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## WHOOPING CRANE NESTING BEHAVIOR, PARENTAL CARE, AND ECOLOGY AT WOOD BUFFALO NATIONAL PARK

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# WHOOPING CRANE NESTING BEHAVIOR, PARENTAL CARE, AND ECOLOGY AT WOOD BUFFALO NATIONAL PARK

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**Abstract:** We studied Whooping crane (*Grus americana*) nesting behavior and movement patterns at Wood Buffalo National Park using an instantaneous scan sampling approach. We also photo-documented important behavioral and ecological observations. Data were collected from 2 to 9 June 2023 from before 3:00 to after 22:00 hours. We completed 88 hours of observation and documented nest swapping about every 3.2 hours. The female incubated/brooded 3.3-10.9% more than the male, and the probability of incubation/brooding declined by 49% after the second chick began pipping and by 99% after both chicks had hatched. The eldest chick was successfully provisioned 16 hours and 33 minutes after hatching. The provisioning rate declined from morning to evening and increased with time since hatch. Parents stayed significantly closer to the elder chick ( $\bar{x} = 0.32$  m) than the second chick ( $\bar{x} = 6.70$  m), despite the first moving 9% further from the nest per hour after hatch. The second chick hatched nearly 40 hours after the first. The eldest chick consumed mainly Odonata spp. and Araneae spp. Adults had a more diverse diet that also included snails (Gastropoda spp.), small fish (Osteichthyes spp.), leeches (Hirudinea spp.), and biting flies (Diptera spp.). The male appeared flightless with only a couple of primary feathers remaining on each wing when the eldest chick hatched. We also describe the features of the whooping crane breeding site and the associated avian community. Though insights are based on data from a single nest, they provide a rich description that can improve our understanding of nesting ecology in a remote landscape.

## PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 16:52-68

**Key words:** Asynchronous hatching, behavior, chick rearing, diet, *Grus americana*, molting, nesting, parental care, whooping crane, Wood Buffalo National Park.

The remnant population of whooping cranes (AWBP) that breeds in and around Wood Buffalo National Park (WBNP) and winters in and around Aransas National Wildlife Refuge (ANWR) in coastal Texas remained quite rare across the 20<sup>th</sup> century, ranging from 15 to 180 total individuals throughout the accordant period of record (1938-2000; CWS and USFWS 2007). However, the population has continued to grow and has more than doubled over the last couple decades (Butler et al. 2023). Nonetheless, the whooping crane remains the second rarest North American breeding bird listed to the U.S. Endangered Species Act after the California condor (USFWS 2020). The breeding grounds are so remote that they were not discovered until the mid-1950s and there remains essentially no road access to these sites (CWS and USFWS 2007). The rarity of the species, the remoteness of its breeding range, and challenges in accessing it have limited the amount of *in situ* observational research conducted on this population during the breeding season. Much of the foundational information regarding whooping crane nesting behavior, such as provisioning and incubation

rates, comes from studies of captive breeding pairs (e.g., Conway 1957, Walkinshaw 1973). Additionally, limited *in situ* behavioral research that has been done at WBNP was largely completed >20 years ago, focused predominantly on predation and diet, and has not been thoroughly replicated (Bergeson et al. 2001, 2001b). Therefore, to fill knowledge gaps, we completed on-the-ground behavioral research leading up to and after hatching at a remote whooping crane nesting location in the northern portion of WBNP. We focused our data collection efforts on the parental care of chicks and eggs.

## STUDY AREA

Our study was conducted about 20 km south of the northern boundary of Wood Buffalo National Park (WBNP) in the Northwest Territories of Canada (60.376694 N, -113.892061 W; 240 m elevation). The nesting site we observed was within the Nyarling River drainage, which was first documented to support nesting whooping cranes in 1970 (Kuyt 1981). Our observation site was on a slightly elevated and wooded ridge about 1.25 m above the nesting wetland. The ridge was dominated by tamarack (*Larix laricina*) and black spruce

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(*Picea mariana*), which generally exceeded 3 m in height. The maximum tree height on the wetland margin was estimated at >30 m using a laser range finder and a clinometer. The understory included bog birch (*Betula pumila*), lingonberry (*Vaccinium vitis-idaea*), roses (*Rosa* spp.), and willows (*Salix* spp.). The palustrine emergent wetland was dominated by herbaceous vegetation including broadleaf cattail (*Typha latifolia*) and sedges (*Carex* spp.) and could generally be classified as a shallow marsh (Timoney 1999). Vegetation was almost completely green during our observations, which contrasted with nest-site photographs taken at WBNP during the same timeframe in early June 2008 in which vegetation remained largely senesced (Nigge 2010). Site depth was visually estimated based on the average whooping crane tarsal length following Caven et al. (2021). We also incidentally assessed maximum water depth at the study site during a walk through the focal wetland during blind setup. The maximum depth within 30 m of the nest appeared to be about 60 cm with locations as shallow as 5 cm. The average wetland depth near the nest was likely about 20 cm. There was about 30% open water habitat within 30 m of the nest. The nest sat 12-15 cm above the water throughout most of the survey period. The wetted width of the wetland was about 65 m across following estimation methods by Caven et al. (2022). The nest itself was about 32 m from our observation location. Our view to the nest had a bearing of 345° (~northwest; Fig. 1).



**Figure 1.** Aerial photograph of the whooping crane (*Grus americana*) nesting wetland with the nest platform at its center taken on 15 May 2023, 18 days before our behavioral observations started. Photo by M. Forsberg.

## METHODS

### Behavioral Sampling

We captured adult whooping crane behavior at and within sight of the nest using a 25-50x80 spotting scope (Maven Optics, Lander, Wyoming, USA) and 10x42 binoculars (Vortex Optics, Barneveld, Wisconsin, USA). Behavioral observations were made from a Tragopan V6 photography blind (<https://photographyblinds.com/>). Photographic data was recorded from an adjacent Tragopan Monal photography blind using a Sony A1 mirrorless camera, a 200-600 mm f3.5-6.3 zoom lens, and a 1.4x teleconverter (Sony Corporation, Minato City, Tokyo, Japan). Researchers were situated within neighboring blinds facing the nest. The blinds were placed behind a single sheet of camouflage mesh to further obscure them. To limit the disturbance to the nesting cranes the researchers lived within their blinds for the duration of the study from 2 to 9 June.

We used an instantaneous scan sampling approach which entailed tallying the number of adult whooping cranes (0-2) displaying a specific behavior at 3-minute intervals (Altmann 1974). Behavioral categories included foraging, social, alert, defensive, flying, walking, preening or loafing, incubation or brooding, and chick provisioning based on crane behavioral literature (e.g., Tacha 1988, Ellis et al. 1998, Yang et al. 2007, Malzahn et al. 2018, Barzen et al. 2018). The male and female were identified based on their vocalization behavior during unison calls (Ellis et al. 1998). However, we were able to record distinctive bill markings for each bird to determine sex visually after the first couple of unison calls. The female was a head shorter and had more orange around the base of its culmen and mandible than the male, which had gray to the base of its lower mandible (Fig. 2). We used their markings to track the sex of the incubating adult and nest swapping events in the absence of unison calling behavior. We also recorded a series of landscape distance measurements pertinent to crane behavior using a Vortex laser range finder (Vortex Optics, Barneveld, Wisconsin, USA) and a compass (i.e., triangulation; side-angle-side). We were able to establish distance estimates from the nest to distinct objects in the wetland footprint (e.g., emergent shrubs) for quick reference during scan sample efforts.



