Whooping Crane (*Grus americana*) family consumes a diversity of aquatic vertebrates during fall migration stopover at the Platte River, Nebraska

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ABSTRACT.—The Aransas-Wood Buffalo population of Whooping Cranes (*Grus americana*) migrates approximately 4000 km through the central Great Plains biannually, between their breeding and wintering grounds. Whooping Cranes depend on stopover sites to provide secure resting locations and the caloric resources necessary to complete their migration, such as the USFWS-designated critical habitat area in the Central Platte River Valley (CPRV) of Nebraska. This area includes braided river habitat characterized by low-elevation and submerged sandbars, which provide important roosting and foraging opportunities for migrating Whooping Cranes. We used long-range photography, videography, and behavioral scan sampling to document forage items consumed by Whooping Cranes during an 11-day stopover in this area during the fall of 2019. We identified 3 adult-plumage Whooping Cranes and 1 colt consuming 16 individual vertebrates of at least 6 different species during the stopover. In total, we documented Whooping Cranes consuming 7 Channel Catfish (*Ictalurus punctatus*), 5 ray-finned fish (Actinopterygii), 1 sunfish (Centrarchidae), 1 carp/minnow relative (Cypriniformes), 1 perch relative (Percidae), and 1 Leopard Frog relative (*Lithobates* sp.). We estimated prey item lengths using the average exposed culmen measurements for adult Whooping Cranes and approximated their nutritional value using log-transformed length–weight regression equations with taxon-specific intercepts and slopes from secondary data sources. We estimated that aquatic vertebrate forage made up a significant portion of Whooping Crane daily energy requirements and provided substantial amounts of calcium, phosphorus, and protein not present at high levels in waste grains also consumed during migration. Additionally, we documented territorial behavior by adult Whooping Cranes during migration and evidence of adults teaching their colt to forage. Our study demonstrates the utility of photography and videography to natural history research and indicates that aquatic vertebrates may be a relatively regular part of Whooping Crane diet in the CPRV.

RESUMEN.—La población de grullas trompeteras (*Grus americana*) de Aransas-Wood Buffalo migra aproximadamente 4000 km dos veces al año a través de las Grandes Llanuras (Great Plains) centrales, entre sus sitios de reproducción y sus sitios de invernada. Las grullas trompeteras dependen de los sitios donde hacen escalas para obtener lugares de descanso y adquirir los recursos calóricos necesarios para completar su migración, tales como, el área de hábitat crítico designada por USFWS en Central Platte River Valley (CPRV) de Nebraska. Esta área cuenta con un hábitat fluvial trenzado caracterizado por bancos de arena sumergidos de baja elevación que constituyen importantes zonas de descanso y alimentación para las grullas trompeteras migratorias. En el otoño de 2019, durante una escala de 11 días, registramos los alimentos consumidos en el área por las grullas trompeteras, utilizando fotografías y videos de largo alcance y análisis conductuales. Identificamos tres grullas trompeteras adultas y una joven consumiendo 16 vertebrados de al menos seis especies diferentes. En total, registramos grullas trompeteras consumiendo siete peces gato americanos (*Ictalurus punctatus*), cinco peces con aletas radiadas (Actinopterygii), un pez luna (Centrarchidae), un pariente del pez carpa/piscardo (Cypriniformes), un pariente de la perca (Percidae) y un pariente de la rana leopardo (*Lithobates* sp.). Calculamos la longitud de las presas usando el promedio del tamaño de culmen de las grullas trompeteras adultas, y estimamos el valor nutricional con ecuaciones de regresión de talla-peso transformadas logarítmicamente con intersecciones y pendientes de taxones específicos provenientes de una fuente de datos secundarios. Estimamos que el consumo de vertebrados acuáticos proporciona una parte significativa de las necesidades energéticas diarias de la grulla trompetera, y grandes cantidades de calcio, fósforo y proteínas que no están presentes en altos niveles, en los granos de desecho, que también se consumen durante la migración. Además, documentamos el comportamiento territorial de las

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grullas trompeteras adultas durante la migración, así como la evidencia de adultos enseñando a sus crías a alimentarse. Nuestro estudio demuestra la utilidad de la fotografía y videografía en la investigación de la historia natural e indica que los vertebrados acuáticos pueden ser parte de la dieta regular de la grulla trompetera en el CPRV.

