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Ecological Factors Influencing Population Dynamics of the Mississippi Sandhill Crane, Grus canadensis pulla

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Ecological Factors Influencing Population Dynamics of the Mississippi Sandhill Crane, *Grus canadensis pulla*

A Dissertation

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy
in
Integrative Biology

by

Henry W. Woolley

B. S. University of Rochester, 2007

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Abstract

My dissertation encompasses three studies involving ecological factors influencing the Mississippi sandhill crane (*Grus canadensis pulla*) population at Mississippi Sandhill National Wildlife Refuge. To examine influences on the historical population I studied trends in nesting, number of chicks fledged annually, and their environmental and biotic drivers during 1991-2018. I expected precipitation to be positively associated with population measures and drought, extreme heat, and predation to be inversely related to population measures. To examine the influence of current habitat food production on the crane population I quantified measures of production in 2018 and 2019 and their relationship to time since an area was burned and crane population dynamics from 1991-2019. I expected measures of habitat food production to be positively associated with crane population measures and inversely related to time since burn. To examine the relationship between land cover, predation, and crane population I used geographic information system (GIS) analysis to classify land cover characteristics and relate those to crane population dynamics and predator trapping during 2018, 2016, 2014, and 2012. I expected to discover a decrease in chick fledging in areas with more edge habitat due to increased predation risk associated with habitat edges. Population size, number of nests, and number of chicks fledged annually increased significantly from 1991-2019. Total population size was positively related to nesting season precipitation, while the number of chicks fledged annually was negatively related to number of extreme heat days from June to August and estimates of bobcat occurrence. The number of chicks fledged annually occurred with approximately equal frequency across management units burned at different times prior to nesting. Herbaceous production bore no relationship to time since burn or arthropod production. Nesting was positively associated with orthopteran density, but number of wild-hatched chicks fledged
annually was unrelated to the production of vegetation or arthropods. I detected no increase in predation related to habitat edge effect. The results indicate that both biotic and abiotic factors drive population dynamics on the refuge and suggest that continued attention to prescribed burns and predator removal is necessary for the establishment of a self-sustaining wild population in the future.

Keywords: arthropod, climate, edge effect, GIS, land cover, orthoptera, production, predators
General Introduction

It has long been known that successful conservation of endangered species requires an understanding of multiple aspects of their biology, including genetics, behavior, and ecology (Soule 1985; Soule and Kohm 1989). Endangered species populations are often small and lack genetic diversity and are thus more vulnerable to loss of viability due to inbreeding depression (Avise 1988). Defining the genetic makeup of endangered species populations can guide strategies for conserving genetic diversity, identify individuals of high genetic value, and optimize the value of ex-situ breeding programs (O’Brien 1994). Assessment of behavior can be an important component to understanding how organisms react to threats and opportunities in their environment. It can be used to identify desirable behaviors that promote survival and undesirable ones that increase vulnerability, and to devise training programs to maximize survival probability of captive-bred individuals after release (Caro 1998, Gosling and Sutherland 2000, Berger-Tal and Saltz 2016). Ecological investigations can quantify the demographic processes that govern population growth or decline, identify crucial interactions involving habitat, food, predators, and parasites, and assess the potential for persistence in current environments or colonizing new ones (Brussard 1991).

The Mississippi Sandhill Crane (*Grus canadensis pulla*) is a federally endangered species that exemplifies the need for an interdisciplinary approach to species conservation because of the influences of genetics, habitat management, and predation on the population. The Mississippi sandhill crane currently exists in a single small population on the Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) in Jackson County, Mississippi (Gee and Hereford 1995). The population is a relict of a formerly contiguous non-migratory population extending from Florida to east Texas and is genetically differentiated from the remaining non-migratory flock in
Florida (Jones et al. 2010). Initially described as a separate subspecies in 1972 (Aldrich 1972), it was listed as endangered by the U. S. Fish and Wildlife Service in 1973. As a result, the MSCNWR was created in 1974 under the authority of the Endangered Species Act (ESA) to maintain suitable habitat for Mississippi sandhill cranes (Gee and Hereford 1995, USFWS 2007). The population size fell to a low of 40 individuals during the 1960s (Valentine and Noble 1970), which prompted the establishment of a captive breeding program. Beginning in 1965, the US Fish and Wildlife Service partnered with the Patuxent Wildlife Research Center to raise Mississippi sandhill cranes in captivity. Captive-reared cranes began to be released on the refuge in 1981, which led to an increase in the wild population from 50 cranes in 1981 to a high of 135 cranes in 1993 (Gee and Hereford 1995). With annual supplementation from captive-reared juveniles, the crane population held steady at 100-120 from 1991-2012, with a recent slight increase to over 130, due mainly to increased recruitment and protection from predators (Hereford and Dedrickson 2018).

Most genetic analyses of the population have focused on analysis of the phylogenetic relationships between Mississippi sandhill cranes and other North American sandhill crane populations using allozymes (Dessauer et al. 1992), mitochondrial DNA (Rhymer et al. 2001) and DNA microsatellites (Jones 2003). In addition, a detailed study of kinship structure using DNA microsatellites was used to map relatedness within the wild and captive populations and revise the studbook used for captive breeding (Henkel et al. 2012). These studies have explored the genetic distinctness of the MSC population and established that alleles in the population are a nested subset of those in Florida, consistent with loss of alleles through drift rather than local adaptation (Henkel et al. 2012). Revisions to the studbook have been used to guide selection of eggs for rearing by foster parents in the captive breeding program to preserve genetic diversity in
the population.

Crane behavior relevant to conservation planning has also been studied in the MSC population, primarily in an effort to understand factors contributing to low rates of fledgling survival on the refuge. Analysis of nesting behavior revealed that captive-reared individuals released on the refuge displayed relatively low rates of nest defense behavior compared to wild-reared birds (Howard et al. 2016). Similar behavioral deficits are common in many species where individuals bred in captivity are used to supplement wild populations. These problems are commonly attributed to the restricted environment, altered social relationships, and limited opportunities for social learning experienced during captive rearing (Curio 1998). As a result, an experimental program to expose captive-reared chicks to predator models has been implemented so that captive-reared birds experience nest defense behaviors expressed by foster parents (Howard et al. 2018).

In this dissertation I explore the ecological correlates of trends in the Mississippi sandhill crane population. The number of nesting pairs has increased relatively slowly, and the number of fledglings added to the population has increased at an even slower rate. The number of chicks fledged per pair has been nearly constant during this time; low chick survival, and thus low recruitment, is the main factor limiting a self-sustaining population (S. G. Hereford, pers. comm.). Ecological relationships between cranes and their food sources, predators, and habitat are not well understood, and may help to explain the relatively slow growth of the population since the supplemental breeding program began 40 years ago.

My first chapter focuses on historical population trends related to weather, predator abundance, and nesting habits of cranes to determine if the population has been affected by large-scale processes operating over long time frames. In this chapter I relate reproduction,
survival, and population growth to annual weather patterns, predator abundance estimated from trapping records, and patterns of fire management. It may be expected that population trends are positively correlated to trends in precipitation and inversely correlated with predator abundance. In chapter 2 I examine the relationship between reproduction and small-scale patterns of food availability. Specifically, I ask how primary production and arthropod availability are related to fire interval, and whether food availability affects the probability of successful fledging by nesting crane pairs. In Chapter 3 I ask how predator occurrence is related to land cover features and whether fledging success is related to land cover features or to proximity of nests to areas of high predator incidence. By evaluating ecological processes at varying scales in these three chapters, I aim to identify interactions and habitat features that have a strong influence on nesting and fledging success. Greater knowledge about which factors influence population dynamics will provide a sound basis for decisions about habitat and predator management and help to achieve the long-standing goal of establishing a self-sustaining wild Mississippi sandhill crane population.
Literature Cited


Chapter 1: Drivers of annual fledging success in the Mississippi sandhill crane population, 1991-2018

Introduction

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 (Cox et al. 2020, Folk et al. 2010, Gee and Hereford 1995). Efforts to synthesize information on factors influencing long-term population trends are uncommon. 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 chapter I examine trends in the Mississippi sandhill crane population during 1991-2018 and evaluate biotic and abiotic factors that may influence those trends. Mississippi sandhill cranes forage and nest primarily in wet pine savanna habitat characterized by few coniferous trees per acre and dominated by grasses and forbs (Gee and Hereford 1995, US Fish and Wildlife Service 2007). 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, US Fish and Wildlife Service 2007). The captive rearing program involves a partnership between the refuge and the Freeport-McMoRan Audubon Species Survival Center in New Orleans, Louisiana and White Oak Conservation Center in Yulee, Florida which conduct 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 hand-reared. Juveniles are released at the refuge in November of their hatch year after they have fledged (Ellis et al. 2000).

The refuge maintained detailed locality-specific records on nesting, reproductive outcomes, weather, fire management, and predator removal during the study periods, allowing me to examine multiple potential drivers of population trends. Specifically, I asked how weather and apparent predator occurrence affected estimated population size, nesting, mortality, and number of chicks fledged annually over time. I expected population trends to respond positively to measures of rainfall and negatively to measures of predator occurrence. I also asked how crane nesting behavior and number of chicks fledged annually were related to prescribed burning of management units, 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 (Chamberlain et al. 2003, Jones et al. 2004, Jones et al. 2002, Littlefield et al. 2001). I 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 Area

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 2007). The refuge is divided into 103 management units (mean 72.4 ha, range 14.0 to 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 I limited each analysis to time periods for which data were available. I 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. 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. The number of captive-reared juveniles released on the refuge each year was obtained from records maintained by refuge staff. I calculated an estimate of annual
adult 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 zero 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 I 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. I 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 mesopredators 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 two 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 around 70-80 days post hatch and remain with their parents for around 10 months. Traps were targeted primarily in areas identified as having high predator activity by refuge staff.
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 using their unique leg band color combination through field observation and camera monitoring. I defined the number of growing seasons since a management unit had a prescribed burn as the burn interval. I 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 zero growing seasons since the last burn and thus having a burn interval of zero.

