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Abstract: Over-summering of migratory bird populations on wintering grounds may occur when individuals forgo migration and remain in non-breeding or wintering habitats. We summarized all reported instances of migratory whooping cranes (*Grus americana*) over-summering on the wintering grounds during 1891-2024. We report 9 individuals over-summering from the Eastern Migratory Population (EMP), 4 reports from Texas during 1891-1941, and between 1-4 individuals over-summering across 23 summers from the Aransas-Wood Buffalo Population (AWBP) post-1941. Although there were many instances of over-summering without clear proximate causes, some documented causes or contributing factors across both populations include injury, disease, death or injury of a mate, or unfamiliarity with the migration route or breeding grounds. We also report on instances of 4 remigial and 3 body molts on over-summering AWBP cranes. The remigial molt is of primary interest as whooping cranes become flightless during this period, resulting in potential increased depredation risk. We documented over-summering AWBP cranes using saltmarsh and freshwater wetlands, and EMP cranes using wetlands and flooded agricultural fields, similar to wintering individuals. As these endangered populations are still quite small, individuals missing breeding seasons or experiencing additional threats while over-summering is a potential concern for population recovery. However, forgoing migration and breeding may lead to increased survival or more productive future breeding attempts.

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Key words: *Grus americana*, migration, whooping crane, wintering grounds.

Migration has evolved across a multitude of taxa, providing greater access to scarce and limiting resources, and potentially increasing individual and group fitness (Flack et al. 2022). However, there are many costs and risks associated with migration and the energetic requirements associated with it. Over-summering on the wintering grounds is utilized in some populations to forgo migration (Johnson 1973, McNeil et al. 1995, Martínez-Curci et al. 2020, Navedo and Ruiz 2020). Over-summering has been attributed to sexual immaturity, molt timing and condition of flight feathers, limited fat stores, parasite loads, and difficult conditions on the breeding grounds the previous year (Johnson 1973, McNeil et al. 1995, Sørensen et al. 2017, Martínez-Curci et al. 2020). Conditions on the wintering grounds could also play a role, as environmental conditions upon arrival on wintering grounds can impact physical condition during both the winter and spring for passerine

species (Aloni et al. 2019). Over-summering of juveniles on the wintering grounds has been documented in 15 avian taxonomic families (Newton 2011). Summers et al. (1995) concluded that first-year shorebirds with longer migration distances, larger body size, and longer lifespans are more likely to over-summer on the wintering grounds. Hockey et al. (1998) theorized that the lower foraging proficiency of first-year shorebirds made them more likely to forego migration. While young birds are often the focus of over-summering, adult Montagu's harriers (*Circus pygargus*), semipalmated sandpipers (*Calidris pusilla*), red knots (*Calidris canutus*), and other species have also been observed to over-summer (Sørensen et al. 2017, Martínez-Curci et al., 2020, Tavera et al. 2020). Individuals of breeding age that forgo the breeding season on their traditional summering grounds would reduce the number of reproducing individuals that year, which may have implications for genetic diversity. However, forgoing migration and breeding may lead to increased survival or more productive future breeding attempts, for example, over-summering semipalmated

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sandpipers had higher survival than their migrating counterparts (Tavera et al. 2020).

Whooping cranes (*Grus americana*) are an endangered species that have been extensively monitored since the 1930s and have been the focus of a decades-long international recovery (Canadian Wildlife Service [CWS] and U.S. Fish and Wildlife Service [USFWS] 2007). Two migratory populations of whooping cranes exist today, the extant Aransas-Wood Buffalo Population (AWBP) and the reintroduced Eastern Migratory Population (EMP). The AWBP winters primarily on and near Aransas National Wildlife Refuge (NWR) in Texas and breeds and summers in and near Wood Buffalo National Park in Canada. However, non-breeding subadult whooping cranes occasionally summer in Saskatchewan and Alberta well south of Wood Buffalo National Park (Harrell and Bidwell 2014). The EMP winters in the southeastern U.S. and summers primarily in Wisconsin. All whooping cranes descended from the AWBP, which dropped to 15-16 individuals in 1941 (CWS and USFWS 2007). The AWBP has increased in size, and in the winter of 2022-23, 536 whooping cranes (95% CI = 444-644) were estimated within the primary wintering areas (Butler et al 2023). Since 2001, 348 whooping cranes have been released or hatched into the EMP, 75 of which were alive in 2023 (Thompson et al. 2022b, ICF 2024). In small populations, any loss of individuals or decrease in reproductive potential can significantly impact recruitment rates. Maintaining the greatest number of reproducing individuals possible is important for preserving and enhancing the genetic diversity and eventual recovery of the species. Understanding the drivers and impacts of over-summering on small populations of endangered species will allow for conservation action that encompasses a greater portion of the population.

Here, we present all known published and unpublished reports of over-summering whooping cranes in the AWBP and EMP from 1891 to 2024. We include information about the circumstances and potential causes of over-summering events, report on the occurrence of molting while over-summering on the wintering grounds and report the ultimate outcome of the over-summering cranes and any known breeding information from subsequent years. We also share details of the habitats used where available.

