadult individuals on the winter areas along the Texas coast over a 5-year period may influence future range expansion and population dynamics. The first strategy incorporated the known life-history characteristics of subadults spending most time on the winter grounds in close proximity to their parents' territory; whereas we added a habitat quality parameter in strategy 2 to mimic their tendency to visit habitats known for plentiful food supply. Birds utilizing strategy 1 remained in close proximity to their parents' territory each year and encountered low to average habitat qualities, and birds of strategy 2 traveled farther distances and associated with higher quality habitats. Our model is the first attempt at predicting subadult *G. americana* movement behavior on the winter range and explores the implications on future range expansion between 2 different movement strategies–site fidelity and habitat quality. Future development of this model will incorporate a trade-off parameter between the 2 strategies to better resemble subadult movement and allow for more accurate predictions of *G. americana* winter range expansion and carry-over effects.

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Key words: *Grus americana*, habitat quality, movement strategy, site fidelity, subadults, whooping crane, winter range expansion.

PEOPLE OF A FEATHER FLOCK TOGETHER: A GLOBAL INITIATIVE TO ADDRESS CRANE AND POWER LINE INTERACTIONS

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Abstract: *The Cranes: Status Survey and Conservation Action Plan* of the IUCN/SSC Crane Specialist Group (1996) identified overhead power lines as a significant global threat to many crane species worldwide. The demand for electricity from growing economies and efforts to alleviate poverty through rural electrification are likely to increase in most of the developing world. Most of the sites where power line collisions occur are remote and communications among individuals have been very limited. To our knowledge, South Africa is the only crane range state with a comprehensive national program to deal with the threat of power line collisions (the Eskom-Endangered Wildlife Trust (EWT) Strategic Partnership). Coordination is critical at this stage, in order to share lessons, develop capacity, pool resources, and accelerate collective learning towards finding innovative solutions to mitigate this impact on threatened crane populations. In order to initiate this international collaboration, key role players participated in a workshop in Yueyang, China, in December 2012 aimed at stimulating discussion and promoting the coordination of efforts. Key outcomes of this workshop included: 1) a briefing document detailing the baseline information on global impact of power line collisions, the identification of hotspots and the process to be followed to address the impacts in these areas, and a comprehensive list of research and mitigation needs, and 2) the establishment of a global Cranes and Power Lines Working Group comprised of regional subject matter experts working in partnership to address this threat through the sharing of expertise and acting as an informed stakeholder group.

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Key words: cranes, Cranes and Power Lines Working Group, mitigation, power lines, South Africa.

EVALUATION OF LONGEVITY AND WEAR OF COLORED PLASTIC LEG-BANDS DEPLOYED ON SANDHILL CRANES IN WISCONSIN

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Abstract: We investigated durability and retention of colored plastic leg bands deployed on sandhill cranes (*Grus canadensis*) by the International Crane Foundation since 1991. Overall, band retention was high (>90%) across 20 years of observation. A logistic regression model showed that 4 variables (band height, sex of bird, year of band deployment, and radio presence/absence) significantly affected long-term band retention. Short bands (2.5 cm) were 4.5 times more likely to fall off than tall bands (7.5 cm). Males were 2.3 times as likely to lose short bands as females, although females showed more wear on recovered tall bands over time. Low-quality plastic likely increased band loss in 1996-97. The largest factor affecting short band retention was the attachment of a radio transmitter which increased the weight and wear on plastic thickness. Short bands with radios attached were 4.0 times as likely to be lost as short bands without radios. Attaching a radio to a short band decreased its average and maximum lifespan by 5 years compared to short bands without radios attached. We provide 3 recommendations to maintain, or possibly increase, lifespan of short bands on sandhill cranes: 1) introduce bands made of solid plastic in 2 halves that snap together around a crane's leg rather than wrap around it, 2) mount leg-band transmitters on tall bands, or 3) use backpack harness-mounted transmitters instead of leg-mounted transmitters. These recommendations can significantly increase band retention, thereby reducing band loss, in a marked population of a long-lived avian species.

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Key words: band longevity, *Grus canadensis*, plastic leg-bands, sandhill crane.

SURVIVAL OF THE ROCKY MOUNTAIN SANDHILL CRANE

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Abstract: The sandhill crane (*Grus canadensis*) is one of the longest lived of game bird species. Species with its life history tend to have relatively constant adult survival rates over time, mitigating environmental stresses by reducing reproductive effort. Given its low natural mortality rate, crane populations are not robust to large harvest rates, even if compensatory mortality is applicable. We evaluated survival of Rocky Mountain Population sandhill cranes during 1969-1992, based on a mark-resight/recovery program. This included time periods before and after initiation of sport harvest. Most cranes were banded as juveniles, on the breeding grounds, and the resighting period was centered in the winter. Therefore we estimated survival of the first 6 months, and then annual survival thereafter. We modeled crane survival as a function of age, body condition, and pre- or post-sport harvest. We also modeled relative vulnerability of cranes to hunting vs. non-hunting sources of mortality. Survival estimates were adjusted for loss of field-readable marks over time. Juvenile survival for the first 6 months was dependent on body condition, and on whether hunting occurred. Hunting also reduced survival from age 0.5 to 1.5 years, but had no effect on survival for age >1.5 years. Up to age 4.5, cranes were more vulnerable to non-hunting sources of mortality, relative to cranes age >4.5 years. The apparent lack of hunting impact on adult crane survival is based on data only until 1992. A new banding program for cranes could test whether harvest is more additive with current harvest levels.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:121

Key words: *Grus canadensis*, hunting mortality, Rocky Mountain Population, sandhill crane, survival.

THE USE OF SATELLITE TELEMETRY TO EVALUATE MIGRATION CHRONOLOGY AND DISTRIBUTION OF EASTERN POPULATION SANDHILL CRANES

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Abstract: The Eastern Population (EP) of sandhill cranes (*Grus canadensis tabida*) is rapidly expanding in size and geographic range. Limited information exists regarding the geographic extent or migration chronology for EP cranes. To address these information needs, we trapped and deployed Platform Transmitting Terminals (PTTs) on 33 sandhill cranes from 2009 through 2011 to assess movements throughout the year. Tagged cranes settled in summer areas of Minnesota (10%), Wisconsin (34%), Michigan (28%), and Ontario, Canada (21%). Cranes departed for initial fall staging stopover sites by early October through Wisconsin, Michigan, Illinois, Indiana, Ohio, Kentucky, and Tennessee before reaching their winter terminus. We identified staging and transient stopovers; Jasper-Pulaski FWA, Indiana, and Hiwassee Wildlife Refuge, Tennessee, were used as stopover sites most frequently during migration. Cranes arrived at their winter terminus by mid-December in Indiana (28%), Kentucky (10%), Tennessee (69%), Georgia (10%), and Florida (31%). Cranes departed on spring migration by February and travelled on routes similar to those used during fall migration to their respective summer areas. Seventy-nine percent of marked cranes (n = 23) returned to their initial summer area after a second spring migration. The estimated difference among mean center of the previous year's summer area was 0.53 km. The information we collected on EP sandhill crane movements provides insight into distribution and migration chronology that will aid in assessment of the current U.S. Fish and Wildlife Service Cooperative Fall Abundance Survey and can aid state and federal managers in identifying and protecting key staging and winter areas.

