North American Crane Working Group

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP

2022

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Woolley, H. W., S. G. Hereford, and J. J. Howard. 2022. Drivers of annual fledging in the Mississippi Sandhill Crane Population 1991-2018. Proceedings of the North American Crane Workshop 15:90-102.

DRIVERS OF ANNUAL FLEDGING IN THE MISSISSIPPI SANDHILL CRANE POPULATION 1991-2018

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Abstract: We studied trends in nesting, number of chicks fledged annually, and their environmental and biotic drivers in the wild population of Mississippi sandhill cranes (*Grus canadensis pulla*) on Mississippi Sandhill Crane National Wildlife Refuge during 1991-2018. Population size, number of nests, and number of chicks fledged annually increased slowly but significantly over the course of the study. Increases in population size were related to both number of wild-reared chicks fledged annually and number of captive-reared chicks released each year, but wild-reared chicks had significantly higher survivorship than captive-reared chicks. Hurricanes transiently raised mortality rates but only Hurricane Katrina caused a sustained population decline among adult birds. Total population size was positively related to precipitation during the nesting season, while number of chicks fledged annually was negatively related to annual number of extreme heat days and estimates of bobcat (*Lynx rufus*) occurrence. Cranes displayed high philopatry to their initial nest location and nested repeatedly in the same general home range regardless of the time since an area had last been treated by prescribed burning. Number of chicks fledged annually occurred with approximately equal frequency across management units burned at different times prior to nesting. The results indicate that both biotic and abiotic factors drive population dynamics on the refuge and suggest that additional attention to prescribed burns, predator removal, and behavioral conditioning of captive-reared birds prior to release may promote faster population growth and establishment of a self-sustaining wild population in the future.

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Key words: burn history, fledging rate, *Grus canadensis pulla*, Mississippi sandhill crane, nesting, population, predators, reproduction, weather.

Effective avian population management requires an understanding of the abiotic and biotic factors that influence population dynamics of a species. Bird populations are strongly affected by climate (Grant and Grant 1989, Rotenberry and Wiens 1991), often through extreme events such as drought (Grant and Grant 1989, Bolger et al. 2005, Albright et al. 2010). Birds are also particularly vulnerable to nest predation, which may substantially reduce population size (Ricklefs 1969), and after hatching chicks are quite vulnerable to predation until fledging (developing feathers capable of flight). An understanding of the relative influence of these factors on population dynamics is essential for devising effective long-term management strategies for avian populations.

The need for a clear understanding of the drivers of population dynamics is particularly acute for nonmigratory North American cranes. They have suffered from constrained habitat geographically and in southern regions are affected by human development and high summer temperatures (Gee and Hereford 1995, Folk et al. 2010, Cox et al. 2020). There exists a wealth of short-term studies focusing on 1 or more factors influencing the size of crane populations but efforts to synthesize information on factors influencing long-term population trends are less common. Such data can be of significant value to population managers in identifying factors threatening population viability as well as compensatory management strategies. Insights from long-term studies can be particularly valuable in devising strategies to offset long-term threats to crane populations posed by climate change (Butler et al. 2017, Liu et al. 2020).

In this study we examine trends in the Mississippi sandhill crane (*Grus canadensis pulla*) population during 1991-2018 and evaluate biotic and abiotic factors that may influence those trends. The Mississippi sandhill crane is a federally endangered subspecies of sandhill crane found only on or near the Mississippi Sandhill Crane National Wildlife Refuge in Jackson County, Mississippi. Mississippi sandhill cranes forage and nest primarily in wet pine savanna habitat characterized by few coniferous trees per acre and dominated by grasses

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and forbs (Gee and Hereford 1995, U.S. Fish and Wildlife Service 2005). The population has been actively managed since 1981 but has experienced low levels of natural reproduction and has been maintained primarily by supplemental releases of captive-reared birds (Gee and Hereford 1995, U.S. Fish and Wildlife Service 2005). The captive rearing program involves a partnership between the refuge and associated organizations conducting *ex-situ* breeding programs. Some captive-reared Mississippi sandhill cranes that are released on the refuge come from wild eggs collected from the refuge and hatched and raised offsite, and others come from captive flocks held offsite. Captive-reared chicks are either parent-reared or costume-reared. Juveniles are released at the refuge in November of their hatch year after they have fledged (Ellis et al. 2000).

The refuge has maintained detailed locality-specific records on nesting, reproductive outcomes, weather, fire management, and predator removal during the study periods, allowing us to examine multiple potential drivers of population trends. Specifically, we asked how weather and apparent predator occurrence affected estimated population size, nesting, mortality, and number of chicks fledged annually over time. We expected population trends to respond positively to measures of rainfall and negatively to measures of predator occurrence. We also asked how crane nesting behavior and number of chicks fledged annually were related to prescribed burning of management units, which is the primary management tool used to maintain savanna vegetation on the refuge. Fire increases plant species richness in wet pine savanna habitats (Kirkman et al. 2001) and may also increase abundance of important insect food taxa such as Orthoptera (Branson et al. 2006, Kral et al. 2017). Fire may also alter predator activity by reducing woody vegetation and small mammal prey base (Littlefield et al. 2001; Jones et al. 2002, 2004; Chamberlain et al. 2003). We expected crane nesting to be more frequent and number of chicks fledged annually to be higher in recently burned management units than in those burned infrequently.

