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Diurnal time–activity budget and habitat use of Whooping Cranes (*Grus americana*) in the reintroduced Louisiana nonmigratory population

Phillip L. Vasseur,^{1*} Sammy L. King,² and Michael D. Kaller³

ABSTRACT—Time–activity budget studies provide valuable insights for better understanding animal behavior relative to spatial and temporal habitat use. We examined a reintroduced, nonmigratory Whooping Crane (*Grus americana*) population to determine how time–activity budgets change relative to crane age, sex, habitat type, and season. Our study area encompassed natural marshes and working wetlands primarily in southwestern Louisiana. From June 2012 to January 2016, we conducted continuous focal sampling on individuals ($n = 27$) from the first 4 captive-reared cohorts released in the state. We classified age groups as juveniles, subadults, and adults, and identified 5 main habitat types utilized by cranes in Louisiana: crawfish ponds, rice fields, agricultural levees/farm roads, fallow fields, and natural wetlands. On average, cranes spent approximately 53% of their diurnal time–activity budget foraging. Maintenance/rest (28%), vigilance (12%), locomotion (6%), and other/unknown (2%) behaviors accounted for the remainder of the time observed. Foraging most frequently occurred in fallow fields and crawfish ponds where cranes likely encountered greater invertebrate biomass and density. Cranes tended to spend less time foraging and more time on maintenance as they aged, which could indicate age-dependent differences based on experience on the landscape. Vigilance levels were not significantly affected by age, but males tended to be more vigilant than females. As this young population continues to mature, additional study of breeding pairs and family groups may elucidate other behavioral differences in response to the dynamic habitat conditions in the region. Received 30 March 2022. Accepted 8 December 2022.

Key words: behavior, crawfish pond, foraging, Gruidae, rice field, wetlands.

Presupuesto diurno de actividades y uso de hábitat por la grulla *Grus americana* en la población reintroducida no migratoria de Louisiana

RESUMEN (Spanish)—Los estudios de presupuesto de actividades - tiempo dan un punto de visto valioso para entender el comportamiento animal con respecto al uso espacial y temporal del hábitat. Examinamos una población reintroducida no migratoria de grulla *Grus americana* para determinar cómo cambia el presupuesto actividad- tiempo según la edad y sexo de la grulla, el tipo de hábitat y la estación. Nuestro estudio comprende pantanos naturales y humedales activos principalmente en el sudoeste de Louisiana. De junio del 2012 a enero del 2016, hicimos un muestreo focal continuo de individuos ($n = 27$) de las 4 primeras cohortes criadas en cautiverio liberadas en el estado. Clasificamos los individuos por edad, como juveniles, subadultos y adultos, e identificamos 5 tipos principales de hábitat que usaban las grullas en Louisiana: estanques de langostinos, campos de arroz, diques agrícolas/caminos agrícolas, campos de cultivo en descanso y humedales naturales. En promedio, las grullas gastaron 53% de su presupuesto diario de actividades-tiempo forrajeando. El resto del tiempo observado se repartía entre comportamientos de mantenimiento/descanso (28%), vigilancia (12%), locomoción (6%) y otra/desconocido (2%). El forrajeo más frecuente se observaba en campos de cultivo en descanso y en estanques de langostino donde las grullas posiblemente encontraban mayor densidad y biomasa de invertebrados. Las grullas tendían a pasar menos tiempo forrajeando y más tiempo en mantenimiento conforme envejecían, lo que podría indicar diferencias dependientes de la edad según experiencia en el paisaje. Los niveles de vigilancia no cambiaban significativamente con la edad, pero los machos tendían a ser más vigilantes que las hembras. Conforme la joven población continúa su maduración, estudios adicionales de parejas reproductivas y grupos familiares pueden dilucidar otras diferencias conductuales en respuesta a las condiciones dinámicas del hábitat de las región.

Palabras clave: campo de arroz, comportamiento, estanque de langostinos, forrajeo, Gruidae, humedales.

The Whooping Crane (*Grus americana*), 1 of 2 crane species (Gruidae) endemic to North America, is classified as an endangered species and is therefore considered to be facing a high risk of extinction in the wild (Smith 2019, BirdLife

International 2021). The only sustainable wild breeding population winters in and around Aransas National Wildlife Refuge along the central Gulf Coast of Texas and summers in and around Wood Buffalo National Park, Canada (Mirande and Harris 2019). The International Whooping Crane Recovery Plan outlines objectives necessary for the eventual downlisting of the species, which includes establishing and maintaining additional self-sustaining wild populations through experimental releases (CWS and USFWS 2007).

Attempts to establish experimental, nonessential populations outside the species' current range but within its historical range have been made with

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separate reintroductions in the western and eastern United States (migratory populations) and in Florida and Louisiana (nonmigratory populations; French et al. 2018, Hartup 2018). The Eastern Migratory Population (EMP) and Louisiana Non-migratory Population (LNMP) are the only active reintroductions with estimated population sizes of 79 and 73 individuals, respectively, as of December 2021 (Thompson 2021; E. Szyszkoski, Louisiana Department of Wildlife and Fisheries, 2021, pers. comm.). The LNMP is the most recent reintroduction attempt commencing with an initial release of 10 juveniles in 2011 in the southwestern part of the state (King et al. 2018).

Historically, southwestern Louisiana supported migratory and resident populations of Whooping Cranes that primarily inhabited the coastal prairies and coastal marshes of the Chenier Plain (Allen 1952, Austin et al. 2018a). However, the species was extirpated from Louisiana by 1950 due in part to dramatic landscape changes associated with an expanding human population in the region (Allen 1952, Gomez 1992, King et al. 2018). Much of the native coastal prairie was converted to rice (*Oryza sativa*) agriculture (Meacham 1986) and later crawfish (*Procambarus* spp.) aquaculture (Gary 1973, McClain and Romaine 2004, Irwin 2014). Canals developed by the oil and gas industry and the construction of roads further altered the hydrology of the region (Theriot 2014).