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Key words: Eastern Population, *Grus canadensis tabida*, migration, movements, PTT, sandhill crane.

NATIONAL WHOOPING CRANE ENVIRONMENTAL EDUCATION PROGRAM

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Abstract: The International Crane Foundation and Hamline University's Center for Global Environmental Education have formed a partnership to develop a 4-part national whooping crane (*Grus americana*) environmental education program involving interactive multimedia tools. This work started in Texas through a partnership with Texas A&M University-Corpus Christi's Harte Research Institute. The first module, *Estuaries in the Balance: The Texas Coastal Bend*, focused on how estuaries work and the vital importance of the quantity and timing of freshwater inflows in sustaining high-quality habitat for wintering whooping cranes, as well as on sustaining important fisheries and industries for local economies. Target audiences are students and teachers in grades 4-8, families, and the general public. The curriculum is multi-disciplinary and adheres to state academic standards in science and social studies. The program is available via the web and distributed to schools, zoos, national wildlife refuges, and through partnership with Texas Parks and Wildlife Department. Development is currently underway for the second multimedia module, *To the Brink and Back*. This program will engage users in an exploration through time of the whooping crane as a species and the crane's relationship with humans. It will bring to life the history of the species' decline and recovery within the context of the larger conservation movement, whooping crane conservation and reintroduction, the fate of other selected endangered and extinct species, and important legislation that has affected whooping cranes.

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Key words: environmental education program, *Grus americana*, partnership, whooping crane.

THE ROLE OF POPULATIONS AND SUBSPECIES IN SANDHILL CRANE CONSERVATION AND MANAGEMENT

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Abstract: The scientific literature on sandhill cranes (*Grus canadensis*) is organized into 9 breeding populations (Cuban, Florida, Mississippi, Eastern Flyway, Mid-Continent, Rocky Mountain, Lower Colorado River, Central Valley, and Pacific Flyway) and 6 subspecies. Several populations are composed of multiple subspecies, with subspecies occurring in multiple populations, and some populations are further divided into subpopulations that may also include multiple subspecies. Populations with "flyway" nomenclatures are not necessarily restricted to the North American flyway specified. The organization of sandhill crane distribution was adopted when cranes were limited by loss of wetland habitat and overhunting, which caused distinct breeding populations separated by unoccupied areas. Using this approach, management actions were tailored to meet local and regional recovery goals with great success. Sandhill crane populations are now larger than they were only a few decades ago and their distribution continues to expand. However, as crane populations and crane research have grown, unoccupied areas between populations have become populated, and genetic analyses have suggested that revision of subspecific designations may be warranted. This can lead to substantial confusion when evaluating an author's intended scope of inference for a given study. In this presentation, we define and review support for the existing organization of populations, subpopulations, and subspecies. We then discuss the implications of recent genetic and citizen science analyses to the existing organization. We close with an open question of what costs and benefits to crane conservation and management might occur if population designations were redefined.

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Key words: *Grus canadensis*, populations, sandhill cranes, subpopulations, subspecies.

ANNUAL VARIATION OF YOUNG OF THE YEAR IN THE ROCKY MOUNTAIN POPULATION OF SANDHILL CRANES

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Abstract: The sandhill crane (*Grus canadensis*) has the lowest annual production of young of any harvested bird in North America. Within the Rocky Mountain Population (RMP), the percent of juveniles (<1 year old) has been observed to fluctuate considerably among years (3-12%). Recognizing the mechanisms that drive this variation is important for understanding population dynamics and making future harvest decisions. The 3-year average of the percent of juveniles during migration at the San Luis Valley, Colorado is one of the parameters used to calculate the allowable number of harvest permits for the RMP. Reliable predictions of the production of young would be helpful in understanding limitations of population growth, and evaluating the importance of the juvenile survey in an optimal harvest decision strategy. Following previous hypotheses of the influence of large-scale drought on RMP crane juvenile production, and given predictions of future climate trends, we evaluated whether climate variables (e.g., winter snow depth, freezing temperatures during brooding) and drought indices (e.g., Palmer Drought Severity Index, Palmer Drought Z Index) could explain observed annual variation. Data were collected from 1972 to 2013. We fit these data using a Bayesian beta linear regression model. We found the Palmer Drought Severity Index a good predictor of juvenile production. Drought indices below zero were correlated with below-average juvenile production. Drought indices may be useful to adjust the harvest formula so a conservative number of permits are issued when juvenile production is expected to be low.

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Key words: annual variation, drought index, *Grus canadensis*, harvest, juvenile production, RMP, Rocky Mountain Population, sandhill crane.

AGE-SPECIFIC MIGRATORY AND FORAGING ECOLOGY OF EASTERN POPULATION GREATER SANDHILL CRANES

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Abstract: Migratory birds adapt behavior to exploit changes in food resources. Altering foraging behavior and migratory chronology are common adaptive strategies that are linked to food density and distribution during migration. In some species, hatch-year (HY) individuals do not complete structural growth prior to migration. Therefore, food density and distribution, nutritional requirements, and foraging experience can also affect foraging behavior. We studied these relationships in Eastern Population greater sandhill cranes (*Grus canadensis tabida*) at Manitoulin Island, Ontario, Canada, during autumn migration 2011 and 2012. Our goal was to elucidate how changes in food density and variation affect behavior. We collected observational data that included: 1) waste grain depletion, 2) number and age of cranes using focal fields (functional response), and 3) individual behavioral time budgets of after hatch-year (AHY) and HY cranes using focal fields (behavioral response). We also conducted an experiment in 2012 to test for a causal relationship between grain and behavioral response. We manipulated grain in 0.25-acre plots in a sub-sample of focal fields ($n = 12$) to emulate natural grain depletion. Results from our negative binomial generalized linear mixed-effects analysis of the functional response dataset showed no evidence for differences between AHY and HY field use. Our modelling procedure provided support (63% AIC support) for positive additive effects on functional response from field area, distance to nearest roost wetland, time of day, total grain density at the 5-km scale, and relative grain density at the 5-km scale. Our results did not provide evidence for within-field grain density or variation effects on functional response. Total and relative grain effects on field use were more important at the 5-km scale (i.e., a community food effect) than we had anticipated. Results from our linear mixed-effects modelling of the behavioral response dataset collected in observational fields provided evidence for more efficient foraging by HY cranes. Our top model (32% AIC support) showed negative additive effects (decreased foraging efficiency) from month of observation, crane age, and total grain and positive additive effects (increased foraging efficiency) from proximity to nearest roost wetland and grain variation (0.358 ± 0.19). Though the difference (± 1 SE) in foraging efficiency between age groups was relatively small (−0.01 ± 0.006), our findings did not support our prediction that HY cranes feed less efficiently on seasonally novel food sources (i.e., spend more time searching compared to feeding relative to adult conspecifics). Analysis of our experimental dataset provided additional support for positive additive effects on foraging efficiency from variation (1.134 ± 0.36). The inclusion of grain variation but not grain density in our top models accords with the inverse relationship that often exists between heterogeneity of food distribution and foraging efficiency.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:124

Key words: autumn migration, Eastern Population, foraging, grain density, *Grus canadensis tabida*, Manitoulin Island, sandhill crane.