**Figure 2. Male whooping crane (*Grus americana*) loss of primary feathers evident during wing-spreading behavior. Note the greater amount and brighter nature of the orange at the base of the female whooping crane's bill which helped us identify the individual cranes in the absence of unison calling or wing spreading behavior. Photo by M. Forsberg during observations in June 2023.**

We also used the average height of the whooping crane (~1.5 m; Urbanek and Lewis 2020) to estimate shorter distances and confirm triangulation-based estimates. We recorded the distance of the nearest parent to the nest, the distance of each chick to the nest, and the distance of the nearest parent to each chick as accurately as possible during scan sampling efforts. Finally, we recorded any potential chick or egg predators in the area and the adult cranes' reactions to them.

Nesting observations were divided into 5 separate developmental periods for analysis including: 2 eggs, 1 egg and 1 pipping, 1 egg and 1 chick, 1 pipping and 1 chick, and finally 2 chicks. Sky conditions were categorically described as clear, partly cloudy, cloudy, and rainy during each observation. Data were collected from 2 to 9 June (day of year 153-160) during almost all portions of the day (0210-22 16 hr) as the observer was awake and alert. However, >95% of observations were collected between 0630 and 2105 hours.

### Diet and Natural History Observations

We noted the diet items that adult and juvenile whooping cranes were foraging on via a spotting scope and/or zoom photography when visually apparent throughout our study (see Caven et al. 2021). On 3 separate occasions for a total duration of 9 minutes, when foraging adults were sufficiently close, we recorded the number of foraging attempts (probes, stabs, etc.) adult

cranes made into the wetland and the accordant number of swallows made to determine capture efficiency on a per minute basis (see Barzen et al. 2018, Thompson et al. 2018). Swallowing events were determined via the characteristic head jerking movements cranes make when they consume food (Barzen et al. 2018, Thompson et al. 2018). These wetland foraging observations were made on 6 and 7 June between 0930 and 1800 hours. We also noted that adult cranes were consuming several flies out of their feathers during midday incubation periods. We recorded the number of flies swallowed per minute on 8 separate occasions spanning 36 total minutes (2-6 min per sampling period) while adults were incubating to also document this component of their breeding-season diet. These observations were made from 4 to 7 June between 1100 to 1900 hours while fly-specific foraging behavior was occurring.

We conducted 6 5-minute avian point count surveys between 0630 and 2030 hours from 4 to 7 June to determine the dominant birds associated with the whooping crane nesting site. We counted all distinct calls and visual observations from the blind during survey periods. Therefore, double counting was likely and counts simply represent an index of relative abundance and favor more vocal species (Gregory et al. 2004). Nonetheless, this process likely provided a reasonable estimate of what avian species were abundant at this site. We also noted species incidentally detected right before or after surveys, which were not officially documented during point counts. Additionally, we noted any behavioral, biological, or ecological phenomena that may be novel or add richness to the literature regarding whooping cranes breeding at WBNP. We made narrative descriptions, photo-documented, and recorded the time and date of such instances.

Finally, we recorded narrative behavioral and habitat notes during a single afternoon visit to a second remote whooping crane nesting site in Alberta, Canada, near the Salt Plains area of WBNP on 12 June 2023. Observations at this site were made from a wooded bluff about 25 m elevation above the nesting wetland and at a much longer distance (~400 m) than our primary observations.

### Statistical Analyses

All statistical analyses were conducted in the open-source software program R version 4.0.2 (R Core Team 2020). We examined variation in incubation/brooding

rates as well as provisioning rates by temporal (e.g., time of day) and chick development-related (e.g., stage) covariates using binomial family generalized linear models (GLM) with a “logit” link function with the “stats” package in R (McCullagh and Nelder 1989, R Core Team 2020). We examined model fit using Aldrich-Nelson pseudo- $R^2$  with a Veall-Zimmermann correction with the “DescTools” package in R (Smith and McKenna 2013, Signorell 2022). We evaluated variation in incubation/brooding and provisioning rates by sex using two-way tests of equal proportions (i.e., Z-test) with confidence intervals developed following Newcombe (1998) using the “stats” package (R Core Team 2020). We examined variation in the distance of the nearest parent to the nest and the distance of the elder chick (i.e., chick 1) to the nest in relation to developmental and temporal covariates using Poisson

family GLMs with a “log” link function using the “stats” package (McCullagh and Nelder 1989, R Core Team 2020). We examined differences in the distance that the nearest parent was to chick 1 (elder) and chick 2 (younger) using a two-tailed Mann-Whitney U Test (Bauer 1972). All graphics reflecting statistical tests were produced via the “effects” (Fox and Weisberg 2018) and/or the “ggplot2” packages in R (Wickham 2016).

### RESULTS

We completed 1,753 individual scan samples of behavior, which equates to about 5,259 minutes of observation, or about 87.7 hours of observation time over 8 days (just under 11 hr per day). We also shot 14,005 high-resolution photographs and captured 9.9 hours of 4K video and associated audio.