Statistical Analyses

Statistical analyses were carried out in R version 3.5.0 (R Core Team, 2018). I calculated regressions 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. I 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. I 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. I 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 nine environmental factors on three 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. I 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, I 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; I 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, I 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-Lepczyzyk et al. 2016, Rockwell et al. 2012, Carstens et al. 2019). Therefore, I 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 I 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. I 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 detect lag effects. I analyzed the relationship between all three population parameters and all predators summed, and for the four most numerous predators: bobcats (*Lynx rufus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and red fox (*Vulpes vulpes*). Current-year and previous-year trapping data were 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, I 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 from 1991-2018. To determine if pairs nesting for the first time showed a preference for recently burned management units, I compared nesting territory availability of management units with different burn intervals to locations of 87 first-time nests by newly formed pairs. I used Chi-square tests with the R function Chi-square to compare frequency of nesting in units with burn intervals of 0, 1, 2, 3, and 4 or more years. I also used Chi-square tests to determine whether the number of nests producing fledglings varied significantly with burn interval.
I examined nest site fidelity of 62 pairs in which both members were positively identified and that nested in two or more consecutive years in georeferenced locations. I used UTM coordinates of 292 nests to calculate the mean distance between consecutive nests produced by a pair. I also tallied instances in which pairs changed the location of consecutive nests between management units with different burn intervals. I 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.

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 individuals (Figure 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 (Figure 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 ($r^2 = 0.66, P < 0.001$), and although annual variability was high, the number of chicks fledged annually increased by 0.14 per year ($r^2 = 0.18, P = 0.023$). 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 adult 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 two periods of decline, 1995-97 and 2005-9 (Figure 1). Both declines were associated with landfalling 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 1995-1997 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 in 2005 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 (Figure 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 (Figure 1). From 2006-2009 cranes initiated 123 nests but fledged only 5 wild-reared chicks compared to the 12 chicks fledged from 110 nests from 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 size.
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; Captive-reared chicks; Wild-reared chicks.
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 nor wild-reared chicks were 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 years, whereas captive-reared chicks survived an average of 4.2 ± 0.2 years (Figure 2). A log rank test revealed that survivorship of wild- and captive-reared chicks differed significantly ($\chi^2 = 6.9$, $df = 1$, $P = 0.009$).

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.
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).

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

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

† February-June
†† Daily high temperature exceeding 36°C

Over the entire study period there were a total of 22 extreme heat days (daily high temperature 36°C and above) during nesting season (mean 0.9, range 0-8) and 153 that occurred during the chick-rearing period (mean = 6.4, range 0-27). Measures of precipitation and drought
exhibited intermediate levels of variation. The best fit model for annual population size included a positive effect of nesting season precipitation and mean annual daily high temperature (coefficient ± standard error = 0.279 ± 0.08 and 7.965 ± 3.889 respectively, $P = 0.002$ and 0.053, respectively, AIC = 177.05; Figure 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 (coefficient ± standard error = -0.201 ± 0.061, $P = 0.003$, AIC = 101.42; Figure 3; Table 2). No other models were within 2 ΔAIC. Nesting and annual morality rate were unrelated to any measure of environmental variation.

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 (February-June) precipitation on total population size. B: Effect of extreme heat days during the chick-rearing period (May-August) on number of chicks fledged annually.
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, during 1995-2018.

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimate</th>
<th>Std Error</th>
<th>$P$</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nesting season</td>
<td>0.279</td>
<td>0.08</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>precipitation†</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean annual daily high temperature</td>
<td>7.965</td>
<td>3.889</td>
<td>0.053</td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td></td>
<td></td>
<td></td>
<td>177.05</td>
</tr>
<tr>
<td>Chicks Fledged</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annually</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extreme heat days during the chick-rearing period (May-August) ††</td>
<td>-0.201</td>
<td>0.061</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td></td>
<td></td>
<td></td>
<td>101.42</td>
</tr>
</tbody>
</table>

† February-June
†† Daily high temperature exceeding 36°C

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).

<table>
<thead>
<tr>
<th>Predator</th>
<th>Total removed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raccoon (<em>Procyon lotor</em>)</td>
<td>530</td>
</tr>
<tr>
<td>Virginia opossum (<em>Didelphis virginiana</em>)*</td>
<td>254</td>
</tr>
<tr>
<td>Coyote (<em>Canis latrans</em>)</td>
<td>159</td>
</tr>
<tr>
<td>Bobcat (<em>Lynx rufus</em>)</td>
<td>50</td>
</tr>
<tr>
<td>Red fox (<em>Vulpes vulpes</em>)</td>
<td>14</td>
</tr>
<tr>
<td>Gray fox (<em>Urocyon cinereoargenteus</em>)</td>
<td>7</td>
</tr>
<tr>
<td>Domestic dog (<em>Canis familiaris</em>)</td>
<td>6</td>
</tr>
<tr>
<td>Feral cat (<em>Felis catus</em>)</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>1,022</td>
</tr>
</tbody>
</table>

*Not a known predator of Mississippi sandhill cranes

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 ± standard error = -0.652 ± 0.194, \( P = 0.015 \), AIC = 32.61; Figure 4; Table 4). A model including the number of current-year bobcats plus raccoons trapped had a lower AIC (31.33), but the term for raccoons was not significant and model ∆AIC was within 2 of the simpler model (Table 4) 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.
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.

Table 4. Generalized linear model analysis of current-year predator trapping influences on number of Mississippi sandhill crane chicks fledged annually at Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, during 2011-2018.

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimate</th>
<th>Std Error</th>
<th>P</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bobcats trapped</td>
<td>-0.652</td>
<td>0.194</td>
<td>0.015</td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td></td>
<td></td>
<td></td>
<td>32.61</td>
</tr>
<tr>
<td>Bobcats trapped</td>
<td>-0.923</td>
<td>0.243</td>
<td>0.013</td>
<td></td>
</tr>
<tr>
<td>Raccoons trapped</td>
<td>0.03</td>
<td>0.019</td>
<td>0.172</td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td></td>
<td></td>
<td></td>
<td>31.33</td>
</tr>
</tbody>
</table>
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 seasons differed significantly from the availability of management units ($\chi^2 = 28.8; df = 4; P < 0.001$; Figure 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, but preferred those over units burned 4 or more 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 four 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 ($\chi^2 = 2.16; df = 4; P = 0.71$; Figure 5). The mean distance between consecutive nests constructed by a given pair was $410 \pm 41$ 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 one management unit moved into an adjacent management unit. Pairs were equally likely to move from one management unit into a more recently burned unit ($n = 22$) as into a unit burned longer ago ($n = 13$) ($\chi^2 = 2.31; df = 1; P = 0.13$).
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.
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 than the average annual mortality of 11.8 ± 1.7%. My study identifies three 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. I estimated first year survival at 69% and five-year survival at 34%, which are very similar to survival estimates for captive-reared birds released on the refuge from 1989-1992 (72% and 42% respectively; Ellis et al. 2001). However, the mean lifespan of captive-reared birds in my study (4.2 years) was lower than the average age of first nesting in this population (5 years). Mean lifespan of wild-reared birds was 60% greater (6.7 years), 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 exhibit 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, my data indicate that many birds
are lost before they gain the necessary experience.

Another constraint on growth of the population was the low rate of fledging success 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 is well below rates measured for other sandhill crane populations. Fledging rates in non-migratory Florida sandhill cranes \((\text{Antigone canadensis pratensis})\) have been estimated at 46% in the Okefenokee swamp of Georgia (Bennett and Bennett 1990\(a\)) and at 35% in northcentral Florida (Nesbitt 1992). Migratory sandhill crane \((\text{Antigone canadensis})\) populations may have fledging rates exceeding 80% per pair (Dimatteo 1992, Burke 2003) but fledging rates of the Malheur National Wildlife Refuge population in Oregon over 24 years were more comparable to those in this study, averaging 13.9 \(\pm\) 8.4% (Littlefield 2003). A majority, historically 75-85%, of the refuge population is derived from captive-reared birds, which are known to display lower frequencies of antipredator defensive behavior than wild-reared birds (Howard et al. 2016). I 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 from 1966-2006 were found to be negatively affected by drought conditions (Cox et al. 2020). Florida whooping crane nest productivity from 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 positively related specifically to nesting season precipitation, but I 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 effect of chick-rearing period rather than nesting season extreme heat events on fledging success 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 kph 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. From 1995-1997 the captive population was moved from Patuxent Wildlife Research Center in Laurel, MD to Audubon Species Survival Center in New Orleans, LA and White Oak Conservation in Yulee, FL, which caused the drop in release numbers in 1996 and 1997. Similar disruption to the supplemental breeding program occurred after Hurricane Katrina 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, personal communication, August 25, 2021).

Although tropical storms appeared to increase mortality in the refuge population, their direct effects were transient and relatively minor compared to other factors.

Although numerous mammalian species are known to prey on sandhill crane eggs and young, I 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 I lacked data required to evaluate their impact. The negative relationship between the number of chicks fledged annually and the number of bobcats trapped suggests that bobcats are the most important predator of crane chicks on the refuge. My evidence is circumstantial, since I do not have direct estimates of bobcat density and rely instead on trapping records as a proxy for bobcat occurrence. However, bobcats are 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 crane chicks and is consistent with previous studies
documenting bobcat predation on sandhill cranes in Georgia (Bennett and Bennett 1990b) 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 three other
mammalian predators trapped during this study, including coyotes (Littlefield 1995, 2003,
Littlefield and Lindstedt 1992, Nesbitt and Badger 1995), raccoons (Bennett and Bennett 1990a,
Littlefield 1995, 2003), and red foxes (Drieslein and Bennett 1979), but the 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, my 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, I 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 1990b). 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. They also may have comparatively 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 I found no indication that crane population metrics were related to occurrence of coyotes or raccoons, I 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. Understanding the spatial and temporal population dynamics of these key predator species, along with those of alternative prey such as rabbits or mice, could provide important insight.

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 proportion 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 is most consistent with initial home range selection based on a general assessment of habitat quality by young birds prior to the onset of breeding, with fidelity to the home range generally overriding yearly conditions for nest site selection.

Overall, my 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 is 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 I 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.
Literature Cited


https://doi.org/10.5751/ACE-01519-150107


animals to avoid predators. Conservation Biology 14:1317-1326.


Chapter 2: Primary production, arthropod abundance, and nesting success of Mississippi sandhill cranes

Introduction

Primary production is regarded as a significant predictor of habitat quality in many systems because it regulates carbon and energy availability for animals and governs production at higher trophic levels (Chapin et al. 2012). Primary production may regulate biomass at higher trophic levels through food limitation in bottom-up trophic cascades (White 1978, Hunter and Price 1992). It is generally expected that primary production should influence the diversity and biomass of higher trophic levels, including insects (Hutchinson 1959). However, the relationship between production and insect biomass is not straightforward (Yang et al. 2017, Asmus et al. 2018). Although increases in primary production may increase biomass of arthropod consumers and higher trophic levels through bottom-up regulation (Hurd and Wolf 1974, Kirchner 1977, Siemann 1998, Haddad et al. 2000, Gruner and Taylor 2006, Wimp et al. 2010, Lind et al. 2017), the exact impact of changing production depends on plant palatability (Asmus et al. 2018) and whether insects consume fast or slow-decomposing species (Belovsky and Slade 2018). In addition, vegetation alters soil microclimate, and higher primary production may suppress insect biomass through changes in physical environment (Yang et al. 2017). Changes in primary production at a given site may thus either increase or decrease insect biomass or alter insect community composition rather than biomass (Asmus et al. 2018). These studies suggest that the effects of primary production on higher trophic levels are not generally predictable and must be evaluated for each site on a case-by-case basis.