EVALUATION OF A VACUUM TECHNIQUE TO ESTIMATE ABUNDANCE OF AGRICULTURAL GRAIN

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Abstract: Estimation of waste grain density and distribution in harvested agricultural fields is needed to develop energetic carrying capacity models for non-breeding granivorous gamebirds. We aimed to evaluate the efficacy of the Penny et al. blower-vacuum method for sampling waste barley at our study site as part of a larger study of Eastern Population sandhill crane (*Grus canadensis*) foraging and migratory ecology. To determine if the Penny et al. vacuum technique adequately sampled waste barley, we developed an experiment that compared the efficacy of the vacuum technique to hand-picking. In 2011, we used our Stihl Model BG 65E Blower-Vac and modified it similar to Penny et al., and in 2012 we used the Penny et al. Stihl Model BG 85. We sampled grain during autumn and conducted 2 analyses to evaluate the devices, including: 1) we sampled points (n = 25) in 3 different fields using the vacuum sampling device for 10 seconds, hand-picking, and digging 2 cm into the substrate to collect remaining seeds, and 2) we randomly placed known abundances of dyed barley seeds in sampling frames, and sampled for 10 seconds. In each of the 3 fields, we used 3 different seed densities that were 90, 50, and 10% of the maximum density recorded in fields at the study site (n = 12 per field, 36 total). Hand-picking was more effective (mean seed recovery = 98%) than the vacuum technique in both years. We detected no substantial vacuum model, seed density, or field effect.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:125

Key words: agricultural fields, Eastern Population, *Grus canadensis*, sandhill crane, vacuum sampling, waste grain density.

CHARACTERIZATION OF STOPOVER SITES USED BY WHOOPING CRANES AS DETERMINED FROM TELEMETRY-MARKED BIRDS

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Abstract: An essential component to conservation of Aransas-Wood Buffalo whooping Cranes (*Grus americana*) is identifying locations and characteristics of migration stopover sites, but this type of information is limited due to the rarity of whooping cranes and remoteness of their stops. Data from the Whooping Crane Tracking Partnership provides an unprecedented opportunity to locate stopover sites along the entire migratory corridor. Much of the information about these sites, however, cannot be remotely sensed and is available only from ground-based, time-sensitive measurements of habitat characteristics. In 2012 the Platte River Recovery Implementation Program (Program) and researchers from the U.S. Geological Survey and Crane Trust initiated a ground-based study spanning from northern Texas to North Dakota to evaluate habitats that over 30 telemetry-marked whooping cranes have used as stopover sites during their migration. Herein, we present the overall study approach, show images of the diversity of habitats visited, and summarize preliminary results from site evaluations. Over 200 stopover sites have been characterized to date, thereby greatly improving our understanding of sites selected by migrating whooping cranes. Stopover site evaluations depend largely on private landowners allowing access to their properties, and we are grateful for the access landowners have provided to the project during the past several migration seasons. The Program and other organizations will apply knowledge gained from this study to inform habitat management practices and conservation strategies along the central Platte River and throughout the migration corridor.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:126

Key words: Aransas-Wood Buffalo, *Grus americana*, migration stopover, Tracking Partnership, whooping crane.

MESHING NEW INFORMATION FROM THE WHOOPING CRANE TRACKING PARTNERSHIP WITH SPECIES RECOVERY GOALS—NEXT STEPS

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Abstract: The International Whooping Crane Recovery Plan (2007) has established population goals and objectives for downlisting whooping cranes (*Grus americana*) from "endangered" to "threatened". Delisting criteria have not been established as of yet. In addition to population goals and objectives, the plan outlines a number of recommended actions that need to be taken to move species recovery forward. We expect that data generated from the Whooping Crane Tracking Partnership will provide key metrics that will enhance our understanding of population demographics for the last remaining natural population of whooping cranes (i.e., the Aransas-Wood Buffalo population, AWBP). If ongoing whooping crane reintroduction projects are not able to establish additional, self-sustaining whooping crane populations, the AWBP will have to continue increasing both its overall range and population size in order for this species to reach current downlisting goals (i.e., alternative downlisting criteria 1B). Thus, information gleaned from the tracking partnership on AWBP demographics such age-specific mortality rates, causal mortality factors and habitat use throughout the species' range will provide critical information to future recovery efforts. We examine preliminary data from the Whooping Crane Tracking Partnership and suggest near-term recovery actions and long-term planning efforts that will enhance species conservation efforts specific to the AWBP.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:127

Key words: Aransas-Wood Buffalo population, downlisting, *Grus americana*, recovery, Tracking Partnership, whooping cranes.

HEALTH ASSESSMENT OF JUVENILE WHOOPING CRANES IN WOOD BUFFALO NATIONAL PARK

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Abstract: During 2010-2012, 31 (19 males, 12 females) pre-fledging, juvenile whooping cranes (*Grus americana*) were captured for satellite tagging and health assessment at Wood Buffalo National Park (WB), Canada. All WB birds were in good to excellent physical condition and exhibited normal responses to capture. The mean ± SE body weight was 4472 ± 87 g (range 3311-5200 g). Feather condition was generally good and no external parasites were observed. Morbidity associated with capture was noted in 4 individuals: 1 crane avulsed a toenail and 3 others sustained self-induced lacerations likely from kicking out at capture. Preliminary analysis of laboratory data revealed numerous differences in the hematology, clinical chemistry, trace element and serum protein electrophoresis values of WB versus captive-reared juvenile whooping cranes, likely due to increased exposure to potential antigens in WB birds over captive and dietary differences between the 2 populations. Prevalence of the protozoan parasite *Haemoproteus* sp. was similar between WB (10%) and captive (17%) juveniles. Four of 30 (13%) WB juveniles were seropositive for West Nile virus, and 11 of 28 (39%) were seropositive for Infectious Bursal Disease virus. All 26 WB juveniles tested were seronegative for Inclusion Body Disease of Cranes, and 31 juveniles were negative for Avian Influenza by RT-PCR of cloacal swabs. Moderate to heavy growths of *E. coli* were isolated from cultures of cloacal swabs of WB juveniles; none were positive for *Salmonella* sp. or *Campylobacter* sp. By comparison, *Campylobacter* sp. is commonly isolated from captive juveniles. This study provides baselines for many health parameters in wild whooping cranes.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:127

Key words: *Grus americana*, health assessment, juveniles, whooping crane, Wood Buffalo National Park.