METHODS

Study Site

The Mississippi Sandhill Crane National Wildlife Refuge, located 5 km north of Gautier in Jackson County, Mississippi, is comprised of 7,450 ha of pine savanna and flatwoods habitat managed primarily to maintain high quality habitat for Mississippi sandhill cranes (U.S. Fish and Wildlife Service 2005). The refuge is divided into 103 management units ($\bar{x}$ = 72.4 ha, range 14.0-301.0 ha), 99 of which are burned as conditions allow to maintain and expand wet pine savanna habitat used by cranes for nesting and foraging. Management units are burned, usually between October and June, on a 2-3-year rotation when possible, although some units are situated in locations that experience conditions suitable for burning only rarely (i.e., close to major highways or housing developments) and may experience burn intervals of 5-10 years.

Data Sources

Data were not consistently collected for all variables for the entire period between 1991 and 2018, and we limited each analysis to time periods for which reliable data were available. We examined crane population data and weather records from 1995 to 2018. Crane population data were obtained from annual year-end analyses of monitoring conducted by refuge personnel. Annual nest counts were obtained from aerial and ground surveys and camera-trap monitoring, and the number of wild-reared chicks fledged each year was determined by in-person and camera trap monitoring conducted by refuge personnel. Not all nests could be located with certainty, and some fledglings could not be attributed to any known nest. Number of captive-reared juveniles released on the refuge each year was obtained from records maintained by refuge staff. We calculated an estimate of annual mortality as prior year population size plus additions from newly fledged wild-reared birds and captive releases, minus the year-end population.

Daily precipitation and temperature data were obtained from the National Weather Service station on the refuge and were used to calculate the Keetch-Byram Drought Index (KBDI) as revised by Alexander (1990). KBDI estimates the moisture deficit of substrate in terms of millimeters of water required to saturate the soil, with 0 representing completely saturated soil and 200 representing maximally dry conditions (Keetch and Byram 1968, Alexander 1990).

No systematic surveys of predator density on the refuge were available for the period of the study, so we used predator trapping records as a proxy for predator occurrence. Trapping records only include location and type of predator trapped, and do not include trapping effort per year. We assume for the purposes of this study that the number of predators removed per year is positively correlated with predator occurrence in that year. Refuge staff provided data on the number and type of mammalian meso-predators trapped by refuge contractors during 2011-2018. Predator traps were set annually from October or November until June, with some exceptions. In 2011, trapping continued until 1 August, while in 2017 trapping ended in April, and in 2018 trapping ended in March. Trapping season for a given year was calculated as predators trapped during the fall of the previous calendar year plus the spring of the chick fledging year. Previous trapping season was calculated as predators trapped during the fall 2 calendar years previous to fledging year plus the spring of the calendar year previous to fledging year. The trapping season overlaps with the crane nesting period, which is roughly February through May; juveniles fledge at about 70-80 days post hatch and remain with their parents for about 10 months. Traps were targeted primarily in areas identified by refuge staff as having high predator activity.

Nest locations and prescribed burn records for each management unit were available for 1991-2018. Nest locations were obtained from aerial, ground, and a few boat surveys carried out by refuge staff on and around the refuge between March and June each year. A total of 626 nests were recorded in management units on the refuge, and another 101 nests were recorded in areas within 1 km of the refuge boundary. GPS locations accurate to 10 m were available for 606 nests. When possible, crane pairs associated with located nests were identified to maintain records of bonded pairs and associated territories in the population. Cranes were identified by using their unique leg band color combination through field observation and camera monitoring. We defined the number of growing seasons since a management unit had a prescribed burn as the burn interval. We defined growing seasons as starting in March and ending in October; hence a management unit burned during October of the previous year was classified during the following spring nesting season as having 0 growing seasons since the last burn and thus having a burn interval of 0.

Data Analysis

Statistical analyses were carried out in R version 3.5.0 (R Core Team 2018). We calculated regressions by using the lm function to determine how population size, number of nests, and number of wild-reared chicks changed with year since the beginning of the sample period. We also used regression to determine the relationship between number of nests and population size. Increases in population size might be driven by both the number of wild-reared fledglings and the number of captive-reared chicks released on the refuge. However, wild- and captive-reared individuals are known to differ in behavior (Howard et al. 2016) and may not contribute equally to population increase. We compared the influence on population size of the number captive-reared or wild-reared chicks added each year, both alone and in combination, using Akaike's Information Criterion (AIC) to select the best fit model. We used non-parametric Kaplan-Meier survival analysis in the R package survival v 3.1-12 to compare survival rates of 32 captive-reared and 545 wild-reared chicks for which both birth and death years were known using the log rank test.

The effects of 9 environmental factors on 3 population parameters (population size, number of nests, and number of chicks fledged annually) were investigated by generalized linear modeling using the glm function in the basic R stats package. We used AIC values to identify the best fit model and all other models with ΔAIC within 2 of the best fit model in each case. However, we discarded models with extra terms as uninformative if the additional terms were not statistically significant and ΔAIC of the more complex model was within 2 of the simpler model (Arnold 2010). The models included annual total precipitation, annual mean daily high temperature, and KBDI; we chose to focus on daily high rather than daily mean temperature because eggs and chicks are generally well-protected from low temperatures by brooding adults whereas high temperatures may stress eggs and hatchlings (Guthery et al. 2001, 2005; van de Ven et al. 2020). Since conditions during nesting season may have a greater effect on fledging outcomes than overall annual patterns, we also included nesting season (February through May) values for these variables in the models. In some grassland ecosystems annual net aboveground production lags rainfall by a year (Oesterheld et al. 2001, Sherry et al. 2008, Reichmann et al. 2013, Dudney et al. 2017), and lagged rainfall effects are known to influence bird breeding success (Spalding et al. 2009, Fantle-Lepcyzyk et al. 2016, Rockwell et al. 2012, Carstens et al. 2019). Therefore, we also included prior year total rainfall. Finally, temperatures above 36°C may cause heat stress in whooping cranes (*Grus americana*) (Fitzpatrick et al. 2015), so we included the number of extreme heat days on which the maximum temperature exceeded 36°C during nesting season (February through May) and the chick-rearing period (May through August).

