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COMPARISONS OF MIGRATION PATTERNS BETWEEN PARENT-REARED AND COSTUME-REARED WHOOPING CRANES IN THE EASTERN MIGRATORY POPULATION, 2012-2023

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Abstract: Whooping cranes (*Grus americana*) have been raised and released into the Eastern Migratory Population (EMP) since 2001. Cranes either were costume-reared and learned their migration route by following an ultralight aircraft, were costume-reared and released in fall near adult cranes (known as direct autumn release), or were parent-reared by captive adult whooping crane pairs and released in the fall near adult whooping cranes. Compared to costume-rearing, parent-rearing encourages conspecific learning prior to release, but needs further research to understand how it may influence post-release behaviors including migration. This study compared the migratory timing and length of parent-reared whooping cranes and ultralight-led, costume-reared whooping cranes in the EMP during 2012-2023. Using GPS data from satellite transmitters, we determined when cranes were migrating or stationary and categorized movements as summering, stopover (2 or more relocations in an area that spanned overnight hours), migratory, or wintering. No differences in timing, distances, or duration of migration were detected during the spring between parent-reared cranes and costume-reared cranes. However, parent-reared cranes migrated shorter distances ($W = 65, P = 0.02$), migrated shorter durations ($W = 61, P = 0.04$), and completed migration earlier in the year during the fall ($W = 65, P = 0.02$). These results were expected given that costume-reared cranes were taught specific routes with numerous stopovers to Florida during ultralight-led migrations while parent-reared cranes experienced a greater variety of wintering locations and migratory routes from other cranes. Individual cranes from both rearing groups (parent and costume-reared) sometimes followed different migration routes from year to year. These results suggest that rearing and release techniques have some effects on post-release selection of migratory routes but not the timing of migratory initiation. Future work should include comparisons with direct autumn release costume-reared cranes.

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Key words: captive rearing, *Grus americana*, migration, movement, reintroduction, satellite telemetry, whooping crane.

The Eastern Migratory Population (EMP) of whooping cranes was established by a reintroduction effort that was initiated in 2001, when all whooping cranes were reared by caretakers who wore costumes equipped with crane puppets (Wellington et al. 1996, Hartup 2019). During 2001-2010, costume-reared whooping cranes were raised at Necedah National Wildlife Refuge (NWR) in central Wisconsin and guided through their first autumn migration via ultralight aircraft (UL) to the Gulf Coast of Florida (Urbanek et al. 2010a). Beginning in 2005, costume-reared whooping cranes were also released at Necedah NWR near other cranes in the fall before migration in a method known as Direct Autumn Release (DAR; Hartup 2019). In 2011, releases of UL and DAR cranes shifted from Necedah NWR to eastern Wisconsin and were focused at White River Marsh State Wildlife

Area (SWA) and Horicon NWR; from 2016 onwards, the UL method was no longer used (Thompson et al. 2022b).

In addition to costume-rearing, whooping cranes in the EMP were parent-reared beginning in 2013, where chicks were raised by captive whooping cranes then released among wild EMP cranes before autumn migration (Thompson et al. 2022b). Between 2013 and 2019, 1-year post-release survival rates for parent-reared cranes (69.0%) were similar to costume-reared cranes (64.4%) (Thompson et al. 2022a); however, the parent-rearing method could offer several benefits over costume-rearing. For example, the parent-rearing method allows chicks to learn behaviors from adult cranes during the rearing period. Cranes naturally have long rearing periods (up to a year), during which they can learn feeding and foraging behaviors, predator avoidance, and migratory behavior from their parents (Drewien et al. 1997, Mueller et al. 2013). While this could theoretically support the learning

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of parenting and reproductive behaviors, there is currently no evidence that parent-rearing improves reproductive success in reintroduced cranes (Spalding et al. 2010). Parent-rearing also minimizes potential habituation to humans through reduced human contact and requires less labor and resources than costume-rearing (G. Olsen, personal observation). Finally, parent-reared whooping crane chicks are less prone to incidents of toe, carpal, or limb deformities than costume reared chicks while in captivity (Kelley and Hartup 2008).

While there are advantages to parent-rearing compared to costume-rearing, more research needs to be done on how rearing methods may influence post-release behavior. Most EMP cranes exhibit successful migratory, foraging, and breeding behavior (Urbanek et al. 2010a, Thompson et al. 2022b), and, with the exception of high mortality during a 16-month period of drought, the annual survival rate of the EMP (7.1%) during the first 7 years after introduction has been comparable to the annual survival rate of the wild Wood Buffalo-Aransas population (9.7%) (Urbanek et al. 2010a). Reproductive success of the EMP population, however, has been low due to widespread nest desertion (Urbanek et al. 2010b, Converse et al. 2013, King et al. 2015, Barzen et al. 2018) and low chick survival (Converse et al. 2019, McLean 2019, Thompson et al. 2022b).

Captive rearing techniques may also affect post-release migratory behavior. For instance, in the Asian houbara (*Chlamydotis macqueenii*), captive-reared individuals migrated shorter distances and durations than their wild-counterparts in the same population (Burnside et al. 2017). Genetic effects such as accidental selection of genes beneficial to captivity or relaxation of natural selection in the captive environment (Araki 2007) could also potentially alter migratory behavior. Additionally, rearing methods may affect post-release social behaviors (Utt et al. 2007), and consequently could affect intraspecific learning of migratory or habitat use behaviors such as on their breeding grounds (Johns et al. 2005) or wintering grounds (Teitelbaum et al. 2019b). To date, direct comparisons of migratory phenology between rearing methods have not been made, so this study aimed to identify if these groups exhibit differences in migratory behavior. In this study, we analyzed the migration phenology of parent-reared and costume-reared whooping cranes from 2012 to 2023 to examine similarities or differences in migratory phenology and distance.