Birds rely on insects as primary prey (Nyffeler et al. 2018), and insectivorous bird population numbers and reproductive ability are affected by insect availability (Narango et al. 2018). However, the exact relationships between bird population dynamics, insect biomass, and
primary production are poorly known in most systems. This gap in knowledge can be particularly troublesome for bird conservation efforts. Management programs aimed at providing high-quality bird nesting habitat generally rely on manipulating habitat structure to provide suitable resources. The effects of habitat manipulation may be difficult to assess because of the inter-relatedness of many habitat elements. Understanding how management strategies alter primary production, and whether insect availability is either directly or indirectly affected, can enhance the viability of insectivorous bird populations.

The Mississippi sandhill crane is an endangered subspecies found only on the Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) in Jackson County, Mississippi. The refuge is managed through controlled burning to maintain savannas favorable for the support of the wild population of the Mississippi sandhill crane (Hereford 1994). Gulf Coast grasslands are adapted to frequent fire intervals of 2-3 years (Stambaugh et al. 2011) and in the absence of periodic fire, encroachment of woody vegetation begins to transition grassland to shrubland in a few years (Briggs et al. 2005). Terrestrial orthopterans (e.g., grasshoppers, crickets, and katydids) and some Coleoptera are common in the wet pine savannas of MSCNWR and are thought to be an important part of the crane diet, especially during nesting season as a source of protein for growth of crane chicks (USFWS 2007). Defining the relationships between fire, primary production, insect abundance, and breeding success is essential to devising effective habitat management strategies for the Mississippi sandhill crane population.

In this study I explored the links between primary production, arthropod biomass, and orthopteran density in a subtropical savanna in Mississippi. I asked if these measures vary according to schedules of prescribed burning, and whether they influence the probability of crane chicks fledging (developing feathers capable of flight) at MSCNWR. Fledging was used because
after fledging colts (young sandhill cranes) are less vulnerable to predation and thus can be expected to be recruited into the population. Much effort has been devoted to measuring primary production in grasslands in both temperate and tropical environments (French 1979), but the subtropical savannas of the Gulf Coastal plain have received little attention to date. Most studies of Gulf savannas focus on vegetation structure and diversity and the influence of fire regime on species richness (Keddy et al. 2006, Platt et al. 2006, Glitzenstein et al. 2012). Primary production is known to vary substantially from year to year in other temperate grassland ecosystems according to fire regime (Briggs and Knapp 1995, Heisler and Knapp 2008) and production generally increases due to nutrient release after fire with a delay of variable length (Senthilkumar et al. 1998, Lett and Knapp 2005).

I first estimated primary production of the savanna graminoid community in management compartments burned at varying intervals prior to sampling. I also estimated total arthropod biomass and orthopteran density and identified the major species of Orthoptera present in the savannas at MSCNWR. I predicted that primary production would peak in the second or third year after burning due to a lag effect, while arthropod biomass and orthopteran density would peak in the first year after burning due to increased nutrient availability in new growth.

I then asked if patterns of primary production and arthropod biomass and orthopteran density were related to the probability of successful fledging of chicks produced by crane pairs nesting in sampled management compartments. I also asked whether there was evidence that patterns of production were related to historical variation in fledging success among management compartments. Historically, different areas of MSCNWR have seen varying occurrences of nesting and fledging of Mississippi sandhill cranes (Table 5). A strong relationship between primary production, arthropod biomass, or orthopteran density and current or historical fledging
success would be evidence that variation in food availability is an important determinant of population dynamics at MSCNWR and would improve the basis for future management decisions. I predicted that both current and historical fledging success would be positively related to orthopteran density, and possibly to primary production and arthropod biomass as well because cranes use roots and tubers of herbaceous vegetation as a food source (Iverson et al. 1982) and can be expected to rely on arthropods other than orthopterans as well.
Table 5. Comparison of nesting and fledging numbers by management compartment at Mississippi Sandhill Crane National Wildlife Refuge, Gautier, Mississippi, during 1991-2018.

<table>
<thead>
<tr>
<th>Compartment</th>
<th>Nests</th>
<th>Chicks fledged</th>
<th>Proportion fledged</th>
</tr>
</thead>
<tbody>
<tr>
<td>G-06</td>
<td>76</td>
<td>13</td>
<td>0.17</td>
</tr>
<tr>
<td>G-12</td>
<td>39</td>
<td>8</td>
<td>0.21</td>
</tr>
<tr>
<td>G-14</td>
<td>34</td>
<td>4</td>
<td>0.12</td>
</tr>
<tr>
<td>O-06</td>
<td>33</td>
<td>5</td>
<td>0.15</td>
</tr>
<tr>
<td>G-11</td>
<td>31</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>G-15</td>
<td>31</td>
<td>5</td>
<td>0.16</td>
</tr>
<tr>
<td>O-03</td>
<td>29</td>
<td>4</td>
<td>0.14</td>
</tr>
<tr>
<td>G-02</td>
<td>27</td>
<td>1</td>
<td>0.04</td>
</tr>
<tr>
<td>G-08</td>
<td>24</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>O-05</td>
<td>21</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>G-03</td>
<td>18</td>
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<td>0.00</td>
</tr>
<tr>
<td>O-16</td>
<td>17</td>
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<td>0.12</td>
</tr>
<tr>
<td>F-02</td>
<td>16</td>
<td>1</td>
<td>0.06</td>
</tr>
<tr>
<td>O-02</td>
<td>13</td>
<td>3</td>
<td>0.23</td>
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<td>G-16</td>
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<td>0.00</td>
</tr>
<tr>
<td>O-10</td>
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<td>0.18</td>
</tr>
<tr>
<td>G-19</td>
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<td>2</td>
<td>0.20</td>
</tr>
<tr>
<td>F-03</td>
<td>8</td>
<td>0</td>
<td>0.00</td>
</tr>
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Methods

Study Area

This study was conducted during 2018-2019 on the Mississippi Sandhill Crane National Wildlife Refuge. The refuge consists of 7,450 hectares of wet pine savanna in Jackson County, Mississippi. It is composed of three major units, Fontainebleau, Ocean Springs, and Gautier; each unit is further subdivided into management compartments to facilitate vegetation management via prescribed burning. Management compartments generally contain large areas of wet savanna interspersed with individual occurrences or scattered stands of longleaf pine (*Pinus palustris*). Some areas, particularly along watercourses or in infrequently burned compartments, are characterized by a dense shrub layer or tree stands dominated by slash pine (*Pinus elliottii*) and mixed hardwoods.

Sampling locations were selected in consultation with refuge staff to provide wide geographic coverage of the refuge and to include management units at different stages in the burn cycle. Crane nesting and fledging location data were provided by refuge staff. A total of 30 management compartments were sampled, 15 each in 2018 and 2019 (Figure 6). Compartments on Ocean Springs and Gautier units were sampled in both years, while the smaller Fontainebleau unit was sampled only in 2018. The compartments represent every area of the refuge save for the isolated block of the Ocean Springs unit south of Interstate Highway 10 (Compartments O-11, O-12, and O-18, Figure 6). Nesting attempts between 1991-2019 in the 30 compartments sampled in 2018 and 2019 ranged from a high of 78 to a low of zero.

Selection of compartments was constrained by the schedule of prescribed burning and as a result, compartments were not equally distributed across the burn cycle. Refuge staff attempt to achieve a 2-3 year burn interval (time since a unit was last burned), and most compartments
available for sampling were burned 1-2 years previously. Relatively few compartments go as long as three years between burns, and these were often inaccessible and thus under-represented in this study. Of the compartments studied, 5 were sampled in the same year as a prescribed burn (0 burn interval), 13 had been burned a full year prior to sampling, 5 were burned 2 years prior, 3 were burned 3 years prior, 2 were burned 4 years prior and 2 were burned 5 years prior (Table 6).

Figure 6. Management compartments at the Mississippi Sandhill Crane National Wildlife Refuge sampled during the study, 2018-2019. N = 30, 15 each in 2018 and 2019.
Table 6. Management compartments with burn interval (years since last burn) at Mississippi Sandhill Crane National Wildlife Refuge sampled for arthropods and primary production in 2018 and 2019.

<table>
<thead>
<tr>
<th>Compartment</th>
<th>2018 Sampling Locations</th>
<th>2019 Sampling Locations</th>
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<tr>
<td></td>
<td>Burn Interval</td>
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<tr>
<td>F03N</td>
<td>2</td>
<td>G03NE</td>
</tr>
<tr>
<td>F03S</td>
<td>5</td>
<td>G05N</td>
</tr>
<tr>
<td>G02E</td>
<td>1</td>
<td>G06M</td>
</tr>
<tr>
<td>G05S</td>
<td>3</td>
<td>G08NW</td>
</tr>
<tr>
<td>G06N</td>
<td>1</td>
<td>G11SW</td>
</tr>
<tr>
<td>G06S</td>
<td>0</td>
<td>G12N</td>
</tr>
<tr>
<td>G11NE</td>
<td>2</td>
<td>G12S</td>
</tr>
<tr>
<td>G13</td>
<td>1</td>
<td>G14M</td>
</tr>
<tr>
<td>G14N</td>
<td>1</td>
<td>G14SE</td>
</tr>
<tr>
<td>G15N</td>
<td>0</td>
<td>O03W</td>
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<tr>
<td>O03E</td>
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<td>O04</td>
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<tr>
<td>O05S</td>
<td>0</td>
<td>O06SW</td>
</tr>
<tr>
<td>O06SE</td>
<td>1</td>
<td>O07NW</td>
</tr>
<tr>
<td>O07S</td>
<td>0</td>
<td>O08N</td>
</tr>
<tr>
<td>O10N</td>
<td>1</td>
<td>O19E</td>
</tr>
</tbody>
</table>
Experimental Design

Each compartment was sampled eight times at monthly intervals during the growing season (March-October). During each sampling event data related to annual net primary productivity (ANPP), overall arthropod biomass, and orthopteran density was collected. ANPP of herbs and forbs in each compartment was estimated using trough-peak analysis of live and recently dead matter (Sala and Austin 2000). All standing live and dead vegetation in a 0.25 m² plot was clipped at ground level, bagged, and returned to the laboratory for analysis. Two 0.25 m² plots were sampled per compartment each month. The location of each sample was determined by reference to a haphazardly placed marker and the location of reference markers was changed for each monthly visit. The samples were processed in the laboratory within 72 hours of collection. Herbaceous and woody vegetation in each sample were separated, after which live and dead material in each subsample was bagged separately, dried overnight at 100º C, and weighed. The change in live and dead biomass from month to month was calculated for the growing season and each positive increment in biomass of green vegetation was added to positive increments of dead vegetation to estimate ANPP (Scurlock et al. 2002).