The relationship between population parameters and predator trapping was analyzed using a generalized linear model with the glm function in the basic R stats package. We examined whether year-end population size, estimated annual mortality, and number of wild-reared chicks fledged annually were related to the number of predators trapped during the current-year trapping season starting in November of the previous year and continuing to June of the year of interest, or the previous-year trapping season to test for lag effects. We analyzed the relationship between the 3 population parameters and all predators summed, and for the 4 most numerous predators: bobcats (*Lynx rufus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and red fox (*Vulpes vulpes*). Current-year and previous-year trapping was analyzed separately since current-year predator populations are likely dependent on previous-year populations. Best fit environmental and predator trapping models were identified as those having the lowest AIC.

To investigate the relationship between nest location, chick fledging, and burn interval, we compared the nesting territory availability of management units with burn intervals of 0, 1, 2, 3, and 4 or more years to the location of 626 nests on management units that are known to have fledged 48 chicks during 1991-2018. To determine if pairs nesting for the first time showed a preference for recently burned management units in their initial nest sites, we compared nesting territory availability of management units with different burn intervals to locations of 87 first-time nests by newly formed pairs. We used chi-square tests in R to compare frequency of nesting in units with burn intervals of 0, 1, 2, 3, and 4 or more years. We also used chi-square tests to determine whether the proportion of nests producing fledglings varied significantly with burn interval.

We examined nest site fidelity of 62 pairs in which both members were positively identified and that nested in 2 or more consecutive years in georeferenced locations. We used UTM coordinates of 292 nests to calculate the mean distance between consecutive nests produced by a pair. We also tallied instances in which pairs changed the location of consecutive nests between management units with different burn intervals. We used a chi-square test to determine whether pairs were more likely to switch into more recently burned units than into units burned longer ago.

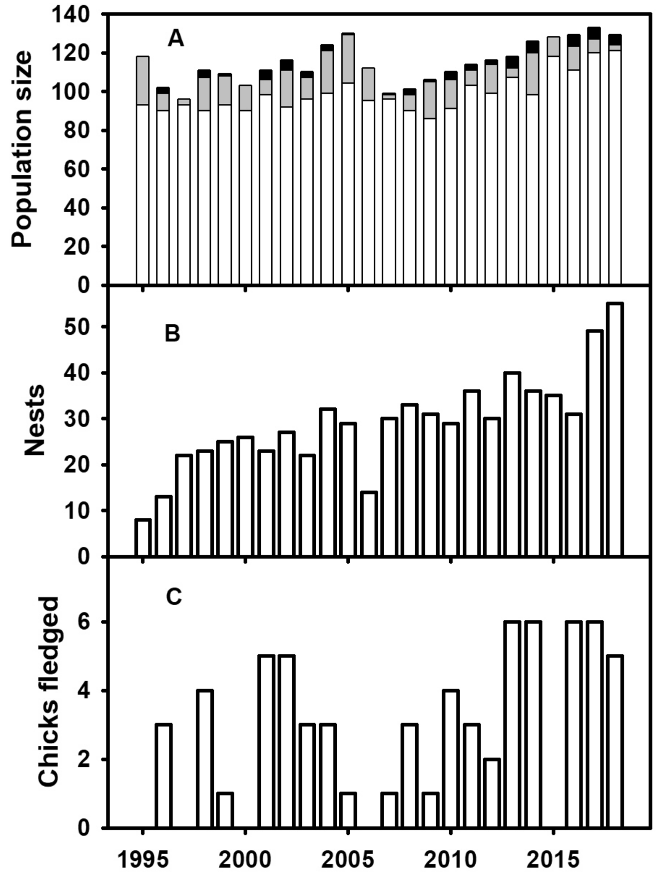

Figure 1. Population trends in the Mississippi sandhill crane population on the Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, 1995-2018: (A) Year-end population size measured in October (adults white, captive-reared chicks gray, wild chicks black), (B) Number of nests, (C) Number of chicks fledged.

RESULTS

Population Trends

During 1995-2018 the total Mississippi sandhill crane population ranged from 96 to 130 individuals, with an average of 114.6 ± 2.2 (SE) individuals (Fig. 1). Over the same period the population produced 699 nests and 68 fledglings for an average of 29.1 ± 2.1 nests and 2.8 ± 0.5 fledglings per year (Fig. 1). Yearly population census, number of nests, and fledglings all increased significantly over the 23-year period but at different rates. Total population increased at a rate of 0.92 individuals per year (r^2 = 0.34, P = 0.002) while number of nests increased at a rate of 1.2 per year (r^2 = 0.66, P < 0.001). Although annual variability was high, the number of chicks fledged annually increased by 0.14 per year (r^2 = 0.18, P = 0.023).