TERRITORY AVAILABILITY BEST EXPLAINS FIDELITY IN SANDHILL CRANES

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Abstract: We investigated dynamics of mate and site fidelity among color-banded sandhill cranes (*Grus canadensis*). Over 22 years, 81 permanent mate switches (70%) occurred in 115 pairs: 24 switches (31%) were divorces and the rest occurred following mate disappearance. The asynchronous migration, incompatibility, and better option hypotheses did not explain divorces in this population well. Productivity of divorced pairs prior to separation was lower than non-divorced pairs, but divorcing did not improve individual productivity and productivity of divorced pairs following separation was lower than non-divorced pairs. Following divorce or mate disappearance, territory retention was high (divorce = 100%, mate loss = 83%) while males and females did not differ in original territory retention. Long-term territory retention led to higher lifetime productivity and divorcing prolonged territory retention, especially for pair bonds that may have been unstable. Divorcing birds typically paired with experienced territory holders, although invasion into a pair bond by a non-territorial bird occurred. Post-divorce, relocating birds moved to adjacent territories with a vacancy rather than re-distribute to random territories. Because territories in this population are limited, an opening on a proximate territory offers a potential advantage: a bird can stay with a current mate and territory, even if reproductive history is poor, or it can seek a new but familiar mate on an adjacent territory to potentially improve productivity in an unknown future. Pairing with familiar birds may minimize the risk of losing a territory altogether. Divorces are best explained by a new "territory limited" hypothesis rather than existing hypotheses.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:128

Key words: *Grus canadensis*, mate fidelity, sandhill cranes, site fidelity, territory.

MISSISSIPPI SANDHILL CRANE CONSERVATION UPDATE 2011-13

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Abstract: The Mississippi sandhill crane (*Grus canadensis pulla*) is an endangered non-migratory subspecies found on and near the Mississippi Sandhill Crane National Wildlife Refuge in southeastern Mississippi. From 2011 to 2013, conservation efforts for the recovery of this population included management activities such as protection and law enforcement, restocking, predator management, farming, prescribed burning, mechanical vegetation removal, hydrological restoration, pest plant management, and education. To maintain open savanna, we burned 4,060 hectares (10,033 acres), with 69% during the growing season. To restore open savanna, over 4,040 hectares (1,000 acres) of woody vegetation were removed using mechanical methods. To bolster the population, we released 42 captive-reared juveniles as part of 7 cohorts. To protect cranes, nests and young, contractors conducted 17,400 trap-nights, removing 93 large predators and 200 raccoons (*Procyon lotor*). Crane and habitat monitoring assessed life history parameters including radio-tracking, visual observations, and an annual nest census. We collected over 5,150 observation records including 1,760 radio-fixes. We discovered 18 after-hatch-year carcasses. Of 14 with known or suspected causes of death, 6 were due to predation, 2 to disease (including first cases of encephalitis), and 8 to trauma. During the 3-year period, there were 36, 30, and a record 39 nests resulting in 3, 2, and 5 fledglings, the latter including only the third set of twins recorded. The December 2012 population was approximately 120 cranes, up slightly from the previous total.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:128

Key words: *Grus canadensis pulla*, management, Mississippi sandhill crane, monitoring.

MIGRATION ROUTES AND WINTERING AREAS OF PACIFIC FLYWAY LESSER SANDHILL CRANES

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Abstract: Some lesser sandhill cranes (*Grus canadensis* canadensis) breed in the Homer area of the Kenai Peninsula, Alaska, and those birds are part of the Pacific Flyway lesser sandhill crane population. We captured 10 of the Homer summer lesser sandhill cranes in 2008, using noose lines, and fitted each crane with a satellite transmitter to track their migration routes to and from their wintering areas. On their migration south, they traveled east to Prince William Sound before they turned southeast and flew along the Alaska coast and the Alaska panhandle before they proceeded inland to British Columbia. From there they traveled southeast to eastern Washington and Oregon before arriving about a month later in the Central Valley of California for the winter, a distance of 3,860 km (2,400 miles). They used 3 wintering areas in the Central Valley, including the Sacramento-San Joaquin Delta, the Merced Grasslands, and the San Joaquin River National Wildlife Refuge (NWR). Their spring migration route was similar to their fall migration; however, the return trip took twice as long. The most important site used for staging during migration was Columbia NWR, near Othello, Washington.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:129

Key words: *Grus canadensis* canadensis, Kenai Peninsula, lesser sandhill crane, migration, Pacific Flyway, wintering areas.

A MODEL FOR MITIGATING LOSS OF CRANES FROM POWER LINE COLLISIONS

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Abstract: Mortality from power line collisions is a serious issue for cranes. We developed a geospatial model to facilitate mitigation of take of greater sandhill cranes (*Grus canadensis tabida*) from proposed power lines in the Sacramento-San Joaquin Delta Region of California that should result in no net take. The model uses our data on local night roost site population estimates and of distances that greater sandhill cranes are likely to fly within 6 km from their roosts to develop crane use probability polygons around night roosts. We estimated crane overflights for each polygon within the 6-km radius, transected by a proposed power line per day (assuming 4 daily overflights and that 25% birds fly out in the cardinal direction of the line from the roost site), multiplied by the number of days in the wintering period then divided by the proportion of the line crossing the crane use area within each polygon. We then calculated expected mortalities using mortality rates/overflight reported in the literature. After estimating annual losses, we proposed using the same model to estimate the number of cranes "saved" by marking, burying, or removing existing powerlines (considering the efficacy of line markers to reduce mortality; generally less than 80%) in the area to achieve full mitigation of expected losses. Such a model could be applied to mitigate new power lines in areas where collision risk is high for similar species such as swans and other large birds.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:129

Key words: California, geospatial model, greater sandhill cranes, *Grus canadensis tabida*, mitigation, mortality, power line collisions.

SPACE USE OF WINTERING WHOOPING CRANES

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Abstract: Two hundred and fifty productive pairs or 1,000 individuals are the number of whooping cranes (*Grus americana*) of the Aransas-Wood Buffalo population needed for achieving recovery goals and subsequent downlisting to 'threatened' status. What is not known is how much habitat and/or area is required to support this goal. We can begin to understand the space needs of cranes by employing data collected by telemetry-marked bird locations at fixed intervals. Kernel density estimators are used to evaluate the seasonal ranges and potential territory sizes. We assess variation in seasonal range size with timing of arrival at the wintering grounds, age class, and habitat quality. Understanding how whooping cranes use space, both temporally and geographically, will increase our ability to identify area needed for cranes and aid in refining land conservation priorities to achieve recovery objectives.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:130

Key words: Aransas-Wood Buffalo population, *Grus americana*, space use, whooping cranes.