Arthropod biomass was estimated from sweep samples, the standard method for collecting community-level insect samples in medium to tall herbaceous vegetation (Southwood 1966). Two sweep samples were taken in each compartment between 9 AM and 4 PM, each consisting of ten sweeps over a 5 m transect using a 12-inch sweep net. The location of each sweep sample was determined as previously described for ANPP. Each sweep sample was stored separately on ice until returned to the laboratory, where samples were dried overnight at 60º C, weighed using a 0.0001g digital scale, and stored in alcohol. Alcohol specimens were examined under a dissecting microscope and identified to order and where possible to family using keys in

It was initially expected that sweeping would capture an unbiased sample of the insect fauna, and that adult specimens of Orthoptera in these samples would be identified to species. However, a pilot study in 2017 showed that adult Orthoptera in particular were adept at avoiding capture by sweep nets and were under-represented in these samples, leading to a serious underestimate of true orthopteran abundance. In addition, in most cases only adult Orthoptera possess the characteristics required for reliable assignment to species and this presented a serious problem for the experimental design. To obtain a more accurate estimate of abundance, in 2018 and 2019 the number of Orthoptera flushed from a 1 x 10 m transect by an observer beating the vegetation was recorded. This method had the advantage of providing an estimate of density in a 10 m² area. Two transects were sampled on each compartment per month, and the location of transects was varied each visit as described above.

Although some adult Orthoptera were obtained from sweep samples and identified to species, most of the Orthoptera used for identification of common species were obtained through stalking and hand netting during supplemental visits to the refuge independent of the monthly sampling periods. Orthoptera were netted while walking slowly through savannah during daylight hours. A total of 66 person-hours were spent hand-netting specimens between the months of May and October in 2018 and 2019. Specimens were held on ice after capture and returned to the laboratory where they were pinned and identified to species. Orthoptera were identified using keys in Otte (1981, 1985), Helfer (1987), and Capinera et al. (2004). Mass of adult orthopterans was estimated using dried specimens after pinning; mass of the pin was recorded and subtracted from total mass of insect + pin. Reference specimens are held in the Department of Biological Sciences, University of New Orleans.
Statistical Analyses

Statistical analyses were carried out in R version 3.5.0 (R Core Team, 2018). I used the package car to perform repeated measures ANOVA to determine if ANPP, arthropod biomass, and orthopteran density differed across the refuge, with different burn intervals, or from month to month within each year. I used the function GLM in the basic stats package to determine if ANPP, arthropod biomass, or orthopteran density differed between 2018 and 2019. I used the function lm for linear regression to determine if ANPP depended on burn interval or if arthropod biomass or orthopteran density depended on ANPP or burn interval. I used the GLM function for logistic regression to determine if the likelihood of fledging depended on ANPP, arthropod biomass, or orthopteran density sampled during the nesting year, and I used lm for multiple regression to determine if historical nesting and fledging numbers were related to ANPP, arthropod biomass, or orthopteran density from 2018 and 2019.

Results

Aboveground Net Primary Production

Mean ANPP of non-woody vegetation for all sampled burn compartments was 370 ± 145 g*m⁻² in 2018 and 383 ± 106 g*m⁻² in 2019. Repeated measures ANOVA showed that ANPP during 2018 did not differ significantly among refuge units ($F_{2,11} = 1.93, P = 0.19$) or burn interval ($F_{1,11} = 0.05, P = 0.87$). ANPP during 2019 also did not differ significantly among refuge units ($F_{1,12} = 1.88, P = 0.20$), or burn interval ($F_{1,12} = 0.86, P = 0.37$). A separate ANOVA comparing Gautier and Ocean Springs found that mean ANPP of compartments in the two units
did not differ significantly in 2018 and 2019 \( (F_{1,24} = 0.88, P = 0.36) \). Although the need to analyze 2018 and 2019 compartments separately reduced sample size, linear regression combining all observations from 2018 and 2019 did not result in a significant relationship between ANPP and burn interval (Figure 7).

![Figure 7. Aboveground net primary production (ANPP) vs. burn interval in 30 management compartments at Mississippi Sandhill Crane NWR, 2018-2019.](image)

Total arthropod biomass

Six insect orders made up the majority of specimens caught in sweep samples: Coleoptera, Lepidoptera, Hymenoptera, Hemiptera Mantodea, and Orthoptera. Coleoptera were abundant in sweep samples but were most often leaf beetles (Chrysomelidae) and weevils
(Curculionidae) with a dry mass of less than 20 mg. Lepidoptera larvae in sweep samples were generally less than 5 mg in mass and difficult to identify but appeared to primarily belong to the families Noctuidae and Geometridae. Adult Lepidoptera were elusive and uniformly less than 5 mg in mass. They appeared to be primarily Elechistidae (grass miners) or Pyralidae (snout moths), the larvae of which are predominantly miners living within plant tissues. Most Hymenoptera in sweep samples were ants, and most Hemiptera were very small leaf bugs (Miridae), minute pirate bugs (Anthocoridae), and damsel bugs (Nabidae) weighing 10 mg or less. Mantids were often large, with some specimens exceeding 100 mg. However, mantids were relatively uncommon in sweep samples and were generally too damaged during collection to be successfully identified. Orthoptera in sweep samples were overwhelmingly nymphs lacking characters required for identification to species, but were relatively large, ranging from 10-150 mg.

Repeated measures ANOVA showed that the mass of arthropods collected in sweep samples during 2018 did not differ significantly among refuge units ($F_{2,26} = 0.72, P = 0.50$), burn interval ($F_{1,26} = 0.69, P = 0.41$), or over the course of the year ($F_{7,182} = 0.50, P = 0.83$). Arthropod mass during 2019 also did not differ significantly among refuge units ($F_{1,26} = 0.13, P = 0.72$), or burn interval ($F_{1,26} = 0.57, P = 0.46$). However, arthropod mass during 2019 varied significantly over the course of the year ($F_{7,182} = 2.10, P = 0.046$). In both years arthropod mass was initially low and increased steadily from March to June, at which point mass remained essentially constant for the remainder of the sampling year (Figure 8). Although both years showed similar patterns, the variance in arthropod mass was substantially higher in 2018 than in 2019, which may account for the lack of a significant seasonal trend in 2018. A separate ANOVA comparing Gautier and Ocean Springs found that arthropod mass in the two units did not differ significantly
in 2018 and 2019 ($F_{1,24} = 0.35, P = 0.56$). Regression analysis showed that ANPP was not significantly related to arthropod mass in sweep samples ($P = 0.83$). Finally, a regression analysis relating total arthropod mass collected in each burn compartment to burn interval for all 30 sampled compartments showed no significant relationship ($t = 0.04, P = 0.968$, Figure 9).

Figure 8. Arthropod mass in standardized sweep samples at Mississippi Sandhill Crane NWR, 2018-2019.
Figure 9. Mean arthropod mass vs. burn interval in 30 management compartments at Mississippi Sandhill Crane NWR, 2018-2019.

Orthopteran species and density

Over 400 individuals of 15 species were caught via hand-netting, but only 162 were adult specimens with characteristics required for identification to species (Appendix). Seven species accounted for the majority of likely food sources in wet pine savannas, two large, common tetigoniid species, *Conocephalus fasciatus* and *Scudderia furcata*, ranging from 90-170 mg in adult dry mass and five abundant, medium-sized acridid species, *Amblytropidia mysteca*, *Dichromorpha viridis*, *Mermeria picta*, *Orphulella pelidna*, and *Paroxya atlantica*, ranging from 60-150 mg in adult dry mass (Appendix). The remaining species were encountered only
occasionally in savanna vegetation although some were abundant in woody vegetation adjacent unsuited to crane movement (Appendix).

Repeated measures ANOVA revealed that mean monthly orthopteran density in 2018 did not vary significantly among the Gautier, Fontainebleau, and Ocean Springs units \((F_{2.26} = 0.54, P = 0.56)\) or with burn interval \((F_{1.26} = 1.35, P = 0.26)\). However, monthly density differed significantly within compartments over the course of the year \((F_{7.182} = 6.12, P < 0.001)\). Mean monthly orthopteran density during 2019 showed similar patterns, with no significant differences between the Gautier and Ocean Springs units \((F_{1.27} = 2.32, P = 0.14)\) or with years since a compartment was last burned \((F_{1.27} = 0.18, P = 0.68)\). Monthly density in 2019 again differed significantly over the course of the year \((F_{7.189} = 3.84, P = 0.001)\). In both years density of Orthoptera was low early in the year and reached a peak in July (2018) or August (2019) before declining once again in autumn (Figure 10). Although late season densities were higher in 2019 than 2018 (Figure 10), a separate ANOVA comparing overall densities in the Gautier and Ocean Springs units during 2018 and 2019 revealed no significant difference among years \((F_{1.24} = 3.10, P = 0.091)\). Regression analysis showed that ANPP was not significantly related to Orthoptera density \((P = 0.47)\). Finally, a regression combining 2018 and 2019 data to compare mean monthly density of Orthoptera in each of the 30 compartments to burn interval revealed a significant negative relationship between orthopteran density and burn interval \((Y = -0.011X + 0.123, P = 0.045, \text{Figure 11})\).
Figure 10. Monthly orthopteran densities at Mississippi Sandhill Crane NWR, 2018-2019. Estimated from 1x10 m transects.

Figure 11. Mean density of Orthoptera vs. burn interval in 30 management compartments at Mississippi Sandhill Crane NWR, 2018-2019.
Relationship of resources to current and historical nesting success

During 2018 13 nests on the 15 units under study produced 2 fledglings, while during 2019 7 nests produced 5 fledglings in the 15 sample units. A logistic regression revealed no relationship between the likelihood of fledging in 2018 and 2019 and ANPP ($P = 0.536$), arthropod biomass ($P = 0.595$), or orthopteran density ($P = 0.364$) in the management compartments sampled in 2018-2019. Multiple regression showed frequency of nesting from 1991-2019 was not related to ANPP ($P = 0.519$) or arthropod biomass ($P = 0.083$) but was however significantly related to orthopteran density ($P = 0.008$, Figure 12, Table 7). Frequency of fledging from 1991-2019 bore no significant relationship to primary production ($P = 0.245$), total arthropod biomass ($P = 0.695$), or orthopteran density ($P = 0.988$) in the management compartments measured in 2018-2019. Rather, frequency of nesting was the only significant predictor of frequency of fledging ($P = 7.25 \times 10^{-5}$, Figure 13).