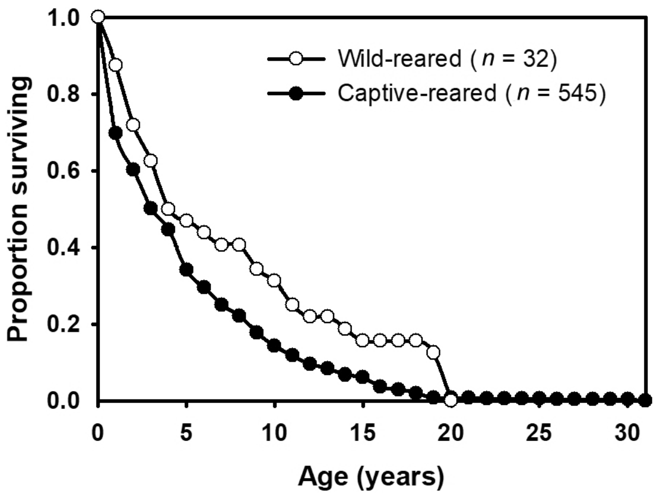

Figure 2. Survivorship curves for wild-reared (*n* = 32) and captive-reared (*n* = 545) Mississippi sandhill cranes released on the Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, 1995-2018.

The number of nests per year increased significantly with population size (r^2 = 0.24, P = 0.009), and number of chicks fledged annually increased significantly with nest number (r^2 = 0.23, P = 0.01). The rate of fledging per nest averaged 9.5 ± 1.5% over the study period and did not change significantly over time (P = 0.745). Mean annual mortality for the population was 11.8 ± 1.7% and did not change significantly over time (P = 0.136).

During the study period the population experienced 2 periods of decline, 1995-1997 and 2005-2009 (Fig. 1). Both declines were associated with land-falling hurricanes on the central Gulf Coast, Erin and Opal in 1995, and Katrina in 2005. Annual mortality exceeded 28% in the year following these hurricanes, the highest rates observed in the study. From 1995 to 1997 the total population declined from 118 to 96, but the number of adults and subadults remained stable while the number of captive-reared birds released on the refuge declined from 25 to 3. After Hurricane Katrina the population experienced a sustained decline from 124 to 99 in 2007, while adults and subadults declined from 104 to a low of 86 in 2009 (Fig. 1). Both the number of captive-reared fledglings released on the refuge and fledging of wild-reared chicks were also reduced in the wake of Hurricane Katrina. Releases of captive-reared chicks dropped from a high of 25 in 2005 to 2 in 2007. Although nest numbers recovered fully by 2007, fledging of wild-reared chicks remained low for several years (Fig. 1). During 2006-2009 cranes initiated 123 nests but fledged only 5 wild-reared chicks compared to the 12 chicks fledged from 110 nests during 2002-2005. Although both releases of captive-reared birds and fledging of wild-reared chicks increased subsequently, the total refuge population did not fully recover from Hurricane Katrina until 2013, when the number of adults and subadults reached 107. Two other hurricanes, Georges (1998) and Nate (2017) made landfall in the vicinity of the refuge and were associated with higher-than-average annual mortality (17.4% and 11.6%, respectively) but did not result in detectable effects on total refuge population.

Year-end population count was best predicted by a model containing both the number of captive-reared chicks released and the number of wild-reared chicks fledged (r^2 = 0.31, P < 0.01, AIC = 169.9). Neither model containing only captive-reared or wild-reared chicks was within 2 ΔAIC of the best fit model. Regression coefficients suggested that number of wild-reared chicks fledged bore a stronger relationship to population size (coefficient ± 95% CI = 2.5 ± 0.37) than number of captive-reared chicks released (0.73 ± 1.5). Kaplan-Meier survival analysis showed that wild-reared chicks survived an average of 6.7 ± 1.1 (SE) years, whereas captive-reared chicks survived an average of 4.2 ± 0.2 years (Fig. 2). A log rank test revealed that survivorship of wild- and captive-reared chicks differed significantly (χ^2 = 6.9, df = 1, P = 0.009).

Weather and Predator Trapping

Environmental variables differed markedly in the degree to which they varied over the study period (Table 1). Coefficients of variation suggested that mean daily high temperature during the year and nesting season were relatively invariant, but the number of extreme heat days during nesting and chick-rearing seasons was far more variable (Table 1). Over the entire study period there were a total of 22 extreme heat days (daily high temperature 36°C and above) during nesting season ($\bar{x}$ = 0.9, range 0-8) and 153 that occurred during the chick-rearing period ($\bar{x}$ = 6.4, range 0-27). Measures of precipitation and drought exhibited intermediate levels of variation. The best fit model for annual population included a positive effect of nesting season precipitation and mean annual daily high temperature (coefficient ± SE = 0.279 ± 0.08 and 7.965 ± 3.889, respectively; P = 0.002 and 0.053, respectively; AIC = 177.05; Fig. 3; Table 2). No other models were within 2 ΔAIC. The best fit model for number of chicks fledged annually included only a significant inverse relationship with chick-rearing period extreme heat days

Table 1. Environmental conditions at Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, 1995-2018.

Parameter	Mean ± SE	Range	C.V.
Annual precipitation (cm)	177 ± 7.36	113-260	0.20
Annual mean daily high temperature (ºC)	26.3 ± 0.10	25.4-27.0	0.02
Annual mean Keetch-Byram Drought Index	321 ± 12.61	220-456	0.19
Nesting season precipitation (cm)[a]	71.1 ± 4.79	33.7-128.7	0.33
Nesting season mean high temperature (ºC)[a]	25.7 ± 0.15	24.8-27.2	0.03
Nesting season Keetch-Byram Drought Index[a]	262 ± 20.64	115-537	0.39
Previous year annual precipitation (cm)	176 ± 7.34	113-260	0.20
Extreme heat days during the chick-rearing period (May-Aug)[b]	6.38 ± 1.28	0-27	0.98
Nesting season extreme heat days[b]	0.92 ± 0.38	0-8	0.20

[a] Feb-Jun.
[b] Daily high temperature exceeding 36ºC.