SOCIAL LEARNING OF MIGRATORY PERFORMANCE

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Abstract: Successful bird migration can depend on individual learning, social learning, and innate navigation programs. Using 8 years of data on migrating whooping cranes (*Grus americana*), we were able to partition genetic and socially learned aspects of migration. Specifically, we analyzed data from the Eastern Migratory Population wherein all birds were captive bred and artificially trained by ultralight aircraft on their first lifetime migration. For subsequent migrations, in which birds fly individually or in groups but without ultralight escort, we used deviations from a straight-line path between summer and winter ranges on the migratory route of individual birds as a proxy for migratory performance. We built a hierarchical linear mixed model to examine how much of those deviations at each observed location on the migratory route could be explained by individual age, age of the oldest individual(s) in a migratory social group, group size, and genetic relatedness on both individual and group levels. The age of the oldest individual(s) in a group improved migratory performance by ~5.5% per year of age, decreasing the average deviation from a straight-line path by ~4.2 km per year of age for each relocation event (posterior mode: –4.2 km, 95% highest posterior density interval [HPDI]: –1.1 to –7.2 km). We found no significant effects of individual migratory age, group size, or mean group genetic variance. Our results show that social learning enhances group navigation performance for long-distance migrants and that the benefits of experience accrue over many years.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:130

Key words: *Grus americana*, migration, social learning, whooping crane.

PARENT-REARING AND RELEASING WHOOPING CRANES IN WISCONSIN

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Abstract: Four whooping crane (*Grus americana*) chicks were successfully reared at USGS Patuxent Wildlife Research Center, Laurel, Maryland, and released on Necedah National Wildlife Refuge, Wisconsin, in 2013. The chicks were reared by whooping cranes that had successfully reared sandhill crane (*G. canadensis*) chicks, and were, therefore, rated as proven parents. All whooping crane chicks received periodic health examinations. Chicks were vaccinated for West Nile Virus and Eastern Equine Encephalitis. Chicks were hatched during an 8-day period in early June. After fledging in net-covered pens at Patuxent, they were shipped by aircraft to Necedah NWR, 19 September, and placed in temporary pens for 4-6 days before release. Two of the crane chicks successfully integrated and moved off refuge. One crane was located (27 November 2013) in central Kentucky on the wintering area of the pair of adult cranes that the chick was accompanying. The other chick was in northern Indiana along the Kankakee River, and then flew in 1 day to southeastern Tennessee near Hiwassee Wildlife Refuge. Two chicks died after release. One was killed 7 days post-release by a vehicle along one of the east-west roads that cross the refuge. The other chick was killed by a canid predator 2 weeks post-release while on the territory of the adult birds it was accompanying. The parent-rearing technique was successful in rearing and releasing whooping cranes into the targeted population. Two of the released birds formed bonds with wild adult pairs, and 2 of the released birds successfully migrated from central Wisconsin to known wintering areas of cranes.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:131

Key words: *Grus americana*, Necedah NWR, parent-rearing, Patuxent, whooping crane, Wisconsin.

BEHAVIORAL COMPARISON OF COSTUME AND PARENT-REARED WHOOPING CRANE CHICKS

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Abstract: During June through August 2013, 4 whooping crane (*Grus americana*) chicks that were reared by adult parent whooping cranes for eventual release in Wisconsin were monitored and behaviors recorded. Also, during the same period, 11 whooping cranes were costume-reared by humans for eventual release in Louisiana. Behaviors were also monitored for this group. All behavioral observations were recorded as 5 minute focal observation periods. Times of observations were selected randomly between 0800 and 1500 hours primarily to avoid conflicts with other activities. No observations were possible overnight because of potential for disturbance. Results for whooping cranes will be compared to a similar study done in 2010. Behavioral activities were divided into 2 categories, posture or movements, such as standing, hock sitting, walking, running, and resting on sternum, and activity such as foraging, vigilant, non-vigilant, sleeping, drinking, grooming or preening. Thus a crane chick would be scored for both a posture and an activity, such as standing and foraging, or walking and vigilant. For most behaviors, there were no differences between parent-reared and costume-reared chicks, but differences were observed in the amount of time the 2 groups spent in vigilant behavior and in foraging.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:131

Key words: behavioral comparison, costume-rearing, *Grus americana*, parent-rearing, whooping crane.

A TECHNIQUE FOR AGING CRANES

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Abstract: Wild birds are traditionally aged, using feather characteristics, as hatch year (HY), after hatch year (AHY), second year (SY), and after second year (ASY); often only HY and AHY. For wild birds, no accurate method of aging exists. This is especially important for long-lived bird species such as cranes. Having a method of accurately aging wild cranes will improve assessment of age-specific survival and fecundity and result in more accurate age distribution information. Bird banding studies give researchers and managers information that is age-specific if the age of the bird is known at banding. However, this information is often not known for AHY birds. For cranes, it is extremely difficult to catch and band full-flighted individuals. Pentosidine is a compound that results from the non-enzymatic glycosylation of collagen. Pentosidine is considered stable and irreversible. It is found in a variety of organs and tissues, including skin, and will accumulate slowly during the entire lifetime of an animal. Pentosidine has been tested as a chronological aging method in a number of bird species, and we have been developing this technique using known-age sandhill cranes (*Grus canadensis*) and whooping cranes (*G. americana*) to develop techniques for using pentosidine as an aging tool or biomarker for endangered Mississippi sandhill cranes (*G. c. pulla*) and whooping cranes in the wild.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:132

Key words: aging technique, cranes, *Grus*, pentosidine.

MIGRATION ECOLOGY OF ARANSAS-WOOD BUFFALO WHOOPING CRANES

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Abstract: Aransas-Wood Buffalo whooping cranes (*Grus americana*), like many other migratory birds, make major moves between summer and wintering grounds twice each year. Birds in this population travel approximately 4,000 km through the Great Plains of North America. Using data from the Whooping Crane Tracking Partnership, we estimated some basic migration parameters from 57 individuals marked with transmitters that collected multiple GPS locations per day. Our preliminary results indicate that whooping cranes have a protracted migration period, wherein in some migrations, birds arrive at terminal areas (e.g., wintering grounds) before others leave initial locations (e.g., summering areas). Cranes used an average of 10 stopover sites during migration and the most common staging duration was 1 day (>60% of sites). Marked birds generally followed a migration corridor as determined from past sightings and staging within the corridor was more uniformly distributed than may have been apparent from sightings. We identified instances where birds used stopover sites from season-to-season, but this behavior was less common than use of novel sites. To date, we have documented 2 mortalities during migration. Basic data about the migration of this species coupled with other site-specific information will be used to further the conservation and management of this endangered population

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:132

Key words: Aransas-Wood Buffalo, *Grus americana*, migration, Tracking Partnership, whooping crane.