The Aransas-Wood Buffalo population of Whooping Cranes (AWBP; *Grus americana*) migrates through the central Great Plains biannually, traveling approximately 4000 km between their breeding grounds in and surrounding Wood Buffalo National Park in Canada and their wintering grounds in and surrounding Aransas National Wildlife Refuge along the Gulf Coast of Texas, USA (Allen 1952, Kuyt 1992, Pearse et al. 2018). This migration corridor averages about 300 km in width and traverses the Central Platte River Valley (CPRV) in Nebraska, which the U.S. Fish and Wildlife Service (USFWS) designated as one of 5 critical habitat areas in the Central Flyway for the AWBP (others include Cheyenne Bottoms State Wildlife Management Area [WMA], KS; Quivira National Wildlife Refuge [NWR], KS; Salt Plains NWR, OK; and Aransas NWR, TX) (USFWS 1978, Pearse et al. 2018). The CPRV provides secure roosting and foraging habitat for Whooping Cranes as well as caloric resources critical for survival, migration, and ultimately subsequent biological processes (Myers 1983, Moore et al. 1995, Farmer and Parent 1997, Haig et al. 1998, Farmer et al. 2005, Webb et al. 2010, Carey 2012, Baasch et al. 2019a). The AWBP numbered <20 individuals in the early 1940s but has since rebounded to about 500 individuals as a result of wetland habitat conservation and other efforts throughout their range. However, continued protection and management of stopover resources is necessary to sustain population recovery (Aronson and Ellis 1979, Meine and Archibald 1996, Austin and Richert 2001, 2005, CWS and USFWS 2007, Harrell and Bidwell 2020, Caven et al. 2020). Whooping Cranes have been reported to eat agricultural waste grains, native plants and their tubers, invertebrates, and vertebrates, including fish, frogs, snakes, salamanders, and small mammals (Allen 1952, USFWS 1978, 1981, Kauffeld 1982, Howe 1987, Kuyt 1987, Austin and Richert 2005, Geluso et al. 2013, Caven et al. 2019a). However, the vast majority of Whooping Crane diet knowledge was obtained from the wintering or breeding grounds. Knowledge has mostly been gathered visually at long distances where morphometric and species-specific information was challenging to ascertain, and a substantial portion of that knowledge represents conjecture based on the availability of potential prey items in certain habitats (Chavez-Ramirez 1996, Bergeson 1998, Bergeson et al. 2001, Austin and Richert 2001, Classen 2008, Caven et al. 2019a). While detailed information about variation in and breadth of Whooping Crane diet during migration is limited, even less is known about the rate at which various food items are consumed and their ultimate nutritional value during migration.

Given the scarcity of information that exists regarding the specific forage items Whooping Cranes consume during migration, the frequency at which these items are consumed, and their nutritional importance, we report morphometric details and nutritional value estimates from aquatic vertebrates consumed by Whooping Cranes during a fall stopover of extended duration (11 days) using data derived from high-resolution, long-range photographs. We also extrapolate behavioral time budget data collected from scan sampling efforts to estimate the nutritional value of aquatic vertebrates consumed during this stopover. Finally, we examine the hydrological contexts in which this long-duration stopover occurred.

METHODS

Study Area

The central Platte River in Nebraska is an over-appropriated river basin that currently struggles to maintain its braided, open planform with natural flow (Smith 1971, Simons and Associates, Inc. 2000, Caven et al. 2019b). During the 1800s, the main channel of the central Platte River exceeded 1.6 km in width and was surrounded by lowland grasslands, but it subsequently has become much narrower without management intervention (−60% to −90%; Williams 1978, Currier 1982, Johnson 1994, Caven et al. 2019b, Simons and Associates, Inc. 2000). The CPRV has also become more wooded, and many lowland grasslands have been developed into agricultural crop fields over the past century (Williams 1978, Currier 1982, Johnson 1994). The Crane Trust,

located south of Alda, Nebraska, USA, manages over 25 km of river channel (including side channels) to maintain an open, shallow, braided planform for many migratory species, including Whooping Cranes. Observations reported here were collected within this stretch of the CPRV (40.780489°, −98.469832°; 584 m elevation), where main channel widths have been maintained by the Crane Trust to be >300 m wide.

Data and Analyses

We observed a Whooping Crane group of 4 individuals during a fall stopover on the Platte River from 31 October to 10 November, 2019. The group was composed of a family unit including 2 adults and a juvenile that was joined by an additional adult-plumage bird. Both parents and the juvenile were banded, while the other adult-plumage bird was not. We recorded all diurnal behavioral observations from a riverine location, but the family group was also documented foraging in a cornfield and wet meadow within 2 km of the river. We used an "instantaneous scan sampling" approach, which included counting the number of Whooping Cranes displaying a particular behavior at 1-min intervals (Altmann 1974). Behavioral categories included foraging, social (conspecific), social (interspecific), alert/defensive, flying/walking, loafing, and preening. However, for the purposes of this study, we examined only the proportion of time spent foraging, including movement foraging, relative to other behaviors. Therefore, foraging included walking, scanning, and occasionally pecking at the ground as well as time spent continuously foraging or drinking (Cronin et al. 2005, 2007). Observations were made during 7 days of the estimated 11-day stopover using an 80-mm spotting scope (20–60×; STS 80, Swarovski Optik, Wattens, Austria), binoculars (Vortex Diamondback 10 × 50, Vortex Optics, Barneveld, WI, USA), and a digital camera (Nikon DSLR, Nikon Inc., Tokyo, Japan) with a long-range zoom lens (Tamron SP 150–600 mm, Tamron Co., Ltd., Saitama, Japan). We focused on using our camera equipment when Whooping Cranes appeared to be consuming visually discernable food items. To ensure that we did not disturb Whooping Cranes, all photographs and videos were taken under natural light conditions (i.e., no flash photography). Following the U.S. Fish and Wildlife Service and

Nebraska Game and Parks Commission guidelines (USFWS and NGPC 2015), observations were made at distances >610 m (~0.4 mi, 2000 ft.) unless Whooping Cranes approached a biologist observing from within a concealed blind.