Despite these substantial habitat alterations, Louisiana contains vast amounts of diverse natural and agricultural wetland habitats that support a myriad of wildlife species including an abundance of waterbirds (Bolduc and Afton 2004, Pickens and King 2014). Over 280 species of birds utilize the rice/crawfish landscape of the historical coastal prairie region during some portion of their annual cycle (Huner et al. 2009). The timing and type of management practices implemented in these working wetland systems create a spatially and temporally diverse matrix of habitats, ranging from mudflats to flooded fields, which have international importance for numerous waterbird species (Huner et al. 2002, 2009; Foley 2015). An improved understanding of the patterns of behavior expressed by cranes could provide indications of habitat quality such as food availability and predation risk (Jia et al. 2013, Van Schmidt et al. 2014, Zheng et al. 2015), and documenting how Whooping Cranes released in Louisiana utilize its

altered landscapes over time can assist in conservation and reintroduction efforts.

Time-activity budget studies provide valuable insights for better understanding crane behavior relative to spatial and temporal habitat use (Chavez-Ramirez 1996, Aviles 2003, LaFever 2006, Zhou et al. 2010). Globally, time-activity budget studies have linked activities of cranes in wild populations to the natural wetlands and managed (e.g., plowed, fallow, flooded, burned) areas they inhabit. For example, Red-crowned Cranes (*G. japonensis*) wintering in the Yancheng Nature Reserve in China spent more time foraging and less time vigilant in grasslands, whereas the pattern was opposite in farmlands (Li et al. 2013). Hooded Cranes (*G. monacha*) wintering at Shengjin Lake in China adjusted their foraging patterns in response to fluctuations in water levels (Zhang et al. 2015) and increased vigilant behavior in areas with intensive human disturbance (i.e., rice fields; Li et al. 2015). Similarly, cranes wintering at Poyang Lake National Nature Reserve in China shifted their diets in response to a reduction in a preferred food item by feeding on energy-rich crops in adjacent uplands (Burnham et al. 2017, Hou et al. 2021). Jia et al. (2019) also noted considerably different activity patterns among several crane species in shared habitat at Poyang Lake, which may reflect differences in their foraging methods. Black-necked Cranes (*G. nigricollis*) breeding in the Ladakh region of India spent the majority of their daily activity budget foraging and resting in marsh meadows where food resources were more abundant and diverse (Khan et al. 2014).

Much of what is known about the life history, ecology, and behavior of Whooping Cranes in the wild is based on studies of the Aransas-Wood Buffalo Population (hereafter AWBP; CWS and USFWS 2007). Additional research on reintroduced populations has provided further insights into demographics (Converse et al. 2013a, Servanty et al. 2014), diet (Zimorski et al. 2013, Barzen et al. 2018a), habitat selection (Maguire 2008, Van Schmidt et al. 2014, Pickens et al. 2017, Barzen et al. 2018c), migration (Mueller et al. 2013, Urbanek et al. 2014), reproduction (Folk et al. 2005, Spalding et al. 2009, Converse et al. 2013b, King et al. 2013, Barzen et al. 2018b), and causes of mortality (Cole et al. 2009, Miller et al. 2010, Yaw et al. 2020). Investigations into Whooping Crane

behavior through the use of time–activity budget studies have been conducted for the AWBP on its wintering grounds in Texas (Chavez-Ramirez 1996, LaFever 2006, Tiegs 2017), on captive birds and the EMP in Wisconsin (Fitzpatrick et al. 2015, Thompson et al. 2018), and the nonmigratory population in Florida (Kreger et al. 2005, 2006). Our study is the first to document the spatiotemporal behavioral responses of a captive-reared, reintroduced Whooping Crane population in Louisiana.

We investigated the nonmigratory Whooping Crane population released into Louisiana with the following objectives: (1) develop a time–activity budget for Whooping Cranes in natural marsh and working wetland systems (i.e., rice agriculture and crawfish aquaculture); (2) examine how activity budgets change through time as cranes age (juvenile, subadult, adult) and through space (within/among different types of habitat); (3) compare any behavioral differences between sexes; and (4) determine the effects of seasonal differences relative to various abiotic and biotic factors. We hypothesized that Whooping Crane behaviors would differ based upon age, sex, habitat type, and season.

Methods

Study area

Our study area encompassed natural marshes and working wetlands primarily in southwestern Louisiana, USA (Fig. 1), a region historically composed of coastal marshes and coastal prairies (i.e., the Chenier Plain). Captive-reared, juvenile Whooping Cranes were initially released onto the ~29,000 ha White Lake Wetlands Conservation Area (WLWCA; 29.8807N, –92.5219W), a state-owned property in Vermilion Parish mostly composed of fresh marsh. Dominant taxa included maidencane (*Panicum hemitomon*), bulltongue (*Sagittaria lancifolia*), *Eleocharis* spp., swamp sawgrass (*Cladium mariscus*), *Ludwigia* spp., and *Typha* spp. (Visser et al. 2000). Northern portions of the property are leased to the public and managed as farmland, pastureland, or left fallow. The average annual salinities of freshwater marshes at WLWCA and elsewhere in the Chenier Plain region were <0.5 ppt; oligohaline marsh types have a mean of 0.5–5.0 ppt and were dominated by saltmeadow cordgrass (*Spartina*

