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First Description of Nesting Behavior of a Same-sex Pair of Whooping Cranes (*Grus americana*) in the Reintroduced Eastern Migratory Population

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Abstract.—Accounts of same-sex nesting behaviors have been observed in several wild and captive bird species, but the evolutionary adaptation of this behavior remains unclear. There have been reports of male-male and female-female territorial pairs of Whooping Cranes (*Grus americana*) in two reintroduced populations. However, this is the first documentation of nesting behavior of a same-sex pair of Whooping Cranes. The incubation rhythm and nesting behaviors of a female-female Whooping Crane pair nesting at McMillan Marsh Wildlife Area in Marathon County, Wisconsin, USA, were documented using a nest camera. The female-female pair displayed comparable nest constancy (99.7%) and incubation behaviors to male-female Whooping Crane pairs in the same population. Both females of the pair incubated the nest; however, the older female incubated for longer periods of time than the younger female (235.8 ± 20.7 min and 168.3 ± 17.2 min, respectively). The pair exchanged incubation duties 5.7 ± 0.2 and 1.1 ± 0.2 times daily during daylight hours and nighttime hours, respectively. The two females incubated the nest for at least 28 days, but fate of the eggs was not determined. Ultimately, the cause of this pairing remains unknown. This behavior could have implications for the breeding success of this small, reintroduced population of Whooping Cranes. Received 4 October 2019, accepted 26 August 2020.

Key words.—breeding, *Grus americana*, incubation, nest, reintroduced population, same-sex sexual behavior, Whooping Crane, Wisconsin

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Same-sex nesting behavior has been documented in a variety of bird species in captivity (Chinstrap Penguin, *Pygoscelis antarcticus*, Zuk 2006; Zebra Finch, *Taeniopygia guttata*, Elie *et al.* 2011; Greater Flamingo, *Phoenicopterus roseus*, Regaiolli *et al.* 2018) and in the wild (Roseate Tern, *Sterna dougallii*, Nisbet and Hatch 1999; Bearded Vulture, *Cybaetus barbatus*, Bertran and Margalida 2003; Black-necked Crane, *Grus nigricollis*, G. Archibald, pers. commun.). However, it is difficult to determine the evolutionary adaptation of same-sex pairs studies of potential causes of same-sex reproductive behavior (Bailey and Zuk 2009), including the influence of a sex-skewed population (Nisbet and Hatch 1999; Adkins-Regan and Krakauer 2000; Young and VanderWerf 2014), an inability to distinguish members of the opposite sex (Bagemihl 1999), or individuals practicing breeding for when an opposite-sex mate is available (Flamingo species, *Phoenicopterus* spp., King 2006). Additionally, if same-sex partners are related, kin selection may motivate individuals to help raise young if the eggs had been fertilized by another individual. The causes and implications of same-sex breeding be-

havior remain unclear and are likely varied (Bailey and Zuk 2009).

The first nesting record of a same-sex pair of Whooping Cranes (*G. americana*) was in the reintroduced Florida Non-migratory Population (hereafter FNMP; Dellinger 2018). The two females built a nest, and one Whooping Crane laid a single egg which was depredated (Dellinger 2018). This pairing was attributed to a small, female-skewed population, assuming females had the drive to breed but there were no available males in the population (Dellinger 2018). Another small reintroduced population of Whooping Cranes, the Eastern Migratory Population (EMP) in the USA, is male sex-skewed; a same-sex male pair has been together beginning in 2012 until the time of this writing. Although the male-male pair appears to occupy a breeding season territory and migrates together, we have never documented nesting or copulating. However, despite the male skewness in the EMP, in 2017 we documented the first two female-female pairs of Whooping Cranes incubating eggs on nest mounds. In 2019, one of these female-female pairs of Whooping Cranes nested again,

which we will discuss here. The objective of this study was to describe in detail the nesting behavior and incubation characteristics of a female-female pair of Whooping Cranes at McMillan Marsh Wildlife Area in Marathon County, Wisconsin, USA as recorded by a nest camera.