Following survey efforts, 2 biologists independently evaluated photographs and videos of discernable food items consumed by the Whooping Cranes and identified vertebrate species to the lowest taxonomic level possible based on identifiable characteristics and knowledge of available biological communities (Chadwick et al. 1997, Ballinger et al. 2010). We used the following morphological features for fish: fin placement (dorsal, adipose, caudal, pectoral, and anal), body depth-to-length ratio, and apparent presence or absence of scales (if discernable; Page and Burr 2011). We identified anurans using morphological features described in Ballinger et al. (2010). We estimated the length of each aquatic vertebrate by comparing it to the average upper bill length (exposed culmen) for an adult Whooping Crane (i.e., 138 mm; Johnsgard 1983, Caven et al. 2019a). For instance, a fish that appeared to be 120% of the length of a Whooping Crane culmen from relative on-screen measurements would be an estimated 166 mm total length (138 mm*1.2; Caven et al. 2019a). Similarly, we estimated water depth at foraging locations based on the degree to which the Whooping Crane tarsus was submerged ($\bar{x}$ tarsal length = 28 cm; Johnsgard 1983, Caven et al. 2019a). When there were multiple pictures of a foraging event, we used the photographs that provided the clearest view of the diet item consumed and relevant Whooping Crane physical attributes (bill or legs) to make body length and water depth determinations, respectively. We estimated the weight of vertebrates using log-transformed regression equations based on length (total length for ray-finned fish and snout–vent length for anurans) and taxon-specific slopes and intercepts from multiple data sources (Holland and Peters 1992, Schneider et al. 2000, Deichmann et al. 2008):

$$\text{Log}_{10}(\text{Weight}_g) = Y\text{-intercept}(a) + \text{Slope}(\beta)*\text{Log}_{10}(\text{Length}_{mm}).$$

We used species-specific length–weight regression slopes and intercepts, when available,

to estimate the live weight of fish consumed (e.g., Channel Catfish [*Ictalurus punctatus*]; median values, Holland and Peters 1992). When diet items were identified to a higher taxon (e.g., order), we used parameter estimates from regionally common representatives (e.g., Bluegill [*Lepomis macrochirus*] to represent Centrarchidae; Schneider et al. 2000) or closely related taxa (Southern Leopard Frog [*Lithobates sphenocephalus*] to represent *Lithobates* sp.; Deichmann et al. 2008). For diet items simply classified as "ray-finned fish," which is a taxonomic class that encompasses all other fish detected during this study, we used values associated with Channel Catfish because that was the species we most frequently observed being consumed.

We assessed the energetic value of vertebrate diet items using taxon-relevant estimates of calories per kilojoule per gram of wet weight provided by Turner (2017) for ray-finned fish (e.g., River Carpsucker [*Carpiodes carpio*] to represent Cypriniformes) and Fargallo et al. (2020) to represent anurans (e.g., Perez's frog [*Pelophylax perezi*] for *Lithobates* sp.). Finally, we estimated the protein and nutrient content of prey items using mean values from species of small fish assessed by Hossain et al. (1999; $\bar{x}$ protein = 14.8% fresh matter; $\bar{x}$ calcium = 1.9% and $\bar{x}$ phosphorus = 2.25% dry matter). We approximated the dry weight of fish consumed in our study to facilitate nutrient (e.g., calcium) value estimation using the mean moisture content of fish assessed by Hossain et al. (1999). Finally, we examined how the consumed fish related to the dietary needs of Whooping Cranes using data and equations from Ellis et al. (1996; $K = 78$) and median weight estimates from Urbanek and Lewis (2020; ~7.5 kg). Our estimates of daily energy requirements may be higher than other energetic models that use lower median weight estimates (e.g., 7.2 kg); we chose 7.5 kg because wild Whooping Cranes tend to be larger than their captive-reared counterparts (Pearse and Selbo 2012, Urbanek and Lewis 2020):

$$\text{Daily Energy Requirement}_{\text{Kcal/d}} = 1.5 * \text{BMR}$$

and

$$\text{BMR} = K_{\text{Kcal constant}} (\text{Weight}_{\text{kg}})^{0.75},$$

where BMR is basic metabolic rate.

Finally, we evaluated the hydrological contexts of these foraging events by summarizing river discharge values during the 11-day stopover, in the years leading up to it, and throughout the period of record (1934–2019) using data from the nearest U.S. Geological Survey gage station (No. 06770500; 19 km downstream from our study site; USGS 2021).

RESULTS

We identified Whooping Cranes consuming 16 individual aquatic vertebrates during 347 min of observation time at the main channel of the Platte River between the dates of 31 October and 7 November 2019, with observations ranging from 14 to 98 min daily ($\bar{x} = 49.6$ min, SD = 31.4 min). No observations were made from 8 to 10 November 2019. Scan sampling data indicated that an average of 59.9% of diurnal observation time was spent foraging (SD = 12.4%, range 37.8% to 76.4% of time per day). In total, we estimate that the Whooping Cranes we observed foraged for 199.6 min during our observation periods, collectively consuming one discernable aquatic vertebrate for every 12.5 min of foraging time. This would equate to approximately 4.8 fish per hour of observation time considering the group as a whole, or 1.2 to 1.6 fish/h for each individual Whooping Crane, depending on the number actively foraging (i.e., the adult from outside of the family group was regularly observed foraging alone on macroinvertebrates during the study). The number of minutes foraging per aquatic vertebrate consumption event ranged from every 3.0 min on 7 November to >43.5 min with no recorded consumption event during observations on 4 November 2019.