STUDY AREA

Eastern Migratory Population

Whooping cranes in the EMP were released in Wisconsin at Necedah NWR, Horicon NWR, and White River Marsh State Wildlife Area (SWA; Urbanek et al. 2014b, Thompson et al. 2022b). They were released during fall near adult whooping cranes to follow on migration, excluding the portion of costume-reared juveniles guided on their first migration by an ultralight aircraft, who were then released on the wintering grounds (2001-2016; Wellington et al. 1996, Hartup 2019, Thompson et al. 2022a). EMP cranes primarily summer in Wisconsin, and winter in Illinois, Indiana, Kentucky, Tennessee, Alabama, Georgia, and Florida (Urbanek et al. 2014b, Thompson et al. 2022b). Throughout the annual cycle, EMP whooping cranes use freshwater wetlands which are typically shallow and dominated by grasses and forbs, having little to no woody vegetation, as well as various upland habitats, such as grasslands and agriculture fields, including corn, soy, wheat, alfalfa, and cranberry beds (Thompson 2018, Barzen et al. 2019, Gondek 2020).

Aransas-Wood Buffalo Population

Most observations of over-summering for this population fell within their traditional wintering grounds, the Texas Gulf Coast, in and around the Aransas NWR (ANWR). Whooping cranes typically begin arriving on the Texas coast in October and November and depart for their summering grounds in March and April (Pearse et al. 2020b). The primary coastal habitats are dominated by salt grass (*Distichlis spicata*), saltwort (*Batis maritima*), smooth cordgrass (*Spartina alterniflora*), glasswort (*Salicornia* sp.), and bushy seaside tansy (*Borrchia frutescens*; CWS and USFWS 2007).

METHODS

Eastern Migratory Population

We collected data for this study from 9 individual cranes on the wintering grounds in the EMP from 2010 to 2022; however, these represent the only known over-summering instances in the EMP since reintroduction began in 2001. The growth of the EMP

is supported by releasing captive-reared juveniles into the population. To instill appropriate behaviors before being released into the population, a biologist in a costume (costume-reared) or a foster whooping crane parent (parent-reared) raises juvenile whooping cranes that have hatched in captivity (Wellington *et al.* 1996, Hartup 2019, Thompson *et al.* 2022a). Occasionally, releases of juvenile cranes are delayed or cranes are recaptured after release, in the fall due to extenuating circumstances (e.g., injury, failure to migrate, etc.), which may result in whooping cranes being released on the wintering grounds (Thompson *et al.* 2022a). We use the terms over-summer, over-summering, or over-summered to refer to individuals that remained on the wintering grounds during the typical breeding season.

All birds in this study had a VHF transmitter, and 5 birds were also equipped with solar-powered GPS transmitters, 2 with global system for mobile communications (GSM) transmitters (67-15, 70-16) and 3 with platform terminal transmitters (PTT; 61-15, 62-15, 80-19; Urbanek 2018). Biologists collected blood prior to release, to determine the sex of the whooping cranes using genetic techniques (Griffiths *et al.* 1998, Duan and Fuerst 2001). All field work and banding were conducted under ESA 10a1a Recovery Permit #TE048806 and United States Bird Banding Lab permit #24022.

After banding, juvenile whooping cranes are released in the EMP. In this study, 3 EMP whooping cranes were costume-reared and ultralight-led on their first migration south (27-07, 12-09, 10-11), 4 were costume-reared and released on the summering grounds (61-15, 62-15, 63-15, 67-15), and 2 parent-reared and released near adults on their summering grounds (70-16) or wintering grounds (80-19). Following release, all birds were monitored regularly through visual observations and remote sensing.

We defined the period of time when birds were on their wintering grounds as the number of days between the first and last days they were observed on wintering grounds (i.e., outside of Wisconsin). Cranes were determined to have arrived on their wintering grounds if they remained in the same location for >5 consecutive days. We excluded years where monitoring efforts were minimal, resulting in little data collection, and periods determined to be migration stopovers (i.e., less than 16 days before moving) from the dataset. We included periods determined to be over-summering on the wintering grounds and 29 years of normal

migratory movement for comparison. We included the potential proximate causes or contributing factors to over-summering when the information was available.

Aransas-Wood Buffalo Population

We compiled a literature review of all reported instances of over-summering on the wintering grounds for the AWBP since 1891. We excluded historical summer reports from outside Texas from Allen (1952), Austin *et al.* (2017), and Austin *et al.* (2019). We also excluded 4 reports of breeding during the late 19th century in Texas and Mexico as these may have been individuals outside the AWBP (Allen 1952; Oberholser 1974; Austin *et al.* 2017, 2019). Austin *et al.* (2017) summarized distribution records until 1941, when the AWBP was at its nadir, so we grouped over-summering reports as 1891-1941 and 1942-2024. Some reports prior to 1938 could include extirpated populations that were not within the AWBP. Additionally, we compiled unpublished reports and observations from USFWS, as well as observations from International Crane Foundation (ICF) staff, volunteers, boaters, tour guides, and ANWR staff and contractors in the months of June-September. The months of June-September should exclude all migrating individuals except for outliers, as the 95th percentile departure date from Texas is 30 April, and the 5th percentile arrival date is 27 October (Pearse *et al.* 2020b). We searched eBird reports (eBird.org 2024) along the Texas coast. The years 2014 and 2015 each included a report from 20 September that may have been early migrants (outliers), not over-summering individuals. Thus, we did not include eBird data in the results. We used the conventional naming system of the time to refer to individuals. We utilized color bands to differentiate individuals when available and reported data from 1 individual marked with a PTT (North Star Science and Technology LLC, Baltimore, MD, USA), which generally provided 4-5 locations for each crane daily via the Argos satellite system (Argos, Inc., Landover, Maryland, USA; Pearse *et al.* 2020a). For that individual, we used similar methods as used for the EMP to report the period of time that individual used the wintering grounds (the number of days between the first and last day on the wintering grounds) both in the year it over-summered as well as the years it did not. We included the exact ages if they were known, otherwise, we included the most

detailed age classification available. White plumage birds represented either subadults or adults, and we classified individuals as unknown age if the age or plumage was not reported.