METHODS

Study Area

This study was conducted in McMillan Marsh Wildlife Area in Marathon County, Wisconsin, USA (44° 43' N, 90° 10' W). The nesting marsh of this pair of Whooping Cranes is owned by the Wisconsin Department of Natural Resources, however; the Whooping Cranes also used private agricultural lands adjacent to the marsh. McMillan Marsh Wildlife Area is approximately 2,666 ha of wetlands, forests, and grasslands. The nest site was in an open wetland area dominated by cattails (*Typha* spp.).

Bird Monitoring

The identification numbers of the three Whooping Cranes in this study are male 19_17, and females 2_15 and 28_05. All three individuals were raised in captivity at the U.S. Geologic Survey's Patuxent Wildlife Research Center in Laurel, Maryland, USA or the International Crane Foundation in Baraboo, Wisconsin, USA. Both females were raised by aviculturists in Whooping Crane costumes, and the male was raised by captive adult Whooping Cranes. Prior to the release of the birds, the sex of each bird was determined by the captive institutions using genetic techniques (Griffiths *et al.* 1998; Duan and Fuerst 2001). All birds were outfitted with a unique combination of colored leg-bands, as well as leg-band mounted Very High Frequency (VHF) transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) and satellite transmitters (Platform Terminal Transmitters or PTT; Microwave Telemetry, Columbia, Maryland, USA). Female 28_05's satellite transmitter was non-functional during this study. Female 28_05 was raised and released during fall 2005 at Necedah National Wildlife Refuge in Juneau County, Wisconsin, USA. Female 2_15 was raised at White River Marsh in Green Lake County, Wisconsin, USA, during 2015. The two females were first seen together during spring 2017. During fall 2017, male 19_17 was released into the area used by females 28_05 and 2_15, and all three, along with another juvenile male 25_17, migrated south and wintered together in Jackson County, Alabama, USA (Boardman and Tidmus 2017). The locations, behaviors, and associations of Whooping Cranes in the EMP were monitored using a combination of satellite telemetry, VHF telemetry, or leg-band identification. Aerial surveys or ground-based observations were conducted by members of the Whooping Crane Eastern Partnership.

Nest camera

We deployed a camera near the nest which was initially found via aerial survey. We installed the camera (Trophy Cam model 119466, Bushnell, Overland Park, Kansas, USA) on a metal post approximately 7.7 m from the nest, according to methods described by McKinney (2014) and Jaworski (2016). The camera was set to automatically take one photo every 5 min, 24 hr per day, and one additional photo per 5-min interval if it detected motion.

From each photo we recorded the number of Whooping Cranes present, behavior, and individual identity (if possible). We also recorded the incubating Whooping Crane's position, and if the position had changed since the last photo, in order to determine if the camera had missed the motion of a nest exchange or egg manipulation. We used behavior categories, organized in tiers described in McKinney (2014) and used in Jaworski (2016). Tiers increased in specificity from Tier 1 which was the number of Whooping Cranes present, to Tier 4 which was fine scale behaviors. To calculate percentage of time in each behavior, we used photos taken in 5-min intervals and excluded the motion-detected photos, per methods used by McKinney (2014) and Jaworski (2016). Daylight hours were considered 30 min before sunrise until 30 min after sunset, and outside of that time frame was considered nighttime hours. Two observers tagged photos and initially tagged the same set of 250 photos to ensure agreement on behaviors and data collection methods.

We used a Welch's two-sample t-test in the statistical program R to assess any differences in the duration of incubation bouts between 2_15 and 28_05 (R Core Team 2019). All measurements were calculated in R and are reported as mean \pm standard error (SE).

RESULTS

During an aerial survey on 7 May 2019, the pilot detected a Whooping Crane nest at McMillan Marsh Wildlife Area, in Marathon County, Wisconsin. At the time of the survey, one Whooping Crane was laying on the nest, and two additional Whooping Cranes were nearby. The identities of the three could be determined via VHF telemetry; however, due to the individuals' proximity to each other, the pilot could not tell which Whooping Crane was on the nest. The Whooping Cranes present at the nest were male 19_17 and females 2_15 and 28_05. The two females had been associating with each other since March 2017 and had used the McMillan Marsh Wildlife Area in the past. After the release of male 19_17 during fall 2017, he returned briefly during spring 2018, and re-

turned again on 31 March 2019. He left the area for a maximum of 4 days during April 2019 before returning to McMillan Marsh. Male 19_17 died on 9 May 2019 due to a powerline collision just east of the marsh.