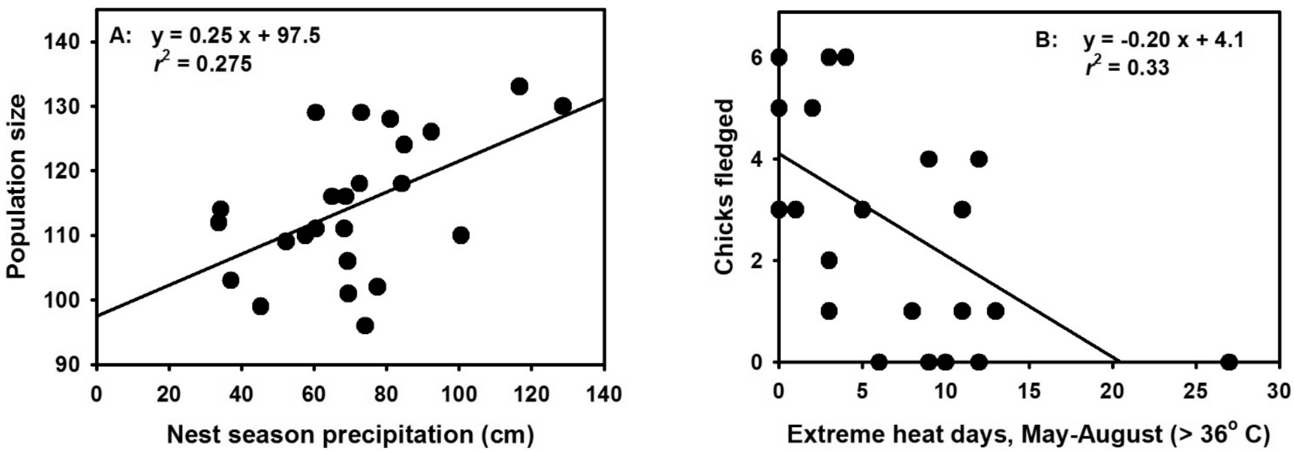

Figure 3. Relationship of Mississippi sandhill crane population size and number of chicks fledged annually to environmental variables on the Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, 1995-2018. A: Effect of nesting season (Feb-Jun) precipitation on total population size. B: Effect of extreme heat days during the chick-rearing period (May-Aug) on number of Mississippi sandhill crane chicks fledged annually.

(coefficient ± SE = –0.201 ± 0.061, P = 0.003, AIC = 101.42; Fig. 3; Table 2). No other models were within 2 ΔAIC. Nesting and annual mortality rate were unrelated to any measure of environmental variation.

A total of 1,022 mammals were trapped and removed from the refuge from November 2010 to March 2018, with annual totals ranging from 54 to 270 per trapping season (November-June). Of these, 768 were potential predators while 254 were Virginia opossums (*Didelphis virginiana*), which are not known to pose a threat to Mississippi sandhill crane chicks or eggs and were trapped accidentally. The most common predators removed were raccoons, coyotes, bobcats, and red fox (Table 3). Crane population size and estimated annual mortality were unrelated to any measure of predator trapping. The best fit model for number of chicks fledged annually included only a negative relationship with the number of current-year bobcats trapped (coefficient ± SE = –0.652 ± 0.194, P = 0.015, AIC = 32.61; Fig. 4). A model including the number of current-year bobcats trapped and the number of current-year raccoons trapped as separate terms had a lower AIC (31.33), but the term for raccoons was not significant (P = 0.172) and model ΔAIC was within 2 of the simpler model so this model was not chosen as the best fit. The number of chicks fledged annually was unrelated to any measure of previous-year predator trapping.

Nesting Patterns and Site Fidelity

The distribution of crane nests in management units with burn intervals of 0, 1, 2, 3, and 4 or more growing

Table 2. Generalized linear model analysis of environmental influences on Mississippi sandhill crane annual year end population size, annual nesting, and number of chicks fledged annually at Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, 1995-2018.

Model	Estimate	SE	*P*	AIC
Population				
Nesting season precipitation[a]	0.279	0.08	0.002	
Mean annual daily high temperature	7.965	3.889	0.053	
Model				177.05
Chicks fledged annually				
Extreme heat days during the chick-rearing period (May-Aug)[b]	-0.201	0.061	0.003	
Model				101.42

[a] Feb-Jun.
[b] Daily high temperature exceeding 36ºC.

Table 3. Mammals removed from Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, by trapping during 2011-2018 trapping seasons.

Predator	Total removed
Raccoon (*Procyon lotor*)	530
Virginia opossum (*Didelphis virginiana*)[a]	254
Coyote (*Canis latrans*)	159
Bobcat (*Lynx rufus*)	50
Red fox (*Vulpes vulpes*)	14
Gray fox (*Urocyon cinereoargenteus*)	7
Domestic dog	6
Feral cat	2
Total	1,022

[a] Not a known predator of Mississippi sandhill cranes.

seasons differed significantly from the availability of management units ($\chi^2 = 28.8$; $df = 4$; $P < 0.001$; Fig. 5). This pattern disappeared when management units burned 4 or more growing seasons previously were excluded from analysis ($\chi^2 = 2.35$; $df = 3$; $P = 0.50$), suggesting that cranes exhibited little preference among management units burned 0-3 growing seasons previously. The distribution of initial nest sites of new crane pairs also differed significantly from the distribution of management units with different burn intervals ($\chi^2 = 12.5$; $df = 4$; $P = 0.014$), but this difference again disappeared when units burned 4 or more growing seasons previously were excluded from the analysis ($\chi^2 = 1.80$; $df = 3$; $P = 0.60$). The proportion of nests that successfully fledged chicks did not differ significantly among management units with burn intervals of 0, 1, 2, 3, or 4 or more growing seasons ($\chi^2 = 2.16$; $df = 4$; $P = 0.71$; Fig. 5). The mean distance between consecutive nests constructed by a given pair was 410 ± 41 m ($n = 230$). Pairs constructed consecutive nests in management units of different burn intervals in 35 instances. In all 35 cases, cranes nesting near the border of 1 management unit moved into an adjacent management unit. Pairs were equally likely to move from 1 management unit into a more recently burned unit ($n = 22$) as into a unit burned longer ago ($n = 13$) ($\chi^2 = 2.31$; $df = 1$; $P = 0.13$).