STUDY AREA

Necedah NWR supports 8,470 ha of forested, non-forested, and open wetlands (USFWS 2004), including sedge (*Carex* spp.) meadow wetlands and emergent marshes (Strobel and Giorgi 2017). Necedah NWR also supports prairies, oak (*Quercus* spp.) savanna, and oak-pine (*Pinus* spp.) forest (Strobel and Giorgi 2017). Hydrology in some areas is actively managed to promote growth of high-energy waterfowl foods (USFWS 2004). Whooping Cranes were also released in eastern Wisconsin, in an area known as the Wisconsin Rectangle or the Eastern Rectangle, which is a 2,021,800-ha region with row crop agriculture and wetlands and contains Horicon NWR and White River Marsh SWA (Van Schmidt et al. 2014, Thompson et al. 2022b). Wetlands in the Rectangle area are mostly dominated by cattails (*Typha* spp.) (Van Schmidt et al. 2014, Thompson et al. 2021).

Winter release sites for ultralight cranes included Saint Marks NWR in Florida and Wheeler NWR in Alabama. Saint Marks NWR covers 27,744 ha, of which 29% of the land cover consists of saltwater marsh dominated with black needlerush (*Juncus roemerianus*) or smooth cordgrass (*Spartina alterniflora*) (USFWS 2006). Another 10% of the land cover consists of freshwater lakes, marshes, and impoundments dominated with sawgrass (*Cladium jamaicense*), needlerush (*Juncus* spp.), cattail (*Typha* spp.), arrowhead (*Sagittaria* spp.), and pickerelweed (*Pontederia cordata*) (USFWS 2006). Wheeler NWR covers 14,614 ha and contains some naturally occurring wetlands as well as 809 ha of open water and seasonally flooded fields (Cantrell and Wang 2018). Wheeler NWR also contains agricultural land that practices harvest gleanings and crop shares which provide supplemental food to wildlife during cold months (Cantrell and Wang 2018).

METHODS

Rearing and Release Techniques

The whooping cranes included in this study were raised at the U.S. Geological Survey's Patuxent Wildlife Research Center in Laurel, Maryland (currently part of the U.S. Geological Survey, Eastern Ecological Science Center) or at the International Crane Foundation in Baraboo, Wisconsin. Cranes were

Table 1. Demographic information of whooping cranes in this study. Release locations are Wisconsin counties, White River Marsh State Wildlife Area (WRM), or Necedah National Wildlife Refuge (NWR) in Wisconsin. Cranes were either raised in captivity by adult cranes and were released in the fall near adult cranes prior to fall migration (PR), or were costume-reared and led south on their first migration by ultralight aircraft (UL). Ultralight-led cranes were raised at WRM but then were led south on their first migration and released on the wintering grounds or southern terminus of the UL migration at St. Marks NWR, Florida, or Wheeler NWR, Alabama.

ID	Sex	Release Date	Release location	Age at release (days)	Rearing method
27-14	F	22 Sep 2014	Necedah NWR	101	PR
14-15	F	20 Sep 2015	Necedah NWR	119	PR
20-15	M	20 Sep 2015	Necedah NWR	115	PR
39-16	M	24 Sep 2016	Adams County, Wis.	115	PR
19-17	M	14 Sep 2017	Marathon County, Wis.	120	PR
79-19	F	8 Oct 2019	WRM	129	PR
84-21	F	15 Sep 2021	Necedah NWR	123	PR
4-11	F	8 Feb 2012	Wheeler NWR	279	UL
7-11	F	8 Feb 2012	Wheeler NWR	275	UL
2-13	F	21 Jan 2024	St. Marks NWR	251	UL
8-13	F	21 Jan 2014	St. Marks NWR	248	UL
9-13	M	21 Jan 2014	St. Marks NWR	247	UL
3-14	F	23 Dec 2014	St. Marks NWR	224	UL
7-14	F	23 Dec 2014	St. Marks NWR	219	UL
8-14	F	23 Dec 2014	St. Marks NWR	218	UL
10-14	F	23 Dec 2014	St. Marks NWR	216	UL
2-15	F	14 Feb 2016	St. Marks NWR	285	UL
10-15	F	14 Feb 2016	St. Marks NWR	280	UL

either costume-reared or parent-reared in captivity prior to release. Parent-reared crane chicks were individually housed with a pair of adult whooping cranes (Sadowski et al. 2018, Thompson et al. 2022a). Adult cranes were selected for parent-rearing based on previously demonstrated ability to raise chicks (Thompson et al. 2022a). Parent-reared cranes were released at Necedah NWR, White River Marsh SWA, or on private properties in Marathon or Adams Counties, Wisconsin from 2014 to 2021 (Table 1).

All costume-reared cranes in this study were part of the UL program and were released from 2011 to 2015. While location data were also collected on an additional 3 costume-reared, DAR cranes, only 1 of these cranes survived long enough to provide migration information so DAR cranes were excluded from this analysis. Costume-reared cranes were group-housed in outdoor pens, and taken for daily walks, taught swimming lessons, and trained to follow ultralight aircraft by costumed caretakers (Sadowski et al. 2018). Costume-reared cranes were guided by ultralight aircraft typically from early to mid-October to late November to early January on specific routes from White River Marsh SWA to their winter release locations in St. Marks NWR, Florida or Wheeler NWR, Alabama (Urbanek et al. 2010c, 2016). Once at the wintering location, these cranes were kept in

enclosures for a few days for acclimation to the local environment, health evaluations, and banding before they were released, and they were given supplemental feed from feeders located in the pens throughout their first winter (Urbanek et al. 2010c, 2016). More specific information on rearing techniques is provided by Wellington et al. (1996), Sadowski et al. (2018), Hartup (2019), and Thompson et al. (2022a) and ultralight release techniques by Urbanek et al. (2010c; 2016).