In total, we documented Whooping Cranes consuming 7 Channel Catfish (*Ictalurus punctatus*; Fig. 1), 5 ray-finned fish (Actinopterygii), 1 sunfish (Centrarchidae; Fig. 2), 1 carp/minnow relative (Cypriniformes), 1 perch relative (Percidae), and 1 Leopard Frog relative (*Lithobates* sp.; Fig. 3, Table 1). In addition, we regularly observed Whooping Cranes foraging on diet items that were too small to positively identify, such as macroinvertebrates. We were able to identify 5 smaller diet items to the phylum Arthropoda during the 31 October to 7 November 2019 study period, but based on the frequency we observed Whooping Cranes

Fig. 1. Three Whooping Cranes (WHCR) foraging in the Platte River on 7 November 2019. A banded adult (green/white—left leg) captured a Channel Catfish (*Ictalurus punctatus*) estimated to be 159 mm total length (based on average WHCR culmen length) in approximately 9 cm of water (based on average WHCR tarsus length). Photo credit: J. Malzahn.

Fig. 2. Two Whooping Cranes (WHCR; 1 adult and 1 juvenile) foraging near the edge of a sandbar in the main channel of the Platte River. The juvenile captured a sunfish (Centrarchidae) estimated at 83 mm total length (based on average WHCR culmen length) in about 7 cm of water (based on average WHCR tarsus length) after it was initially stabbed by a banded adult Whooping Crane (not pictured). Photo credit J. Malzahn.

probing sandbars and entering the water, our estimate of aquatic animal prey consumed is very conservative.

Fish ranged from 83 to 179 mm in total length ($\overline{x}$ = 142.1 mm, SD = 23.4 mm), and the lone anuran observed had a 69-mm snout–vent length. The estimated weights for detected diet items ranged from 8.8 to 65.3 g based on log-transformed regression equations ($\overline{x}$ = 23.7 g, SD = 13.2 g). Vertebrates ranged in estimated energetic value from 9.0 to 96.1 Kcal ($\overline{x}$ = 27.1 Kcal, SD = 20.4 Kcal) and included an estimated 1.3–9.6 g of protein ($\overline{x}$ = 3.5 g, SD = 1.9 g), 46.4–344.4 mg of phosphorus ($\overline{x}$ = 124.8, SD = 69.6 mg), and 38.9–288.7 mg of calcium ($\overline{x}$ = 104.6 mg, SD = 58.4 mg). In total, the documented vertebrate prey items provided an estimated 406.8 Kcals of energy, 52.4 g protein, 1872 mg phosphorus, and 1569 mg calcium to the Whooping Crane group. We estimated that a 7.5 kg Whooping Crane would require

Fig. 3. Four Whooping Cranes (WHCR) foraging on the Platte River on 31 October 2019. A banded adult (green/white—left leg) captured a *Lithobates* sp. estimated to be about 69.0 mm snout–vent length (based on average WHCR culmen length) in roughly 17 cm of water (based on average WHCR tarsus length). Photo credit: M. Forsberg.

530.1 Kcals per day for physical maintenance during migration.

We also recorded some noteworthy behavioral observations during this study. First, when they were capturing aquatic vertebrates, the Whooping Crane parents regularly defended their riverine foraging area against the additional adult-plumaged Whooping Crane through agonistic behavioral displays that we interpreted as territoriality (e.g., "pre-attack," per Ellis et al. 1998). Secondly, on 4 total occasions, the Whooping Crane parents assisted their colt in capturing a fish by first injuring it and then leaving the fish moving on the edge of a sandbar for the colt to claim.

Vertebrates were captured in water depths ranging from 3 cm to 18 cm ($\bar{x}$ = 9.1 cm, SD = 5.4 cm), and, from 31 October to 10 November 2019, discharge averaged 2541 ± 32 cfs ($\bar{x}$ ± SE; 72 ± 1 cms; cfs = cubic feet per second [ft^3/s] and cms = cubic meters per second [m^3/s]). Flows at Grand Island Nebraska had not dropped to 0 cfs (0 cms) in 6 years at the time these foraging observations were recorded, and flows had only dropped to 0 cfs (0 cms) during 2 (2012 and 2013) of the last 13 years. This deviates from the historic record in which flows dropped to 0 cfs (0 cms) in 39.1% of years from 1934 to 2019, which equates to the river going dry every 2.6 years. Similarly, mean summer flows (June–August) were 2824 ± 791 cfs (80 ± 22 cms) during the last 6 years

(2014–2019) and 1414 ± 191 cfs (40 ± 5 cms) for the period of record (1934–2019).

DISCUSSION

While the CPRV has been the target of considerable research during the past 4 decades, little is known about Whooping Crane diet in riverine habitats at this stopover location or elsewhere within the migration corridor (Lingle et al. 1991, Austin and Richert 2001, Urbanek and Lewis 2020). Caven et al. (2019a) recently provided the first published record of a Whooping Crane consuming fish in the Platte River. These observations also represented the first published record of Whooping Cranes consuming Channel Catfish during migration in the Great Plains (Caven et al. 2019a). A limited number of records exist that describe Whooping Cranes consuming aquatic vertebrates during migration, but these records provide little taxonomic or morphometric information regarding the prey items (Allen 1952, USFWS 1978, 1981, Kuyt 1987, Austin and Richert 2001). One exception is Geluso et al. (2013), which documented multiple Whooping Cranes consuming Plains Leopard Frogs (*Lithobates blairi*) in shallow palustrine wetlands in the Rainwater Basin region of Nebraska. We documented Whooping Cranes consuming at least 6 different taxa of fish and 1 anuran at the Platte River in the

TABLE 1. Aquatic vertebrates consumed by a Whooping Crane group comprised of 3 adult-plumage birds and 1 juvenile on the main channel of the Platte River from 31 October to 7 November 2019 during diurnal observations, including species (lowest taxa with ≥90% certainty of identification) and estimated length in millimeters, weight in grams, energetic value in Kcal, protein in grams, phosphorus (P) in milligrams, and calcium (Ca) in milligrams, as well as the date of consumption event, Whooping Crane age class, and estimated water depth in which the forage items were consumed.