DISCUSSION

Crane population size and reproductive performance increased during the study period, suggesting that management strategies aimed at increasing the wild population were generally effective. However, the rate of population increase was low compared to the number of birds added to the population through natural reproduction and supplemental releases. Natural reproduction and supplemental releases combined averaged 13.6 ± 1.1% of the annual population, but this was only slightly higher

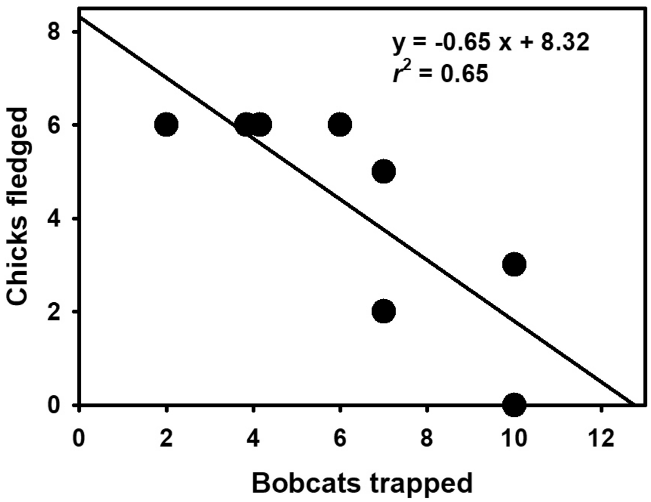

Figure 4. Relationship of number of Mississippi sandhill crane chicks fledged annually to number of bobcats trapped and removed from the Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, 2011-2018.

than the average annual mortality of 11.8 ± 1.7%. Our study identifies 3 factors that contributed to high mortality and the low rate of population growth: characteristics of individuals within the population, weather patterns, and predation.

One important factor limiting the growth of the population is the low survival rate of captive-reared birds. We estimated first-year survival at 69% and 5-year survival at 34%, which are very similar to survival estimates for captive-reared birds released on the refuge during 1989-1992 (72% and 42%, respectively; Ellis et al. 2001). However, the mean lifespan of captive-reared birds in our study (4.2 yr) was lower than the average age of first nesting in this population (5 yr). Mean lifespan of wild-reared birds was 60% greater (6.7 yr), suggesting that captive-reared birds may lack some survival skills learned by wild-reared birds. Deficiencies in behavior critical to post-release survival have been observed in captive-reared individuals in a number of *ex-situ* breeding programs, likely due to more restricted opportunities for social learning in captivity (Griffin et al. 2000, Griffin 2004). A previous study found that captive-reared cranes released to supplement the refuge population exhibited lower levels of antipredator defense behavior than wild-reared birds (Howard et al. 2016). Captive-reared fledglings may lack other behaviors that promote survival, and although the long lifespans of some captive-reared birds indicate that they can acquire the necessary skills, our data indicate that many birds are lost before they gain the necessary experience.

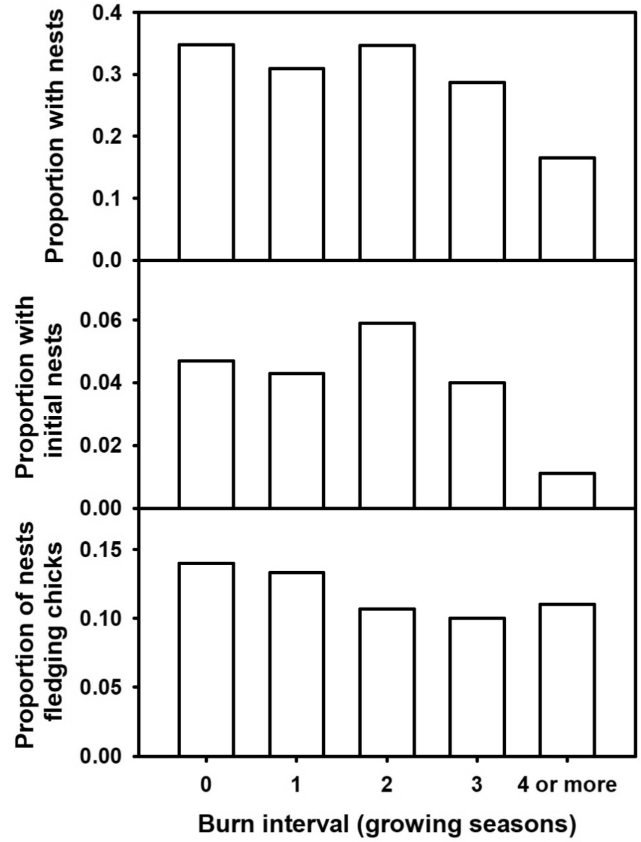

Figure 5. Mississippi sandhill crane nesting and fledging frequency in relation to burn interval of management units on the Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, 1995-2018: (Top) Proportion of available nesting territories with different burn intervals that had nests, (Middle) Proportion of available nesting territories with different burn intervals that had initial nests, (Bottom) Proportion of nests from territories with different burn intervals that fledged chicks.