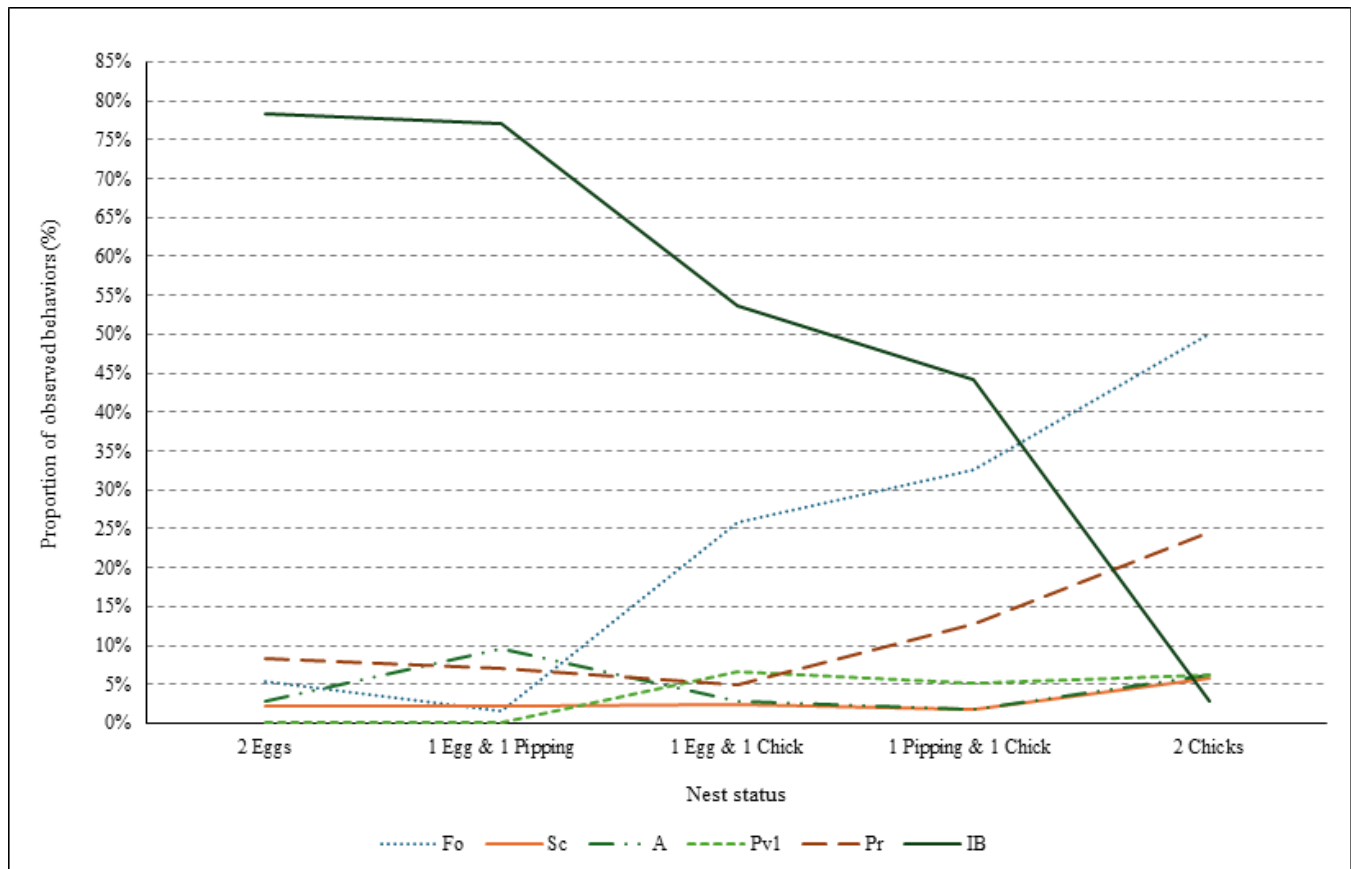


Figure 3. Adult whooping crane (*Grus americana*) time budget by nest status. Adult time budget is expressed as the proportion of total behaviors observed by nest reproductive status as 2 eggs, 1 egg and 1 pipping, 1 egg and 1 chick, 1 pipping and 1 chick, and 2 chicks. Behavioral rates plotted include Foraging (Fo), Social (Sc), Alert (A), Provisioning to chick one (Pv1), Preening/loafing (Pr), and Incubation/brooding (IB). Defensive, flying, and walking behaviors were relatively infrequent and did not demonstrate a strong trend and therefore were not plotted in this graphic but are summarized in the results section of this manuscript.

## Adult Time Budget and Nest Attendance

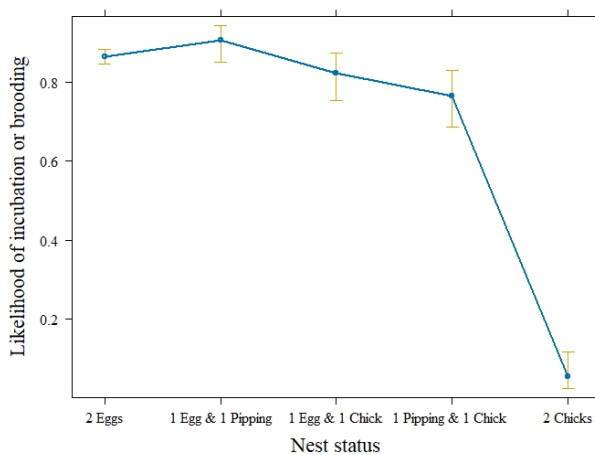
While in view adult whooping cranes spent their time incubating/brooding (64.7%), foraging (14.5%), and preening/loafing (9.8%), while alert behavior (3.6%), conspecific social behavior (2.6%), provisioning to chicks (1.9%), walking (1.9%), flying (0.9%), and defensive behavior (0.2%) totaled less than 11.0% of adult time budgets. However, these behavioral patterns varied widely by chick development status. For instance, adult foraging behavior increased substantially from the pre- to post-hatch period, peaking at 50% after both chicks were hatched (Fig. 3, Appendix 1). Social behavior also peaked after both chicks had hatched but at a much lower rate (5.8%). Clearly, provisioning only occurred after the eldest chick hatched and it comprised between 5.1% to 6.7% of adult behavior from that developmental stage forward (Fig. 3, Appendix 1). Preening behavior also increased from the pre- to post-hatch period, peaking at 24.5% of adult time after both chicks had hatched. Incubation and/or brooding went from being the most frequently observed adult behavior pre-hatch (78.4% of behavioral observations when there were 2 eggs) to the fifth most observed behavior after both chicks had hatched (2.9% of observations; Fig. 3, Appendix 1). Alert behavior was elevated when the first egg started pipping and again after both chicks had hatched (Fig. 3, Appendix 1). Trends were less pronounced regarding other behaviors such as flying, walking, and defensive behavior.

There was only 1 parent in view during the majority of our behavioral observations (60.1%). However, our sample was biased toward the period when there were 2 eggs in the nest (Appendix 2). The proportion of time when both

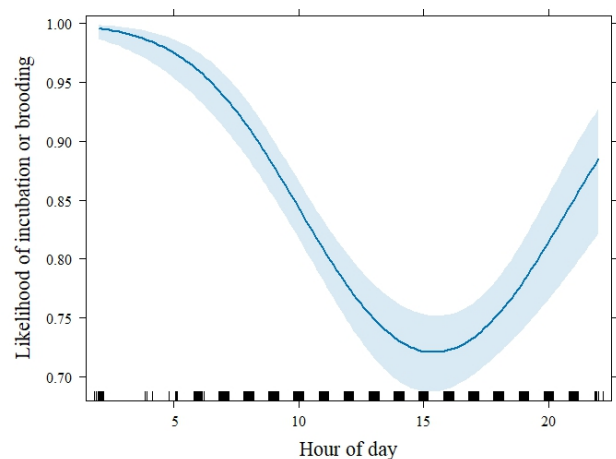
parents were present in the nesting area increased as chick development progressed ( $\chi^2 = 639.5$ ,  $P < 0.001$ ; Appendix 2). For instance, both parents were present 19.0% of the time that there were 2 eggs (residual = -20.3,  $P < 0.001$ ), 69.2% of the time that there was 1 egg and 1 chick (residual = 8.5,  $P < 0.001$ ), and 96.2% of the time that there were 2 chicks (residual = 16.8,  $P < 0.001$ ; Appendix 2).

## Incubation/Brooding Rate

Omitting the period with 2 chicks in which we did not record regular nest attendance, we documented 26 nest swaps in total across 82.25 hours of observation. This equates to about 1 nest swap per 3.16 hours (~190 min) or about 7.59 nest swaps per day. The male incubated during 46.4% of observations and female during 53.6%, with 95% confidence intervals, suggesting the male likely incubated 3.3-10.9% less than the female ( $\chi^2 = 13.9$ ,  $P = 0.0002$ ). Incubation/brooding behavior was observed in >80% of scan samples during earlier developmental stages including when there were 2 eggs ( $\bar{x} \pm SE$ ;  $86.5 \pm 1.0\%$ ), 1 egg and 1 pipping ( $90.6 \pm 2.3\%$ ), as well as 1 egg and 1 chick ( $82.2 \pm 3.1\%$ ; Fig. 4). However, this rate dropped to  $76.5 \pm 3.6\%$  when the second chick started pipping, and to  $5.6 \pm 2.2\%$  after both chicks hatched. Incubation/brooding rates were thus statistically similar across the first 3 chick development stages. Nonetheless, our model suggested the probability of incubation/brooding behavior declined by 49.3% (95% CI = 21.1-66.7%;  $Z = -3.1$ ,  $P = 0.002$ ) in the 1 pipping and 1 chick stage, and by 99.1% (95% CI = 98.0-99.7%;  $Z = -10.9$ ,  $P < 0.001$ ) when there were 2 hatched chicks (Fig. 4).