We visited the nest on 14 May 2019 to deploy the camera, and there were two eggs present. The nest was approximately 1.2 m in diameter and was made up mostly of cattail (*Typha* spp.) vegetation. During camera deployment, 28_05 was threat displaying, but then returned to the nest 9 min 12 sec after we left. We did not assess egg development or fertility while at the nest. The pilot saw both females off-nest on 6 June. We returned to collect the camera on 12 June 2019, and the vegetation had grown significantly. We did not find any eggs, eggshell fragments, or signs of predation or hatch. There were no photos of predators or other animals at the nest.

The camera recorded a total of 8,444 photos between 14 May and 12 June 2019, including photos taken after the pair stopped incubating on 4 June 2019. The camera recorded 6,271 photos from the time of camera deployment until nest abandonment. Of the 250 photos tagged by both observers,

there was 99.6%, 100%, 99.6%, and 82.4% agreement on Tiers 1-4, respectively. Most disagreements in Tier 4 were due to slight differences in the straightness of a Whooping Crane’s neck, indicating either alert or other behavior, which were not analyzed in this study. Ultimately, the fate of the eggs could not be determined from the photos taken at the nest. During the incubation period, nest constancy was high (99.7%). There were only five instances where the Whooping Cranes were off the nest, three during daylight hours and two instances at night. The maximum time off nest was 20 minutes (12 min).

Both adult females incubated the nest during daylight and nighttime hours (Fig. 1). Female 28_05 incubated 56.2% and 63.1%, and 2_15 incubated 43.8% and 36.9% of daylight and nighttime hours, respectively. Overall, the pair exchanged incubation duties on average every 202.1 ± 13.7 min, and the incubating bird shifted position or stood up and presumably manipulated the eggs, on average every 54.2 ± 2.4 min. Female 28_05 incubated for longer periods of time than 2_15 (Fig. 2, $t(145.1) =$

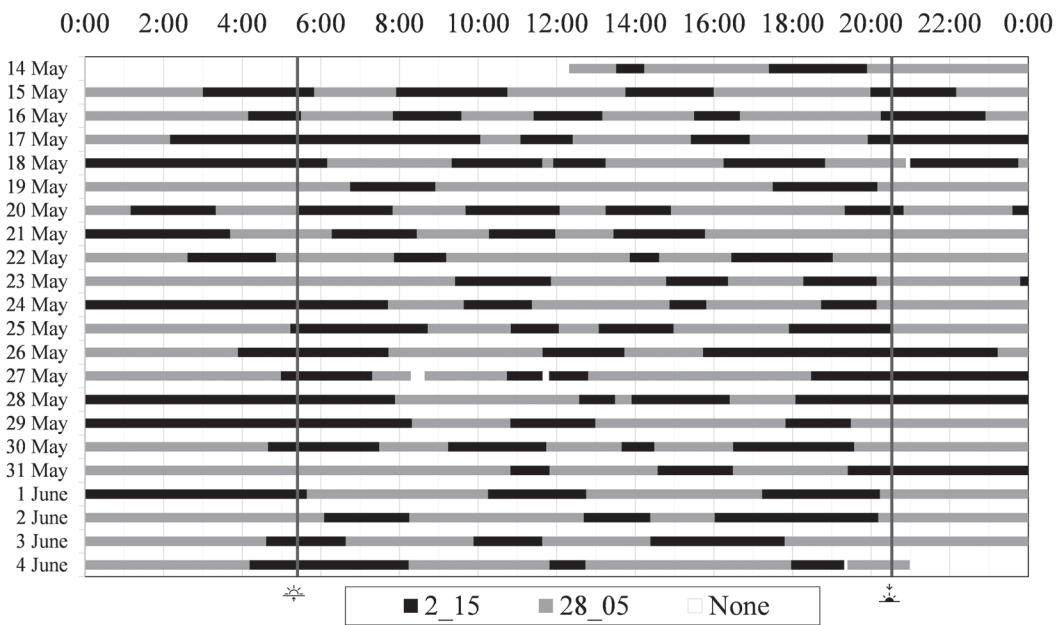


Figure 1. Incubation rhythm for a female-female Whooping Crane (*Grus americana*) pair on a nest at McMillan Marsh Wildlife Area in Marathon County, Wisconsin, USA, during 2019. Vertical black bars depict average sunrise and sunset times during the period between 14 May and 4 June 2019.