In the summer of 2023, we deployed 3 trail cameras (Outfitter Gen. 3 Cabela's, Springfield, Missouri, USA) on 2 freshwater wetlands after observing individuals at these wetlands. Cameras were set to take photos every 5 minutes from 0600 to 1800 hours. Additionally, we had motion detect set to trigger every 2 seconds.

When available, we included the potential proximate causes or contributing factors to over-summering. We included all information on molting reported or observed while over-summering. We determined remigial molt by observations of missing primaries or of bright white secondaries relative to dingy body feathers (Folk et al. 2008). Additionally, we reported the observed habitats used by over-summering individuals. All field work was conducted under ESA 10a1a Recovery Permit #TE048806. Recent observations and camera deployments for the AWBP were done under ANWR Research & Monitoring Activity Special Use Permit #21530-22-001.

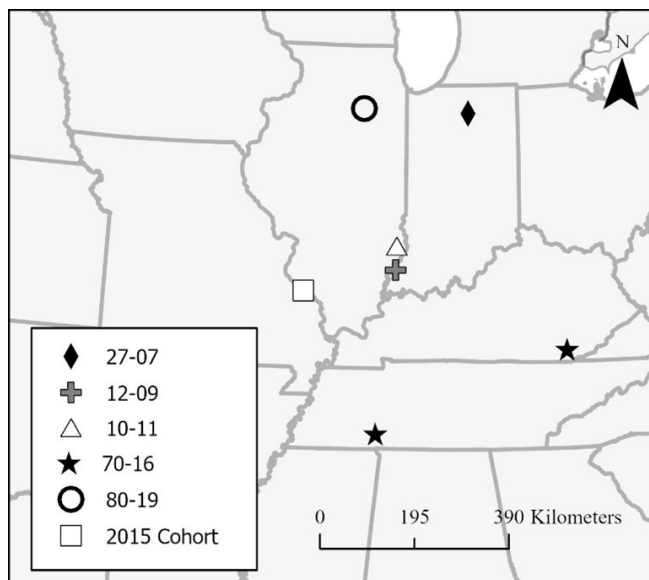


Figure 1. Map of whooping cranes in the Eastern Migratory Population that over-summered on the wintering grounds. Each symbol on the map represents a unique individual crane, except for the 4 birds from the 2015 cohort who over-summered together (61-15, 62-15, 63-15, 67-15).

RESULTS

Eastern Migratory Population

Since 2001, 9 whooping cranes (5 males, 4 females; 1-6 years old) have over-summered on their wintering grounds, spending an average of 321.2 uninterrupted days (range: 294-417 days, $n = 9$) within the wintering range of the EMP (Fig 1., Table 1). In years these cranes did not over-summer, they spent an average of 97.5 days on the wintering grounds (range 64-161, $n = 28$). Assumed causes of over-summering in the EMP include death of a mate, unfamiliarity with breeding grounds, possible injury, translocation, and insufficient knowledge of the migratory route.

The first recorded instance of over-summering for an EMP whooping crane was in 2010, when a 3-year-old female (27-07) over-summered in Indiana. 27-07 was costume-reared and ultralight-led to Chassahowitzka NWR in Citrus County, Florida. During the guided migration, 27-07 was reluctant to fly and was crated and driven along much of the migratory path, limiting her familiarity with the route. During her first 2 summers (2008-09), she may have over-summered in Indiana or Illinois, however we received infrequent reports and were not able to confirm. During spring 2010, 27-07 was seen in Wisconsin on 27 April; however, by 12 May she had returned to Indiana and was consistently in Kosciusko and Marshall Counties until she disappeared was last seen on 13 March 2011 (305 days).

In 2015, a 6-year-old male (12-09) over-summered in Indiana (WCEP 2016). As a juvenile, 12-09 was costume-reared and guided south to St. Marks NWR in Wakulla County, Florida (Urbanek et al. 2014a, b). Data on 12-09's migrations are limited, but in years with more observations, 12-09 migrated normally and spent an average of 101 days on his wintering grounds in Indiana (range 98-104, $n = 2$). Following the loss of his mate in Indiana, 12-09 briefly returned to the breeding grounds at Necedah NWR (4 May 2015) but was observed back in Gibson County, Indiana on 25 May 2015, remaining through 22 March 2016 (302 days). In the years following, 12-09 continued to winter in Gibson County and spent an average of 83 days (range 73-93, $n = 3$). In 2019, he also repaired and nested in Juneau County, Wisconsin near a runway for an air force base, resulting in unsuccessful hazing attempts, and his ultimate removal from the EMP in September 2019 (ICF 2020, Thompson et al. 2022b).