Date	WHCR age	Taxon of aquatic vertebrate prey consumed	Water depth (cm)	Length (mm)	Weight (g)	Kcal	Protein (g)	P (mg)	Ca (mg)
31 Oct 2019	Adult	Actinopterygii	6	152	23.6	24.2	3.5	124.5	104.3
31 Oct 2019	Adult, juvenile	Ictalurus punctatus	4	146	20.9	21.4	3.1	110.2	92.4
31 Oct 2019	Adult	Lithobates sp.	17	69	26.1	26.8	3.9	137.7	115.4
31 Oct 2019	Adult	Actinopterygii	4	110	8.8	9	1.3	46.4	38.9
31 Oct 2019	Adult	Ictalurus punctatus	3	125	13	13.3	1.9	68.6	57.5
31 Oct 2019	Adult	Ictalurus punctatus	4	138	17.6	18	2.6	92.8	77.8
31 Oct 2019	Juvenile	Ictalurus punctatus	3	152	23.6	24.2	3.5	124.5	104.3
1 Nov 2019	Adult	Actinopterygii	18	155	25.1	25.7	3.7	132.4	111.0
1 Nov 2019	Adult, juvenile	Actinopterygii	11	—	—	—	—	—	—
2 Nov 2019	Adult	Actinopterygii	—	140	18.4	18.8	2.7	97.0	81.3
5 Nov 2019	Adult, juvenile	Centrarchidae	7	83	9.7	16	1.4	51.2	42.9
7 Nov 2019	Adult, juvenile	Ictalurus punctatus	14	152	23.6	24.2	3.5	124.5	104.3
7 Nov 2019	Juvenile	Ictalurus punctatus	11	144	20	20.5	3.0	105.5	88.4
7 Nov 2019	Adult	Ictalurus punctatus	9	159	27.1	27.8	4.0	142.9	119.8
7 Nov 2019	Adult	Cypriniformes	17	179	65.3	96.1	9.6	344.4	288.7
7 Nov 2019	Adult	Percidae	9	155	32.2	40.6	4.8	169.8	142.3
$\bar{x}$			9.1	137.3	23.7	27.1	3.5	124.8	104.6
SD			5.4	29.4	13.2	20.4	1.9	69.6	58.4

fall of 2019. To our knowledge, this represents the first published record of a Whooping Crane consuming an anuran at the Platte River. We identified this prey item to genus (*Lithobates* sp.) but were unable to determine the species with certainty. However, the observation likely provides support for Geluso et al. (2013), which suggested that Leopard Frogs (*Lithobates* spp.) may be relatively common prey items for Whooping Cranes during migration, given their wide distribution throughout the Great Plains.

We documented Whooping Cranes consuming a diversity of fish taxa, including species of Centrarchidae, Cypriniformes, and Percidae, but *Ictalurus punctatus* (Channel Catfish) was the most commonly consumed species per our observations. This may be because Whooping Cranes are specifically selecting for Channel Catfish because they are a preferred diet item or because they are commonly slowed by disease in the spring and fall (enteric septicemia), which can make them more attainable (Brugger 1993, Stickley et al. 1995, Glahn et al. 1999, 2000). However, it could also be the case that *I. punctatus* is more detectable by our methods, since it has pectoral spines that serve as an antipredator defense, which may increase the handling time for Whooping Cranes (Duvall 2007). Regardless, these observations in combination with Caven et al. (2019a), which documented an individual consuming ≥5 Channel Catfish during the 2018 spring migration, suggest that this species may occasionally be a relatively regular component of the Whooping Crane diet at the Platte River.

As Urbanek and Lewis (2020) note, Whooping Cranes tend to forage on "small aquatic animals," but measurements are relatively scarce in the literature. Whooping Cranes in this study consumed fish ranging from 83 to 179 mm total length. Great Blue Herons (*Ardea herodias*) tend to select for a similar size range of Channel Catfish (110–160 mm) despite their generally smaller stature than Whooping Cranes (Stickley et al. 1995, Glahn et al. 1999). It is possible that this size category of Channel Catfish, or fish generally, is relatively easy to handle and processes for medium- to large-sized wading birds. Our results indicate a broader diet of aquatic animals than previously described for Whooping Cranes that use the Platte River and other

rivers in the Great Plains during migration (Austin and Richert 2001, National Research Council 2004, Urbanek and Lewis 2020). Though records of aquatic vertebrate consumption during migration are rare, they have been consistently detected on the breeding and wintering grounds and in reintroduced populations relying heavily on wetland habitats (Chavez-Ramirez 1996, Bergeson 1998, Bergeson et al. 2001, Geluso and Harner 2013, Zimorski et al. 2013, Van Schmidt et al. 2014, Dinets 2016, Barzen et al. 2018, Urbanek and Lewis 2020). For instance, research indicates that Whooping Cranes consistently consume small fish such as Brook Stickleback (*Culaea inconstans*) at their breeding grounds near Wood Buffalo National Park, and they even select ponds that contain fish as nesting sites over ponds that do not contain fish (Bergeson et al. 2001, Sotiropoulos 2002, Classen 2008). It is possible that Whooping Cranes will select fish and other aquatic vertebrates over other diet items when these prey are readily abundant (Allen 1952). However, availability is partially dependent on the health of the riverine ecosystem and its fishery (Goldowitz 1996, Marchetti and Moyle 2001, Perkin et al. 2015).