Prior to release, the sex of each crane was determined by genetic techniques (Griffiths et al. 1998, Duan and Fuerst 2001) and each crane was banded with a unique combination of leg bands and transmitters for long-term monitoring of individuals (Urbanek 2018). All cranes in this study were also tagged with a leg band-mounted satellite transmitter known as a platform transmitting terminal (PTT-100 solar powered, leg band-mounted; Microwave Telemetry Inc., Columbia, Maryland USA).

Data Analysis

We processed location data from satellite transmitters using the Douglas Argos Filter (Douglas et al. 2012) on the Movebank website (Kays et al. 2021). All subsequent analysis was performed in

R version 4.3.1 (R Core Team 2023). We filtered to location class (LC) 1, which represents a maximum error radius of 1,000 m or better. In the case of duplicate timestamps, we averaged coordinates between all data points. Through this filtering process, we identified and removed redundant relocations or erroneous relocations that would otherwise indicate a crane moving at impossibly fast speeds or moving to implausible locations. To reduce computational load and capture more accurate speeds between relocations, we subsampled the filtered data, so relocations were at least 1 hour apart, resulting in a total of 6,185 relocations for parent-reared cranes and 12,920 relocations for costume-reared cranes. Since relocations spanned multiple UTM zones, we projected the data from the WGS84 to USA Contiguous Albers Equal Area Conic coordinate system so that we could use the *sf* package (Pebesma 2018) for spatial analysis.

To determine migration phenology, we first defined summering and wintering sites for each individual crane. We removed location data from each bird's release date to the end of the release year, then visualized the data by month to identify the months when most crane locations were concentrated in the north (Teitelbaum et al. 2019a). We then used the *adehabitat* package (Calenge 2006) to generate individual summering ranges for each year as 95% minimum convex polygons using location data from May to September. While whooping cranes in this population typically exhibit site fidelity around their original release sites during the summer months (Maguire 2008, Teitelbaum et al. 2019a, Urbanek et al. 2010a, Thompson et al. 2022a), they sometimes shortstop during winter migration, leading to variability in overwintering locations (Teitelbaum et al. 2016). Therefore, for each year, we searched for any site that was at least 30 km south of their summer range and where the crane remained within a 15-km radius for at least 15 days during the months between October to April (Teitelbaum et al. 2016) and designated the southernmost of these sites as a wintering site. We excluded the first fall and spring migrations following release and incomplete migrations where a crane perished mid-migration from analysis.

We defined the start of fall migration as the last timestamp before the bird left its summer range

without returning between the months of September to December and defined the end of fall migration as the first timestamp when the bird entered its wintering site of that year. We similarly defined the start of spring migration as the last timestamp before the bird left this wintering site without returning, and the end of spring migration as the first timestamp after the bird entered its summering range.

We examined relocations that occurred during migratory periods to identify stopover locations. We defined stopovers as any set of 2 or more relocations within a 15-km radius where the bird stayed between the times of 2200 and 0300 hours (Baasch et al. 2019). If a bird left this 15-km radius, then returned to it, it was considered back within that particular stopover site. Stopover sites were defined within each migration, were required to be at least 50 km away from migration start locations and end locations and were considered unique if they were at least 30 km apart from each other. We averaged migratory start dates, end dates, distances, and durations per crane then used two-sample Student's *t* or Wilcoxon ranked sum tests to compare these migratory statistics between parent-reared and costume-reared cranes. Given the time and location differences between costume and parent-reared crane data, we checked if climatic conditions may have been harsher between rearing-groups. To do this, we queried daily climatic data from the 5 nearest weather stations within a 100-km radius of each fall migration starting location between the months of September and December of that year. We used two-sample Student's *t* or Wilcoxon ranked sum tests to check if mean monthly temperature or precipitation differed between costume-reared or parent-reared cranes for each month. We repeated this weather analysis for the starting locations of spring migration between the months of December and March to determine if overwinter conditions differed between rearing groups. We also examined wind speeds during migration by querying wind speeds from the nearest weather station in a 100-km radius for each relocation between the start and end of migration. To obtain weather data, we used Global Surface Summary of the Day data (NOAA 1999) using the *GSODR* package (Sparks et al. 2017).

Table 2. Number of migrations completed (N), mean migration dates and ranges, and mean migration durations and distances with standard error for individual, parent-reared whooping cranes between 2016 and 2023 or individual, costume-reared whooping cranes between 2012 and 2019 in the Eastern Migratory Population.