Table 1. Eastern Migratory Population whooping cranes documented over-summering on the wintering grounds 2010-2020. Reports include individual identity, age, sex, possible reason for over-summering, and outcome.

Bird ID	Year	Age/Sex	Winter state	Possible reason	Outcome
27-07	2010	3 yo female	Indiana	Unfamiliarity with migratory route	Last seen in Indiana March 2011.
12-09	2015	6 yo male	Indiana	Mate died in Indiana	Migrated normally in subsequent years. Nested in 2019 with female 69-16.
10-11	2016	5 yo male	Illinois	Mate died in Illinois	Migrated normally in subsequent years. Nested with 7-11 in 2014. Nested with 27-14 from 2018-21 and hatched chicks in 2019 and 2021.
61-15, 62-15, 63-15, 67-15	2016	All 1 yo, 2 males, 2 females	Illinois	Unknown. Possibly related to translocation from Michigan to Wisconsin spring 2016	62-15 died from impact trauma in Illinois in Dec 2016. 61-15 died from unknown causes in Wisconsin in Sept 2017. 67-15 may have over-summered again in 2017 but we could not confirm, then migrated normally after 2017, nested from 2019-24, and hatched chicks in 2022. 63-15 migrated normally in subsequent years, nested and hatched chicks from 2020-23, and fledged a chick in 2020.
70-16	2017	1 yo male	Alabama/Kentucky	Did not know the migratory route, possible wing injury	Removed 2018 in Kentucky due to impact trauma. Never made it back to Wisconsin.
80-19	2020	1 yo female	Illinois	Unfamiliarity with breeding grounds	Migrated normally in subsequent years. Revisited Illinois briefly in the summer of 2022.

In 2016, 5-year-old male whooping crane 10-11 over-summered in Lawrence County, Illinois. Male 10-11 was costume-reared at White River Marsh SWA to be guided south on his first migration. Due to poor flying conditions and a grounding order from the Federal Aviation Administration before completing the final leg of the trip, 10-11 and his cohort were crated and driven to their release location at Wheeler NWR in Morgan County, Alabama (WCEP 2012). Following an unorthodox first migration in 2011, 10-11 migrated as predicted and was documented on his wintering grounds for an average of 101.5 days (range 86-117, $n = 2$). In the winter of 2015-16, 10-11 paired with female 7-09 in Lawrence County, Illinois. By March 2016, however, 7-09 was found dead on their wintering grounds, likely due to predation. After a brief return to Wisconsin on 19 and 20 April 2016, 10-11 was observed back on his wintering grounds on 8 May 2016 where he remained alone until 26 February 2017 (294 days) before migrating north to Wisconsin. In 2018, 10-11 repaired, hatched 4 chicks (2019-2021), and was observed on his wintering grounds for 113 days on average (range 64-158, $n = 4$).

Also in 2016, a group of 4 1-year-old cranes (males 62-15 and 63-15, females 61-15 and 67-15)

over-summered on the wintering grounds in Randolph County, Illinois. These 4 cranes were raised and released at Horicon NWR prior to their first fall migration. In fall 2015, they migrated together to Randolph County, Illinois, where they wintered (79 days). The following spring, they migrated to Macomb County, Michigan, and on 5 May 2016, all 4 cranes were captured and translocated to Marquette County, Wisconsin (Thompson *et al.* 2022*b*). By 22 May 2016, the group of 4 returned to Randolph County, Illinois. In December 2016, 62-15 died from impact trauma on the wintering grounds. The 3 remaining cranes spent at least 296 days in Illinois, then returned to Wisconsin by 3 April 2017. In September 2017, 61-15 died from unknown causes. Female 67-15 may have over-summered in Illinois again in 2017; however, we had inconsistent reports and were not able to confirm. However, 67-15 migrated normally after 2017, was observed on the wintering grounds in Morgan County, Alabama for an average of 85.7 days (range 69-67, $n = 6$), and nested and hatched 2 chicks (2019-2024). Male 63-15 migrated normally in subsequent years, was observed on the wintering grounds in Randolph County, Illinois for an average of 105.2 days (range 78-127, $n = 6$), nested and hatched 5 chicks (2020-2023), and fledged 1 chick in 2020.