THE SPATIAL AND TEMPORAL USE OF HABITATS BY A REINTRODUCED POPULATION OF WHOOPING CRANES IN LOUISIANA

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Abstract: Forty pen-reared juvenile whooping cranes (*Grus americana*), comprising 3 release cohorts, have been released at the White Lake Wetlands Conservation Area in Vermilion Parish, Louisiana, since 2011 as part of a recovery effort to establish a self-sustaining wild population. Paramount to the survival of the Louisiana crane population (LAWC) is identifying habitats used by these cranes and understanding how habitat use changes spatially and temporally. We used CropScape, a USDA landuse GIS raster, for the years 2011 and 2012 to classify habitat type for 27,797 GPS satellite telemetry location points for 40 cranes from April 2011 through October 2013. We used these data to investigate the independent and interactive effects of year, time of day, and season on individual and cohort habitat use across the Louisiana landscape. We identified 15 habitat types used by the LAWC across 3 years. The number of habitat types used by the cranes increased each year (9 in 2011, 10 in 2012, and 13 in 2013). Eighty-one percent of the total crane location points were located in 3 habitat types: herbaceous wetlands (41%), rice (21%), and crawfish (17%). This study contributes important ecological information relative to habitats used by a reintroduced crane population across space and time. This information has been absent in our current understanding of overall crane use of natural resources and it provides us with the ability for comparisons between reintroduced and wild cranes.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:133

Key words: *Grus americana*, habitat use, Louisiana, whooping cranes.

BEHAVIOR ECOLOGY OF PEN-REARED, REINTRODUCED WHOOPING CRANES WITHIN THE LOUISIANA LANDSCAPE

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Abstract: Theoretically, whooping crane (*Grus americana*) behavior can be linked to long-term individual/population survival and fitness as individuals should behave in ways that maximize their success. Thus, understanding the behavioral ecology of the 40 pen-reared whooping cranes released in Louisiana is central to the successful establishment of a self-sustaining wild whooping crane population in Louisiana. We conducted time activity budgets on 4 whooping cranes (2 from L-10 cohort and 2 from L-11 cohort) between June 2012 and December 2012. Data were summarized from 12 observations, representing 9 hours of time activity. We will use these data to investigate: 1) crane behavior patterns relative to allocation of time by behavior type within and among cohorts and between individuals and flocks; 2) how these patterns change over space and time and compare to the wild population of whooping cranes; and 3) the correlation and characteristic of behavior by habitat type. Preliminary results show that overall, cranes spent more time (66%, $n = 4$) foraging than other behaviors. Cranes spent 14% and 11% of their time in preening and alert activities, respectively (n = 4). Cranes spent almost twice as much time loafing than walking (8% and 4%, respectively; $n = 4$). Sleeping cranes comprised the least amount of crane diurnal activities (2%, $n = 4$). This study provides novel quantitative information on behaviors exhibited by a pen-reared, reintroduced whooping crane population in the wild and provides a strong foundation for the effects of habitat quality, captive-rearing methods, disturbance rates and types, and other environmental factors on whooping crane behaviors.

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Key words: behavior, *Grus americana*, Louisiana, reintroduced ,whooping crane.

CAPTURE OF SANDHILL CRANES USING ALPHA-CHLORALOSE

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Abstract: The International Crane Foundation has captured greater sandhill cranes (*Grus canadensis tabida*) in Wisconsin using oral delivery of alpha-chloralose (AC). The goals of this study were to assess the efficacy of modest changes implemented in 2002 with drug deployment (regimented baiting limited to early fall) and post-capture treatments (fluid administration) intended to reduce capture-associated morbidity and mortality, especially exertional myopathy (EM). We reviewed 317 captures made between 1990 and 2011. Capture efficacy (the proportion of capture attempts where all cranes in a targeted social group were successfully immobilized) improved from 59% to 72%; however, there was no statistically significant difference in sedation scores. The proportion of cranes that were diagnosed with EM decreased from 7/188 (3.7%) to 3/129 (2.3%), and the overall mortality observed among the captured cranes decreased from 9/188 (4.8%) to 4/129 (3.1%). Time in confinement (elapsed time between capture and release, including processing and recovery in a portable pen) was reduced by 3 to 4 hours in birds that received subcutaneous fluids compared to those that did not ($F_{2,213} = 6.6$, $P = 0.002$), but no preventive association was found between fluid administration and the development of EM. The findings of this follow-up study suggest that these management changes in bait deployment resulted in modest improvement in the efficacy of the field capture technique and were associated with decreased morbidity and mortality rates with little change in sedative effect. This method is associated with very low morbidity compared to alternative practices used to capture groups of cranes.

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Key words: alpha-chloralose, capture, *Grus canadensis*, sandhill crane, Wisconsin.

A COMPREHENSIVE HABITAT TYPE DATASET FOR WHOOPING CRANE CONSERVATION PLANNING IN TEXAS, USA

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Abstract: Using land use and land cover data sets to develop species-specific habitat maps is challenging, especially if the species uses both upland and wetland areas. The last wild flock of whooping cranes (*Grus americana*) winters in a limited area along the northwestern Gulf coast in and around Aransas National Wildlife Refuge, Texas. While National Wetland Inventory data can provide a base map for estuarine coastal marsh and palustrine inland marsh extent, the adjacent upland and shallow sub-tidal vegetative cover are not represented. To adequately quantify potential habitat coverage and evaluate landscape patterns for conservation planning, we combined 3 databases (CHTD) to develop a preliminary habitat type dataset for whooping cranes. Using historical crane survey points from 2004-2010, we identified the habitat-type with each location, ranked the use, then created potential habitat type maps using the CHTD and calculated extent by rank. Use of habitat types at the micro level was not possible given the error within each of the databases used; however, the meso level provided valuable spatial coverage and amount of habitat available under current conditions. The mesohabitat type matrix was crosswalked to land cover classes in the Sea Level Affecting Marsh Model, and potential changes predicted for various sea-level rise scenarios. Overall, habitat types currently used by whooping cranes will decrease in the current wintering area. We identified the data gaps and information necessary to evaluate habitat quality at various spatial and temporal scales. Recommendations for improving the datasets as well as directions conservation strategies should take are also considered.

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Key words: Aransas National Wildlife Refuge, CHTD, comprehensive habitat type dataset, *Grus americana*, Texas, whooping crane.