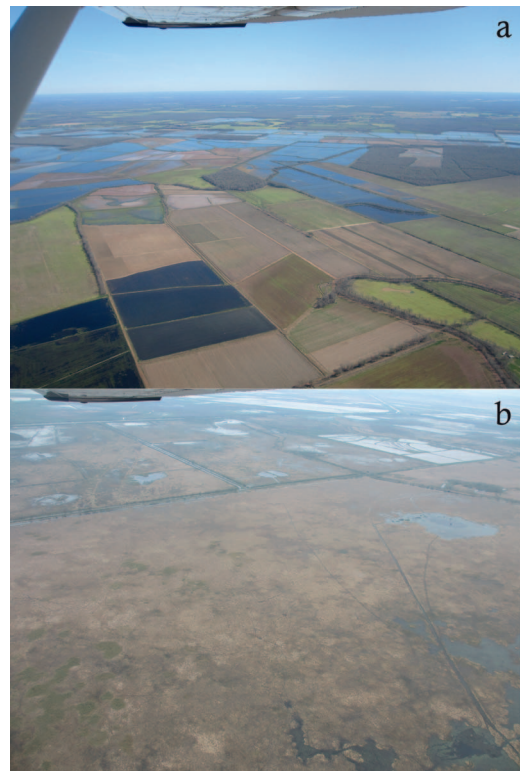


Figure 1. Aerial photographs representative of (a) working wetlands and (b) marsh habitat in southwestern Louisiana. Photos by E. Szyszkoski, Louisiana Department of Wildlife and Fisheries.

patens), whereas mesohaline marsh types had means of 5.0–18.0 ppt and were dominated by smooth cordgrass (*Spartina alterniflora*) and saltgrass (*Distichlis spicata*; Visser et al. 2000).

Nearly all (>99%) of the coastal prairie landscape, which historically was a tallgrass prairie system, has been converted to pasture, agriculture, and development (Vidrine et al. 2001). The region is now dominated by working wetlands that are typically privately owned lands managed as shallow-water, moist-soil agricultural systems. Intra- and inter-annual rotation of crops result in variable water depth and vegetation cover depending on season and specific agricultural practices (Foley 2015). Thus, the landscape is dynamic in both spatial and temporal scales. In southwestern Louisiana, these working wetlands are predominantly utilized for the commercial production of crawfish and/or rice but they are also highly productive bird habitats (Remsen et al. 1991,

Huner et al. 2002). Management for wintering waterfowl is another common practice on working wetlands, providing recreational and economic opportunities for those used as hunting leases (Elphick et al. 2010, Stafford et al. 2010). Huner et al. (2009) provide a more detailed discussion of the various management practices and the socio-economic importance of working wetlands as avian habitat.

Whooping Crane releases and monitoring

Between March 2011 and December 2015, 75 captive-reared Whooping Cranes were released in 6 cohorts of 6- to 9-month-olds. Pickens et al. (2017) provide details on the acclimation process at the WLWCA pen and subsequent release. Within a few days of arrival, each juvenile Whooping Crane received a numbered US Geological Survey size 8A rivet band on the lower left leg and a unique combination of colored, plastic bands on the upper parts of both legs. Thus, the age and sex (which was determined at the captive rearing facility prior to arrival) of all Whooping Cranes in the LNMP could be determined visually with these markers. We equipped each crane with a solar-powered satellite transmitter (e.g., platform transmitter terminal) affixed to the color bands on 1 leg to enable remote tracking of the population. Additional details regarding the types of transmitters used for various cohorts and satellite tracking are provided in Pickens et al. (2017). We programmed older transmitter models to collect daily location data at 0000 h, 0800 h, and 1600 h (local standard time) corresponding to a roost, morning, and afternoon point, respectively. Newer transmitter models transmitted data via cellular networks and could produce numerous location data daily. In this study, location data were not used in statistical analyses but were valuable for determining locations of individuals on the landscape to facilitate monitoring.

Behavioral observations

Ellis et al. (1991) described the behavioral repertoire of cranes in great detail, and we followed their terminology and classification system with some modifications. We categorized behaviors into one of 7 classes: foraging, locomotion, maintenance, resting, vigilance, other, and unknown. Foraging behaviors included food

capture attempts, food item handling time, consumption (e.g., pecking, probing, gleaning, stabbing, thrashing), and drinking, which we observed infrequently. A foraging crane could be either stationary or walking in search of food as indicated by a lowered head position and scanning the ground while moving. Locomotion included behaviors such as running, flying, and walking while not actively foraging. Maintenance involved actions associated with care of the body including preening, bathing, and other comfort movements like stretching, scratching, and ruffling feathers. Resting was indicated by a relaxed posture of the head and neck (i.e., S-shaped) by a stationary crane as well as sleep-related behavior such as tucking the head along the body with eyes either open or closed. Vigilance was identified when a crane exhibited alert behavior typified by a straightening of the neck and head-turning as it scanned its surroundings possibly due to a disturbance or a perceived or actual threat. Other behaviors included those infrequently observed such as dancing, vocalizing, and aggression. If the observer's view of the crane was lost because of an obstruction or some other factor and it was out of view for <1.5 min, the crane's behavior was classified as unknown for that time period. Instances where a crane was out of view for >1.5 min during an observation period were rare, but we removed these cases from the dataset and did not include them in analyses.

We developed time-activity budgets by conducting continuous focal sampling (Altmann 1974, Martin and Bateson 2007) for 5 min periods. We used binoculars (8–10×) and spotting scopes (20–60×) to observe cranes at a minimum distance of 100 m and maximum distance of 500 m. Observations were usually made from a vehicle (truck or utility terrain vehicle) or on foot. Observers on foot attempted to camouflage themselves behind vegetation or allowed for a greater observation distance. We recorded data directly in the field using a standardized form or dictated observations into a digital voice recorder, which we later transcribed. We used a video camera (Sony Vixia HF-R10, 20× optical zoom, Sony Corporation, Tokyo, Japan) to record some observations, which we also transcribed. An acclimation period of 5–10 min preceded the initiation of a behavioral observation. At the start of an observation, the observer recorded the initial

behavior of the focal individual and noted each time the crane changed its behavior until the end of the 5 min period. We were thereby able to use the start and end times of each distinct behavior (i.e., duration) to calculate the total amount of time (in seconds) a crane exhibited all occurrences of that behavior during the entire observation period (i.e., total duration).