ID	Start date	Range	End date	Range	Distance (km)	Duration (days)	N	Years migrated
Fall Parent-Reared								
14-15	6 Nov	(18 Oct-8 Nov)	30 Nov	(10 Nov-28 Dec)	1,063 ± 17.6	23.2 ± 5.10	7	2016-2022
19-17	15 Oct	–	13 Nov	–	1,291	29	1	2018
20-15	11 Nov	(4 Nov-18 Nov)	13 Dec	(26 Nov-29 Dec)	1,436 ± 15.1	31.4 ± 9.46	2	2016-2017
27-14	15 Oct	(3 Oct-22 Oct)	15 Nov	(6 Oct-2 Feb)	584 ± 11.4	31.3 ± 23.80	4	2019-2022
39-16	8 Nov	–	12 Nov	–	961	3.6	1	2017
79-19	11 Nov	(1 Nov-21 Nov)	18 Nov	(3 Nov-28 Nov)	451 ± 78.7	6.7 ± 4.74	3	2021-2022
84-21	27 Sep	–	3 Oct	–	681	6.1	1	2022
Spring Parent-Reared								
14-15	17 Feb	(27 Jan-13 Mar)	24 Mar	(4 Mar-21 May)	1,086 ± 6.9	35.6 ± 14.00	7	2017-2023
20-15	13 Mar	(9 Mar-16 Mar)	3 Apr	(24 Mar-18 Apr)	1,486 ± 68.3	21.2 ± 11.60	2	2017-2018
27-14	3 Mar	(24 Jan-15 Mar)	26 Mar	(16 Mar-25 Mar)	575 ± 14.0	17.7 ± 9.87	4	2020-2023
39-16	5 Mar	–	24 Mar	–	897	18.6	1	2018
79-19	1 Mar	(27 Feb-7 Mar)	15 Mar	(Mar 1-May 24)	453 ± 79.7	12.7 ± 5.33	3	2021-2023
Fall Costume-Reared								
10-14	6 Nov	-	8 Dec	-	1601	32.9	1	2015
10-15	23 Oct	(3 Oct-11 Nov)	9 Dec	(3 Dec-14 Dec)	971 ± 94.1	47.4 ± 8.15	3	2016-2018
2-13	10 Nov	-	24 Nov	-	1,581	13.9	1	2014
2-15	28 Oct	(28 Sep-6 Dec)	5 Dec	(24 Nov-25 Dec)	1,198 ± 48.2	37.6 ± 11.00	4	2016-2019
3-14	22 Nov	(11 Nov-7 Dec)	23 Dec	(9 Dec-6 Jan)	1,548 ± 54.4	30.8 ± 1.04	2	2015-2016
4-11	12 Nov	(25 Oct-29 Nov)	13 Dec	(2 Nov-20 Jan)	990 ± 113.	31.6 ± 14.20	4	2012-2015
7-11	6 Nov	(27 Sep-26 Nov)	10 Dec	(11 Nov-11 Jan)	829 ± 88.7	35.0 ± 11.602	5	2012-2016
7-14	10 Nov	-	24 Nov	-	1,603	14.0	1	2015
8-13	16 Oct	-	22 Nov	-	1,558	37.2	1	2014
8-14	15 Nov	(12 Nov-18 Nov)	27 Nov	(27 Nov-28 Nov)	1,755 ± 153.0	12.4 ± 2.49	2	2015-2016
9-13	13 Nov	-	28 Feb	-	1,655	107.5	1	2014
Spring Costume-Reared								
10-15	20 Feb	(17 Feb-23 Feb)	25 Mar	(16 Mar-2 Apr)	1066 ± 0.697	33.2 ± 5.83	2	2017-2018
2-15	11 Feb	(9 Feb-12 Mar)	22 Mar	(22 Mar-30 Mar)	1169 ± 254.	38.9 ± 3.27	3	2017-2019
3-14	13 Feb	(21 Jan-7 Mar)	21 Mar	(21 Mar-21 Mar)	1540 ± 63.5	36.5 ± 22.6	2	2016-2017
4-11	26 Feb	(4 Feb-15 Mar)	27 Mar	(21 Mar-4 Apr)	987 ± 112.	29.7 ± 10.1	4	2013-2016
7-11	9 Mar	(7 Mar-12 Mar)	29 Mar	(21 Mar-13 Apr)	935 ± 107.	20.0 ± 5.85	4	2013-2016
7-14	22 Mar	-	29 Mar	-	1602	7.6	1	2016
8-14	5 Apr	-	22 May	-	1903	16.9	1	2016
9-13	15 Mar	-	21 Apr	-	1702	36.6	1	2015

RESULTS

For parent-reared cranes, we identified a total of 17 complete spring migrations and 19 fall migrations across 8 individual cranes during the years 2016-2023 (Table 2). In total, parent-reared cranes in our study used 14 fall and 20 spring stopover sites. For costume-reared cranes, a total of 31 fall migrations and 23 spring migrations were completed across 9 individual cranes, and they used a total of 32 spring stopovers and 32 fall stopovers during the years 2012-2019.



Figure 1. Right panel: all locations (unfilled circles) of 8 parent-reared whooping cranes from May to September for each year between 2016 and 2023. Left panel: all locations (unfilled circles) for 12 costume-reared cranes between May to September for each year between 2012 and 2019.

Parent-reared cranes in this study moved farther west during summers than costume-reared cranes (Fig. 1). For parent-reared whooping cranes, summering locations between May through September occurred in North Dakota, South Dakota, Minnesota, Michigan, Illinois, Indiana, Iowa, and Wisconsin. For costume-reared cranes, all summering locations occurred in Wisconsin. Of the 4 parent-reared cranes that moved outside of Wisconsin, 3 of these were under breeding age (<3 years) and 1 was over breeding age (7 years). In some cases, whooping cranes would summer in the same relatively confined location each year, while others would move between or within states during summer months. This behavior is sometimes referred to in the literature as “spring wandering” (Teitelbaum et al. 2019a). Consequently, the areas of summering ranges spanned between 1.95 km² to 1,121,012 km². While these ranges are useful as spatial barriers to detect migration events, they do not accurately represent home ranges due to large tracts of unused space for wandering cranes. Wintering sites for parent-reared cranes occurred in Alabama, Louisiana, Indiana, Tennessee, and Illinois (Fig. 2), while wintering sites for costume-reared cranes occurred in Florida, Alabama, Indiana, Tennessee, and Georgia (Fig. 3). Six costume-reared cranes (2-13, 8-14, 3-14, 10-14, 8-13, and 7-14) returned to their release sites in Saint Marks NWR, and costume-reared cranes 10-15 and 4-11 wintered in Wheeler NWR (which was the release site for crane 4-11). Three costume-reared cranes (7-11 during 2015, 2-15 during 2017, and 4-11 during 2015) and parent-reared crane 79-19 during 2021 wintered at a higher latitude from wintering sites from their previous year. In a few instances, costume-reared cranes would partially migrate then move over 100 km to a more southern location in January or February, as seen in crane 7-11’s 2014 and 2013 migrations, 4-11’s 2014 migration, and 3-14’s 2016 migration.

