

EVOLVING RESPONSE OF THE WOOD STORK (*MYCTERIA AMERICANA*) TO
URBANIZATION AND HYDROLOGICAL CHANGE IN THE UNITED STATES

by

Katherine R. Shlepr

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by

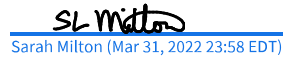
Katherine R. Shlepr

This dissertation was prepared under the direction of the candidate's dissertation co-advisors, Dr. Dale E. Gawlik, Harte Research Institute for Gulf of Mexico Studies, Texas A&M University-Corpus Christi, and, Dr. Sarah L. Milton, Department of Biological Sciences, and has been approved by all members of the supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

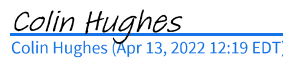
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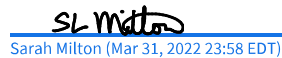
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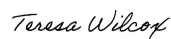
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ABSTRACT

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Urbanization and land development, climate change, pollution, the spread of invasive species, and sea level rise are unprecedented challenges that have led to 25% of avian species worldwide facing an elevated risk of extinction. Under rapidly changing environmental conditions, traditional population models are not ideal because they typically assume that demographic parameters are static in order to estimate the probability of species extinction over a chosen timeframe. This assumption disregards species' potential to adapt to environmental change; adaptations which could alter not only a species' extinction outlook but also its legal protection status. The goal of my PhD research is to re-evaluate the risk of extinction of one threatened species, the Wood Stork (*Mycteria americana*), by accounting for potential adaptation in the context of planned and predicted changes in the southeastern United States. Since the 1970s, Wood Storks have shifted the timing of their breeding season, expanded their range northward and into

novel habitats in urban areas, and begun consuming non-native fishes. I investigate these observations by comparing the physiology and diet of Wood Storks nesting in the historical core of their U.S. range (tree islands in the flooded Everglades marsh) with storks occupying novel habitats in urban and temperate locations. Faster growth rate, improved body condition, and increased survival by nestlings in urban areas would be evidence that colonies on the leading edge of the species' range may be capable of sustaining growth of the whole population. In a third and final chapter, I forecast nest abundance and distribution patterns in the entirety of the U.S. range given various hydrological scenarios. Increased Wood Stork population size and stability are recovery criteria which must be met before the species can qualify for removal from the federal Endangered Species List. More broadly, understanding Wood Stork response to human development in the Everglades illuminates general patterns in avian species response to extreme changes in landscape, and could serve as a framework for proactively incorporating evolutionary potential into the framework of Endangered Species Act recovery in other species which have a high adaptive capacity.

In honor of my parents

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URBANIZATION AND HYDROLOGICAL CHANGE IN THE UNITED STATES

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1 INTRODUCTION

1.1 MODELS: TOOLS TO FIGHT THE LOSS OF BIODIVERSITY

The modern scientific consensus is that we have reached a crisis point in the loss of global biological diversity. Within the context of the debate about whether the Earth's sixth mass extinction event has already begun (Barnosky et al. 2011), we can look to avian species—the taxa that is most completely documented—to see that a full quarter of them face an elevated risk of extinction (Vulnerable, Near Threatened, Endangered, or Critically Endangered on the IUCN Red List (International Union for the Conservation of Nature and Natural Resources 2017). In North America, the best available data suggest there has been a net loss of 3 billion birds, or 29% of the North American population, since 1970 (Rosenberg et al. 2019). And in the United States, 101 of the 349 reported avian species are formally classified as Threatened or Endangered under the Endangered Species Act (ESA), which requires a rigorous review of the evidence of decline prior to species listing (U.S. Fish and Wildlife Service 2019). The number one cause of species loss in the world is habitat destruction (Groom et al. 2005), which may be more broadly cached as a category of human-induced rapid environmental change (Sih et al. 2011). Climate change, which has been intensified by human activities (Eyring et al. 2021), is also a pervasive threat, though it is harder to prove as a driver of species loss since the linkages between climate change and species loss are nearly always indirect.