From June 2012 to January 2016, we conducted behavior observations on solitary individuals and flocks from the first 4 cohorts (hatch years 2010–2013). We defined a flock as the close association of 2 or more cranes that use a common area and move collectively to new locations throughout life-cycle periods. Due to the small size of the nascent population, a limited number of cranes was available to monitor, so we attempted to monitor all cranes in the population. In cases where a flock was gathered, we made behavior observations on the entire flock by randomly selecting focal individuals without replacement until all individuals of the flock were sampled. However, we averaged the data for all individuals sampled in a flock to avoid pseudoreplication effects (Hurlbert 1984).

Initially, we followed solitary individuals and flocks throughout the day to conduct behavioral observations during each of the 4 diurnal sampling periods. Later, as the population increased with the addition of new cohorts and as monitoring priorities shifted, we did not follow focal cranes throughout the day but instead observed them multiple times (up to three 5 min periods) during 1 diurnal period. In these instances, the 5 min observation periods were separated by ~15 min and we averaged the data from multiple observations within a sampling period to get mean values. We believed this sampling approach would enable us to adequately identify the full spectrum of behaviors displayed by Whooping Cranes while managing other aspects related to monitoring the growing population.

For each observation, we classified the type of habitat the focal individual occupied. Because of the intra-annual variability of agricultural practices in the region, some individual fields combined crawfish and rice production on a seasonal rotation. Therefore, we classified fields based on observed farming activities—the presence of commercial traps indicated an active crawfishing operation. We classified fields with flooded rice

that did not have crawfish traps present as rice-only production. We recorded environmental data such as cloud cover, precipitation, temperature, wind speed and direction, and estimated the water depth, vegetation height, and visual obstruction around the crane based on the morphology of the crane. We also noted the distance from the focal crane to water and high ground, and recorded other Whooping Cranes or waterbird species in the vicinity of the focal crane (<9 m away). Sampling took place within 4 diurnal periods: early morning (0600–0900 h), late morning (0900–1200 h), early afternoon (1200–1500 h), and late afternoon (1500–1800 h). Our monitoring efforts were conducted throughout the year because Whooping Cranes in the Louisiana population are nonmigratory, and therefore, year-round residents. We defined 4 seasons (similar to Pickens et al. 2017) as follows: spring (Feb–Apr), summer (May–Jul), fall (Aug–Oct), and winter (Nov–Jan).

Statistical analyses

We used a set of generalized linear mixed models (GLM; PROC GLIMMIX, SAS 9.4, SAS Institute, Inc., Cary, North Carolina, USA) to investigate the effects of several variables on Whooping Crane time-activity budgets. Models included sex, habitat type, season, and their interactions as fixed effects and vegetation obstruction, time of day, and water depth as fixed covariates. The fixed covariates were retained in all models, except a null model used as a reference. Although the effect of age was initially of interest, during our analyses, the age variable was highly correlated with season and was removed from analyses. We used the Laplace method for estimation of interpretable Akaike information criterion (AIC) values. Because time budget data were converted to percentages and both beta distribution and binomial distributions may be used to analyze percentage data, we compared global models (all fixed effects with interactions and covariates) with each distribution type by $\hat{c}$, AIC, mean absolute error (MAE), and root mean square error (RMSE) as these objective functions provide different but complementary information about the model (Chai and Draxler 2014, Kéry and Royle 2016); we selected the better fitting distribution for analyses. The logit link, binomial distribution GLM was overfit ($\hat{c} =$

Table 1. Diurnal time–activity budget (mean % ± SE) of behaviors displayed in various habitats utilized by Whooping Cranes in the Louisiana Nonmigratory Population as determined by continuous focal animal sampling during 5 min observation periods from 2012 to 2016. Sample size (*n*) is the number of independent focal observations made in each habitat type.

Behavior	Crawfish pond (<i>n</i> = 39)	Rice field (<i>n</i> = 40)	Ag levee/farm road (<i>n</i> = 34)	Fallow field (<i>n</i> = 15)	Marsh/wetland (<i>n</i> = 17)	Total (<i>n</i> = 145)
Foraging	67.0 ± 4.6	54.6 ± 5.6	24.1 ± 5.2	74.9 ± 6.9	51.0 ± 7.7	52.5 ± 2.9
Maintenance/rest	19.0 ± 4.6	27.7 ± 4.7	45.9 ± 5.1	13.0 ± 6.2	24.0 ± 6.8	27.7 ± 2.5
Vigilance	8.3 ± 1.7	11.3 ± 2.4	14.9 ± 3.4	8.4 ± 2.3	15.0 ± 5.1	11.5 ± 1.3
Locomotion	4.1 ± 1.2	4.8 ± 2.0	12.5 ± 2.3	2.6 ± 1.2	5.9 ± 2.7	6.3 ± 0.9
Other/unknown	1.6 ± 0.7	1.6 ± 0.7	2.5 ± 0.8	1.1 ± 1.1	4.1 ± 1.9	2.1 ± 0.4

0.18, AIC = 716, MAE = 0.11, RMSE = 0.17), thus, estimates would be questionable. Therefore, we used the logit link, beta distribution GLM version in further analyses ($\hat{c}$ = 1.03, AIC = −402, MAE = 0.26, RMSE = 0.38) and selected the logit link, beta distribution GLM with the best combination of $\hat{c}$, AIC, MAE, and RMSE for interpretation of the variables in the best model. We considered a *P* value < 0.05 as statistically significant.

Results

We collected behavior data on 27 Whooping Cranes (16 females, 11 males) for a total of 1,635 min of continuous monitoring over 327 observations. Once we averaged data for individuals in flocks to avoid pseudoreplication, this resulted in 145 independent observations. We most often observed foraging behaviors, which accounted for ~53% of the mean diurnal time–activity budget of all cranes sampled (Table 1). We combined maintenance and resting into 1 class (maintenance/rest = 28%) as these behaviors typified relatively inactive periods for cranes. Vigilance accounted for 12% of the daily time–activity budget followed by locomotion at 6%. Finally, we combined other and unknown behaviors into one class (other/unknown = 2%) because neither accounted for much of the daily time budget on its own.