Mean fall temperature ($P > 0.05$ for each month) or precipitation ($P > 0.05$ for each month) between parent-reared and costume-reared cranes did not differ for the months of September, October, November, or December. Mean overwinter temperature ($P > 0.05$ for each month) or precipitation ($P > 0.05$ for each month) between parent-reared and costume-reared cranes did not differ for the months of December, January, February, or March.

For parent-reared cranes, the median fall migration start date was 4 November (interquartile range [IQR]: 19 October-14 November), and median end date was 23 November (IQR: 6 November-29 November).

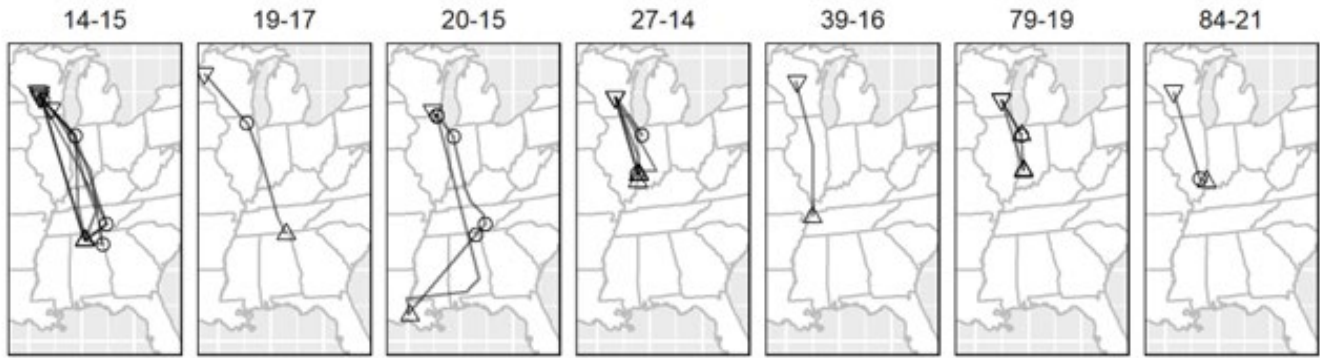


Figure 2. Fall migration paths of individual parent-reared whooping cranes in the eastern migratory population during 2016-2022 using relocation data filtered between fall migration start and end dates. Triangles represent start and end locations and circles represent stopovers.

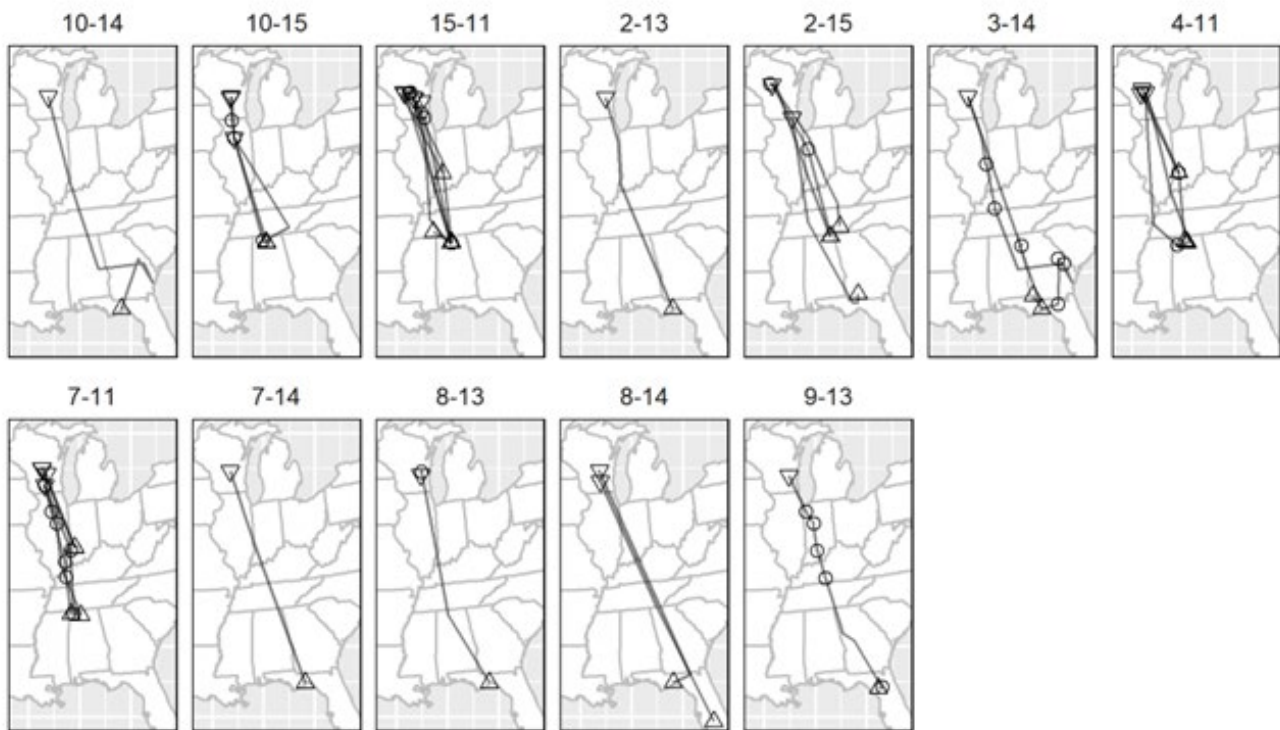


Figure 3. Fall migration paths of individual costume-reared whooping cranes in the eastern migratory population during 2012-2019 using relocation data filtered between fall migration start and end dates. Triangles represent start and end locations and circles represent stopovers.