Conservation biology, which has been deemed a “crisis discipline” since its inception (Soule 1985; Kareiva and Marvier 2012), is the study of how to mitigate the

global loss of biodiversity. Models are one of the most important tools of conservation biology because they explicitly represent the best understanding of how ecological components (e.g., the number of individuals in a population, community composition, habitat factors, abiotic conditions) relate to one another. This type of mechanistic understanding, where cause-and-effect relationships are stated and quantified, is valuable because it is what allows us to break down the complex reality (which can be observed) into comprehensible components. These components can be systematically discussed and (ideally) manipulated through scientific experimentation to continuously improve our understanding of the causes of biodiversity loss. Knowing what drives the biodiversity loss provides the opportunity for decision-makers—be they landowners, policymakers, infrastructure managers, wildlife biologists, or others—to act in accordance with the preservation of biodiversity rather than its demise.

The simplicity of an ecological model relative to the reality of nature is what makes the model a valuable tool, but it also poses a challenge. When users forget or ignore aspects of nature that were left out the model for the sake of simplicity, the model may be misapplied and lose its value as a tool. One assumption that is commonly used in conservation modeling is that of “stationarity”, whereby relationships between model components are assumed to be static through time. These relationships, which are represented as mathematical equations, are typically derived from empirical data. For example, a population model combines information on the life history and demographics of a species and its habitat with the goal of forecasting the future population size of that species under different environmental scenarios. Such a forecast may usefully inform decisions related to species conservation *if* there is reason to believe the species’ response

to habitat conditions will remain constant through the forecasted period. Studies (Sih et al. 2011; Cattau et al. 2018; Beckmann and Berger 2003) now show that this assumption is unwarranted since evolution (change) is continuously happening in response to rapid anthropogenic changes in the environment. The pragmatic question, though, is whether we expect the evolutionary changes that will occur over the timeframe of interest to measurably affect the variable of interest, population size. How to gauge the likelihood of significant evolutionary changes within a given time period for a particular species or population is a foremost question today in the field of conservation biology.

1.2 MODELS APPLIED: WOOD STORK CONSERVATION

This dissertation illustrates the use of modeling as a tool in conservation biology using a focal species, the Wood Stork (*Mycteria americana*; hereafter, “stork”). The stork makes for an interesting case study for several reasons. First, it is a species of conservation interest, having status as a Threatened species under the ESA (U.S. Fish and Wildlife Service 2014) but Least Concern globally (International Union for the Conservation of Nature and Natural Resources 2017). Second, the legal status that the stork has in the U.S. has allowed for detailed, long-term research and monitoring, meaning that data which may be used to explore this question of modeling in conservation are abundant. Finally, following the severe population decline that led to their listing under the ESA, the stork has rebounded in the U.S. despite continuation of the stressor, widespread habitat degradation, that caused the initial decline. Hence, as a capable adaptor, the stork is a challenge to that “stationarity” assumption built into traditional population models.

1.2.1 Everglades Trophic Hypothesis

The Everglades Trophic Hypothesis is a location-specific conceptual model that posits the number of predators at the highest trophic level (alligators, otters, wading birds) is controlled by the concentration and availability of intermediate trophic aquatic prey (crustaceans and fishes), which in turn is dictated by the hydrological state of the landscape. The hydrological condition of the Everglades changes seasonally, so that high water levels brought on by wet season rainfall provide abundant high-quality habitat for crustaceans and fishes to reproduce in the summer and fall. The wet period is followed by months where the water levels steadily recede, thereby forcing the aquatic prey species to concentrate in deep-water refugia. This winter and fall concentration of crustaceans and fishes provides optimal foraging conditions for high trophic predators to reproduce (Trexler and Goss 2009). This hypothesis is grounded in field observations (Kahl 1964; Kushlan et al. 1975; Ogden et al. 1976), has been tested by experimental field manipulations (Gawlik 2002; Cocoves et al. 2021) and computer models (Fleming et al. 1994), and is now integrated into the monitoring protocol of the Comprehensive Everglades Restoration Plan (RECOVER 2005; Frederick et al. 2009; Trexler and Goss 2009).