**Figure 4.** Predicted likelihood of whooping crane (*Grus americana*) parental incubation of eggs or brooding of chicks by nest status. Parental incubation of eggs or brooding of chicks (0-1) by nest reproductive status including 95% confidence intervals.



**Figure 5.** Predicted likelihood of whooping crane (*Grus americana*) parental incubation/brooding (0-1) by hour of day (1-24). The black bars on the x-axis represent observed data points

The model examining incubation/brooding rates in relation to chick developmental stage had a pseudo- $R^2$  value of 0.32 suggesting decent fit. The incubation/brooding rate demonstrated a quadratic relationship to hour of day ( $Z_1 = -6.38, P_1 < 0.001, Z_2 = 5.92, P_2 < 0.001$ ), with rates being highest in the early morning (>93% before 0700 hr) declining to mid-day (<73% at 1500 hr) and increasing again into the evening (>85% after 2100 hr; Fig. 5). This model was significant but had a pseudo- $R^2$  value of 0.08, suggesting limited explanatory power.

### Provisioning Rate

The first attempt to provision chick 1 was 14 hours and 20 minutes after hatch. We first visually confirmed successful provisioning of chick 1, in which the chick definitively consumed food, 16 hours and 33 minutes after hatch. On several occasions chick 1 took 2-5 attempts to swallow the food provisioned to it and occasionally appeared to swallow food items only partially. We documented no provisioning to chick 2 through the first 8 hours and 23 minutes after it hatched, and we departed the study site following those observations. A nest camera positioned at the site

recorded another 14 hours of time-lapse photography at 30-second intervals before the family departed the area. This camera recorded an adult holding provisions at the nest while chick 2 was present but did not provide definitive evidence of provisioning to the younger chick through the first 24 hours and 23 minutes of life. We documented 41 cases of provisioning across 401 behavioral samples following the hatch of chick 1 for an estimated provisioning rate of  $10.2 \pm 1.6\%$  of chick 1's time. However, the provisioning rate varied by time of day (Fig. 6). The provisioning rate declined at a pace of about 16.8% each hour of the day from about 0600 to 2000 hours (95% CI = 9.1-24.4%:  $Z = -3.9, P < 0.001$ ). This equates to a predicted provisioning rate of >25% at 0600 hours but <3% at 2000 hours (Fig. 6). This model had a pseudo- $R^2$  value of 0.11. Parental provisioning increased with time since hatch for chick 1, rising at a rate of 2.8% per hour of life (95% CI = 0.5-5.2%:  $Z = 2.3, P = 0.019$ ; Fig. 7). However, this model had a relatively low pseudo- $R^2$  value of 0.04. When the sex of the provisioning adult was identified through field markings, it was the male in 61.1% of instances. However, the apparent difference in provisioning rate by adult sex was not statistically significant ( $\chi^2 = 1.8, P = 0.182$ ).

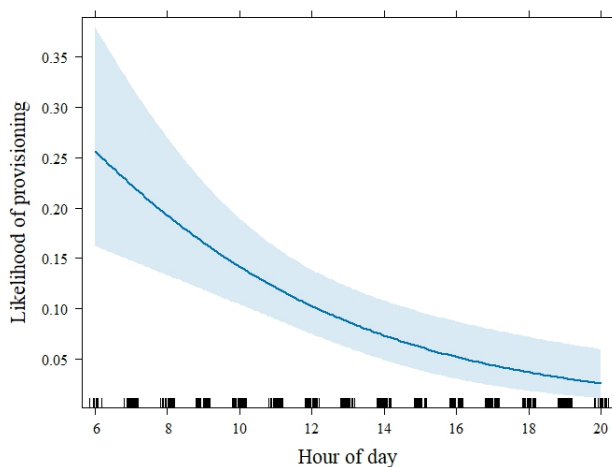


Figure 6. Predicted likelihood of whooping crane (*Grus americana*) parental provisioning (0-1) to the first-born chick by hour of day (1-24). The black bars on the x-axis represent observed data points.

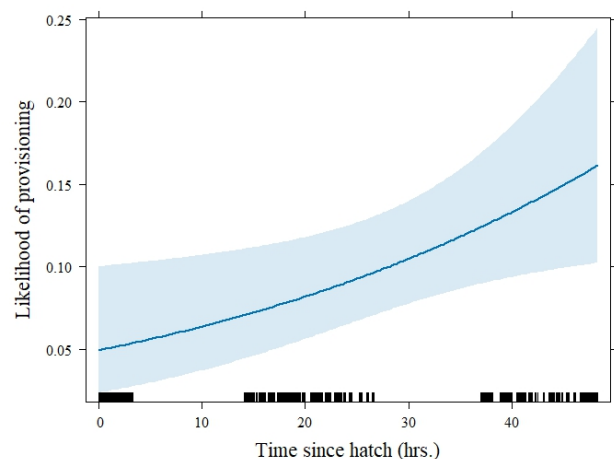
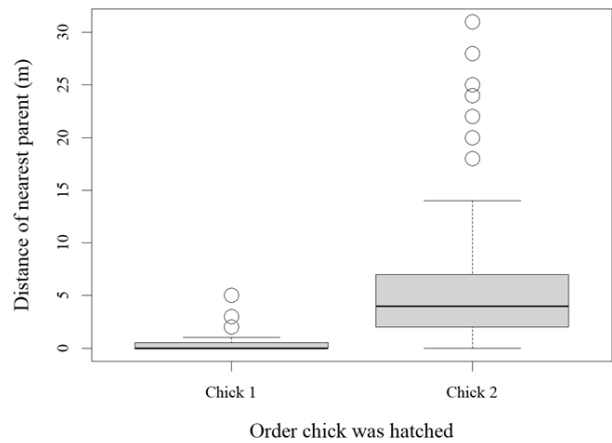


Figure 7. Predicted likelihood of whooping crane (*Grus americana*) parental provisioning (0-1) by time since hatch in hours (1-48). The black bars on the x-axis represent observed data points