For costume-reared cranes, the median fall migration start date was 7 November (IQR: 10 October-14 November), and end date was 28 November (IQR: 24 November-14 December).

The median spring migration start date for parent-reared cranes was 1 March (IQR: 19 February-9 March) and end date was 19 March (IQR: 14 March-25 March).

For costume-reared cranes, the median spring migration start date was 5 March (IQR: 16 February-11 March) and end date was 26 March (IQR: 21 March-1 April).

Maximum speed during migration, calculated as distance over time between non-stopover relocations during migration, was 60.4 km/hr during the fall and 20.6 km/hr during the spring for parent-reared cranes. For

costume-reared cranes, maximum speed during migration was 82.5 km/hr during the fall and 49.5 km/hr during the spring. Wind conditions were similar between stopover and non-stopover relocations and between rearing groups. Between start and end dates of migrations, mean daily wind speeds and mean maximum wind speeds were 7.8 and 14.6 km/hr during stopover relocations of parent-reared cranes, 6.8 and 13.4 km/hr during non-stopover relocations of parent-reared cranes, 7.4 and 14.5 km/hr during stopover relocations of costume-reared cranes, and 6.5 and 13.3 km/hr during non-stopover relocations of costume-reared cranes. Wind speed and max wind speed were uncorrelated with the migratory speed of cranes (Spearman's ranked correlation test: $P > 0.05$ for both).

Median migration duration for parent-reared cranes was 16.2 days (25-75% interquartile range [IQR]: 6.0-29.0 days) during the fall and 17.1 days (IQR: 9.5-32.8 days) during the spring. Median duration for costume-reared cranes was 31.7 days (IQR: 14.8-56.4 days) during the fall and 30.2 days (IQR: 14.6-39.0 days) during the spring. Mean Euclidean distance of parent-reared cranes from start to end points of migration during the fall was 891.3 ± 335.03 [SD] km, and during the spring was 889.9 ± 353.52 km. For costume-reared cranes, these distances were $1,216.5 \pm 360.67$ km during the fall, and $1,200.9 \pm 369.75$ km during the spring.

Parent-reared cranes made a median of 1 stopover (IQR: 0-2, $n = 17$ migrations) during spring migration and 0 stopovers (IQR: 0-1, $n = 19$ migrations) during fall migration. Costume-reared cranes made a median of 1 stopover (IQR: 0.5-2, $n = 18$ migrations) during spring migration and 1 stopover (IQR: 0-1, $n = 25$ migrations) during fall migration. The median time parent-reared cranes spent on stopovers during fall was 7.5 days (IQR: 2.7-11.4, $n = 14$ stopovers) and spring was 4.2 days (IQR: 3.7-9.7, $n = 23$ stopovers). The median time costume-reared cranes spent on stopovers during fall was 5.7 days (IQR: 1.7-19.5, $n = 27$ stopovers) and spring was 8.1 days (IQR: 5.4-14.5, $n = 23$ stopovers). During the fall, parent-reared cranes made stopovers in Wisconsin, Tennessee, Illinois, Indiana, and Alabama, and costume-reared cranes made stopovers in Wisconsin, Illinois, Alabama, Indiana, Kentucky, Georgia, and Florida. During the spring, parent-reared cranes made stopovers in Wisconsin, Kentucky, Illinois and Indiana (Fig. 4), and costume-reared cranes made stopovers in Wisconsin, Illinois, Alabama, Indiana, Kentucky, and Georgia (Fig. 5). Both parent-reared and costume-reared whooping cranes varied in stay lengths and number of stopover sites within migrations, and they often would select novel stopover locations each migration.

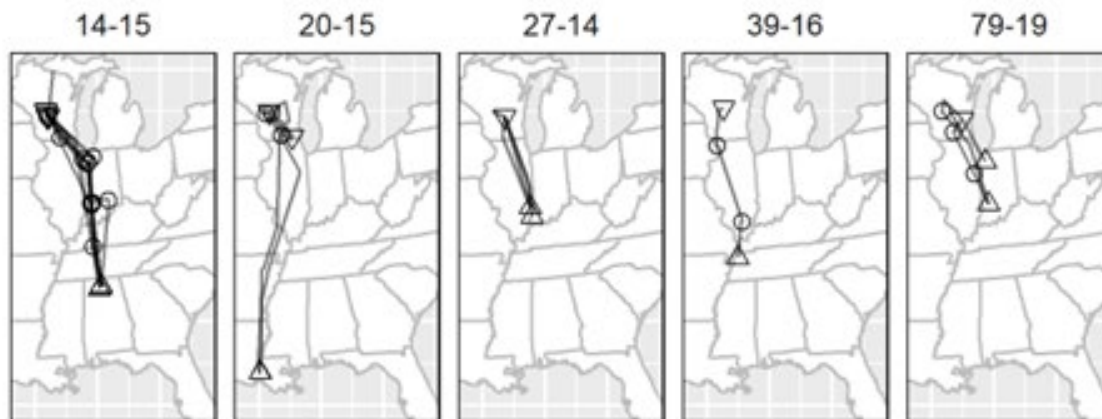


Figure 4. Spring migration paths of individual parent-reared whooping cranes in the eastern migratory population during 2017-2023 using relocation data filtered between spring migration start and end dates. Triangles represent start and end locations and circles represent spring stopovers.