Though it is generic to all high trophic level predators, the Everglades Trophic Hypothesis is largely based on observations of the stork in the Everglades (Kahl 1964; Kushlan et al. 1975; Ogden et al. 1976; Fleming et al. 1994; Frederick et al. 2009). Specifically, the hypothesis is that the size of the stork population in the Everglades will be determined by the seasonal availability of small marsh fishes. Small marsh fishes are predicted to be most available to storks in long hydroperiod wetlands during a dry winter-

spring following a wet summer-fall, because the wet season allows for a period of high reproduction in fishes which are then forced to concentrate into deep pools as water levels recede across the landscape, making those fish available to the stork as prey (Fig. 1.1; Ogden et al. 1976; Gawlik 2002; Kahl 1964).

The linkages described in the Everglades Trophic Hypothesis facilitated the use of the stork as an indicator of Everglades restoration efforts under the assumption that as historical hydrological conditions are restored, stork numbers will increase (Frederick et al. 2009). However, as linkages between storks, fish communities, and hydrological conditions change over time, the utility of storks as indicators for ecosystem restoration becomes diminished. For example, as storks learn to forage outside natural marsh habitats, then an observed increase in the stork population is potentially unrelated to a change in Everglades health. Therefore, consistent monitoring and revision of model parameters is crucial to ensure that indicator species are truly linked to ecological drivers of the ecosystem.

1.3 STUDY OBJECTIVE

The primary aim of this dissertation was to examine the relationship between the stork and its environment. In particular, I was interested in the impact of the urban environment on stork behavior, and wanted to detect whether the urban environment, or the stork's response to the urban environment, had a population-level effect on the stork. I did not presume to know whether the effect of the urban environment would be beneficial or harmful to the population as a whole. On the one hand, the stork population in the U.S. has rebounded during a period increasing urbanization. On the other hand,

urbanization, is known to devastate avian community diversity in cities around the globe (McKinney 2006, Rosenberg et al. 2019). Through it all, I conducted this research with an eye toward the conservation implications of my findings. The species was down-listed in the U.S. because of its population rebounded in the 2000s, but should we feel confident that this positive trajectory will be sustained?

The chapters that follow are organized hierarchically, from a fine resolution, nest-level model to a range-wide systems model. Chapter 2, “Effect of researcher disturbance and environmental variables on the thermoregulatory response of Wood Stork (*Mycteria americana*) nestlings in subtropical South Florida, USA”, measured the thermoregulatory abilities of nestlings as they aged and were subjected to varying amounts of physiological stress. Data collection took place at both urban and natural marsh colonies in South Florida 2019-2020, and model analysis was conducted at a fine resolution with individual stork nests counting as independent samples. Chapter 3, “Commuters: A new view of how wide-ranging species utilize urban environments”, directly addressed the question of urban resource use and its effect on the reproductive rate of storks. Nest monitoring and diet sampling were conducted at both urban and natural marsh colonies in South Florida 2014-2020. This dataset, started by my predecessors Jessica Klassen and Betsy Evans (Ph.D.s, Avian Ecology Lab, Florida Atlantic University), modelled stork productivity and diet at both the nest and colony levels. Chapter 4, “Range-wide impacts of climate change and urbanization on the future status of a recovering waterbird”, compiled colony-level nest monitoring data from across the stork’s range, South Florida to North Carolina, 2002-2019, and paired environmental data from the same time period. Associations between environmental drivers and the stork response were modelled, and

then these equations were inserted into a complex systems model for the purpose of forecasting the stork population size under future environmental conditions. The final chapter, “Synthesis”, revisits themes from this introduction in the context of what I learned over the course of my study.