We identified 5 main habitat types utilized by Whooping Cranes in the LNMP, 4 of which (crawfish ponds, rice fields, agricultural levees/farm roads, and fallow fields) are typical of managed, working wetland systems in southwestern Louisiana. We also monitored cranes in fresh marsh at WLWCA and other natural wetlands in the region. However, we conducted fewer obser-

vations in coastal marshes compared to working wetland habitats due to logistical difficulties accessing remote areas in the marsh.

Reported statistical significance is based on the best-fitting GLM (Table 2). Differences in behaviors were greatest among habitat types ($F_{16,391}$ = 6.54, *P* < 0.001). Whooping Cranes in fallow fields spent the greatest amount of time foraging (75%; β = 0.43 [0.41 SE], t_{391} = 1.05, *P* = 0.29), whereas those on agricultural levees and farm roads spent the least amount of time foraging (24%; β = −1.39 [0.33 SE], t_{391} = −4.27, *P* < 0.001). When considering the other working wetland habitat types, cranes spent more time foraging in crawfish ponds (67%; β = 1.00 [0.47 SE], t_{391} = 2.14, *P* = 0.03) compared to rice fields (55%; β = 2.15 [0.24 SE], t_{391} = 7.41, *P* < 0.001). The time spent foraging in marshes (51%; β = −0.99 [0.38 SE], t_{391} = −2.58, *P* = 0.01) was similar to the overall mean (53%). Maintenance/rest behaviors were by far most often displayed on agricultural levees and farm roads (46%; β = 0.89 [0.31 SE], t_{391} = 2.94, *P* = 0.003). Vigilance did not significantly differ among habitat types but tended to be highest in marshes (15%; β = −0.03 [0.30 SE], t_{391} = −0.11, *P* = 0.91) and on levees and farm roads (15%; β = −0.11 [0.30 SE], t_{391} = −0.38, *P* = 0.71), moderate in rice fields (11%; β = −1.55 [0.34 SE], t_{391} = 2.14, *P* < 0.001), and lowest in fallow fields (8%; β = −0.12 [0.32 SE], t_{391} = 0.32, *P* = 0.71) and crawfish ponds (8%; β = −0.41 [0.38 SE], t_{391} = −1.07, *P* = 0.28). Locomotion was most frequent on agricultural levees and farm roads (13%; β = 0.34 [0.36 SE], t_{391} = 0.94, *P* = 0.35).

An evaluation of temporal patterns revealed some seasonal effects on time–activity budgets (Table 3) but we found no statistically significant

Table 2. Generalized linear mixed models comparing root mean square error (RMSE), mean absolute error (MAE), $\hat{c}$, and Akaike information criterion (AIC) to investigate the influences of sex, habitat type, and season on time–activity budgets of Whooping Cranes in the Louisiana Nonmigratory Population. For RMSE, MAE, and AIC, lower values are better. For $\hat{c}$, a value of 1 indicates fit, and values >1 and <1 indicate under- and over-fitting, respectively. Covariates included in all models were vegetation obstruction, water depth, and time of day. Models are sorted by lowest AIC.

Model	$\hat{c}$	AIC	MAE	RMSE
Covariates + sex + habitat	1.00	–494	0.28	0.40
Covariates + habitat	0.98	–490	0.29	0.40
Covariates + sex + habitat + season	1.00	–486	0.28	0.40
Covariates + habitat + season	0.98	–471	0.29	0.40
Covariates + sex + habitat + season + sex*season	0.97	–463	0.27	0.38
Covariates + sex	0.94	–438	0.30	0.40
Covariates + season	0.93	–424	0.30	0.40
Covariates + sex + season	0.93	–422	0.30	0.40
Covariates + sex + habitat + season + sex*habitat + season*habitat + sex*season	1.02	–417	0.26	0.38
Covariates + sex + habitat + season + sex*habitat + season*habitat + sex*season + sex*season*habitat	1.03	–402	0.26	0.38
Covariates + sex + habitat + season + sex*habitat	0.99	–396	0.28	0.39
Covariates + sex + habitat + season + season*habitat	0.99	–392	0.27	0.39
Covariates + sex + habitat + season + sex*habitat + sex*season	0.99	–344	0.26	0.37
Covariates + sex + habitat + season + season*habitat + sex*season	0.99	–335	0.26	0.38
Covariates + sex + habitat + season + sex*habitat + season*habitat	1.00	–310	0.27	0.38
Null (for reference)	1.14	–248	0.35	0.40

differences among behaviors and season ($F_{3,391} = 1.82$, $P = 0.14$) or time of day ($F_{3,391} = 0.63$, $P = 0.60$). However, cranes foraged 62% during the fall compared to 41% during the spring. Whooping Cranes tended to spend more time displaying maintenance/rest behaviors during the spring compared to other seasons. Mean temperatures during sampling periods were 17.0 °C in the spring, 27.8 °C in the summer, 26.1 °C in the fall, and 15.6 °C in the winter. Regarding daily variation in behavior, time spent foraging was fairly consistent throughout the day (Fig. 2). Maintenance/rest tended to be highest during the early morning whereas vigilance tended to be lowest in the late afternoon, although these were

not strong relationships. Locomotion exhibited 2 peaks—the first occurring in late morning and the second in the late afternoon.

We also compared behaviors among age groups that we classified as juveniles (<1.5 years), subadults (1.5–3 years), and adults (3+ years; Fig. 3). Comparisons were based on observational data, due to the correlation between age and season as previously noted. Juveniles spent more time foraging (66%) than subadults (51%) and adults (42%), and there was an inverse relationship between foraging and time spent in maintenance/rest—juveniles (19%), subadults (29%), adults (36%). Vigilance levels were similar among juveniles (10%), subadults (12%), and adults

Table 3. Diurnal time–activity budget (mean % $\pm$ SE) of behaviors displayed during the spring (Feb–Apr), summer (May–Jul), fall (Aug–Oct), and winter (Nov–Jan) by Whooping Cranes in the Louisiana Nonmigratory Population as determined by continuous focal animal sampling during 5 min observation periods from 2012 to 2016. Sample size (n) is the number of independent observations made during each season.