EGG PRODUCTION BY FIRST-TIME BREEDERS IN THE EASTERN MIGRATORY POPULATION OF WHOOPING CRANES

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Abstract: In 2001 a project to reintroduce a migratory population of whooping cranes (*Grus americana*) into central Wisconsin began. In 2005, the first pairs began breeding. From 2005 to 2013, first nesting attempts by 42 different pairs were documented. Of those nests, 38 (90%) were initiated by pairs in which the females had no prior nesting experience. Of the remaining 4 pairs, 3 females had 1 year of experience each and 1 had 3 years of experience. Age at first breeding for the majority of females was 3 or more years; however 2 different females each produced a single egg when they were only 2 years old, in 2011 and 2012, respectively. Both eggs were collected after full-term incubation (between 35 and 46 days). Infertility was suspected, but due to their deteriorated condition, it could not be confirmed. These 2 eggs represent the first documented record of whooping cranes less than 3 years of age producing eggs. Egg production by individuals in the Eastern Migratory Population was compared to the naturally occurring population of whooping cranes, and to the reintroduced nonmigratory whooping cranes in Florida. In both the wild and Florida populations, no 2-year old females were confirmed laying eggs. Minimum age at time of first egg production for whooping cranes at 2 major captive breeding centers was 4 years.

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Key words: age, egg production, first-time breeders, *Grus americana*, Eastern Migratory Population, whooping crane.

NATAL DISPERSAL OF WHOOPING CRANES IN THE REINTRODUCED EASTERN MIGRATORY POPULATION: THE FIRST TEN YEARS

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Abstract: When managing a reintroduced population, it is important to quantify natural behavior, such as natal dispersal, to determine if the population is behaving "normally" compared to natural populations. In 2001 the Whooping Crane Eastern Partnership began raising and releasing costume-reared whooping cranes (*Grus americana*) into eastern North America in an effort to supplement the globally-endangered wild population. We measured natal dispersal distances for whooping cranes that dispersed from their release (i.e., "natal") area to their first breeding territory or nesting location on and around the Necedah National Wildlife Refuge in central Wisconsin. Using a generalized linear model, we determined that natal dispersal distances (range: 0.6-72.6 km, $n = 84$) were not predicted by sex, cohort, year of establishment, or age of the bird when it first became territorial. As more territories become occupied, there would be an extra cost to acquiring a territory farther from the natal area or displacing another territorial adult. However, the proportion of mature cranes that were territorial did not decrease over time. The reintroduced population is a decade old and most individuals have been costume-reared and released in the same general area. A lack of sex-biased natal dispersal has also been observed in the only remaining wild population of whooping cranes in central North America. Continued monitoring of this young, but maturing, reintroduced population will allow us to further determine if these trends are preliminary or truly represent results from a wild population.

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Key words: *Grus americana*, natal dispersal, reintroduced population, whooping crane.

CHANGES IN WINTER DISTRIBUTION OF THE REINTRODUCED EASTERN MIGRATORY WHOOPING CRANE POPULATION

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Abstract: From 2001 to 2012, 196 costume-reared juvenile whooping cranes (*Grus americana*) were released in the eastern U.S. to reintroduce a migratory population of this endangered species. Techniques included leading juveniles from Wisconsin to wintering areas by ultralight aircraft (UL) or direct autumn release (DAR) in Wisconsin prior to their first autumn migration. With few exceptions, UL cranes released on the Florida Gulf Coast wintered in inland freshwater habitats in subsequent winters. The population wintered in 4 general regions: Florida/southern Georgia, coastal Carolina, the mid-South (primarily Tennessee and northern Alabama), and the North (Indiana, Illinois, and Kentucky). The UL releases resulted in concentration of the early population in Florida. Later DAR releases and short-stopping by UL birds increased numbers in the mid-South. Winter climate played a large role in wintering in the North. Drought resulted in changes in wintering locations, especially in Florida. Other factors influencing changes in distribution included habitat degradation and associations with other cranes, especially new mates and birds released by different techniques. Breeding pairs and direct autumn-released birds exhibited greater winter site fidelity than non-breeders or ultralight aircraft-led birds, but fidelity was low for all groups. Most prevalent causes of mortality were predation in Florida and gunshot farther north. Because most pairing occurred in central Wisconsin, the widespread winter distribution had no apparent negative effect on pair formation. There was no clear relationship between winter region and subsequent incubation success. The widespread winter distribution of the population poses no apparent risk to the outcome of the reintroduction.

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Key words: direct autumn release, *Grus americana*, migratory population, reintroduction, ultralight aircraft, whooping crane, winter distribution changes.

PAIR FORMATION IN THE REINTRODUCED EASTERN MIGRATORY WHOOPING CRANE POPULATION

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Abstract: During 2001-2013, we examined pair formation in the eastern migratory population (EMP) of endangered whooping cranes (*Grus americana*) reintroduced into central Wisconsin. Released cranes were costume-reared in captivity and either led by ultralight aircraft (UL) to winter areas in Florida or released directly in the core Wisconsin area in autumn (DAR). Of 183 members of the population, 141 (77%) formed 346 pair bonds of 1-4 types. The primary cause of failure to form breeding pairs was mortality. For females, the secondary cause was dispersal from the core reintroduction area and association with sandhill crane (*G. canadensis*) flocks. For males, the secondary cause was insufficient numbers of females with which to pair in the core area. Most pairs did not form within groups. Mean age of breeding pair formation was greater for males because of the unequal sex ratio in the core. Mortality was the primary cause of breeding pair dissolution; mate stealing by males was a secondary cause. Mean re-pairing time was likewise greater for males. The core area was critical to pair formation, where minimally 87% of breeding pairs formed. Formation was concentrated in the arrival period at the end of spring migration. Reintroduction techniques based on costume-rearing facilitated prolific pair formation and successfully established the critical base of the EMP. Size of initial release cohorts, adequate number of females to compensate for dispersal, and importance of a core release area with sufficient concentrated habitat are factors that should be considered in planning future reintroductions.

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Key words: eastern migratory population, *Grus americana*, pair formation, reintroduction, whooping crane, Wisconsin.

A PRELIMINARY LOOK AT THE DEVELOPMENT AND TIMING OF CUES INFLUENCING PHILOPATRY IN CAPTIVE-BRED WHOOPING CRANES RELEASED USING THE MODIFIED DIRECT AUTUMN RELEASE METHOD

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Abstract: The philopatric traits which cranes exhibit have been a tool used in whooping crane (*Grus americana*) reintroduction projects. When a new core breeding area was selected in east-central Wisconsin, the Direct Autumn Release Project was modified to take advantage of existing facilities on the previous core breeding area at the Necedah National Wildlife Refuge (NWR) and to learn more about the development of philopatric cues. Whooping crane chicks were transferred from the existing facilities at Necedah to the new desired breeding grounds at the Horicon NWR when they were 82-107 days old. The chicks were released as a group near a known communal pre-migration roost of whooping or sandhill cranes (*G. canadensis*) in mid to late October. All other rearing and release protocols were consistent with those from 2005-2010. Juvenile whooping cranes were released on Horicon NWR in 2011 ($n = 8$) and 2012 ($n = 6$). Nine birds (4 males, 5 females) returned to Wisconsin on their first migration north. Eight of the 9 survived to the fall. Satellite transmitter information on the 3 females from the 2011 cohort provide the only consistent location information to inform us on philopatry; i.e., areas used, frequency of use, and how use may change throughout the year and from year to year. Only 1 of the females with satellite transmitters (33%) returned to either refuge the first year. Including all tracking data available increases the sample size to 8 birds. Three of 8 (37%) were documented exhibiting philopatric tendencies to Horicon. More information needs to be gathered once cranes released at Horicon begin setting up nesting territories potentially as early as spring 2014.