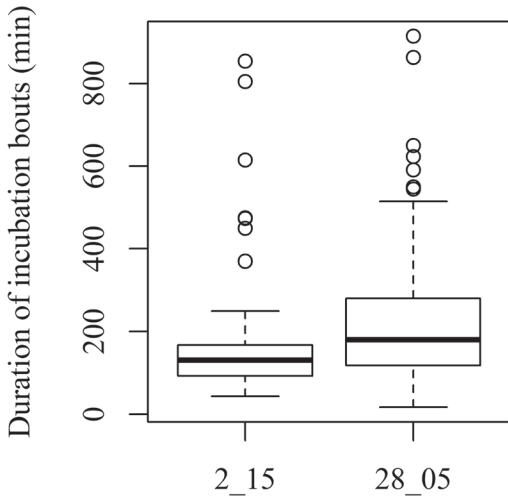


Figure 2. Duration of incubation bouts (min) for a female-female Whooping Crane (*Grus americana*) pair nesting in Marathon County, Wisconsin, USA, during 2019. Numbers on x-axis represent leg-band identification numbers of individual birds.

-2.51, $P = 0.01$). Average incubation bout duration was 235.8 ± 20.7 min and 168.3 ± 17.2 min for 28_05 and 2_15, respectively. The two females exchanged incubation duties at some point during 14 of the 21 nights documented in this study (Fig. 1). Often, they exchanged incubation duties multiple times in one evening, for an overall average of $1.1 \pm$

0.2 exchanges per night (Fig. 1). During the daylight hours, the two females switched incubation duties an average of 5.7 ± 0.2 times per day ($n = 21$ full days). Although 28_05 incubated more often and for longer periods of time than 2_15, there did not seem to be a pattern in the timing of incubation exchanges (Fig. 1).

During both daylight and nighttime hours, the percentage of time spent incubating the nest was high (92.1% and 97.3%, respectively; Table 1). Additionally, this female-female pair also spent a high percentage of time at the nest with their head up (77.4% and 74.6%, during daylight and nighttime hours respectively). Time spent in all behaviors was similar to male-female Whooping Crane pairs in the EMP (Table 1). We also documented three instances of the female-female pair unison calling at the nest. Female 2_15 was standing and identified by her uniquely-colored leg bands in two of the photos, while the second individual, presumably female 28_05, was incubating the nest. In the third instance, after nest-abandonment, both females returned to the nest and were documented standing and unison calling.

During nesting season 2020, this female-female pair nested and laid 3 eggs. We

Table 1. Proportion of time during daytime hours (30 min before sunrise until 30 min after sunset) and nighttime hours (30 min after sunset until 30 min before sunrise) spent in each behavior category by a female-female pair of Whooping Cranes (*Grus americana*) breeding at McMillan Marsh State Wildlife Area, Wisconsin, USA. For comparison, listed here are least mean square and 95% confidence intervals of time spent in each behavior during daylight hours for nesting male-female Whooping Crane pairs from successful (eggs hatched) and unsuccessful (eggs did not hatch) nests, and male-female Sandhill Crane (*G. canadensis tabida*) breeding pairs at Necedah National Wildlife Refuge (NNWR) during 2014 (McKinney 2014).

	M-F Pairs at NNWR During Daytime (McKinney 2014)				
	This Study F-F Pair		Whooping Cranes		Sandhill Cranes
	Daytime	Nighttime	Successful	Unsuccessful	Overall
Incubation	0.921	0.973	0.959 (0.938 – 0.980)	0.827 (0.792 – 0.862)	0.940 (0.920 – 0.960)
Head up	0.774	0.746	0.777 (0.748 – 0.805)	0.788 (0.739 – 0.836)	0.723 (0.696 – 0.751)
Head tucked	0.147	0.227	0.222 (0.194 – 0.251)	0.210 (0.162 – 0.258)	0.271 (0.244 – 0.298)
Preening	0.096	0.020	0.105 (0.090 – 0.119)	0.105 (0.082 – 0.129)	0.152 (0.139 – 0.166)
Manipulating egg	0.029	0.016	0.017 (0.013 – 0.020)	0.026 (0.019 – 0.033)	0.024 (0.021 – 0.0275)
Away from nest	0.001	0.000	0.006 (0.000 – 0.025)	0.127 (0.094 – 0.161)	0.015 (0.000 – 0.086)

swapped two of their eggs for two fertile eggs, and at least one chick hatched. The chick only survived for a few days and was not seen again. After nesting season, female 28_05 was found dead during flightless molt, and female 2_15 had a wing injury and was brought permanently into captivity.