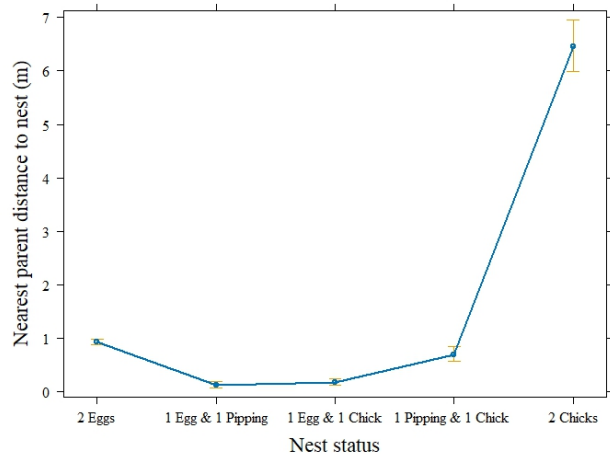
**Movements**

The distance of the nearest parent to the nest averaged 1.1 m and ranged from 0 to 55 m (SD = 4.7, SE = 0.1,  $n = 1,753$ ). The distance of chick 1 to the nest through the first 48 hours and 16 minutes after hatching was 1.3 m and ranged from 0 to 25 m (SD = 3.2, SE = 0.2,  $n = 296$ ). The distance of chick 2 to the nest through the first 8 hours and 23 minutes after hatching was 0.12 m and ranged from 0 to 0.50 m (SD = 0.13, SE = 0.01,  $n = 103$ ). Chick 1 left the nest for the first time 14 hours and 17 minutes after hatch. Chick 2 wandered to the base of the nest 3 hours and 44 minutes after hatching was confirmed, but ultimately it did not leave the area around the nest during our observations. The distance of chick 1 to the nearest parent averaged 0.32 m and ranged from 0 to 5 m (SD = 0.71, SE = 0.04,  $n = 296$ ). The distance of chick 2 to the nearest parent averaged 6.70 m and ranged from 0 to 31 m (SD = 6.96, SE = 0.69,  $n = 103$ ). Parents stayed significantly closer to chick 1 (eldest) than chick 2 ( $W = 1,352.5, P < 0.001$ ) during our observations (Fig. 8).

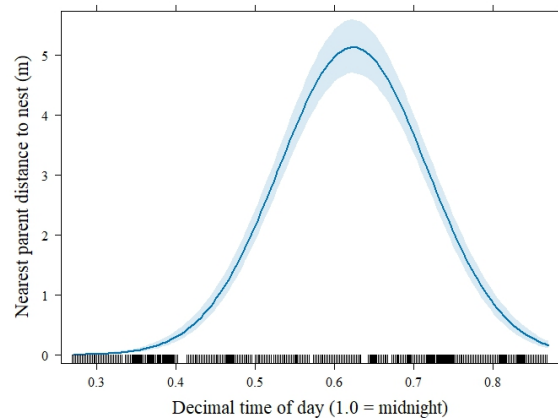
Parents generally stayed within 1 m of the nest aside from the period after both chicks hatched (predicted range = 0.12-0.93 m; Fig. 9). The model predicted a 595% increase in the distance of the nearest parent to the nest after both chicks had hatched compared to when there were 2 eggs ( $B = 1.94, SE = 0.05, Z = 40.10, P < 0.001$ ). This model had a pseudo- $R^2$  value of 0.59, suggesting a good model fit. The distance of the nearest parent to the nest had a quadratic relationship with time of day ( $Z_1 = 19.8, P_1 = < 0.001, Z_2 = -28.6, P_2 = < 0.001$ ; Fig. 10), with predicted distance to nest values <1 m before 1030 hours and after 1930 hours and distance to nest maximized at just over 5 m at 1500 hours (Fig. 10). This model had a pseudo- $R^2$  value of 0.72, suggesting excellent model fit. The distance of the eldest chick from the nest increased at a rate of about 9.4% per hour after hatch with a predicted distance of 6.02 m from the nest 48 hours after hatch ( $B = 0.090, SE = 0.005, Z = 18.5, P < 0.001$ ; Fig. 11). The model had a very strong fit to the data with a pseudo- $R^2$  value of 0.76. There was a strong positive relationship between the distance from the nest of the nearest parent and the eldest chick ( $B = 0.176, SE = 0.005, Z = 33.7, P < 0.001$ ; pseudo- $R^2 = 0.85$ ).



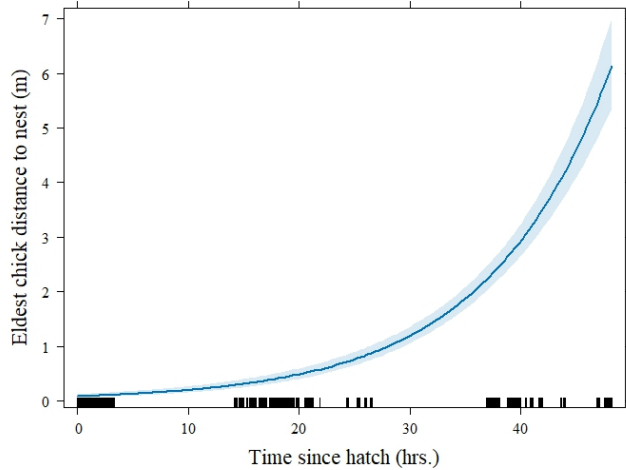
**Figure 8.** Distance of nearest whooping crane (*Grus americana*) parent to chick 1 (elder) and chick 2 (younger) in meters (m) throughout their first hours of life post hatch.



**Figure 9.** Predicted distance of the nearest whooping crane (*Grus americana*) parent to the nest in meters (m) by nest reproductive status.



**Figure 10.** Predicted distance of the nearest whooping crane (*Grus americana*) parent to the nest in meters (m) by decimal time of day (0.0-1.0; 1.0 = midnight). The black bars on the x-axis represent observed data points.



**Figure 11.** Predicted distance of whooping crane (*Grus americana*) chick 1 (elder) to the nest in meters (m) by time since hatch in hours (1-48). The black bars on the x-axis represent observed data points.

### Chick Development

Chick 1 hatched at 1731 hours on 7 June and chick 2 hatched at 0924 hours on 9 June 2024. Pipping was detected in both chicks as the hole in the base of the egg was larger than a dime but smaller than a quarter (Fig. 12). The eldest chick required 8 hours and 17 minutes to hatch after pipping was first noted at 0914 hours on 7 June. Chick 2 required more than twice as long, 20 hours and 24 minutes, to hatch after pipping was first detected at 1300 hours on 8 June. However, it is notable that chick 1 went from pipping to hatched during daylight hours and there was an intervening night between pipping and hatch for chick 2. Ultimately, the second egg was definitively pipping 27 hours and 46 minutes after the first egg did so, but the second chick hatched 39 hours and 53 minutes after the first chick. We did not note how long it took chick 1 to go from hatched to standing. However, chick 2 stood for a duration of >5 seconds for the first time about 1 hour and 52 minutes after hatching.



**Figure 12.** Egg pipping after whooping crane (*Grus americana*) chick 1 was already hatched. The hole at its current state is about 50% larger than when we first noted it for chick 2.

### Diet

The eldest chick consumed predominantly dragonfly and damselfly larvae (61.1%; Odonata spp.) as well as spiders (22.2%; Araneae spp.) whereas the adults had a more diverse diet that also included the previously mentioned items in addition to biting flies (Diptera spp.), snails (Gastropoda spp.), small fish (Osteichthyes spp.), leeches (Hirudinea spp.), and other invertebrates (Fig. 13). Adult whooping cranes consumed approximately  $4.0 \pm 0.4$  ( $\bar{x} \pm SE$ ) large biting flies per minute while being swarmed by them, generally during incubation at midday. The most abundant Diptera spp. appeared to be in the family Tabanidae and the genus *Hybomitra*, based on pictures and samples from the observation area. However, it appeared that there were multiple species harassing the nesting whooping cranes, particularly from late morning through the afternoon. Biting flies were clearly causing the whooping cranes discomfort as they often pulled the flies from their feathers and thereafter appeared with blood on the tip of their culmen. Adult whooping cranes foraging in the wetland probed about  $3.6 \pm 0.5$  times per minute and swallowed about  $2.3 \pm 0.2$  diet items per minute and had a capture rate of about 67% overall for aquatic prey items.