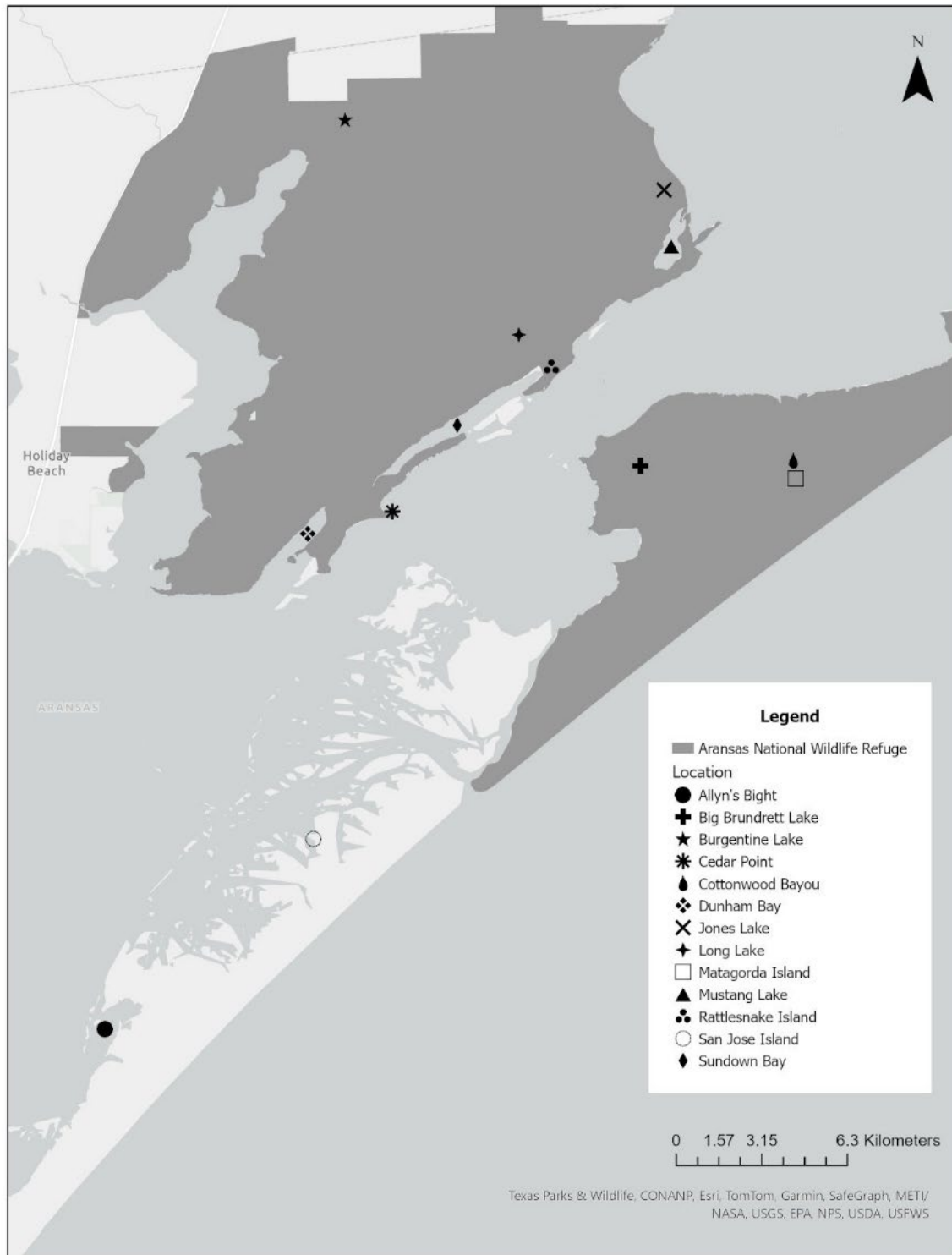


Figure 2. Map of over-summering whooping crane locations on the Aransas-Wood Buffalo Population wintering grounds, Texas, 1942-2024. Locations are denoted by individual symbols. Some locations are general locations such as Matagorda Island and San Jose Island.

The most recent records of whooping cranes over-summering in the EMP were from 2 1-year-old whooping cranes in 2017 and 2020. Male 70-16 (2017) and female 80-19 (2020) were parent-reared but held back from release due to wing injuries. On 16 November 2016, 70-16 was released in Marathon County, Wisconsin near 2 adult whooping cranes. After the pair left on migration without 70-16, he was captured and translocated to Wheeler NWR for release on 14 December 2016 (WCEP 2017, Thompson et al. 2022b). Once on the wintering grounds, 70-16 associated with whooping cranes throughout the winter, but failed to migrate back to Wisconsin with them. In March 2017, 70-16 began migrating north before eventually stopping in Hardin County, Tennessee and Knox County, Kentucky, where he remained until he was discovered caught in a barbed wire fence and on 4 February 2018 (WCEP 2018) and later euthanized. Overall, 70-16 spent 417 days on the wintering grounds (Alabama: 107 days during winter 2016-17; Tennessee: 56 days during spring 2017; Kentucky: 254 days during spring 2017-winter 2018). Additionally, female 80-19 was released at Goose Pond Fish and Wildlife Area in Greene County, Indiana on 5 November 2019 (ICF 2020). In March 2020, she followed whooping cranes back to the breeding grounds at Necedah NWR, but 1 month later she was back on the wintering grounds in Indiana and Illinois (6 April 2020-30 April 2021, 389 days). After over-summering, 80-19 migrated north to Wisconsin, and in winter 2021-22 she returned to Illinois for 161 days. In spring 2022, she flew to Wisconsin, briefly returned to Illinois (18 days), then flew back to Wisconsin, where she stayed for the rest of the summer, and was last seen in October 2022.

Aransas-Wood Buffalo Population

1891-1941

Prior to 1941, there were 3 reports of over-summering whooping cranes in Texas (Allen 1952, Oberholser 1974, Austin et al. 2017). The first occurred in 1891 when groups of 6 and 7 whooping cranes were observed feeding on acorns at the head of Padre Island during late August (Allen 1952). An unknown number of individuals were reported to occasionally over-summer on the King Ranch near Laguna Larga during 1918-1923 (Allen 1952). Additionally, a family group remained on the ANWR for the entirety of the summer in 1941 (Allen 1952).