Behavior	Spring ($n = 42$)	Summer ($n = 21$)	Fall ($n = 35$)	Winter ($n = 47$)
Foraging	41.4 $\pm$ 5.7	53.6 $\pm$ 7.0	62.3 $\pm$ 5.1	54.6 $\pm$ 5.5
Maintenance/rest	36.7 $\pm$ 5.5	27.1 $\pm$ 5.9	21.8 $\pm$ 4.5	24.2 $\pm$ 4.1
Vigilance	11.8 $\pm$ 2.4	8.3 $\pm$ 2.4	9.8 $\pm$ 1.9	13.9 $\pm$ 2.9
Locomotion	7.0 $\pm$ 1.9	10.2 $\pm$ 2.2	4.4 $\pm$ 1.3	5.4 $\pm$ 1.9
Other/unknown	3.2 $\pm$ 0.9	0.8 $\pm$ 0.4	1.8 $\pm$ 0.7	1.9 $\pm$ 0.8

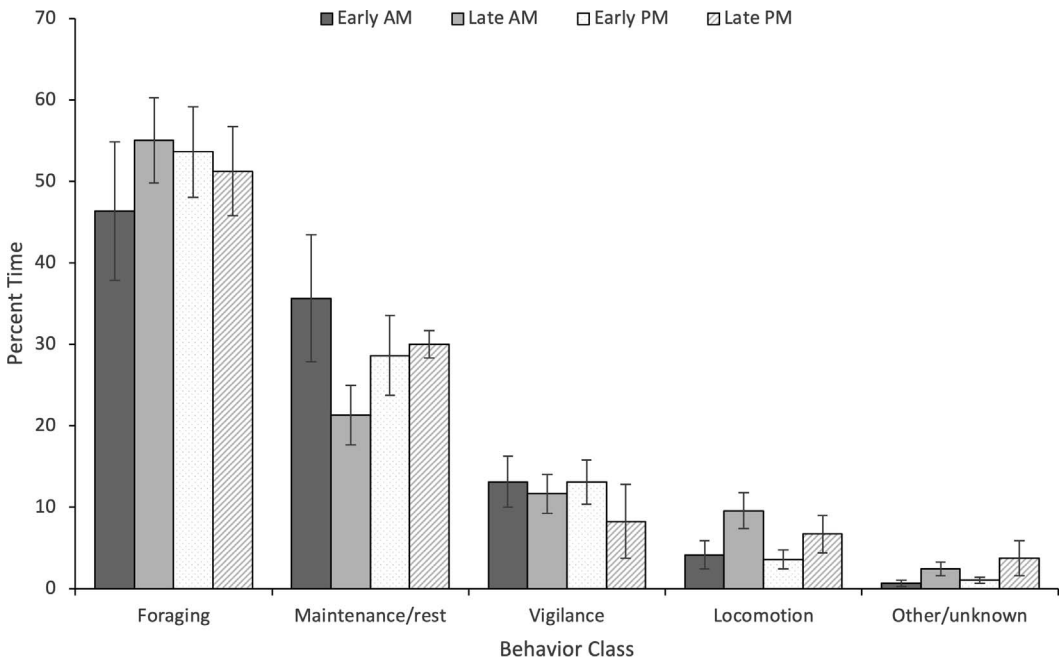


Figure 2. Diurnal time-activity budget (mean % $\pm$ SE) of behaviors displayed by Whooping Cranes in the Louisiana Nonmigratory Population during 4 time periods: early morning (0600–0900 h; $n = 21$), late morning (0900–1200 h; $n = 46$), early afternoon (1200–1500 h; $n = 43$), and late afternoon (1500–1800 h; $n = 35$). Sample sizes indicate the total number of independent focal observations for each time period.

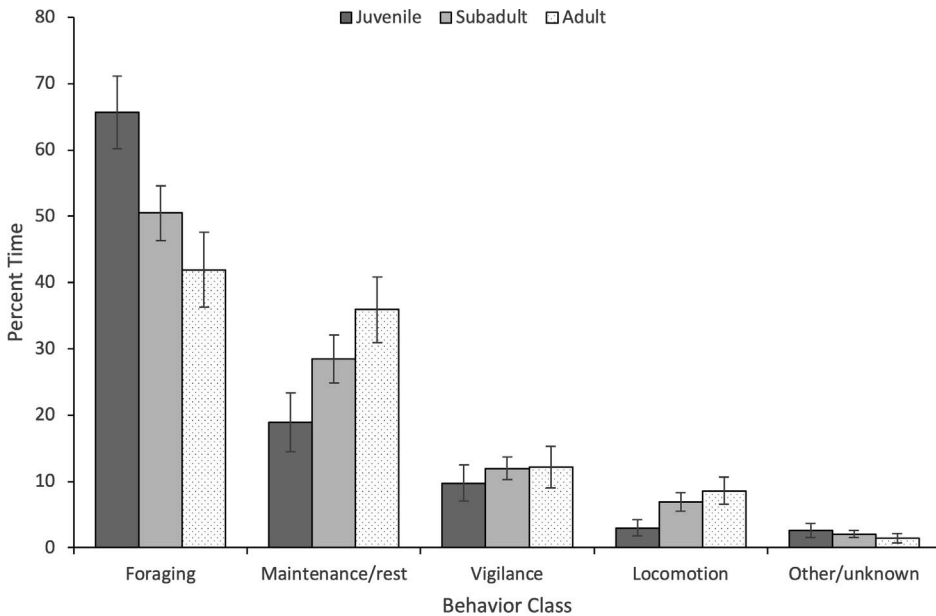


Figure 3. Diurnal time-activity budget (mean % $\pm$ SE) of behaviors displayed by juvenile (<1.5 years; $n = 20$), subadult (1.5–3 years; $n = 20$), and adult (3+ years; $n = 7$) Whooping Cranes in the Louisiana Nonmigratory Population. In total, there were 145 independent focal observations on juveniles ($n = 36$), subadults ($n = 79$), and adults ($n = 30$).