**Figure 13. Adult whooping crane (*Grus americana*) consuming a sedge-dwelling spider (A), a dragonfly larva (B), and a snail (C). Photos by M. Forsberg.**

## Natural History

*Adult molting.*—We did not observe the male flying during the study though we frequently noted the female doing so. The progressive loss of the male’s primary flight feathers became readily apparent by the morning of 6 June as only 2-3 primary feathers persisted on each wing (Fig. 14).

*Female chick attendance.*—The adult female flew out of the nesting area while the first egg was pipping at 1558 hours on 7 June and didn’t return until the eldest chick had hatched at 1731 hours on the same day. The female also flew out of the nesting area after the first chick had hatched at 1115 hours on 8 June and returned at 1151 hours on the same day.

*Potential predators.*—We noted the presence of common ravens (*Corvus corax*) on multiple occasions; it appeared as though the adult female whooping crane purr called to the eldest chick during one such instance as several ravens flew overhead. However, one of the few instances in which we observed defensive behavior occurred as an American bittern (*Botaurus lentiginosus*) approached the nest. The female whooping crane ran at the bittern in a galloping manner while spreading its wings and calling and ultimately flushed the “potential” nest predator.

*Avian Community Data.*—We recorded 26 avian species through point count efforts. The common yellowthroat (*Geothlypis trichas*), Swainson’s thrush (*Catharus ustulatus*), alder flycatcher (*Empidonax alnorum*), swamp sparrow (*Melospiza georgiana*), Wilson’s snipe (*Gallinago delicata*), Tennessee warbler (*Leiothlypis peregrina*), white-throated sparrow (*Zonotrichia albicollis*), sora (*Porzana carolina*), and

the red-winged blackbird (*Agelaius phoeniceus*) were all detected at a rate of  $\geq 0.3$  distinct calls or sightings per survey minute and describe the bird community at the Nyarling whooping crane breeding site during our observation period (Appendix 3).

*Salt Plains Nest.*—We confirmed 2 chicks at this location each foraging with a parent  $>60$  m from the nest. Adults and their attendant chicks were separated into 2 dyads  $>10$  m apart for the majority of the  $\sim 30$ -minute observation period. Adults were foraging and provisioning to chicks on a regular basis. One chick appeared notably more mobile and drifted from its attending parent at times while the other stayed relatively close and moved comparatively shorter distances suggesting the less mobile of the 2 chicks was hatched relatively recently. The habitat could be described as herbaceous-emergent marsh with notable expanses of open water (visually estimated at  $>35\%$  of the wetland footprint). The wetland was about 250 m across its shorter diameter and several times longer than wide. The nest site was around 100 m from the wetland edge, mostly in open water. The extensive wetland included an apparently active American beaver (*Castor canadensis*) lodge. The water level near the outflow was elevated several meters by a large remnant beaver dam which likely increased the wetland’s hydroperiod and extent.

## DISCUSSION

### Chick Development

Published information on whooping crane chick movements and development in a wild setting is very limited (See Urbanek and Lewis 2020). Our findings add explicit quantitative data to existing observational research. Chicks in our study appeared to leave the nest more quickly than those observed by Bergeson (undated), which were “...basically confined to the nest” during the first 24 hours after hatching. The chicks we observed departed the nest platform in just over 14 hours and just under 4 hours, respectively. However, chick 1 stayed within 1 m of the nest for the first 18 hours and 23 minutes after hatching. Additionally, chick 2 stayed within 0.5 m of the nest platform during the first 8 hours and 23 minutes after hatching while it was under active observation. Nonetheless, the distance of the eldest chick to the nest steadily increased following this initial 18-h period. Urbanek and Lewis (2020)

noted 1 chick leaving the nest with a parent just 21 hours after pipping. If pipping was detected at a similar developmental stage as in our study, this may indicate nest departure as early as ~13 hours after hatching, which closely reflects our observations.

### Parental Care of Chicks

Previous research demonstrated differential provisioning rates to whooping crane chicks based on the relative order of their hatch controlling for chick age (Bergeson et al. 2001a, Bergeson undated). We were not able to confirm this finding as our observations of the younger sibling did not extend to the age at which chicks are regularly fed by their parents (Urbanek and Lewis 2020). However, we were able to assess relative parental investment through distance measurements. To our knowledge, whooping crane parental investment in chick survival has not been previously quantified as a factor of parental proximity. However, this approach has been used for other avian species including common loons (*Gavia immer*; Jukkala and Piper 2015). Parents stayed significantly closer to the eldest chick in our study even though it was, on average, significantly further from the nest. This finding validates those in the existing literature which assert that there is increased parental investment in the older chick relative to the younger one (Bergeson et al. 2001, Bergeson undated, Boyce et al. 2005).

Walkinshaw (1973) noted close parental attendance of a Eurasian crane (syn. common crane; *Grus grus*) chick that left the nest before its sibling hatched. Nonetheless, the other Eurasian crane parent generally remained at the nest to incubate the remaining egg. We similarly observed regular nest attendance and incubation by a single parent until the second chick hatched. However, following this milestone, we regularly witnessed both parents clustered close to the eldest chick away from the nest as the younger chick was left unattended at or around the nest. It is possible that the values provided by the second chick are somewhat supplemental to the first, at least during particular developmental stages. Existing hypotheses suggest that the second egg/chick is generally an insurance policy against losing the first for crane pairs or alternatively that the second egg/chick really exists to take advantage of good environmental conditions in a subset of years where 2 offspring can be supported (Boyce et al. 2005). Differential parental behavior based on a chick's relative age has been

documented in a range of avian taxa with asynchronous hatching, with parents generally taking greater risks and investing more energy into protecting and rearing the older chick(s) (Mahr et al. 2014, Węgrzyn et al. 2023). Nonetheless, it is possible that differential parental investment varies across chick development stages. For instance, the nesting pair we observed at the Salt Plains area of WBNP was split into dyads with separate chicks, which appeared more mobile and more mature than the Nyarling River chicks we intensively observed. It is certainly possible that the difference in parental investment decreases as chicks age and is most acute right after hatch when both are ostensibly very vulnerable. Nonetheless, this assertion simply represents hypothesis generation on our part given the limited amount of data reported herein and generally available regarding whooping crane parental investment across chick developmental stages.

Published information on whooping crane provisioning behavior and rates is very sparse. The only comprehensive research comes from Olsen (2022) regarding captive birds studied in 2014 at Patuxent Wildlife Research Center in Maryland. Olsen (2022) covered the period from hatching to fledging and assessed provisioning rates in a different manner than we did but similarly found that parental feeding was initially low as chicks absorbed their remnant yolk sacks but increased steadily across the first days of life. Olsen (2022) did not document hourly variation in provisioning rates as we did, but his observations were made over a longer portion of each chick's life. Additionally, Olsen (2022) observed captive cranes that were likely influenced by different environmental drivers than wild cranes. The elder chick in our study was effectively fed at a younger age (16.5 hr after hatching) than the literature generally indicates (Urbanek and Lewis 2020). For instance, Urbanek and Lewis (2020) report a chick being fed 30 hours after hatching.