1942-2023

Since 1941, 1-4 whooping cranes have been reported over-summering along the Texas Gulf Coast across 23 summers (Table 2, Fig. 2). Individuals that over-summered included various age classes as well as many with white plumage (subadult or adult) or unreported/unknown ages. Some individuals appeared to over-summer multiple years, including 1 individual known as “Lobstick Chick” that over-summered at multiple life stages, identified by the initial injury to neck and subsequent scar. Assumed causes for over-summering include injury, injured mate, and illness (Allen 1952, Stehn 1992).

During 1947-1949, 3 individuals over-summered on ANWR (Allen 1952). The first was noted to have an injury or abnormality to its left wing, but handlers were unable to find a break in the bone during capture. Another individual had a broken wing, and its assumed mate remained with the injured individual throughout the summer before migrating northward without its mate the following spring (Allen 1952). In 1950, 1 individual over-summered in Texas before dying in August of unknown causes (Lewis et al. 1992). This crane known as Mac had been a Louisiana non-migratory crane that had been captured that spring and brought to ANWR. Individuals over-summered during the years 1955, 1956, 1959, 1973, 1980, and 1982 (Lewis et al. 1992).

During the summer of 1988, 2 banded subadult cranes, known as o-R and B-WbW, remained at ANWR. Subadult o-R was captured and diagnosed with avian tuberculosis in April 1989. In August 1989, B-WbW disappeared and was presumed dead, with avian tuberculosis as the suspected cause (Stehn 1992). Three individuals over-summered in 1994, and 2 over-summered in 1995 (U.S. Fish and Wildlife Service, unpublished data).

Over-summering of AWBP cranes was again reported in 2000 when 1 white-plumage individual was observed on San Jose Island by Texas Parks and Wildlife Department staff on 28 July 2000. A single crane was reported at the same location, just east of Allyn’s Bight, on 9 August 2000 and again on 29 August 2000, 2 miles north of refuge headquarters at ANWR, near Bauer’s Pond (T.V. Stehn, USFWS, unpublished data). In 2005, an injured, almost 1-year-old individual known as “Lobstick Chick” remained on ANWR near Dunham Bay with its assumed parents until they migrated north. In April, “Lobstick Chick” was observed with a swollen neck and head. “Lobstick Chick” survived its injury but failed to migrate again in 2006.

Table 2. Aransas-Wood Buffalo Population reports of over-summering whooping cranes on the wintering grounds 1942-2023. Locations shown as ANWR were on the Aransas National Wildlife Refuge. We used bird identification when it was available. For unknown individuals we include the number of individuals each summer.

Bird ID and No. of individuals	Year	Age/sex	Location	Molt	Possible reason	Outcome	Source
3 Unknown ^a	1947-1949*	White plumage	ANWR		Broken wing, assumed mate to unknown bird with broken wing, and injury/abnormality to left wing ^a		Allen 1952
“Mac”	1950	Unknown	ANWR (Burgentine Lake)		The last wild Louisiana whooping crane captured and released at ANWR	Died in August of unknown causes	Lewis et al. 1992
1 Unknown	1955	Unknown	ANWR				Lewis et al. 1992
3 Unknown	1956	Unknown	ANWR			One individual died 1 Jul	Lewis et al. 1992
2 Unknown	1959	Unknown	ANWR				Lewis et al. 1992
1 Unknown	1973	Unknown	ANWR				Lewis et al. 1992
1 Unknown	1980	Unknown	ANWR				Lewis et al. 1992
1 Unknown	1982	Unknown	ANWR				Lewis et al. 1992
o-R and B- WbW	1988	Subadult	ANWR		Avian tuberculosis	o-R was captured in April 1989 and died	Stehn 1992
1 B-WbW	1989	Subadult	ANWR		Avian tuberculosis	B-WbW disappeared in August and was presumed dead	Stehn 1992
3 Unknown	1994	Unknown	ANWR (Rattlesnake Island, Sundown Bay, Matagorda Island)				U.S. Fish and Wildlife Service, unpublished data
2 Unknown	1995	Unknown	ANWR (Sundown Bay, Rattlesnake Island)	At least 1 bird went through a flightless molt during June			U.S. Fish and Wildlife Service, unpublished data
1 Unknown	2000	White plumage	San Jose Island, ANWR (Allyn’s Bight)				T.V. Stehn, U.S. Fish and Wildlife Service, unpublished data
“Lobstick Chick”	2005	1 yo bird	ANWR (Dunham Bay)		Injury	Also failed to migrate in 2006 and 2009	T.V. Stehn, unpublished data

Table 2. Continued.