Table 7. Multiple regression of frequency of Mississippi sandhill crane nesting from 1991-2019 related to ANPP, arthropod biomass, and orthopteran density in 30 management compartments during 2018-2019 at MSCNWR.

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<th>Parameter</th>
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<td>ANPP</td>
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<td>0.034</td>
<td>0.519</td>
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<tr>
<td>Arthropod biomass</td>
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<td>Orthopteran density</td>
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</tr>
<tr>
<td>Model</td>
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<td></td>
<td>0.039</td>
</tr>
</tbody>
</table>
Figure 12. Number of nests from 1991-2019 vs. mean orthopteran density in 30 management compartments during 2018-2019 at MSCNWR.

Figure 13. Number of crane chicks fledged vs number of nests in management compartments at MSCNWR, 1991-2019.
Discussion

The results demonstrate that ANPP, arthropod biomass, and orthopteran density were relatively homogeneous in space and from year to year at MSCNWR. Although variable, no consistent differences were found among Gautier, Ocean Springs, and Fontainebleau units in both 2018 and 2019, suggesting that refuge savannas do not differ markedly in either time or space. This implies that the areas sampled during this study do not vary in their suitability as habitat for the wild crane population, and that the observed variation in nesting effort among refuge units is unlikely to be primarily the result of resource availability.

The herbaceous ANPP of 370 g m$^{-2}$ in 2018 and 385 g m$^{-2}$ in 2019 was comparable to that in several studies of subtropical humid grasslands, which ranged from 187-634 g m$^{-2}$ (Lauenroth 1979). However, methods for measuring grassland ANPP vary considerably from study to study, and some may produce significant underestimates of ANPP (Scurlock et al. 2002). Among directly comparable studies using the same trough-peak method, ANPP in this study was 1.5-2 times higher than that measured in coastal savanna in Georgia (Mitchell et al. 1999). This difference is consistent with lower understory production due to the higher forest cover at the Georgia site and suggests that my methods accurately captured patterns of ANPP at MSCNWR.

This appears to be the first study to attempt to quantify arthropod production in southeastern coastal grasslands, as previous publications have largely focused on community diversity rather than biomass or production. Although arthropod biomass and density of Orthoptera did not differ significantly between the sample years, significant seasonal variation did occur. Arthropod biomass increased significantly from March to November in 2019, while density of Orthoptera showed a significant peak in July and August in both 2018 and 2019. The
lack of a significant seasonal trend in arthropod biomass in 2018 may be due to the high variance in late-season samples, which would tend to obscure significant differences in mean biomass. Both Orthoptera and arthropods in general would be expected to follow the availability of live herbaceous vegetation, which is relatively low in late winter and early spring and increases progressively throughout the growing season. The late decline in density of Orthoptera is likely due to senescence of graminoids in late summer as they channel energy into seed production and root storage in preparation for winter dormancy. The peak density of Orthoptera appears to coincide with the typical fledging period and the availability of large adult insects may be an important subsidy for young cranes. The importance of other arthropod taxa as food sources for cranes is uncertain, but arthropod mass also plateaued in June when crane chicks are at or near fledging and remained high for the rest of the growing season.

Somewhat surprisingly, ANPP bore no significant relationship to either density of Orthoptera or arthropod mass in sweep samples. Previous studies have found that the relationship between ANPP and arthropods is complex, with some characteristics of sites with high ANPP promoting arthropod abundance while others suppressing it. While the low standing plant biomass in recently burned compartments may reduce food availability and thus arthropod biomass (Hurd and Wolf 1974, Kirchner 1977), nutrient pulses from burning may enhance foliage quality, potentially offsetting the effect of lower plant biomass (Haddad et al. 2000). Similarly, increasing standing biomass and ANPP as burn interval increases may have offsetting effects, with high biomass resulting in greater food availability but lower soil temperatures, which are known to inhibit development of eggs laid by arthropods such as grasshoppers in the soil (Yang et al. 2017).

Perhaps the most surprising result of this study was the apparently small effect of burn
interval on ANPP and arthropod biomass. In the absence of fire, succession in gulf coastal grasslands permanently converts graminoid-dominated savannas into shrublands within 5-10 years (Briggs et al. 2005, Grace et al. 2005), which reduces habitat accessibility to cranes and should be expected to profoundly alter both plant and insect communities. However, increasing burn interval was unrelated to ANPP or arthropod mass in sweep samples. One possible explanation for the lack of a strong influence on arthropod availability is community turnover, in which savanna arthropod species are progressively replaced by shrub-associated species without substantially altering either density or mass as measured in this study.

However, the lack of relationship between ANPP of herbs and graminoids and burn interval is not so easily explained. ANPP should be reasonably expected to increase with time as photosynthetic area increases with regrowth after a burn until the point at which it begins to be outcompeted by woody vegetation. As additional time passes and woody vegetation becomes more dominant, herbaceous ANPP should decrease, and the expectation is that herbaceous ANPP should show an increasing or humped relationship with burn interval, depending on the time required for woody vegetation to replace herbaceous vegetation. It is possible that the results of this study simply reflect a high variability in grassland ANPP, and a significant relationship may emerge with a larger sample size. It is also possible that underrepresentation of compartments with burn intervals of 3 or more years may prevent this study from detecting the expected relationship. Burning clearly maintains the ability of cranes to move through and utilize savanna habitat but these results suggest that it does not influence food resource availability as strongly. Future work should attempt to address this issue and clarify the effect of the burn cycle with greater precision.

In contrast to ANPP and arthropod mass, Orthoptera density was shown to have a
significant negative relationship with burn interval. This may be due to most orthopteran species being associated with herbaceous vegetation found in savanna habitat as opposed to woody vegetation that can be expected to begin encroaching into the savanna as burn interval increases. Of the seven most abundant medium to large orthopteran species, six were primarily associated with graminoid vegetation and only one was primarily associated with savanna shrubs. Four of the acridid species, *Amblytropidia mysteca*, *Dichromorpha viridis*, *Mermeria picta*, and *Orphulella pelidna*, are members of the subfamily Gomphocerinae, which is obligately associated with graminoid foods (Otte 1981), while *P. atlantica* is reputed to have a broader diet including both graminoids and many grassland forb species (Helfer 1987). The results suggest that orthopteran abundance in MSCNWR savannas is strongly associated with graminoid availability and much more strongly tied to the burn cycle than that of arthropods in general.

Although arthropod mass and Orthoptera density did not differ significantly among the Fountainbleau, Gautier, and Ocean Springs units, they did vary among management compartments. Variation in arthropod mass among management compartments was unrelated to the probability of fledging during the study, or to the total number of nests established or the number of fledging events in individual management compartments from 1991-2019. However, Orthoptera density in 2018-2019 was significantly related to the number of nests established in individual management compartments from 1991-2019. The significant relationship between Orthoptera density and burn interval would appear to be inconsistent with such a pattern, since current burn interval bears no necessary relationship to conditions in the past. It may be that management compartments recently burned in the current study have been more frequently burned in the past, which would likely be associated with higher Orthoptera densities over time. The nesting and burn records maintained by the refuge do not provide sufficient resolution to
evaluate this idea, but it is worthy of future investigation.

The lack of a relationship between resource availability and current fledging may simply be the result of small sample size; only 7 of 30 management units produced fledglings during the study. Other factors such as predation may exert equal if not greater influence on fledging patterns in a given year. The relationship with orthopteran density rather than arthropod biomass may be due to differences both in characteristics of arthropod taxa and in their habitat use. Adult Orthoptera sampled in this study were consistently 2-8 times larger than arthropods from other orders, making them likely a primary food for cranes, whereas total arthropod biomass included a large number of species that are too small to be common crane food. Some families of large ground-associated Coleoptera such as Staphylinidae, Carabidae, Passalidae, and Tenebrionidae are likely to occur at MSCNWR and would be important resources when encountered, but were almost entirely missed by sweep sampling. However, the abundance and large size of Orthoptera compared to other arthropod taxa supports the idea that they represent a major food resource for cranes and a focus on them appears to be well-founded. Orthoptera sampled in this study were also most common primarily in savanna habitat whereas small arthropods in general may be common throughout both savannas suitable for cranes and shrubby re-growth avoided by them.

Overall, my data are consistent with the idea that Orthoptera provide an important food resource for Mississippi sandhill cranes and suggest that adult cranes may be more likely to nest in areas of high orthopteran density. While crane parents may target areas with abundant food for nesting, the lack of a relationship between any measure of resource availability and fledging success suggests that resources alone are insufficient to guarantee successful breeding. Predation on nests and colts is the primary source of nest failure in the population (Butler 2009) and may eliminate any advantage conferred by high food availability. However, the strong relationship
between number of nests and number of fledglings produced suggests that a few areas on the
refuge are key sources of natural reproduction. It is possible that nesting consistently occurs in
these areas due to a combination of food availability and low predation pressure. Understanding
the characteristics of these core areas and how they are associated with both resources and
predation risk can help improve management decisions in the future and provide guidance
toward attaining the goal of a self-sustaining wild population of Mississippi sandhill cranes.
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Appendix: Common orthopteran species at Mississippi Sandhill Crane NWR collected 2018-2019, with notes on characteristics and occurrence.

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<th>Family: Species</th>
<th>Subfamily</th>
<th>Adult dry mass (g)</th>
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</tr>
<tr>
<td>Trimeroptropis maritima</td>
<td>Oedipodinae</td>
<td>0.3311 1</td>
</tr>
<tr>
<td>Tetigoniidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conocephalus fasciatus</td>
<td>Conocephalinae</td>
<td>0.0905 ± 0.0154</td>
</tr>
<tr>
<td>Amblycorypha floridana</td>
<td>Phaneropterinae</td>
<td>0.4248 1</td>
</tr>
<tr>
<td>Scudderia furcata</td>
<td>Phaneropterinae</td>
<td>0.1691 ± 0.0333</td>
</tr>
</tbody>
</table>

1: Mass of a single intact adult female specimen.
2: Mass is of intact male specimens only.
Notes on individual species of Orthoptera:

Family Tettigidae

*Paratettix mexicanus* (Mexican pygmy grasshopper). Tiny, cryptic species found in moist depressions, especially roadside ditches. Uncommon in open savanna.