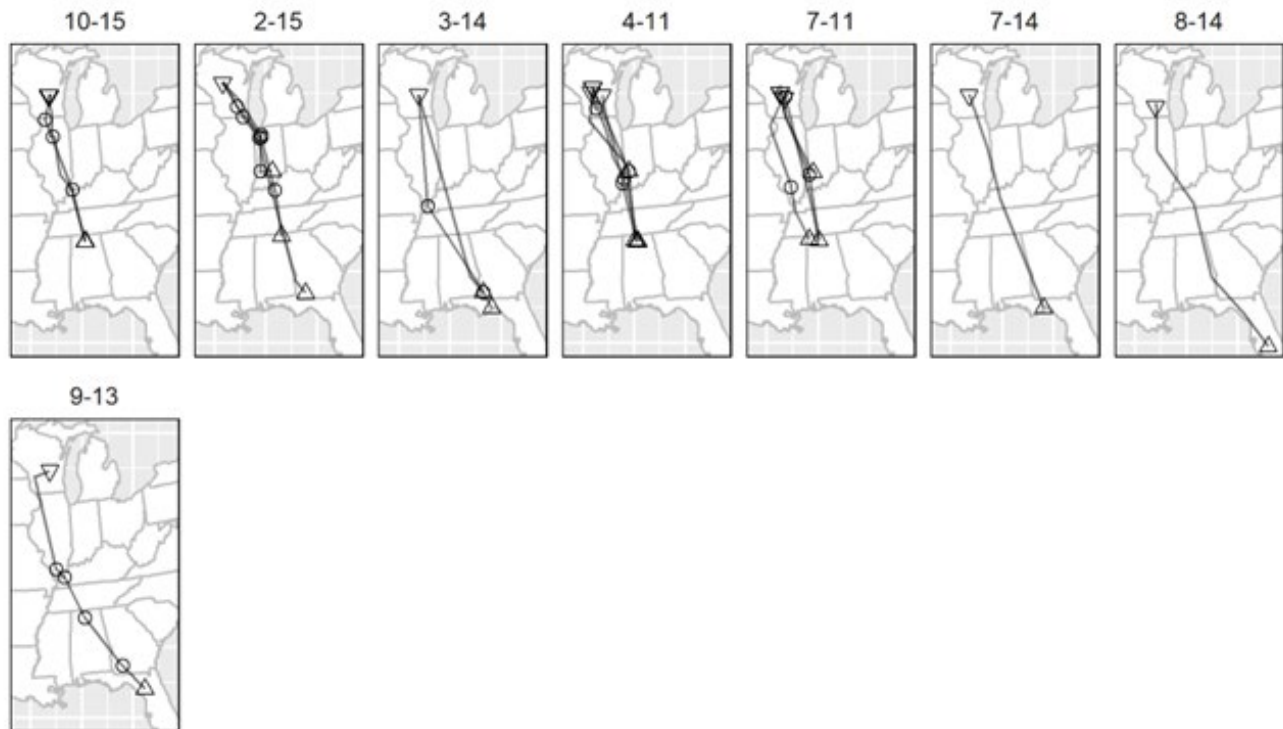


Figure 5. Spring migration paths of individual costume-reared whooping cranes in the eastern migratory population during 2013-2019 using relocation data filtered between spring migration start and end dates. Triangles represent start and end locations and circles represent spring stopovers.

For spring migrations, parent-reared cranes did not differ from costume-reared cranes in the duration of migration ($t_{[10.3]} = 1.1, P = 0.3$), distance of migration ($t_{[7.8]} = 7.04, P = 0.07$), start date of migration ($t_{[105]} = 0.2, P = 0.8$), and end date of migration ($W = 27, P = 0.4$). For fall migrations, parent-reared cranes migrated shorter durations than costume-reared cranes ($W = 61, P = 0.04$), migrated shorter distances ($W = 65, P = 0.02$), and ended migration earlier ($W = 65, P = 0.02$) but did not differ in the start date ($t_{[8.9]} = 1.3, P = 0.2$) of migration. Since more cranes contributed to fall analysis than spring analysis (Table 2), we repeated tests of fall analysis with only the same cranes as in spring analysis. Significant differences were not detected between rearing groups for fall migration initiation date ($t_{[5.2]} = 1.3, P = 0.2$), end date ($W = 33, P = 0.07$), duration ($W = 30, P = 0.2$), or distance ($t_{[7.9]} = 2.1, P = 0.06$), suggesting lack of detection in spring may be an artifact of smaller sample sizes since migratory routes between fall and spring are generally similar.