Bird ID and No. of individuals	Year	Age/sex	Location	Molt	Possible reason	Outcome	Source
“Lobstick Chick” and 2 Unknown	2006	2 yo bird and 2 White plumage	ANWR (Cedar Point/Bludworth Island)	3/3 underwent a body molt			T.V. Stehn, unpublished data
“Lobstick” and 1 Unknown	2009	4 yo adult and Unknown	ANWR	1/2 underwent remigial molt			T.V. Stehn, unpublished data
E44 and 2 Unknown ^b	2016	Adult male and 2 Unknown	ANWR			E44 migrated to Wood Buffalo in 2017, but no transmission or resighting since	Harrell 2016, Sneath 2016, Pearse et al. 2020a, and notes from the Whooping Crane Tracking Partnership
D25	2021	9 yo male	ANWR	Remigial molt		Nested successfully in 2022	ICF staff and notes from the Whooping Crane Tracking Partnership
1 Unknown	2022	White plumage	ANWR (Jones Lake, Mustang Lake)				Photographer and ICF staff
3 Unknown	2023	White plumage	ANWR (Sundown Bay, 3 freshwater wetlands/ponds, Long Lake, Dunham Bay, Matagorda Island)	2/3 underwent remigial molt			Aransas NWR staff, ICF staff, trail cameras, boater, and tour guide observations
Likely 10J and 3 Unknown ^c	2024	2-yo (sex unknown) and 3 white plumage	ANWR (Matagorda Island (Big Brundrett Lake, Sundown Bay)				Aransas NWR staff and contractors, ICF staff, and boaters

^a Unclear from Allen 1952 pages 50, 67, and 142 if all individuals remained in the summers of 1947, 1948, and 1949. Allen (1952:67) remarked the assumed mate “walked at his side through all the summer that followed, only deserting him the next spring when the urge to lift herself into the freedom of the sky, and journey northward with the other migrants, proved irresistible”, but no specific departure date was recorded.

^b Probable fourth bird over-summering on San Jose Island, difficult to verify.

^c Four birds were seen on June 6 and June 11, 2024. Only three were seen the remainder of the summer (June-September). Three individuals and a lone individual on Sundown Lake were seen on October 4, 2024.

In August 2006, a group of 3 white-plumage birds were found on Cedar Point marsh on ANWR, including “Lobstick Chick”, who was identified by the scar on its neck left behind by its 2005 injury. The 3 white-plumage adults who remained in 2006 were noted to undergo a body molt in August. In the summer of 2009, “Lobstick Chick” and another individual remained on ANWR for the entirety of the summer with little interaction between the 2. Observers noted very thin body condition and at least 1 of the 2 experienced a flightless molt (T. V. Stehn, unpublished data).

One adult male, E44, was trapped and marked on 1 February 2014 prior to over-summering in 2016. E44 left the wintering grounds noticeably late that summer on 22 June 2014. The next year E44 spent 173 days on the wintering grounds, arriving on 8 November 2014 and leaving on 30 April 2015. In 2015-2017, E44 spent 500 consecutive days on the wintering grounds, arriving on 23 November 2015 and leaving on 6 April 2017. Following over-summering, E44 migrated back to WBNP in the spring of 2017, with no subsequent data transmission or resighting. In 2016, 2 additional white plumage birds remained on ANWR with E44, and a potential third individual was reported on San Jose Island but was difficult to verify (Harrell 2016, Sneath 2016). In 2021, a 9-year-old male (D25) was seen in May and early June in saltmarsh and photographed without primary feathers (Fig. 3). He was spotted on the breeding grounds at WBNP in 2022 where he successfully nested and was observed with 2 chicks in late July (Whooping Crane Tracking Partnership, unpublished data). On 8 August 2022, a white-plumage individual was photographed at Jones Lake, a freshwater wetland on ANWR. ICF staff saw the individual in saltmarsh on 16 August 2022 from the ANWR Tower and 2 additional times in August and September 2022.



Figure 3. A 9-year-old male (D25) Aransas-Wood Buffalo Population whooping crane was photographed by ICF staff and volunteers in saltmarsh at Aransas National Wildlife Refuge on 3 June 2021. He was observed without primary feathers, indicating remigial molt.

In 2023, 3 white-plumage birds remained on ANWR for the totality of the summer. Two individuals were seen together, and a third was often seen with them. The group was monitored by ICF staff, refuge staff, local boaters and tour guides, and trail cameras deployed on freshwater wetlands from 22 May 2023 until 29 September 2023. The individuals were seen using saltmarsh and at least 3 freshwater ponds on Blackjack Peninsula. Two of the individuals were also reported near Dunham Bay and on Matagorda Island in September. On 12 July, 1 of the 2 individuals seen leaving a freshwater wetland appeared unable to fly well, but on 2 August ANWR staff saw 3 individuals fly into a freshwater wetland. On 3 and 5 August, whooping cranes were photographed and 2 of the 3 cranes showed bright white secondaries on dingier body feathers, indicating a recent remigial molt (Fig. 4). The third individual was not shown clearly enough to determine any recent molting. In 2024, 4 individuals remained on Matagorda Island (with some reports from Blackjack Peninsula); 1 of the birds is suspected to be 10J, a 2-year-old individual with unknown sex; however, the transmitter was not sending reliable transmissions through the summer.



Figure 4. (A) Three over-summering AWBP whooping cranes were photographed in flight by a trail camera (Cabela’s, Springfield, Missouri, USA; Outfitter Gen 3) at a freshwater solar well on Aransas National Wildlife Refuge on 5 Aug 2023. (B) The trail camera captured the contrast between bright white secondaries and dingy coverts, indicating remigial molt during the summer months for 2 of the 3 over-summering birds. Unable to confirm on the third individual due to being out of frame.