Family Acrididae

*Achurum carinatum* (Long-headed toothpick grasshopper). Relatively small, elongate species, cryptic on graminoids. Patchy occurrence in savanna, can be locally common.

*Amblytropidia mysteca* (Brown winter grasshopper) Medium-sized species common everywhere in savanna. Adults were present as soon as the weather warms in February and March, indicating that this species overwinters at least in the adult stage.

*Dichromorpha elegans* (Short-winged grasshopper). Occurred occasionally and patchily in savanna; slightly smaller than the closely related species *D. viridis*. More frequently associated with lush green vegetation than *D. viridis*.

*Dichromorpha viridis* (Short-winged green grasshopper). Medium-sized, abundant year-round in savanna, one of the most common species at MSCNWR and likely a major food item for any vertebrate consuming insects in savanna habitat. Nymphs appeared by April and adults were present by May; some adults persisted year-round although numbers were low during winter months.

*Mermeria picta* (Toothpick grasshopper). Large, elongate, cryptic species, moderately common in savanna. Females are especially large and represent one of the largest prey items in savanna vegetation.

*Orphulella pelidna* (Spotted-winged grasshopper). Medium-small species, more likely than most to be found on the ground rather than on vegetation. A strong flier when
disturbed and difficult to catch as a result. Abundant everywhere in savanna, and adults present year-round. One of the first species seen in early spring, frequently encountered as soon as weather warms in March.

*Melanoplus propinquus* (Southern red-legged grasshopper). Medium-sized species found occasionally in savanna. Strong jumper and elusive because it frequently jumps repeatedly when disturbed. Closely related to the widely distributed *M. femurrubrum*, not all authors distinguish the two species. More common in summer and fall, adults present as early as June.

*Paroxya atlantica* (Atlantic grasshopper). A medium-sized species, present year-round in savanna and often very abundant. Likely an important resource for savanna insectivores.

*Schistocerca americana* (American bird grasshopper). Extremely large, strong-flying species, very rare in open savanna. Most often associated with herb- and shrub-rich understory of pine woodlands, where it was often found on wild blackberry (*Rubus* spp.). Although one of the largest species on the refuge, likely of minor importance at best to savanna-feeding insectivores. Only found in large numbers under pine canopy and within 25-30 m of forest, where adults may be common in summer and fall. Very elusive flier and very difficult to catch.

*Schistocerca damnifica* (Mischievous bird grasshopper). Very large species, characteristics similar to *S. americana* above, but most often associated with moist soils and moisture-loving vegetation in swales and roadside ditches. Very rare in open savanna.

*Trimeroptropis maritima* (Seaside grasshopper). Large, strong-flying species associated with disturbed areas such as roadsides and recent burns. Otherwise uncommon in
savanna.

Family Tettigoniidae

*Conocephalus fasciatus* (Slender meadow katydid). Large, green graminoid-associated species. The most abundant tettigoniid on the refuge. All stages occurred most of the year in savanna, and adults were positively identified as early as February at MSCNWR.

*Amblycorypha floridana* (Florida false katydid). Very large green leaf mimic, the largest tettigoniid at MSCNWR. Uncommon in savanna vegetation and encountered almost exclusively on shrubs. More frequent in pine understory and likely encountered infrequently by savanna insectivores.

*Scudderia furcata* (fork-tailed bush katydid/Southern bush katydid). Large green species, found on both graminoids and shrubs. Common throughout the year, including early spring, although encountered somewhat less frequently than *Conocephalus fasciatus*.

Three additional species in the Oedepodinae (band-winged grasshoppers) were also observed but not collected as adults:

*Chortophaga australior* (Southern green-striped grasshopper). Several nymphs collected in open savanna in June and July, no adults taken.

*Spharagemon* spp. (likely *marmorata*, possibly *bolli*). Adults observed on roadsides from July-September, but these elusive fliers were not collected. Hind tibia observed to be reddish and basal wing disc yellow-orange, which are consistent with these species. Characters required for definitive identification not observable without pinned adult specimens.

*Arphia* spp. (most likely *granulata* or *xanthoptera*). Nymphs with characters consistent
with this group were taken on grasses adjacent to roadsides in July. Adults were observed but not captured July-September.

A single individual of *Nomotettix cristatus* (Tetrigidae) was collected in vegetation growing in a roadside ditch. This is a tiny species with characteristics similar to those of *Paratettix mexicanus* and is rare in open savanna.
Chapter 3: Predator incidence, landcover, and nesting success at Mississippi Sandhill Crane National Wildlife Refuge

Introduction

Nest predation is a major source of nest failure in all bird species (Ricklefs 1969). Ground-nesting birds are especially vulnerable to predation from mammalian predators such as bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and raccoons (*Procyon lotor*) (DeGregorio et al. 2016, Söderström et al. 1998, Reidy and Thompson 2012, Butler 2009, USFWS 2007, 1992). Numerous studies have documented nest predation rates by mammalian predators exceeding 50% for many ground-nesting bird species (Ricklefs 1969, Herring et al. 2011, Johnson et al. 2012, Ellis et al. 2015). Ground-nesting bird populations can experience significant population growth when these predators are reduced or removed (Roos et al. 2018), emphasizing their importance in bird population dynamics. Understanding factors that influence the frequency and impact of these predators on bird population recruitment is essential for effective management of ground-nesting bird populations.

Landscape features often influence the abundance and activity of mammalian predators. They may disproportionately use forest patches that provide woody vegetation cover compared to open habitats such as grasslands (Gese et al. 1988, Keuhl and Clark 2002, Farrell et al. 2018), potentially increasing encounter rate between predators and ground-nesting birds in areas with substantial forest cover. Roads and edges of stands of woody vegetation that provide movement corridors have been shown to be associated with higher usage rates by mammalian predators, a phenomenon known as the edge effect (Wilcove 1985, Andren and Angelstam 1988, Svobodová et al. 2010, Watts and Frick-Rupert 2018). This higher use of edges by these predators also corresponds with an increase in risk of predation to birds in grassland ecosystems (Johnson and Temple 1986, 1990, and Burger et al. 1994).
Given their importance to predators, it is unsurprising that landscape features also have an impact on grassland bird species. Studies have shown that patch area of grassland influences the habitat use of grassland birds (Samson 1980, Herkert 1994, Vickery et al. 1994). Subsequent research has shown that both area and shape of habitat fragments influence grassland bird species and communities. Some grassland bird species nest at lower frequencies near patch edges than in patch interiors (Johnson and Temple 1986). High perimeter-area ratio (PAR) of grassland habitat fragments has been shown to significantly reduce bird species presence and richness (Helzer and Jelinski 1999). One potential explanation of the importance of PAR is the higher predation rates observed on nests adjacent to habitat edges in mixed forest-grassland habitats (Johnson and Temple 1986, 1990, Burger et al. 1994).

The federally endangered Mississippi sandhill crane exists in a small, non-migratory population found in and around the Mississippi Sandhill Crane National Wildlife Refuge (MSCNWR) in Jackson County, Mississippi. The population is characterized by a low rate of natural reproduction and is currently supplemented by annual releases of captive-reared birds. Both total population and number of nesting pairs are approaching recovery objectives outlined in the comprehensive recovery plan for the species (USFWS 1991). However, the number of crane chicks that survive to fledging (developing feathers capable of flight) per pair has remained persistently low since at least 1991; low chick survival, and thus low recruitment, is the main factor limiting a self-sustaining population (S. G. Hereford, pers. comm.). Predation appears to be the most important factor in the low rate of fledging; from 2008 to 2009, 44% of nest failure was attributable to predation, (Butler 2009, USFWS 2007, 1992). At MSCNWR, bobcats, coyotes, raccoons, and red fox (Vulpes vulpes) have been identified as important sources of nest failure for Mississippi sandhill cranes (Butler 2009, USFWS 2007, 1992).
The management regime at MSCNWR has resulted in a landscape mosaic comprised of open savanna dominated by grasses and forbs with very few trees per acre, interspersed with tracts of longleaf pine (*Pinus palustris*) forest. Each management compartment is typically bordered by a refuge access road, a fire line (a wide swath of earth stripped bare of all vegetation which is used as a firebreak), or a thin line of trees that separates the refuge from municipal roads, including Interstate-10. This habitat mosaic may result in high rates of nest predation through proximity of nests to forest cover or movement corridors frequently used by mammalian predators. Cranes typically nest in open wet pine savanna and in proximity to ponds (USFWS 2007), which reduces the risk of nest predation in other ground-nesting species (Robertson 1972, Giroux 1981, Picman 1988, Picman et al. 1993, Jobin and Picman 1997). However, the small spatial scale of the refuge (7,450 ha) and high density of roads and firebreaks may allow predators to locate nests more easily than would be possible in larger, less fragmented landscapes.

The methods that previous studies that have characterized effects of land cover have used to classify land cover have varied. Some studies of habitat edge effects have used site-specific estimation of vegetative cover (Angelstam 1986, Watts and Frick-Rupert 2018), linear distance on a map (Andren and Angelstam 1988), and ground distance measurements (Svobodová et al. 2010) to quantify landcover features. Bogaert et al. (1998) used raster imagery and relied on custom indices to calculate patch size and edge characteristics. Other studies have used geographic information system (GIS) analysis to characterize landscape patches in fragmented landscapes (Li et al. 2007, LaCroix et al. 2008) but have not related landscape features to predation risk. Wilken et al. (2007) used GIS analysis to model edge effects but did not use GIS to classify vegetative landcover. Rastandeh and Zari (2018) used GIS to classify landcover but
did not relate it to predation risk. In a meta-analysis Vetter et al. (2013) use GIS to classify landcover and relate edge effects to predation risk but relied on landcover classification of satellite images taken within 2 years of the studies they review rather than using the satellite image from the same year the data was collected.