DISCUSSION

Overall, migratory behavior of parent-reared whooping cranes followed patterns similar to the ultralight-led, costume-reared cranes in this study. We did not detect a difference in the phenology of spring migration between costume-reared cranes and parent-reared cranes. However, costume-reared cranes migrated for longer durations and longer distances and completed migration later in the year than parent-reared cranes during the fall. These differences during fall migration could be because costume-reared cranes were exhibiting site fidelity to their winter release location in Florida or Alabama (Fondow 2013), and the absence of differences detected during spring may have been because of smaller sample sizes in each rearing group, including 3 fewer costume-reared cranes that migrate to Florida. Other factors could be that UL birds learn to migrate more slowly since UL-led migrations take longer than crane-led migrations and make frequent stops (Tietelbaum et al. 2019a). For instance, compared to the distance between fall stopovers observed in crane-led migrations in the wild Wood Buffalo-Aransas

Population of whooping cranes (307.7 ± 187.6 km; Pearse et al. 2020), the mean segment length between stopovers of UL-led first migrations during 2001-2014 was 58.75 ± 9.19 [SD] km (ICF unpublished data). Additionally, UL birds are less likely to adjust migratory routes to avoid harsh weather than DAR or PR cranes (Abrahms et al. 2021), which may demand more energy and prolong their migrations. In all other cases, migratory patterns of either costume-reared or parent-reared cranes in this study are comparable to previously published information of costume-reared EMP cranes.

Using a dataset of 105 EMP cranes that included UL, DAR, and parent-reared cranes from 2002 to 2018, Abrahms et al. (2021) found that average duration of autumn and spring migrations were 17 days (range 2-122 days) and 27 days (range 3-162 days), respectively, and average daily speeds of 56 km/day (range 0-1,216 km/day) in autumn and 48 km/day (range 0-858 km/day) in spring. Using data from 2001 to 2007 of UL and DAR cranes, Urbanek et al. (2010a) found that juvenile UL whooping cranes initiated spring migration between 25 March and 9 April, while DAR cranes typically migrated in March (mean: 20 March, range 26 February-22 April). For fall migration, they observed start dates from 22 October to 11 December, with most occurring in November. Urbanek et al. (2010a) also noticed some whooping cranes would make staging movements in southern Wisconsin or other areas prior to fall migration. In this study, 4 parent-reared and 4 costume-reared whooping cranes made movements to northern Illinois, northern Indiana, or southern Wisconsin at the beginning of fall migration. Using EMP migratory data from 2010 to 2014, Teitelbaum et al. (2019a) found similar behavior with fall migration typically beginning early November and finishing by December, and spring migration beginning in March and finishing by May. Teitelbaum et al. (2019a) also found birds summering mainly in Wisconsin as well as Iowa, Michigan, Minnesota, and Illinois, and they found birds wintering over a 1,500-km range in latitude from Florida to southern Indiana or Illinois. Finally, both parent-reared and costume-reared whooping cranes exhibited low fidelity to stopover sites and frequently selected new sites during migrations, a behavior also observed in the Arkansas-Wood Buffalo Population (Pearse et al. 2020).

While most whooping cranes included in this study returned to previous wintering sites each migration, 1 parent-reared crane (79-19) and 3 costume-reared cranes (2-15, 4-11, and 7-11) exhibited winter short-stopping at the respective ages of 3, 2, 4, and 4 years. This behavior,

where whooping cranes overwinter at higher latitudes in successive years, has been previously observed in other whooping cranes in the EMP (Teitelbaum et al. 2016) and is influenced by factors such as social group dynamics, increased food or habitat availability in the north, and drought or habitat loss in the south (Urbanek et al. 2016, Abrahms et al. 2021). Interestingly, all cranes in this study that shortstopped their migration were females and may have wintered at new sites as they found males with whom to form a pair bond. Cranes may also overwinter in stopover locations visited from previous migrations, and younger cranes may shortstop with older cranes in the group since migratory behavior is socially influenced (Teitelbaum et al. 2016). Age and rearing methods have also been found to influence migration duration, with rearing and release methods that involve higher intraspecific learning (direct autumn release and parent-rearing) exerting stronger effects with age (Abrahms et al. 2021). Given the social transmissibility of shortstopping behavior, rearing methods that encourage conspecific learning may be especially advantageous during pre-breeding ages when risk of mortality from inexperience is higher (Teitelbaum et al. 2019b).

Some parent-reared whooping cranes in this study traveled from Wisconsin to nearby northern states such as North Dakota, South Dakota, and Minnesota during the end of spring migration or over the summer. In contrast, costume-reared cranes did not move outside of Wisconsin during summer. While the costume-reared cranes in this study did not move as far as the parent-reared cranes, there have been observations of costume-reared cranes moving from Wisconsin to North Dakota (Urbanek et al. 2010a) or Vermont (Gordon et al. 2025). This behavior may familiarize pre-breeding age cranes with potential foraging or breeding habitat outside of their natal grounds; however, natal dispersal distances remain relatively short once whooping cranes reach breeding age (Barzen et al. 2019, Thompson et al. 2021). Spring wandering behavior can lead to young whooping cranes spending a greater percentage of time outside of protected conservation areas and thus run a greater risk of exposure to anthropogenic hazards or limited food availability (Teitelbaum et al. 2019a).

The results of these analyses indicate that parent-reared whooping cranes display similar spring migratory behavior to costume-reared, ultralight-led whooping cranes. However, during fall, costume-reared cranes migrated for longer durations and distances and finished migration later in the year than parent-reared cranes,

partially due to more cranes wintering in Florida, likely as a result of UL release methods. Aside from these differences, parent-reared and costume-reared cranes both exhibit similar migratory behaviors including spring wandering, winter short-stopping, and migratory initiation dates. This supports the use of parent-rearing as an alternative rearing method to costume-rearing, which could benefit reintroduction programs given the method's reduced labor demands and encouragement of conspecific learning. Since this analysis only compares parent-reared birds to ultralight-led, costume-reared birds, we recommend further comparisons of parent-reared cranes to costume-reared, DAR cranes because release methods can also influence post-release behavior (Mitchell et al. 2011, Nagata and Yamagishi 2016).

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