Another constraint on growth of the population was the low rate of fledging among nesting pairs. Nesting rate increased approximately linearly with population size, suggesting that maturing birds are competent at acquiring mates and constructing nests, but the number of chicks fledged annually lagged, increasing at a much lower rate. The overall fledging rate was unchanged over the course of the study, suggesting that the observed increase in number of chicks fledged over time was due to an increase in number of nests rather than increased success in chick rearing. The fledging rate of 9.7% per pair was similar to the rate of 13.9 ± 8.4% documented for the Malheur National Wildlife Refuge population in Oregon over a 24-year period (Littlefield 2003) but was well below rates measured for some other sandhill crane populations. Fledging rates in non-migratory Florida sandhill cranes (*Grus canadensis pratensis*) have been estimated at 46% in the Okefenokee Swamp of Georgia (Bennett and Bennett 1990*a*) and at 35% in northcentral Florida (Nesbitt 1992). A majority of the Mississippi sandhill crane population (historically 75-85%) is derived from captive-reared birds. These captive-reared Mississippi sandhill cranes are known to display lower frequencies of antipredator defensive behavior than wild-reared Mississippi sandhill cranes (Howard et al. 2016). We suggest that low fledging rates may be due to a low frequency of behavior required to defend eggs and chicks from predators.

Population size was positively correlated with nesting season precipitation and annual mean daily high temperature, while number of chicks fledged annually was negatively related to extreme heat days during the chick-rearing period. These effects are consistent with previous studies showing significant relationships between crane population dynamics and weather. Florida sandhill crane recruitment and nest productivity during 1966-2006 were found to be negatively affected by drought conditions (Cox et al. 2020). Florida whooping crane nest productivity during 1992-2007 was negatively correlated with drought conditions (Folk et al. 2010) and positively correlated with winter precipitation (Spalding et al. 2009). Weather may act on crane populations through both direct and indirect mechanisms and it is likely that indirect effects on food availability have a major effect on population size. Grassland primary production is higher in warm, mesic conditions (Lauenroth 1979), increasing food availability for insects and for organisms that rely on them (Barnett and Facey 2016). It is not immediately clear why population size should be related specifically to nesting season precipitation, but we suspect that this may have the effect of increasing food supplies at a particularly stressful time for nesting pairs. The effect of extreme heat days during the chick-rearing period on number of chicks fledged annually is easier to understand since young birds with a high surface-to-volume ratio would be especially sensitive to heat loading. The relationship of fledging with chick-rearing period rather than nesting season extreme heat events suggests that incubating parents are able to maintain suitable conditions for egg development but that hatchlings may be more vulnerable to heat stress once they leave the nest.

Estimates of mortality were high for years in which hurricanes affected the refuge, but these impacts were variable and appear to be primarily due to indirect rather than direct effects. Only Hurricane Katrina in 2005 was associated with evidence of direct storm-related mortality or a decline in the number of adults and subadults. Hurricane Katrina generated wind speeds of 200 km/hour at Pascagoula, 15 km south of the refuge (Knabb et al. 2005), but only 2 birds were verified as likely storm-related deaths. In contrast, Hurricane Katrina reduced primary production by approximately 16% in grasslands of Mississippi (Ambinakudige and Khanal 2010), likely reducing the crane food supply over the following year. Such indirect effects may explain the high year-to-year mortality associated with other hurricanes in which no direct mortality could be verified. Population declines did not occur after every storm, and those beginning in 1995 and 2005 were associated with a decrease in release of captive-bred chicks in succeeding years. It is thus possible that these declines were due as much to a reduction in supplemental releases of captive-reared chicks as to hurricane impacts. During 1995-1997 the captive population was moved from Patuxent Wildlife Research Center in Laurel, Maryland, to Audubon Species Survival Center in New Orleans, Louisiana, and White Oak Conservation in Yulee, Florida, which caused the drop in release numbers in 1996 and 1997. There is a correlation between Hurricane Katrina and the drop of release numbers in 2006. All the chicks that were at Audubon Species Survival Center in 2005 at the time of Hurricane Katrina were transferred to White Oak Conservation after the storm. There were no chicks reared or released from Audubon Species Survival Center in 2006 due to recovery from the storm (R. Dunn, Audubon Species Survival Center, personal communication). Although tropical storms appeared to increase mortality, this effect was transient and had relatively small effects on overall population trends compared to other factors.

Although numerous mammalian species are known to prey on sandhill crane eggs and young, we only found evidence for a negative relationship between the number of chicks fledged annually and the number of bobcats trapped on the refuge. Avian predators are known to be a threat to Mississippi sandhill cranes, but we lack data related to the amount of predation from avian predators, and avian predators are not included in refuge predator trapping. The observed pattern of the number of chicks fledged annually decreasing as the number of bobcats trapped increased could indicate that more bobcats trapped correlates with larger bobcat populations on the refuge. Data related to trapping effort and trapped bobcat age would have been useful to determine whether years with more bobcats trapped were indicative of either an increasing bobcat population with younger animals or older animals that have learned about crane chicks as prey. Our evidence is circumstantial, since we do not have direct estimates of bobcat density and rely instead on trapping records as a proxy for bobcat occurrence. However, bobcats were known or suspected to be responsible for 25 instances of predation on the refuge during the study period, based on direct observation or the presence of tracks and prey caches at kill sites. This suggests that bobcats are indeed an important predator of cranes and is consistent with previous studies documenting bobcat predation on sandhill cranes in Georgia (Bennett and Bennett 1990*b*) and on whooping cranes in Florida (Nesbitt et al. 1997, 2001). Although circumstantial, the evidence suggests that bobcat predation on young birds is likely to significantly reduce the number of chicks fledged annually.