The Platte River has regularly experienced fish kill events during times of low flows (Goldowitz 1996, Sutton 2005, Perkin et al. 2015). Though these events are particularly pronounced and widespread when the Platte River runs dry, they can occur simply as a result of extreme conditions associated with low flows (high temperatures, low dissolved oxygen, etc.; Dinan 1992, Goldowitz 1996, Sutton 2005, Perkin et al. 2015). For instance, many Platte River fish species lose their righting response (i.e., ability to maintain vertical orientation) at temperatures >30 °C and begin to experience premortality muscular spasms at temperatures >33.5 °C (Chadwick et al. 1997, Lutterschmidt and Hutchison 1997, Sutton 2005). Sutton (2005) evaluated the probability of reaching critical water temperatures based on variation in Platte River discharge and found that, while there was only an 11% chance of exceeding 33.5 °C at flows between 1100 and 1499 cfs (31–42 cms), there was a 23% chance of doing so at flows between 500 and 699 cfs (14–20 cms). Though the Platte River has regularly gone dry since the 1930s (every 2.6 years from 1934–2019), it had not

gone dry in an extended period (6 years) at the time of our Whooping Crane foraging observations. Furthermore, mean flows during the summer months in the 6 years previous to our observations ($\bar{x} \pm$ SE = 2824 ± 791 cfs, 80 ± 22 cms) were above the long-term average ($\bar{x} \pm$ SE = 1414 ± 191 cfs, 40 ± 5 cms). As higher summer flows are generally associated with increased fish abundance and diversity, it is possible that the Platte River fishery was in above-average condition and therefore providing more fish foraging opportunities to Whooping Cranes than is typical (Dinan 1992, Goldowitz 1996, Marchetti and Moyle 2001, Sutton 2005, Falke et al. 2011, Kiernan et al. 2012, Perkin et al. 2015).

It is also notable that flows were above average and highly stable during this fall stopover period ($\bar{x} \pm$ SE = 2541 ± 32 cfs, 72 ± 1 cms) and that Whooping Cranes were able to consistently forage on aquatic vertebrates in relatively shallow water despite these above-average flows ($\bar{x} \pm$ SD = 9.1 ± 5.4 cm; range 3–18 cm). As found by Caven et al. (2019a), Whooping Cranes foraged for fish at depths similar to those used by a diversity of wading birds (5–25 cm; Willard 1977). Despite the Whooping Crane's larger stature compared to other North American wading birds (e.g., Great Egret [*Ardea alba*]), the Whooping Cranes did not appear to forage for fish in significantly deeper environments within the Platte River. It is possible that Whooping Cranes benefit from increased foraging success in shallow waters, as has been suggested for a host of other wading birds (Lantz et al. 2011, Beerens et al. 2015). Interestingly, the average exposed culmen lengths of Great Blue Herons (139 mm; Bayer 1985) and Great Egrets (121 mm; Bayer 1985) are similar to those of Whooping Cranes (138 mm; Johnsgard 1983), and it is possible this has an influence on optimal foraging depths (Norazlimi and Ramli 2015).

There remains some uncertainty regarding the Platte River flows that best provide Whooping Crane habitat during migration, and most recommendations are based on maximizing the extent of ideal roosting depths (Currier and Eisel 1984, Faanes and Bowman 1992, Kinzel et al. 2006, Baasch et al. 2019b). Using Sandhill Cranes as surrogates, Kinzel et al. (2006) and Baasch et al. (2019b) found that available roosting habitat in the CPRV was maximized at river discharges between 1200 cfs (34 cms) and 1400 cfs (40 cms) in relatively wide channels (250–275 m). However, Faanes and Bowman (1992) found that flows averaged 2683 cfs (76 cms; range 838–5150 cfs) on the Platte River during Whooping Crane stopovers over a period of 75 years (1912–1987). Our observations demonstrated that Whooping Cranes consistently succeeded in foraging for fish at flows just over 2500 cfs (71 cms) in a reach with relatively wide channels (>300 m). It may be worth considering factors aside from roosting habitat availability when determining ideal flow conditions for Whooping Cranes.

The nutritional value of diet items governs the amount of food Whooping Cranes need to consume, while ingestion rates regulate the amount of energy a crane can take in over a set period of time; therefore, the quality and availability of food resources influence behavior, habitat use, and ultimately survival and reproductive success (McAtee 1912, Lack 1968). Cranes have been reported to consume about 4% of their body weight on a daily basis, achieving an estimated ingestion rate of 0.7 g/min when food is readily available (Mayer et al. 1979, Ellis et al. 1996, Swengel and Carpenter 1996, Pearse and Selbo 2012). The amount of processable energy in Whooping Crane diet items varies, but the metabolizable energy coefficient of fish and other wetland vertebrates tends to be relatively high (Bennett and Hart 1993, Brugger 1993, Nelson et al. 1996, Pearse and Selbo 2012). To meet the daily energy needs of a 7.5-kg Whooping Crane (est. 530.1 Kcal) on aquatic vertebrates alone, it would take about 19.5 vertebrates or 462.8 g of total biomass considering average-sized prey items from our study (Table 1). However, one larger fish can make up a disproportionate percent of a crane's daily caloric needs. For instance, the largest fish consumed in our study was a species of Cypriniformes that was estimated at 179 mm length, 65.3 g, and 96.1 kilocalories, and a Whooping Crane would only need to eat 5.5 similarly sized aquatic vertebrates to meet its daily energetic requirements (about 359.2 g total biomass).