In this study I use GIS analysis of satellite imagery to relate habitat features to records of predator activity and nesting success at MSCNWR. Specifically, I use GIS analysis of satellite images taken during the year of data collection to classify vegetative landcover, characterize landscape features, and test for habitat edge effects. This approach has several advantages over other methods; it allows me to access historical vegetative data, it allows me to characterize the features of entire landscape patches rather than single points, it automates the calculation of area and perimeter of landcover types, and it fully captures the intricacies of patch configuration. This last advantage is important as edge effects may change as edges get closer together in highly fragmented landscapes (Porenksy and Young 2013). I expect that the probability of predator detection will be significantly greater in locations with more forest cover or movement corridors represented by habitat edges than locations with less of these features. I expect the probability of successful fledging will be significantly greater for nests in areas characterized by reduced forest cover or movement corridors than for nests in areas with more of these features. I also expect the probability of predator detection will be higher, and fledging success lower, in locations with a high PAR of woody vegetation, indicating a high degree of habitat fragmentation, than in locations with low PAR. I expect the distance from nest sites to the nearest predator trapped to be inversely related to fledging success, and I expect the total area of water around nest sites to be positively related to fledging success.
Methods

Study Area

MSCNWR is relatively small and consists of 3 major units, Fontaineblau, Gautier, and Ocean Springs, separated from each other by state and interstate highways, and commercial, municipal, and residential developments (Figure 14). The longest continuous linear distance from boundary to boundary of any major refuge unit is slightly more than 6 km in the Ocean Springs section of the refuge, which is the northernmost section. There is substantial wildland/urban interface at MSCNWR with Interstate 10 running through the Gautier section of the refuge and many roads, municipal structures, and housing developments adjacent to much of the refuge. The 3 major units are further subdivided into a total of 103 management compartments (mean 72.4 ha, range 14.0 to 301.0 ha) that the refuge maintains using prescribed burning and other measures to provide suitable crane habitat.
Figure 14. Map of the Mississippi Sandhill Crane National Wildlife Refuge.

Data Sources

Satellite images of the refuge for the years 2018, 2016, 2014, and 2012 were obtained in the form of 4 band .tiff files from the Mississippi Automated Resource Information System (MARIS). These years were the only years for which there were both detailed satellite images and predator trapping data at the time of the study. The images were taken as part of the National Agriculture Imagery Program (NAIP). NAIP satellite imagery was used because the 1-meter ground sample distance (GSD) resolution was more appropriate for the scale of this study than
the 30-m resolution available from Landsat satellite images.

No systematic surveys of predator density on the refuge were available for the period of the study, so predator trapping records were used as a proxy for predator occurrence. Trapping records only include location and type of predator trapped, and do not include trapping effort per year. For the purposes of this study, it is assumed that the number of predators removed per year is positively correlated with predator occurrence in that year, although data related to trapping effort is unavailable. Predator traps were set annually by refuge contractors from October or November until June, except in 2018, when trapping ended in March. Traps were targeted primarily in areas identified as having high predator activity by refuge staff. The four most commonly trapped predator species (Table 8), bobcats (n = 22), coyotes (n = 63), raccoons (n = 177), and red fox (n = 10), were included for analysis of habitat use by predator species. One gray fox (*Urocyon cinereoargenteus*) was trapped in 2018.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Total trapped</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raccoon (<em>Procyon lotor</em>)</td>
<td>177</td>
</tr>
<tr>
<td>Coyote (<em>Canis latrans</em>)</td>
<td>63</td>
</tr>
<tr>
<td>Bobcat (<em>Lynx rufus</em>)</td>
<td>22</td>
</tr>
<tr>
<td>Red fox (<em>Vulpes vulpes</em>)</td>
<td>10</td>
</tr>
<tr>
<td>Gray fox (<em>Urocyon cinereoargenteus</em>)</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>273</td>
</tr>
</tbody>
</table>
Records of GPS locations of crane nests, predator trapping, and refuge boundaries were provided by refuge staff. Nest locations were obtained from aerial, ground, and a few boat surveys carried out by refuge staff between March and June each year; nearly all nests were located to the management unit in which they occurred, and a majority were located to within 10 m by GPS.

Data Processing

Image analysis was conducted using ArcMap version 10.3.1. A total of nine .tiff files were acquired for each year of the study (2018, 2016, 2014, and 2012) to cover the area of the refuge. These 9 satellite images were merged using the Mosaic to New Raster data management tool to form one raster layer for each year of the study. Refuge boundary, nest location, and trapping location data were added as separate layers for each year. Nesting and trapping location layers were merged using the Merge data management tool and 500 m buffers were created around each nesting and trapping location using the Buffer analysis tool. 500 m was chosen as an appropriate buffer because Keuhl and Clark (2002) find that predators including raccoons and red fox are typically found more frequently within 500 m of grassland edges. Many of the buffer areas overlapped so I used the Dissolve All option to dissolve the buffer layer. The resulting layer was then used to clip the satellite image raster layer using the Clip analysis tool to create a new raster layer for land cover classification. This greatly reduced the size of the image files and thus the time required to run land cover classification. Land cover classification was carried out using the Classify Raster spatial analyst tool.

Six land cover classes were created: woody vegetation, herbaceous vegetation, water, bare ground, pavement, and shadow. It was important to include shadow as a separate class
because shadow darkens all other landcover types and thus could result in increased classification errors. Four training locations for each land cover type for each year were used to train the program. The classification was run using maximum likelihood to determine land cover type. To relate individual nesting and trapping locations to the resulting land cover classification layer for each year, the land cover classification layer had to be converted from raster to polygon using the From Raster to Polygon conversion tool. Once the classification layer was in polygon form, an undissolved 500 m buffer layer was created, once again using the Buffer analysis tool. The default attribute table of the land cover classification layer contained area and percent cover for each land cover type, but not perimeter, so it was necessary to add perimeter using the Calculate Geometry function. To determine land cover characteristics within 500 m of each nesting and trapping location the land cover classification layer and the 500 m buffer layer were intersected using the Tabulate Intersection analysis tool. The resulting attribute table was exported as an Excel file using the Table to Excel conversion tool. PAR was calculated in Excel as the perimeter divided by the area of each land cover type for each 500 m buffer area.

Statistical Analyses

All statistical analyses were performed using R 4.1.0. To determine if trapping locations were different from the refuge as a whole, the perimeter, total area, and PAR of woody vegetation patches within 500 m of trapping locations was compared to woody perimeter, area, and PAR within 500 m of 200 random points. Fifty random points were selected in each of 2018, 2016, 2014, and 2012 data layers using ArcMap’s Create Random Points data management tool. A Student’s t test using the function t.test in the basic R statistics package was used to test the hypothesis that trapping locations (n = 274) would have greater woody perimeter, total area, and
PAR compared to a selection of random points (n = 200). Multinomial logistic regression using the multinom function in the nnet R package was used to determine if the likelihood of the most common predator trapped (racoons) to be trapped was different from other predator species based on woody vegetation perimeter, area, and PAR.

The effect of woody vegetation perimeter, total area and PAR on fledging outcomes was analyzed using GLM to perform binomial logistic regression (Helzer and Jelinski 1999). Logistic regression using GLM was used to determine whether nests closer to trapping locations had fewer chicks fledged, with distance to trapping locations determined using the ArcMap geoprocessing tool Near. Logistic regression using GLM was also used to determine whether nests in locations with greater total area of water were associated with an increase in the number of chicks fledged from those areas.

Results

Student’s t test showed perimeter and PAR of woody vegetation patches were significantly higher and total area of woody vegetation was significantly lower within 500 m of trapping sites (P = 0.002, 0.003, and 0.007, respectively), than within 500 m of randomly selected points (Figure 15). Mean total area of woody vegetation around trap sites was 38.2 ± 0.8 ha, while mean total area around random points was 41.8 ± 1.0 ha. Woody vegetation patches around trap sites were thus both smaller and more irregular than those around randomly selected points.
Figure 15. Perimeter, total area and PAR of woody vegetation patches within a 500 m radius of trapping locations (n = 274) or random points (n = 200).
Multinomial logistic regression revealed that the frequency with which predators were trapped varied significantly with landscape features (Table 9). Bobcats and coyotes were trapped in areas with less woody vegetation area than raccoons (\( P = 0.002 \) and \( 1.38 \times 10^{-6} \), respectively), and red fox were trapped in areas with lower woody vegetation PAR than raccoons (\( P = 0.002 \)). However, these differences were characterized by relatively small explanatory power (coefficient = \(-4.48 \times 10^{-6}, -4.19 \times 10^{-6}, \) and \(-6.59 \times 10^{-6}, \) respectively) and may not represent large enough differences in habitat to have a practical effect on the use of habitat by predators.

Table 9. Likelihood of trapping mammalian mesopredators related to woody vegetation landcover characteristics at MSCNWR using most abundant predator (raccoon) as reference.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Coefficient</th>
<th>Std Error</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bobcat (\textit{Lynx rufus})</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perimeter</td>
<td>-1.60 \times 10^{-7}</td>
<td>1.68 \times 10^{-6}</td>
<td>0.924</td>
</tr>
<tr>
<td>Area</td>
<td>-4.48 \times 10^{-6}</td>
<td>1.43 \times 10^{-6}</td>
<td>0.002</td>
</tr>
<tr>
<td>PAR</td>
<td>-0.199</td>
<td>7.88 \times 10^{-12}</td>
<td>0</td>
</tr>
<tr>
<td>Coyote (\textit{Canis latrans})</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perimeter</td>
<td>5.52 \times 10^{-7}</td>
<td>1.09 \times 10^{-6}</td>
<td>0.611</td>
</tr>
<tr>
<td>Area</td>
<td>-4.19 \times 10^{-6}</td>
<td>8.69 \times 10^{-7}</td>
<td>1.38 \times 10^{-6}</td>
</tr>
<tr>
<td>PAR</td>
<td>-0.745</td>
<td>4.96 \times 10^{-12}</td>
<td>0</td>
</tr>
<tr>
<td>Red fox (\textit{Vulpes vulpes})</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perimeter</td>
<td>-6.59 \times 10^{-6}</td>
<td>2.08 \times 10^{-6}</td>
<td>0.002</td>
</tr>
<tr>
<td>Area</td>
<td>1.31 \times 10^{-6}</td>
<td>1.70 \times 10^{-6}</td>
<td>0.44</td>
</tr>
<tr>
<td>PAR</td>
<td>2.11</td>
<td>1.02 \times 10^{-11}</td>
<td>0</td>
</tr>
</tbody>
</table>
Logistic regression revealed no relationship between woody vegetation perimeter, area, or PAR within 500 m of a nest site and the likelihood of fledging (Table 10). Distance from nest to nearest trapping location was not correlated with the probability of fledging ($P = 0.22$). The total area of water coverage within 500 m of nest sites was also not significantly related to fledging outcomes ($P = 0.915$).