It is notable that the first chick seemed to be fed most intensively right away in the morning and that provisioning declined steadily throughout the day. Temporal variation in parental provisioning rates has been noted for other waterbirds species for various reasons (e.g., Emms and Verbeek 1991). Research suggests that foraging may be concentrated in the first half of the day for some avifauna simply because the process can cease when sufficient resources have been gleaned and continued movement may expose individuals to risks such as predation (Bonter et al.

2013). It is likely that vigilance to predation and other risks is compromised during active foraging periods (Higginson 2012). Therefore, it may benefit whooping crane families to predominantly satisfy chick caloric requirements early in the day and improve vigilance thereafter. Nonetheless, this pattern is possibly unique to the contexts of our narrow behavioral study.

It is notable that the female flew out of the nesting area after a chick had hatched. Additionally, the male appeared to have exceeded the female in provisioning efforts, though differences were not significant. This contradicts Blankinship (1976) to some degree, which suggests that the female serves a primary role in chick rearing. However, Bergeson et al. (2001a) demonstrated that this can vary across nests, with the male provisioning more than the female in 1 of 4 nests they studied. It may be that parental roles shift somewhat when 1 of the adults is going through a flightless molt.

Parental presence within the nesting area varied widely across chick developmental stages with both parents being present <20% of the time when there were 2 eggs, but >95% of the time after both chicks had hatched. Concurrent biparental care in avifauna is more common after hatching than during egg incubation as recently hatched chicks typically require more active resource investment (Stearns 1998, Wang et al. 2023). Cooperative parental care can have a range of benefits including increased food provisioning rates and improved predator vigilance (Svagej et al. 2011, Trapote et al. 2023). It is generally accepted that incubation duties are rotational for most crane species (Gruidae) and that parental care of young chicks is generally collaborative, but published data on the subject is limited, particularly regarding parental provisioning behavior (e.g., Bergeson 2001a, Zhang et al. 2017). Our results could potentially inform nesting season survey protocols as observation of a single crane within the nesting wetland may be indicative of that nest remaining unhatched, but more research is needed to confirm this pattern.

### Adult Behavior and Movement Patterns

We estimated a remarkably similar number of nest exchanges per day as Allen (1952) and Walkinshaw (1973) did from captive nesting birds at 7.6 swaps per day, which is about every 3.2 hours. This is slightly more swaps per 24-hour period than noted by Thompson and Gordon (2020) in their assessment of a

nest incubated by a same-sex pair of female whooping cranes, which averaged about 6.8 exchanges daily ( $5.7 \pm 0.2$  diurnal and  $1.1 \pm 0.2$  nocturnal exchanges daily). Similarly, flightless captive whooping cranes breeding at Aransas NWR made about 7.0 nest exchanges per day (Walkinshaw 1965). Taking the limited amount of data on this topic together, it appears that whooping cranes exchange nest attendance duties 7-8 times a day across a wide range of ecological and life-history contexts.

Incubation rates ranged from 86.5-90.6% (95% CI = 84.4-94.2%) during early developmental stages in our study including when there were 2 eggs as well as when there was 1 egg and 1 pipping chick. Our mean egg incubation rates were just slightly lower than the 92.7% reported for nesting whooping cranes by Walkinshaw (1965). Relatively high incubation rates were also reflected in Allen (1952), Walkinshaw (1973), and Urbanek and Lewis (2020). Similarly, Thompson and Gordon (2020) estimated a diurnal incubation rate of 92.1% and a nocturnal incubation rate of 97.3% for a single same-sex nesting pair. Nonetheless, McKinney documented very similar mean incubation rates to our study across whooping crane nests at Necedah National Wildlife Refuge in Wisconsin USA ( $\bar{x} = 89.3\%$ ; 95% CI = 87.2-91.3%). However, McKinney (2014) demonstrated that successful nesting whooping cranes had significantly higher incubation rates compared to unsuccessful nesting pairs ( $\bar{x} = 95.9\%$  vs. 82.7%, respectively). Interestingly, the pair we observed demonstrated an intermediate mean incubation rate relative to what McKinney (2014) associated with successful and unsuccessful pairs. Ultimately, our observations from Wood Buffalo National Park indicate that the pair we observed demonstrated relatively normal incubation rates considering our knowledge largely derived from captive and reintroduced populations. Accordingly, our post-hatch brooding rate ( $5.6 \pm 2.2\%$ ) was also extremely similar to that observed by Bergeson (~6.0%; undated).

Whooping crane adults in our study moved furthest from the nest and were least likely to incubate in the afternoon. Incubation rates were lowest around 1500 hours and generally remained <75% from 1300 to 1700 hours. Similarly, models based on our data projected that parental distance from the nest was maximized at about 5 m at 1500 hours and parents were predicted to remain >3 m from the nest on average between 1300 and 1700 hours. This finding is similar to Walkinshaw (1965) who noted that greater sandhill cranes were

often detected away from the nest in the middle of the day during warm and sunny conditions. Similarly, Zhang et al. (2017) noted a decrease in black-necked crane (*Grus nigricollis*) nest attendance and incubation bout length around midday during warmer temperatures as compared to colder ambient temperatures in the morning. Our detailed nest observations reinforce the existence of this parental behavioral pattern across crane species. Our detailed quantification of this pair's behavior will allow for easy comparison with future crane nesting research.

### Adult and Chick Diets

The adults appeared to have a diet that was about three times as diverse as what they fed chicks. Our findings were similar to Bergeson et al. (2001a) that Odonata larvae were the predominant food source for chicks and a major food source for adults. However, Bergeson et al. (2001a) did not describe the chicks eating any *Araneae* spp., which was the second most provisioned diet item in our study. Ultimately there are very few records of any cranes eating spiders (i.e., *Araneae* spp.). However, using DNA metabarcoding Kataoka et al. (2022) documented spiders in the feces of red-crowned crane (*Grus japonensis*) chicks but not adults. We noted both chicks and adults consuming spiders during our observations. It is possible that spiders represent a common component of crane chick diets on their respective breeding grounds but that observations of spider consumption go underreported considering the challenges of visually documented small diet items through behavioral observation and photography.

### Potential Predators

Allen (1952) and Walkinshaw (1973) noted that whooping cranes were "intolerant" of Ardeidae spp. around their nesting areas. However, they were generally referencing great blue herons (*Ardea herodias*) and great egrets (*Ardea alba*), which can compete with whooping cranes for some diet items and may present a direct threat to chicks (Vennesland and Butler 2020, Caven et al. 2021). Here we note defensive whooping crane behavior toward another species of Ardeidae, the American bittern. This could be related to direct resource competition as American bitterns also depend on aquatic macroinvertebrates (including

Odonata), amphibians, and small fish as major diet items (Lowther et al. 2020). However, it could also be related to perceived egg or chick predation risk as American bitterns have occasionally been known to consume smaller avifauna (Austin and Slivinski 2000).