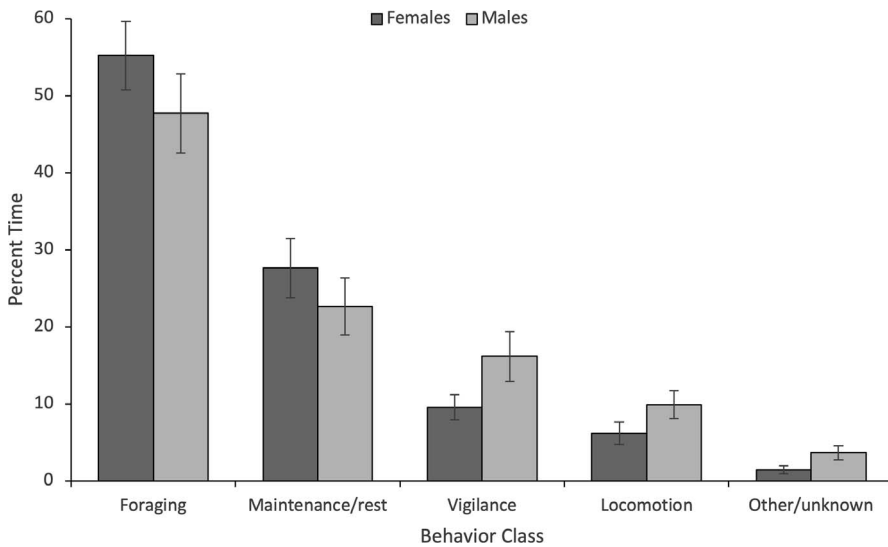


Figure 4. Diurnal time-activity budget (mean % $\pm$ SE) of behaviors displayed by female ($n = 16$) and male ($n = 11$) Whooping Cranes in the Louisiana Nonmigratory Population. In total, there were 114 independent focal observations for females ($n = 74$) and males ($n = 40$).

(12%). Additionally, we made comparisons between females and males, but these were not significantly different (Fig. 4). Females tended to allocate more time than males to foraging (55% vs. 48%) and maintenance/rest (28% vs. 23%), whereas males tended to be more vigilant than females (16% vs. 10%).

Discussion

Our results reveal the behavioral responses of Whooping Cranes in the reintroduced Louisiana Nonmigratory Population to dynamic habitat conditions created by different land management practices in the Chenier Plain of Louisiana. Cranes spent 53% of their average diurnal time-activity budget foraging and tended to forage most often in certain types of working wetland habitats, specifically fallow fields and crawfish ponds. The majority of our focal observations of cranes utilizing fallow fields occurred during the fall and winter. Pickens et al. (2017) showed that fallow fields was a more common land cover type in core-use areas of Whooping Cranes in the LNMP during the fall/winter compared to the spring/summer, and Foley (2015) documented the lowest proportion of fallow land on the Chenier Plain landscape occurred during the summer.

Admittedly, our sample size for fallow fields was relatively small, although this may be explained, in part, by land management practices in the region. Frequent crop rotation may reduce the duration of the fallow period for harvested fields (Ilyashenko and King 2018). Yet, residual plant material may contain a greater number of invertebrate and small vertebrate prey, providing attractive foraging opportunities (Austin and Sundar 2018). Stenert et al. (2009) found higher macroinvertebrate richness and density in the fallow phase than the growing phase in rice fields. Therefore, fallow fields, while not ubiquitous for lengthy periods of time on the southwestern Louisiana landscape, may be primarily targeted by cranes as an important alternative habitat for foraging when it is available.

Foraging rates tended to be lowest during the spring, which is when production in crawfish ponds peaked in the region (Foley 2015). Because crawfish ponds are shallow-water impoundments managed for commercial use, they are highly productive habitats that attract numerous wildlife species (Huner et al. 2009). Foley (2015) examined the mean caloric values and macroinvertebrate energy available in crawfish ponds and rice fields in the Chenier Plain and determined that crawfish biomass was the main contributor to the

caloric value of these working wetlands. An energy content analysis by Huner et al. (1996) showed a crude protein content of 40% and total energy level of 14.1 kJ/g for whole commercial crawfish in Louisiana. Whooping Cranes in the LNMP exhibited strong selection for aquaculture (Pickens et al. 2017), which indicates that cranes utilize these habitats to capitalize on an abundant, high-energy food source (i.e., crawfish). Thus, the energy obtained from crawfish during the spring could have resulted in decreased foraging time to satisfy energetic needs allowing more time to be devoted to maintenance and resting behaviors, which tended to be highest during that season.

An energetic model based on time–activity budgets of wintering Whooping Cranes in the AWBP by Chavez-Ramirez (1996) revealed the most significant source of energy in the cranes' diet in coastal Texas was blue crab (*Callinectes sapidus*). Nelson et al. (1996) experimented with the diet of captive Whooping Cranes and determined that, of the food items tested, blue crab ranked highest for crude protein content (42%) and reported the gross energy of blue crab to be 11.9 kJ/g. Additionally, Fitzpatrick et al. (2018) conducted ecological energetic studies on Whooping Cranes in the EMP and found that agricultural fields were often utilized by cranes. Throughout their winter range, cranes regularly consumed waste corn (*Zea mays*), taking advantage of a particularly energy-rich food item having an energy content of 12.9 kJ/g (Fitzpatrick et al. 2018). Several other researchers have reported the AWBP frequently foraged in cropland, particularly corn and wheat (*Triticum aestivum*) stubble, during migration periods (Howe 1989, Johns et al. 1997, Austin and Richert 2005). Thus, Whooping Cranes in the AWBP, EMP, and LNMP have utilized agricultural areas to incorporate high-energy food sources into their diets.