DISCUSSION

Compared to male-female pairs of Whooping Cranes in the EMP, this female-female pair exhibited similar rates of nest constancy, incubation, and other behaviors at the nest (Table 1; McKinney 2014). Additionally, this pair spent similar proportions of daylight hours incubating the nest (92.1%), as compared to Sandhill Cranes (*G. canadensis tabida*) breeding in Wisconsin (94.0%; McKinney 2014) and Black-necked Cranes (*G. nigricoll*) breeding in China (approximately 90%; Zhang *et al.* 2017a, b). Time spent manipulating eggs and time spent away from the nest were both associated with nest success of male-female Whooping Crane pairs in the EMP and the FNMP (McKinney 2014; Dellinger 2018). The rate of egg manipulation for this female-female pair was more similar to unsuccessful male-female pairs, however the time spent away from the nest during daylight hours was more similar to successful pairs in the EMP (Table 1; McKinney 2014). The overall percentage of time this female-female pair of Whooping Cranes spent in each behavior category measured here fell within normal ranges for male-female pairs of cranes (Walkinshaw 1965; McKinney 2014; Zhang *et al.* 2017b).

This is the first documentation in the EMP of Whooping Crane nesting behavior during nighttime hours. There have been two previous studies of Whooping Crane nesting behavior in the reintroduced EMP, both of which have focused on behavior during daylight hours (McKinney 2014; Jaworski 2016). In this study, both females incubated overnight and often exchanged incubation duties during the night. In the reintroduced FNMP, male-female Whooping Crane pairs also were documented exchanging incuba-

tion duties overnight (Dellinger 2018). In contrast, Walkinshaw (1973) found a captive female Whooping Crane did more nighttime incubation than her male mate, and Conway (1957) observed the same pair and documented the male did more nighttime incubation than his female mate. In some species of cranes, one member of the pair will incubate overnight, and the pair will not exchange duties except during daylight hours. For example, female Sandhill Cranes breeding in Wisconsin, Black-necked Cranes breeding in China, and Eurasian Cranes (*G. grus*) breeding in Germany incubated for longer bouts than males, and typically incubated overnight, or at least during early mornings and late evenings, while males incubated the nest for a few hours in the middle of the day (Zhang *et al.* 2017b; Barwisch 2018; S. Berzins, unpubl. data). While there may be some differences in incubation behavior between male and female cranes, there also appears to be inter- and intra-species variation.

The causes of formation or potential evolutionary advantage of same-sex pairs remains unknown. The female-female pair of Whooping Cranes in the reintroduced FNMP was thought to be a result of a female sex-skewed population (Dellinger 2018). However, the EMP has more male than female Whooping Cranes. Another theory for why same-sex pairs form is an inability of an individual to determine the sex of another individual. Whooping Cranes are sexually monomorphic, however males are typically larger than females, and can be identified by frequency of calls and posture during unison calls (Johnsgard 1983; Volodin *et al.* 2015). It is also unlikely these two female Whooping Cranes are practicing breeding for when an opposite-sex mate becomes available. The two females in this study spent the winter of 2017-2018 with three males, and associated with a fourth male for a portion of the winter. However, during the following spring migration, the two females migrated north alone and did not associate or attempt to breed with any male Whooping Cranes. For the nest described here, there was a male present prior to egg-laying, so it is possible

the egg was fertilized, however the females are not closely related, so there would be no genetic benefit via kin selection to invest in incubation or chick-rearing duties. It is possible the female-female pairing is due to a combination of a sex-biased dispersal, a drive to breed, and a small population size. Female Whooping Cranes in the EMP tend to disperse further than males (Barzen 2018), thus it is possible they will disperse to breeding areas not used by male Whooping Cranes. If they have the drive to breed and only other females are available, that may have caused this unlikely same-sex pairing.

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