We observed Whooping Cranes foraging during 59.9% of diurnal observations. This was similar to the time budgets observed by Jorgensen and Dinan (2016) for 6 Whooping Cranes (including 1 family group) studied at Father Hupp WMA in Nebraska during a fall

stopover from 14 November to 1 December 2015. These cranes spent 54.6% of their time foraging, predominantly in wetland habitats. Assuming that individual cranes consume ≥1.6 fish per hour of foraging time (Pearse and Selbo 2012), that there were about 10 h and 15 min of daylight each day during this stopover period, and that Whooping Cranes spent 60% of their diurnal hours foraging, we would expect cranes to consume about 9.8 fish daily, which would equate to about 266.9 Kcal, 34.4 g protein, 1228 mg phosphorus, and 1025 mg calcium consumed based on the average-sized fish eaten in our study.

It is important to note that our estimates regarding the nutritional value of this stopover are based only on the aquatic vertebrate food items we identified being consumed within the Platte River. Our estimates exclude macro-invertebrates we observed being consumed as well as those we could not visually distinguish (e.g., smaller macroinvertebrates derived from probing sandbars) in addition to any plant matter consumed at riverine locations. Furthermore, our assessment of this fall stopover did not include the nutritive value of waste grains, native plants, and macroinvertebrates derived from croplands and wet meadows where the Whooping Cranes were also observed foraging during our study. We noted that some of the smallest fish eaten (e.g., 110-mm *Actinopterygii*; Table 1) appeared to be consumed the quickest and that Channel Catfish, potentially as a result of their pectoral spines (Duvall 2007), and larger fish generally required longer handling times and therefore may have been easier to visually detect and photograph. Consequently, it is possible that we did not detect the consumption of some smaller fish that could be eaten more quickly. Therefore, we likely underestimated the nutritional values of this fall stopover event.

In addition to meeting a significant portion of their daily energy requirements from wetland vertebrates, individual Whooping Cranes consumed an estimated 1.0 g of calcium, 1.2 g of phosphorus, and 34 g of protein per day from such diet items during their fall stopover (based on extrapolations of our data). Calcium, phosphorus, and protein are essential to a large number of biotic processes, including egg and eggshell formation, bone maintenance and healing, nerve and muscle function/recovery, feather growth, blood clot formation, and metabolic processes (Houston 1997, de Matos 2008, Weber 2009, Muñoz-Garcia et al. 2012, Baggio and Pita 2013). For example, Greater Sandhill Crane (*Grus canadensis tabida*) chicks were fed 5 different diets in an experimental setting to evaluate the effects of protein, metabolizable energy, and sulfur amino acid content on growth and development (Serafin 1982). Serafin (1982) reported observing faster growth rates for Greater Sandhill Crane chicks that were fed a diet higher in protein and sulfur amino acids. Calcium is similarly important to bone growth and maintenance, and calcium requirements for young birds have been reported to be 0.5%–1.3% of the dry weight of their diet (Robbins 1983). The vertebrates consumed during this fall migration stopover event were likely more than sufficient to supply the daily dietary calcium and phosphorous requirements for Whooping Cranes. However, the estimated Ca:P ratio (0.84:1) was slightly below the 1:1–2:1 ratio deemed ideal for many birds (Robbins 1983, Skipper et al. 2020). For comparison, Reinecke and Krapu (1986) stated a that a Sandhill Crane would have to consume nearly 1500 g of corn per day to meet its daily calcium requirements, which would require an unrealistic effort given the 143 g of corn typically consumed during a 3-hour foraging period.

Invertebrates found in agricultural fields can provide some supplemental protein and calcium; however, due to changing agricultural practices (i.e., increasing chemical applications), cornfields generally provide fewer invertebrates than they did historically (Reinecke and Krapu 1986, Marshall et al. 2003, Pisa et al. 2015). Interestingly, Reinecke and Krapu (1986) documented nutrient limitations in Sandhill Cranes that foraged heavily in cornfields, because they deposited fat but not protein. While waste grain (e.g., corn, wheat, etc.) can often meet the daily carbohydrate and energy requirements of Whooping Cranes, animal matter (i.e., vertebrates and macro-invertebrates) found in wetlands, grasslands, and hayfields provides essential nutrients to compensate for the deficiencies of waste grain (National Research Council 1977, USFWS 1981, Reinecke and Krapu 1986, de Matos 2008, Weber 2009, Muñoz-Garcia et al. 2012, Baggio and Pita 2013). Caven et al. (in press) suggest that stopover stay length is positively associated with the availability of preferred

foraging habitats. The average stopover is about 2.5 days, and the majority are <1 day, but the stopover described here was at least 11 days (Pearse et al. 2020). It is possible that the extended stay length of this stopover reflected the high quality of the resources present.