Predation on sandhill crane adults, chicks or eggs has been documented for 3 other mammalian predators trapped during this study, including coyotes (Littlefield and Lindstedt 1992; Littlefield 1995, 2003; Nesbitt and Badger 1995), raccoons (Bennett and Bennett 1990*a*; Littlefield 1995, 2003), and red foxes (Drieslein and Bennett 1979), but relative abundance of these species estimated from trapping records bore no relationship to crane population size or number of chicks fledged annually. This could be related to the abundance of these species; both raccoons and coyotes were common in trap samples and may have maintained dense populations that exerted consistent pressure on cranes regardless of numbers removed, while red fox were infrequently trapped and may not have been common enough to consistently prey on cranes. Alternatively, Littlefield (1995) found that the incidence of nest predation by raccoons increased in years of low coyote density, suggesting the possibility of direct competition between these species, or coyotes excluding raccoons from their foraging territories. An inverse relationship between densities of raccoons and coyotes might result in compensatory predation on cranes, which could produce consistent losses despite fluctuation in the density of each species. However, our data show a positive correlation between annual take of raccoon and coyote ($r = 0.885$), making it unlikely that compensatory predation explains the lack of relationship between population parameters and the number of trapped raccoons or coyotes.

Given the importance of predation by coyotes and raccoons in previous studies, we suspect that the differing impacts of bobcats, raccoons, and coyotes found in this study may stem from differences in population density on the refuge and the relative frequency of predation on eggs versus chicks. Raccoons and coyotes most often consume eggs (Littlefield 1995, 2003), while bobcats appear to most often take chicks and occasionally adults (Bennett and Bennett 1990*b*). Large populations of raccoons and coyotes may exert relatively consistent rates of nest predation regardless of the number of predators trapped in any given year, while having little influence on fledging rates due to cranes' ability to renest. In contrast, a smaller and more variable bobcat population may produce fledgling death rates more closely tied to bobcat abundance. Although we found no indication that crane population metrics were related to occurrence of coyotes or raccoons, we do not believe that this means that they have no impact and suggest that further study may be required to clarify their role in the dynamics of the crane population.

Prescribed burning is the primary management tool used to maintain savanna habitat for Mississippi sandhill cranes, but cranes showed surprisingly broad patterns of habitat use across management units with differing burn intervals. Although nesting pairs preferred more recently burned areas for both their initial and subsequent nests, they primarily discriminated between areas burned less than or more than 4 years previously. Cranes nested infrequently in less recently burned areas, but the number of chicks fledged annually from these nests was comparable to that of more recently burned areas. This suggests that overall habitat quality in terms of resources required for successful reproduction may be broadly comparable in both areas. The avoidance of areas burned 4 or more years previously may be due instead to the post-fire regrowth of woody vegetation in these areas, which would tend to restrict crane movement and visibility.

Patterns of nest fidelity are also consistent with the idea that areas with different burn intervals are generally suitable for successful nesting. Refuge management units are not perfectly aligned with crane territories, with many crane territories extending beyond the boundaries of their associated management unit; however, the core of any given crane territory will be in the associated management unit and most of the territory use will be inside that unit. Although pairs that changed management units between nests tended to choose more recently burned units, only 6% (31 of 518) of successive nests were established in new management units burned more recently than the previous unit. Crane pairs did not appear to make detailed assessments of nest site conditions and move to optimal areas, but instead appeared to be highly philopatric to areas in which they initially nested. Pairs tended to move only small distances between nest sites and generally established nests within the same management unit repeatedly regardless of the burn interval. The behavior of nesting pairs was most consistent with initial home range selection by young birds prior to the onset of breeding, with fidelity to the home range generally overriding current conditions for nest site selection.

Overall, our results suggest that both biotic (predation) and abiotic (temperature and rainfall) factors were major drivers of change in the Mississippi sandhill crane population during the study period. Abundant nesting season rainfall and moderate temperatures, along with low populations of a key predator, the bobcat, appear to be the major factors promoting population increase. Climate change is likely to produce higher temperatures and more extreme heat events, as well as greater variability in rainfall (Ummenhofer and Meehl 2017), presenting greater challenges to effective management of the refuge population in the future. However, consistent predator control, promoting enhanced behavioral competence through enrichment in the captive breeding program, and fire management to maintain or increase suitable nesting habitat offer avenues to offset the deleterious effects of climate change. In 2019 fledging of wild-reared chicks reached a historic high of 15 and 28.8% of nests produced fledglings, nearly triple the historical average. This jump was likely a reflection of concerted efforts over the past decade to increase habitat area and quality, promote appropriate crane behavior, and control predators. Future management strategies should include solutions for potential issues surrounding long-term predator removal such as ecosystem side-effects, cost, and changing societal values. It seems likely that the Mississippi sandhill crane population is capable of attaining production rates comparable to other wild populations, and we believe that continued investment in these strategies can further increase the number of wild-reared chicks fledged annually and ultimately achieve the goal of a self-sustaining wild population even in the face of rising challenges from climate change.

ACKNOWLEDGMENTS

We thank A. Dedrickson and J. Twiss for assistance in collating data used in this study, J. Grace for assistance with study design and guidance with statistical analysis, and B. Shipley for guidance with statistical analysis. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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