### Molting Patterns

Whooping crane molting patterns remain somewhat poorly understood, particularly in the wild (Urbanek and Lewis 2020). A primary feather molt generally occurs every 2-3 years and leaves adult whooping cranes flightless for about 6 weeks (Urbanek and Lewis 2020). Lacy and McElwee (2016) described multiple whooping cranes in the EMP molting rather simultaneously beginning in early June. Interestingly, of the 6 birds detected molting by Lacy and McElwee (2016), 4 represented pairs in which both individuals were molting. This flightless molt can predispose whooping cranes to significant predation risk (Lacy and McElwee 2016, Urbanek and Lewis 2020). First, it is interesting that the male in our study began molting about the same time of year as the reintroduced birds in Wisconsin. Secondly, molting in our study coincided almost perfectly with chick hatching. Given that all remaining whooping cranes ultimately descended from the AWBP, from a genetic perspective, it is possible that this molt timing evolved to coincide with the period in which there were flightless chicks. Interestingly, this pattern had been observed by Canadian whooping crane biologists E. Kuyt and B. Johns, but no data were published on the matter (Urbanek and Lewis 2020). Nonetheless, in captivity the timing of molt is more variable and differs slightly by sex (Lacy and McElwee 2016).

### Avian Community

It is notable that several of the dominant avian species we detected from point counts at the site were, like the whooping crane, wetland species close to the northern edge of their [historic] breeding range (Austin et al. 2019). This includes the common yellowthroat (Guzy and Ritchison 2020), alder flycatcher (Lowther 2020), swamp sparrow (Herbert and Mowbray 2020), Wilson's snipe (Mueller 2020), sora (Melvin and Gibbs 2020), and red-winged blackbird (Yasukawa and Searcy 2020). Given WBNP's low elevation and relatively warm and humid summers (IUCN 2017), wetland

areas of the park may serve as high quality breeding habitat for a number of wetland species that are more frequently detected breeding in more temperate regions of North America. Interestingly, all the aforementioned species can also be found at important migratory stopovers throughout the whooping crane's range such as the Central Platte River Valley (Bomberger Brown and Johnsgard 2013).

## MANAGEMENT IMPLICATIONS

Our insights are largely based on observations from a single nesting site which may not be reflective of general behavioral patterns across the AWBP population. The narrow context of our study makes it hard to derive direct implications from it. Nonetheless, it provides a useful data set on which to base future hypotheses. Additionally, where our findings strongly match other small-scale natural history studies in the literature, this work can provide validation of those findings. For instance, taken together, our study and the literature strongly suggest that nesting whooping cranes make 7-8 nest switches per day across populations. Another limitation of our study is that behavioral data were not collected 24 h per day. Ultimately, we had incomplete coverage of night-time hours, which may marginally impact time budget estimates.

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**Appendix 1. Proportion of all adult Whooping Crane (*Grus americana*) behavior observed per chick developmental stage. The developmental stage with the highest value is bolded for each crane behavioral category. These estimates do not represent rates of behavior over time but present a time budget for the adults. For instance, per our data the eldest chick was provisioned about 10.4% of the time after hatching (behavioral rate). Nonetheless, each parent only spent about 6.0% of their time provisioning the oldest chick (behavioral time budget), which highlights that the parents occasionally overlapped in their efforts to provision but generally took turns doing so.**

Stage	Forage	Social	Alert	Defensive	Flying	Walk	Preen-Loaf	Incubate -Brood	Provision
2 Eggs	5.4%	2.3%	2.8%	0.2%	1.0%	1.7%	8.3%	<b>78.4%</b>	0.0%
1 Egg and 1 Pipping	1.6%	2.1%	<b>9.6%</b>	0.0%	1.1%	1.6%	7.0%	77.0%	0.0%
1 Egg and 1 Chick	25.8%	2.5%	2.9%	0.0%	0.8%	<b>2.5%</b>	5.0%	53.8%	<b>6.7%</b>
1 Pipping and 1 chick	32.6%	1.7%	1.7%	0.0%	0.0%	2.1%	12.7%	44.1%	5.1%
2 Chicks	<b>50.0%</b>	<b>5.8%</b>	6.3%	<b>1.0%</b>	<b>1.4%</b>	1.9%	<b>24.5%</b>	2.9%	6.3%
Total	14.5%	2.6%	3.6%	0.2%	0.9%	1.9%	9.8%	64.7%	1.9%

**Appendix 2. Proportion of time that 1 or 2 Whooping Crane (*Grus americana*) adults were visible in and around the nest during various chick developmental stages.**

Adults attending	2 Eggs	1 Egg and 1 pipping	1 Egg and 1 chick	1 Pipping and 1 chick	2 Chicks	N
One	81.0%	70.1%	30.8%	15.3%	3.8%	1,316
Two	19.0%	29.9%	69.2%	84.7%	96.2%	872
N	1,317	187	240	236	208	2,188

**Appendix 3. Total detections and detections per survey minute of avian species identified across six 5-minute point counts at the Nyarling River Whooping Crane (*Grus americana*) breeding site by species common name, scientific name, and alpha code. We also listed species incidentally detected shortly before or after surveys (I). Surveys were conducted between 6:30 and 20:30 from 4 to 7 June 2023.**

Common name	Scientific name	Alpha code	Total detections	Detections per minute
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE	51	1.700
Swainson's Thrush	<i>Catharus ustulatus</i>	SWTH	50	1.667
Alder Flycatcher	<i>Empidonax alnorum</i>	ALFL	36	1.200
Swamp Sparrow	<i>Melospiza georgiana</i>	SWSP	36	1.200

**Appendix 3. Continued.**

Common name	Scientific name	Alpha code	Total detections	Detections per minute
Wilson's Snipe	<i>Gallinago delicata</i>	WISN	27	0.900
Tennessee Warbler	<i>Leiothlypis peregrina</i>	TEWA	25	0.833
White-throated Sparrow	<i>Zonotrichia albicollis</i>	WTSP	14	0.467
Sora	<i>Porzana carolina</i>	SORA	12	0.400
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	11	0.367
Chipping Sparrow	<i>Spizella passerina</i>	CHSP	6	0.200
Lincoln's Sparrow	<i>Melospiza lincolnii</i>	LISP	6	0.200
Black-capped Chickadee	<i>Poecile atricapillus</i>	BCCH	5	0.167
Song Sparrow	<i>Melospiza melodia</i>	SOSP	5	0.167
American Bittern	<i>Botaurus lentiginosus</i>	AMBI	4	0.133
Canada Jay	<i>Perisoreus canadensis</i>	CAJA	3	0.100
Common Loon	<i>Gavia immer</i>	COLO	2	0.067
Common Raven	<i>Corvus corax</i>	CORA	2	0.067
Northern Shoveler	<i>Spatula clypeata</i>	NSHO	1	0.033
Orange-crowned Warbler	<i>Leiothlypis celata</i>	OCWA	1	0.033
Pied-billed Grebe	<i>Podilymbus podiceps</i>	PBGR	1	0.033
Boreal Owl	<i>Aegolius funereus</i>	BOOW	3	I
Mallard	<i>Anas platyrhynchos</i>	MALL	3	I
American Wigeon	<i>Mareca americana</i>	AMWI	2	I
Northern Flicker	<i>Colaptes auratus</i>	NOFL	2	I
Northern Harrier	<i>Circus hudsonius</i>	NOHA	2	I
Northern Pintail	<i>Anas acuta</i>	NOPI	2	I