Whooping Cranes are generally not territorial during migration and are often gregarious, gathering at times in flocks containing multiple family groups; however, they do display territoriality on the breeding grounds and often on the wintering grounds (Erickson and Derrickson 1981, Caven et al. 2020, Urbanek and Lewis 2020). It is noteworthy that we witnessed adults from the observed family group exhibiting threat displays toward the individual adult-plumaged Whooping Crane regularly flocking with them during this migratory stopover. However, from our observations, the territoriality seemed to be context dependent. The family group behaved aggressively and defended their riverine foraging area when they were successfully capturing wetland vertebrates, but they did not seem to regularly exhibit this behavior when probing sandbars for macroinvertebrates. Interestingly, on the wintering grounds, Whooping Cranes display territoriality within wetland habitats but are more gregarious in upland foraging sites (Chavez-Ramirez 1996, Thompson 2018). Research indicates that territorial behavior in birds can largely depend on the nature and distribution of food resources and parental status (Davies and Houston 1984, Pulliam and Caraco 1984, Carpenter 1987, Powers 1987, Alonso et al. 2004). For instance, avifauna may be more likely to defend higher-quality food resources (Powers 1987). Carpenter (1987) suggests that resource defense generally does not occur when resources are highly abundant or when they are highly limited, because under both those conditions, the resources are typically not worth defending. Additionally, birds are more likely to display territoriality when food resources are evenly distributed, consistently available, and present in concentrations exceeding those in most other local habitats, as opposed to when food resources are unpredictably distributed and ephemeral (Davies and Houston 1984, Pulliam and Caraco 1984, Carpenter 1987). Finally, territorial behavior is often more regularly observed when parents are actively rearing offspring (Alonso et al. 2004). Our observations suggest that Whooping Crane families may occasionally exhibit territorial or resource defense behavior during fall migration, when they have a relatively young colt, and when they are in the presence of high-value forage resources (e.g., aquatic vertebrates) that are defensible.

We also documented adult Whooping Cranes assisting their colts with fish capture on 4 occasions by first injuring, but not killing, the prey item before placing it near their colt for them to secure, kill, and consume. We interpreted this behavior as the Whooping Crane pair "teaching" their colt to capture fish, which, to our knowledge, has not been previously documented during fall migration. Whooping Crane colts stay with their parents for nearly a year—through fall migration, during the winter months, and generally through the spring migration—and have been recorded begging their parents for food at >6 months of age (Urbanek and Lewis 2020). Extended post-fledging care has been observed in several species of birds, predominantly in predatory, long-lived species with low reproductive rates, that need to "learn" to become efficient foragers before they can successfully persist independently (Burger 1980, Watson and Hatch 1999, Nesbitt et al. 2002, López-Idiáquez et al. 2018). This parental investment strategy is relatively widespread in several taxa of waterbirds that depend on efficient fish capture and have specialized foraging strategies (Sulidae, Fregatidae, and Laridae; Burger 1980), and it is widespread in raptors (Bustamante 1995, Eldegard and Sonerud 2012, López-Idiáquez et al. 2018). Research indicates that avian diet is largely learned and can be culturally transferred across multiple generations (Knight and Knight 1983, Lefebvre and Bouchard 2008, Slagsvold and Wiebe 2011). Given the Whooping Crane's K-selected life history and broadly omnivorous diet, it is not surprising that parents continue to help their colts garner food throughout the fall migration. Whooping Crane parents may provide additional assistance to colts attempting to exploit challenging-to-garner diet items, particularly animal prey (i.e., fish), that require distinctive capture techniques (Watson and Hatch 1999, Lefebvre and Bouchard 2008).

Photography and videography can provide important information about animal behavior, natural history, and populations (Hartley 1948, Davies et al. 2012, Pimm et al. 2015, Long and

Azmi 2017, Weise et al. 2017, Caven et al. 2019a, Hawkes et al. 2020). Use of photography and videograpy to observe foraging Whooping Cranes enabled us to document species-specific diet items being consumed without interrupting the cranes' natural foraging activities. Furthermore, analysis of images derived from this study provided important morphometric data that also allowed us to estimate the nutritive value of the aquatic vertebrates we observed being consumed (Caven et al. 2019a). Photography and videography have the benefits of enabling review by multiple people, providing visual evidence that can be corroborated and further investigated at a later date, being an easily archivable format, and not requiring the sacrifice or capture of animals (Pimm et al. 2015, Weise et al. 2017, Caven et al. 2019a). Despite technological improvements that have made long-range photography/videography more accessible and affordable (Pimm et al. 2015), many smaller diet items are still difficult to identify. Our findings are likely biased toward diet items that require longer handling times, such as larger aquatic vertebrates and those with defensive adaptations (Duvall 2007). Additionally, though excellent equations for estimating vertebrate biomass and nutrient content exist, it is also worth considering that our results represent point estimates for weight and nutritive values and include a reasonable amount of uncertainty (Bayer 1985).

CONCLUSIONS

This research improves our understanding of the breadth of Whooping Crane diet during migration, particularly in the CPRV. We recorded Whooping Cranes eating diverse vertebrates of a range of sizes. Our results, in conjunction with Caven et al. (2019a), indicate that Whooping Cranes forage for fish in the Platte River with some regularity when conditions are appropriate and that the cranes consistently consume young Channel Catfish. It is notable that these observations were made following a several-year period during which the Platte River had not gone dry, and that summer flows were generally above average compared to discharge records for Grand Island going back to the mid-1930s. Therefore, it is possible that the fishery was in above-average condition at the time of our observations

(Perkin et al. 2015). Furthermore, Whooping Cranes were consistently successful at capturing fish in shallow water despite relatively robust flows (>2500 cfs, >71 cms). Future research should continue to investigate the immediate and long-term hydrological conditions under which Whooping Cranes choose to forage in the Platte River during the day. Our research indicates that wetland vertebrates occasionally make up a significant portion of Whooping Crane caloric intake during migration and also provide significant sources of essential protein and nutrients that waste grains largely lack. These findings underscore the importance of maintaining functional riverine and palustrine wetland habitats throughout the migration corridor, not only as important roosting sites but also as valuable foraging sites.

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