Rice is one of the most important crops produced in Louisiana based on total acreage and economic value (Saichuk 2009). In the Chenier Plain, most rice production occurs from May to October (summer/fall), with the peak growing season from May to July (Foley 2015). Some fields, particularly in the southern part of the state where the growing season is longer, may be irrigated and fertilized after the first crop is harvested to stimulate growth of a second (ratoon) crop that matures in the fall (Huner et al. 2002,

2009). This ratoon crop may or may not be harvested depending on production costs and commodity prices (Huner et al. 2009, Foley 2015). In cases of a rice–crawfish rotation, ratoon crops are often not harvested primarily to provide forage for crawfish but also to enhance waterfowl hunting, weed control, and water storage (Huner et al. 2002). The majority of our behavioral observations of cranes in rice occurred in the fall and early winter, when Pickens et al. (2017) showed habitat selection for rice fields by Whooping Cranes was strongest. This time frame coincides with the emergence of crawfish from burrows with young from late August into late December (Huner et al. 2002). At this time, crawfish are smaller in size (5–7 cm) and more accessible to other wading birds (e.g., egrets and herons [Ardeidae], ibises and spoonbills [Threskiornithidae]) because of shallow water depths—typically 5–10 cm in rice fields versus 20–50 cm in crawfish ponds (Huner et al. 2002). Despite the potential for greater interspecific competition for crawfish, they are likely an important dietary component for Whooping Cranes in the fall/winter. Cranes may also supplement their diets in these seasons by consuming seeds off mature rice plants and foraging on a greater diversity of invertebrates present in rice fields compared to crawfish ponds (Foley 2015).

Age-specific behavioral differences showed that older Whooping Cranes tended to spend less time foraging and dedicated more time to maintenance/rest behaviors. Juveniles allocated nearly two-thirds (66%) of their diurnal activities to searching for and acquiring food compared to only 42% for adults. This difference may be attributed to experienced adults who have learned over time which habitats are more productive than others during various times of the year. It may also indicate that juveniles have greater nutritional requirements because they are still developing. Aviles and Bednekoff (2007) suggested age-dependent differences in foraging may reflect changes in juvenile and adult diets as well as inefficient foraging by juveniles. Age-related differences were reported by Pugesek et al. (2013) who collected data over a 9 year period on the AWBP wintering in Texas. They showed blue crab abundance was highly variable and juvenile mortality was highest in years when crab densities were lowest, which could support age-

dependent differences in foraging efficiency. Alternatively, the issue on the wintering grounds in Texas may be more complex involving a combination of factors including mortality, early migration, temporary emigration, and incomplete detection (Butler et al. 2014).

Vigilance levels in the LNMP were not significantly affected by age. This could be because the reintroduction was in its early stages and there were no parental adults or family groups to monitor. Other studies have reported higher vigilance rates in adult cranes compared to juveniles. For example, territorial adult Whooping Cranes on their wintering grounds in Texas spent significantly more time alert than juveniles (LaFever 2006, Tiegs 2017). Sandhill Crane (*Antigone canadensis*) adults in pairs and family groups were vigilant 4 times as often as adults without mates or young, and a juvenile was twice as vigilant when by itself compared to a juvenile in a family group (Tacha 1988). Common Crane (*G. grus*) parents were significantly more vigilant than nonparents and juveniles on their wintering grounds in Spain (Alonso and Alonso 1993). Black-necked Crane parents were significantly more vigilant than nonparents (Xu et al. 2013), and more time was spent vigilant when in family groups compared to social groups (Yang et al. 2016). The results of these studies highlight the importance of parental investment in vigilant behavior when allocating resources for the protection of offspring. As more pairs in the LNMP breed and raise young, time-activity budgets on family groups would provide more insightful behavioral comparisons to other crane populations.

It is rare for an entire wild population to have individually marked birds to permit comparisons between males and females in a sexually monomorphic species as we did in this study. Tacha (1988) observed a sample of marked Sandhill Cranes noting vigilant behavior was nearly 3 times more frequent in adult males as in adult females and suggested males served a protective role. However, other factors besides sex (e.g., social status) may have influenced the observed differences in vigilance in that study. Nevertheless, several other studies have found that male birds are more vigilant than their mates (reviewed in Beauchamp 2015), and male vigilance for predators may allow females more time to forage and perform maintenance/rest behaviors (Squires et al.

2007). Juveniles in our study were often in small ($n \leq 3$) same-sex groups or larger ($n > 3$) mixed-sex groups. We typically observed more well-defined, opposite-sex pairings beginning with the subadult age class, and breeding attempts by subadults resulting in fertile clutches have been documented in the LNMP (LDWF 2019). Therefore, it is possible that our finding of higher vigilance in males was attributed to pairings of reproductive-aged birds with males exhibiting behaviors that could enhance female survival. We were, however, somewhat constrained by our sample size due to the young age of the population so further study of time-activity budgets of breeding pairs in the LNMP is warranted to better evaluate sexual differences in vigilance and other behaviors.

The current landscape of southwestern Louisiana is dramatically different from historical habitat conditions that existed when the last resident Whooping Cranes inhabited the region prior to the mid-20th century. Habitat loss and conversion of natural wetlands has transformed the former coastal prairie into a largely agriculture-based ecosystem dominated by rice agriculture and crawfish aquaculture. In many instances, agricultural fields can provide alternative or complementary habitats for cranes and other waterbirds but cannot completely replace the ecosystem functions of natural wetlands (Austin et al. 2018b). However, the matrix of working wetlands and coastal marshes in southwestern Louisiana provides an abundance of resources (King et al. 2018), and cranes in the LNMP have shown strong temporal selection for rice fields and crawfish aquaculture (Pickens et al. 2017). The Chenier Plain consists of >1 million ha of working wetlands, and recent government programs have incentivized producers in the crawfish and rice growing region to enhance and increase availability of shallow-water habitats that benefit waterfowl, shorebirds, and other waterbirds for extended periods of time (Hohman et al. 2018). Such practices create ideal foraging and roosting areas throughout the year that make this landscape compatible for a resident population of Whooping Cranes.

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