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Key words: direct autumn release, *Grus americana*, philopatry, PTT, whooping crane, Wisconsin.

EGG FERTILITY RATE OF THE REINTRODUCED EASTERN MIGRATORY WHOOPING CRANE POPULATION 2005-2012

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Abstract: Early reproductive success is a key factor that determines the probability for a reintroduced population to establish, grow, and persist at carrying capacity. Current attempts at establishing the reintroduced Eastern Migratory Population (EMP) of whooping cranes (*Grus americana*) suffer from similar low productivity despite an annual increase in numbers of pairs that exhibit egg-laying behavior. We aimed to gain a better understanding of the reproductive health of the EMP by using egg fertility rates as a measure of reproductive success. We found the EMP is not following the same trend as the Florida Nonmigratory Population (FNP) but shows similar reproductive characteristics to the viable, self-sustaining Aransas Wood Buffalo Population (AWBP). We compared multiple reproductive characteristics and how experience affects these factors in breeding females between the self-sustaining AWBP and the failed, reintroduced FNP. We found the egg fertility rate of the FNP (1992-2007), EMP (2005-2013) and AWBP (1985-1996) were 48.7, 71.4, and 93.1%, respectively. The age at which males and females in the EMP first produce eggs and first exhibit fertility was younger than the FNP and AWBP. Fertility rates of inexperienced females increase with age, which indicates age affects fertility in this population. By 8 years of age, all EMP females exhibited fertility, similar to AWBP (98%, $n = 28$) whereas, only 46% of FNP ($n = 13$) females exhibited fertility. The onset of earlier reproduction compared to WBNP means younger birds are more likely to breed but less likely to exhibit fertility, thereby reducing overall fertility in the EMP.

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Key words: Eastern Migratory Population, egg fertility, *Grus americana*, reproduction, whooping crane.

REMOTE CAMERAS AID CRANE BEHAVIOR STUDIES: WET MEADOW UTILIZATION BY SANDHILL CRANES ALONG THE PLATTE RIVER, NEBRASKA

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Abstract: The central Platte River in Nebraska supports over 500,000 migrating sandhill cranes (*Grus canadensis*) during spring. These birds use the area to rest, feed, and strengthen pair bonds. The few remaining intact wet meadow grasslands within the Platte River Valley offer sanctuary and vital resources to staging cranes. To better understand how wet meadows are used by cranes, we placed 10 remote cameras set to record motion and time-lapse images along sloughs and uplands within a variety of habitat management scenarios, including hayed, grazed, and burned pastures. Over 60,000 individual sandhill crane behaviors recorded between 7 March and 17 April 2013 were grouped into 6 behavioral categories. These instantaneous behaviors were analyzed at intervals ranging from 10 seconds to 5 minutes, and inferences were made based on time of day, habitat, and other variables. Further understanding of sandhill crane behavior may help researchers and land managers optimize use of native habitats by sandhill cranes.

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Key words: behaviors, camera, *Grus canadensis*, Nebraska, Platte River, sandhill cranes, wet meadow.

RECOVERY AND MANAGEMENT IN A FIELD ENVIRONMENT OF A JUVENILE WHOOPING CRANE FOLLOWING SURGERY TO REPAIR A FRACTURED LEFT CORACOID

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Abstract: On 4 January 2012, while being handled to replace a satellite transmitter, a whooping crane (*Grus americana*) sustained an injury leaving her unable to fly. Rest and medication produced little improvement, so radiographs were obtained and a fractured left coracoid was diagnosed. Surgery to repair the fracture was determined to be the best course of action and was successfully completed on 27 January. The bird was returned to a smaller, dry section of the release pen and remained there for 2.5 days before being moved to a temporary pen at a separate location. Although she appeared less stressed, she remained unwilling to eat and had to be force-fed her medications. Due to continued stress and weight loss, she was returned to the release pen on 2 February. At this time her incision was healing well, but she required medication for several more weeks, and restraint for force feeding would no longer be a viable option. Observations indicated an immediate improvement in her behavior after being returned to the release pen. She began eating and foraging, interacting normally with the other cranes, and willingly took most doses of medication. Sixteen days following surgery she was observed taking a short flight inside the pen and on day 24 she was found in the marsh outside the pen, having flown over the fence to get outside the pen. Seven weeks after surgery, she and 2 other birds moved out of the marsh and settled in an agricultural setting where she still remained 2 years post-surgery.

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Key words: coracoid, field environment, fracture, *Grus americana*, surgery, whooping crane.

WHOOPING CRANES RETURN TO LOUISIANA: THE FIRST THREE YEARS

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Abstract: Despite being proposed as early as the 1970s, a reintroduction of whooping cranes (*Grus americana*) to Louisiana was not approved until 2010. After a 60-year absence from the state, 40 birds in 3 cohorts were released at the White Lake Wetlands Conservation Area (WLWCA) in Vermilion Parish on 3 March 2011, 27 December 2011, and17 December 2012. All birds were hatched and costume/isolation reared at the Patuxent Wildlife Research Center in Laurel, Maryland, for 5.5-9 months before being transferred to a soft release pen at the WLWCA. Environmental conditions varied greatly across years and likely played a role in the survival, dispersal, and habitat choices made by each cohort. All birds eventually moved out of the WLWCA and dispersed widely, using 20 different Louisiana parishes and 3 neighboring states. Many settled in agriculture fields in the area of the historic Cajun Prairie while others used coastal marsh habitats. Survival of the first cohort was poor, with only 1 bird still surviving (10% survival) by mid-April 2013, but survival of the following 2 cohorts was significantly higher with over 70% of each cohort surviving at that time. Major causes of mortality were predation and illegal shooting; however, several additional birds disappeared and were presumed dead from unknown causes. Although the population in 2012 was small, young, and had an uneven sex ratio, 1 pair did form and built 2 nest platforms. The population in 2012 contained 23 individuals (9 males, 14 females) with an additional 10 birds to be transferred and released by the end of 2013.

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Key words: *Grus americana*, Louisiana, reintroduction, White Lake Wetlands, whooping crane.

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