DISCUSSION

This is the most complete record of over-summering in migratory whooping crane populations from 1891 to 2024. We only considered recent observations of AWBP individuals as over-summering birds if they were spotted in June-September, but past reports did not always provide dates. Some of the AWBP individuals reported

as over-summering may not have spent the entire summer but may have left the wintering grounds later or returned earlier than is typical. Also, it is possible if not likely additional individuals over-summered but were not reported between 1891 and 2024. Some of the EMP individuals migrated north to the breeding grounds before returning to the wintering grounds to over-summer. Over-summering of whooping cranes is not well understood, and the potential proximate causes or contributing factors of over-summering include injury, disease, death of a mate, injury of a mate, unfamiliarity with the migration route, or unfamiliarity with the breeding grounds. For most over-summering occurrences in the AWBP, there are no known contributing factors or proximate causes. This is due in part to making observations at a distance, a limited number of observations in some years, and the fact that many of the reports of over-summering birds come from unmarked individuals. Occurrences in the EMP may also be affected by reintroduction techniques, as juvenile captive-reared and released individuals may be unfamiliar with the migration route or the breeding grounds if they were released on or translocated to the wintering grounds.

The large number of over-summering events coming from unmarked birds also makes it difficult to determine if over-summering in the AWBP is more likely to occur with certain age classes. However, we show cranes across various ages have all been documented to over-summer in the AWBP as well as the EMP. Over-summering in shorebirds has been documented in yearlings prior to reaching breeding age, adult birds that have delayed their first breeding, and adults with prior reproductive experience that are skipping breeding (Martinez-Curci et al. 2020). The high ratio of unmarked individuals in the AWBP makes determining the outcome from over-summering and later reproductive contributions of over-summering individuals difficult. In both the EMP and AWBP, however, there are instances of over-summering individuals returning to the breeding grounds and successfully reproducing in later years. The fact that individuals are breeding following over-summering highlights the importance of habitat management and other measures during summer on traditional wintering grounds.

A systematic approach of documenting habitat use of over-summering birds has not been conducted, and anecdotal observations of areas used while over-summering represent all available data. During the winter months, EMP cranes use a variety of habitats

including freshwater wetlands and agricultural areas (Fondow 2013, Thompson 2018), and AWBP birds primarily use saltmarsh and bay habitats (Stevenson and Griffith 1946, Allen 1952, Stehn and Prieto 2010, Smith et al. 2019). Wintering AWBP cranes also will utilize freshwater wetlands and excavated ponds (Stevenson and Griffith 1946, Allen 1952, Ritenour et al. 2016, Kirkwood and Smith 2018, and Butler et al. 2022). Over-summering individuals have been documented utilizing similar habitats to wintering birds. For the AWBP, freshwater resources adjacent to the saltmarsh may be important for over-summering birds, because it is generally thought that cranes must seek freshwater once local bays exceed a salinity of 15-23 parts per thousand (Chavez-Ramirez and Wehtje 2012, Ritenour et al. 2016, Kirkwood and Smith 2018). Freshwater wetlands adjacent to the saltmarsh may be particularly important if some individuals undergo a flightless remigial molt while over-summering.

Relatively little is known about molting in wild whooping crane populations, particularly for the AWBP. Folk et al. (2008) reported information on molting in the Florida Non-migratory Population, while Lacy and McElwee (2014) reported molting in the EMP. Individuals undergoing remigial molt were unable to fly for an average of 44 days (range 38-46, $n = 8$). Seventy percent of individuals first replaced their flight feathers at 3 years of age, while the remainder underwent the first remigial molt at age 2 or 4 years (Folk et al. 2008). Flight feathers were retained from 2 to 4 years (average 2.5 years). Contour feather molt occurred annually between 24 June and 23 October ($n = 53$; Folk et al. 2008). EMP cranes undergoing the remigial molt on the breeding grounds utilized wetland habitats to a greater extent and had smaller home ranges than non-molting individuals (Barzen et al. 2019). Molting while over-summering may place individuals at greater risk for depredation during the flightless period. Depredation risk while flightless could be different on the wintering grounds than on the breeding grounds, particularly if birds need to leave the saltmarsh to obtain dietary freshwater, often crossing upland habitats.

Over-summering on the wintering grounds is not a new occurrence for migratory whooping cranes, and it was documented even when the total population numbers were quite low (Allen 1952, Lewis et al. 1992). If the population continues to grow, over-summering may become more common. Tracking the occurrence of over-summering and the outcomes and

subsequent breeding contributions of these individuals has implications for whooping crane recovery and habitat management on the winter grounds outside of the winter period.

MANAGEMENT IMPLICATIONS

Management that would typically benefit wintering whooping cranes is likely to benefit over-summering birds, as they have been documented in the same types of habitats. Providing freshwater resources adjacent to the saltmarsh could benefit over-summering birds particularly during drought years at ANWR. Natural slough wetlands are important for whooping cranes during migration (Caven et al. 2022) and likely during the winter. Management to keep these wetlands open and useable for cranes during summer months is important and may provide more accessible freshwater resources. However, in dry years the natural slough wetlands can also dry down, and wetlands or ponds supplemented by groundwater may be important resources. Cranes that underwent a remigial molt utilized 3 “Water for Wildlife” ponds at ANWR in the summer of 2023, highlighting the potential importance of these ground water supplemented ponds (Stanzel and Smith 2017).

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