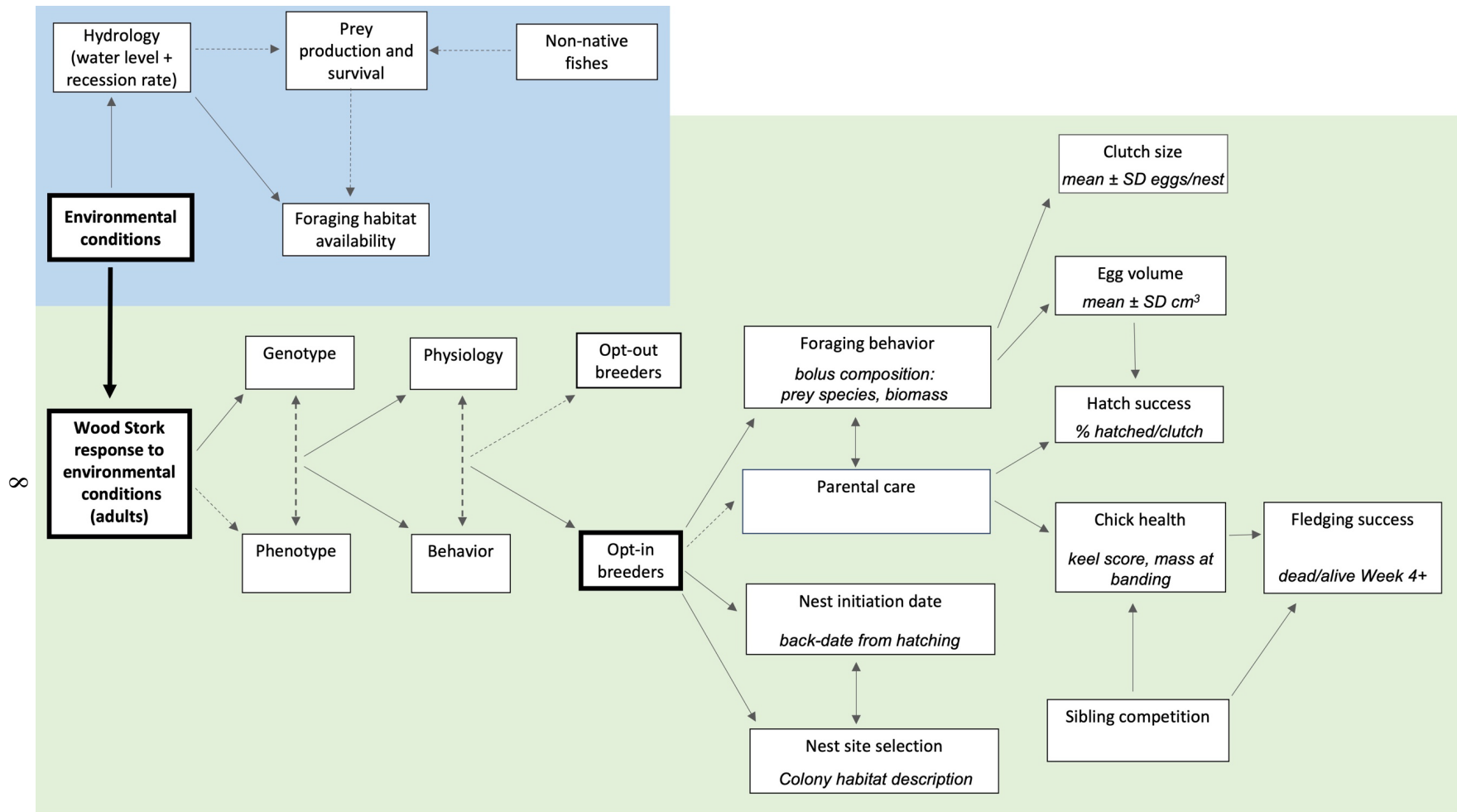


Figure 1.1. Conceptual overview of stork response (green box) to environmental conditions (blue box) studied in this dissertation. Italicized text are metrics used to measure the given component. Dashed arrows indicate relevant components that were not directly observed in this dissertation. Key components observed are highlighted by bold borders.