Table 10. Relationship of woody vegetation characteristics to likelihood of fledging at MSCNWR.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Coefficient</th>
<th>Std Error</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perimeter</td>
<td>$3.44 \times 10^{-6}$</td>
<td>$6.70 \times 10^{-6}$</td>
<td>0.608</td>
</tr>
<tr>
<td>Area</td>
<td>$1.58 \times 10^{-6}$</td>
<td>$6.17 \times 10^{-6}$</td>
<td>0.800</td>
</tr>
<tr>
<td>PAR</td>
<td>1.15</td>
<td>2.02</td>
<td>0.568</td>
</tr>
</tbody>
</table>

Discussion

My results show that predator trapping locations were characterized by greater woody vegetation perimeter and PAR and less total woody area than randomly selected points. Trapping locations in this study were likely biased due to a tendency to be located on or near roads or fire lines, which would tend to increase habitat edges and PAR in the vicinity of trapping sites. The lower area of woody vegetation at trapping locations is less easily understood but may be attributable to setting traps in locations more open than average, where predators would likely be more visible to observers. Given this bias in trapping locations it is not possible to evaluate the relationship of predator occurrence to perimeter, area, or PAR of woody vegetation patches on
Individual predator species did show small but significant differences in their association with landscape characteristics. However, the small coefficients suggest that there were few if any differences of ecological importance in how the four predator species used the landscape. This is in marked contrast to the results of previous studies of mammalian predator habitat preferences and movement patterns. Bobcats in Mississippi are known to prefer areas of pine forest (Chamberlain et al. 2003b) and disproportionately use large forest patches over other habitat types (Nielsen and Woolf 2002). Raccoons also prefer forested habitat (Chamberlain et al. 2003a) but may forage in urban environments with low woody vegetation cover (Prange et al. 2003). Coyotes also frequently use forested areas for shelter but frequently forage in adjacent open habitats (Gese et al. 1988, Holzman et al. 1992). Red fox appear to be broadly generalized and are not consistently associated with any particular habitat type (Goldyn et al. 2003).

The lack of differentiation in habitat associations between predators in this study may be due to the small scale of the landscape at MSCNWR. The refuge is a patchwork of savanna and forest interspersed with urban development, and the longest linear distance from boundary to boundary is only a little over 6 km. Even predators with relatively small home ranges might easily access the entire refuge area, obscuring any tendencies to associate with particular landscape features. Landscape effects might be more important and thus more readily observed over longer distances or in more homogeneous landscapes in which edges may play a more important role as movement corridors (Wilcove 1985, Andren and Angelstam 1988, Watts and Frick-Ruppert 2018).

Predator home ranges have been shown to be variable within species and between sexes and subject to a variety of influences (McNab 1963), including prey density and inter- and intra-
specific competition. Bobcats are mostly solitary and exhibit home ranges in the American southeast from 1 km$^2$ to over 60 km$^2$ with a mean range of $8.5 \pm 1.0$ km$^2$ for males and $5.3 \pm 0.7$ km$^2$ for females (Doughty 2004). Coyotes live in packs with mean home ranges in the American southeast of 13.5 km$^2$ (min 5.4 km$^2$, max 39.2 km$^2$, Ward et al. 2018). Raccoons are considered semi-social animals, often sharing territories with several other raccoons. Male raccoons have larger home ranges than females in central Mississippi ($244 \pm 11$ ha, $153 \pm 13$ ha respectively; Chamberlain et al. 2003a). A review of red fox home ranges shows that the average home range for red fox in America is 5.5 km$^2$ (Trewhella et al. 1988). While all of these home ranges fit within the 7,450 ha area of MSCNWR (Table 11), they are large enough to encompass several nesting or trapping location buffer areas, which are each 19.6 ha and often overlap. At small landscape scales these predators may stop seeing landscape as discrete patches and instead view the landscape as a continuum. At the spatial scale and level of urbanization of the refuge, edge and patch area effects may be difficult to detect.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Home range (km$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coyote (<em>Canis latrans</em>)</td>
<td>13.5</td>
</tr>
<tr>
<td>Bobcat (<em>Lynx rufus</em>)</td>
<td>male $8.5 \pm 1.0$, female $5.3 \pm 0.7$</td>
</tr>
<tr>
<td>Red fox (<em>Vulpes vulpes</em>)</td>
<td>5.5</td>
</tr>
<tr>
<td>Raccoon (<em>Procyon lotor</em>)</td>
<td>male $2.4 \pm 0.1$, female $1.5 \pm 0.1$</td>
</tr>
</tbody>
</table>
The likelihood of crane chick fledging was unrelated to woody vegetation characteristics. This was unexpected; other studies (Andren and Angelstam 1988, Watts and Frick-Ruppert 2018) have shown that greater woody PAR is associated with greater risk of predation. One possible reason is that PAR as measured by GIS landcover classification analysis is capable of classifying at the level of single pixels and is thus consistent with both large, irregular forest patches and many small patches of woody vegetation, or even single trees, too small for predators to use. Some classification images in fact exhibit numerous small patches classified as forest that likely represent one or few trees (Figure 16). Other studies (Andren and Angelstam 1988, Watts and Frick-Ruppert 2018) identify vegetation type by on-site observation, which might result in smoother habitat delineations with less edge than habitat delineations produced by GIS landcover classification analysis. This would weight the PAR of large woody patches, which are presumably preferred by predators, more heavily and likely produce a closer correspondence between PAR and predation risk.
Figure 16. GIS classification of landcover in a 500 m radius around a nest site (yellow dot in center). Woody vegetation (dark green in the image) is very granular, including patches possibly too small to be of importance for predator use.

The distance of a nest to the nearest trapping location was not related to fledging outcomes in this study. The small size of the MSCNWR landscape may again have played an important role in obscuring any relationship between locations where predators were known to occur and the success of nests. Although other studies (Robertson 1972, Giroux 1981, Picman 1988, Picman et al. 1993, Jobin and Picman 1997) have found distance to water to be associated with nesting outcomes, total area of water within 500 m of a nest site was unrelated to fledging
likelihood in this study. This may indicate that water was not a deterrent to predators at MSCNWR, but this appears to be inconsistent with established patterns of nesting outcomes. Nesting in water has been repeatedly shown to deter predation and result in greater fledging rates (Smith and Smith 1992, Drewien et al. 1995, Austin et al. 2007, Ivey and Dugger 2008, Maxson et al. 2008, McWethy and Austin 2009). It is more likely that satellite images did not adequately capture the relationship between nest location and water coverage during nesting season. Images used in this study were not specifically taken during nesting season and water features later in the year may have borne little resemblance to conditions during nesting season.

While the difference between the findings in this study and those of other studies may be due to scale of landscape studied or differences in patch size or methods of determining patch size, there is no doubt that predators are an important influence on fledging success at MSCNWR. The general lack of relationship between landscape characteristics, predator trapping, and fledging success suggests that predator pressure may be pervasive throughout the refuge and that landscape features shown to influence predation risk in other studies are largely irrelevant in this location. The large area of urban-suburban development surrounding the refuge may subsidize predator populations through abundant shelter and food, maintaining higher predator densities than would be possible from foraging on refuge resources alone. This study suggests that nests in all areas of the refuge are equally vulnerable to mammalian predators and that consistent predator control will be required for the future growth of the Mississippi sandhill crane population.


Herring, G., J. T. Ackerman, J. Y. Takekawa, C. A. Eagles-Smith, and J. M. Eadie. 2011. Identifying nest predators of American avocets (Recurirostra americana) and black-


participants. IUCN/SSC Captive Breeding and Specialist Group, Apple Valley, MN. p. 1-146.


General Discussion

The goal of this study was to use a multidisciplinary approach to identify ecological factors that influence an endangered population, the Mississippi sandhill crane, to inform the decisions of managers at Mississippi Sandhill Crane National Wildlife Refuge and help them realize their goal of establishing a self-sustaining population on the refuge. I examined the effects of contemporary climate, predator removal, prescribed burning, resource availability, and land cover characteristics on the population. I expected to find that weather extremes and factors related to predation would negatively impact the population and that increased resource availability would have a positive effect on the population.

My research has provided evidence in support of my some of my assumptions, although the historical data set, which integrates trends across many years, showed relatively clear results while the data related to current trends of resource availability were more ambiguous. Because of high year-to-year variation in fledging perhaps trends only emerge over time as yearly variation evens out. Chapter 1 revealed that climate and predation have influenced historical population patterns and that cranes preferentially chose more recently burned areas of the refuge for nesting. Chapter 2 revealed that while production on the refuge was largely consistent across time and space, burn interval was related to orthopteran density which in turn may have influenced historical nesting, but not fledging success. The relationship of burn interval to orthopteran density makes sense since Orthoptera are graminoid specialists who would experience a loss of food resources as graminoid species decrease with increasing burn interval. ANPP and arthropod biomass were not related to burn interval, which may be due to the burn history of the refuge. If an area is consistently burned every 2-3 years perhaps the plant community becomes dominated by plants adapted to quick recovery, and perhaps those species support a consistent arthropod
community. Because my data set is on the level of the management unit, it is not precise enough to test this hypothesis. Future research using experimental burning could provide useful insight into the relationship between fire, ANPP, and arthropod biomass at MSCNWR. I suspect predation pressures experienced by crane chicks outweigh any effects that food availability may have on fledging success. Perhaps if predation was strictly controlled, effects of food availability may emerge. Chapter 3 revealed that patterns of predation related to habitat edges observed in other studies were not found at MSCNWR and thus are not likely to have a strong influence on the Mississippi sandhill crane population. Presumably, the small geographic scale and high level of urbanization surrounding the refuge may have affected my ability to detect habitat edge effects. Alternatively, this lack of effect may be related to sample size. I elected to use only trapping, nesting, and fledging data from years that had a corresponding satellite image for land cover classification to capture as accurately as possible the conditions during the year of data collection. Vetter et al. (2013) used population data within 2 years of the satellite images they classified, an approach that would increase the sample size of this study and thus may yield more definitive results. Future work could examine this possibility although due to fire management vegetative land cover at MSCNWR may have high year-to-year variation.

Extreme heat and volatility in patterns of precipitation can be expected to increase because of anthropogenic climate change (Ummenhofer and Meehl 2017), likely representing a growing challenge to the crane population. My findings indicate that maintenance of high-quality crane habitat through prescribed burning is of great importance to mitigating the negative effects of climate change. Further work examining resource availability and predation pressure could provide insight necessary for managers to realize the goal of a self-sustaining wild Mississippi sandhill crane population.
Literature Cited


Vita

Henry Woolley grew up in midcoast Maine and received a BS in Environmental Science from University of Rochester in 2007. He has since lived in Baltimore, MD, New Orleans, LA, and currently resides in Hudson, NY. Prior to enrolling in graduate school at University of New Orleans he worked as a BPI certified building analyst, and has had several internships with Americorps, the Student Conservation Association, and the US Fish and Wildlife Service. He hopes to use the skills he has developed while working on his PhD to apply a multidisciplinary investigative approach to contribute to conservation and sustainability.