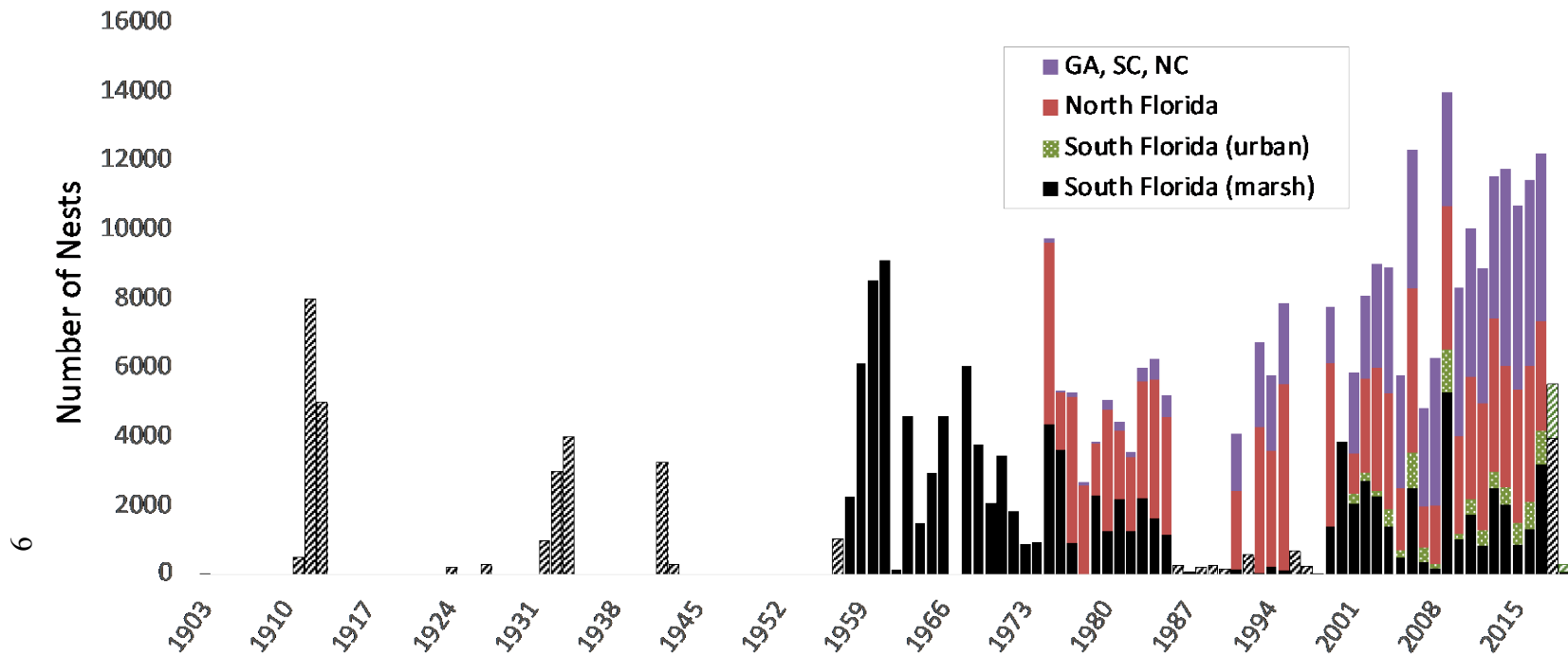


Figure 1.2. Population size of the stork in the U.S. 1903-2019. Hashed bars indicate years when the nest survey was incomplete for the full range of the stork. Data are drawn from Ogden et al. (1976), Crozier and Gawlik (2003), U.S. Fish and Wildlife Service (2021), and Cook and Baranski (2021).

2 THERMOREGULATORY RESPONSE OF WOOD STORK NESTLINGS IN SOUTH FLORIDA

2.1 ABSTRACT

At ambient temperatures above the thermal neutral zone (TNZ), endotherms increase their metabolism to maintain a stable core body temperature (T_b), and failure to thermoregulate effectively leads to rapid death after T_b exceeds a lethal limit. What is unknown is how the thermoregulatory response is impacted by stress-induced hyperthermia when ambient temperatures are above the TNZ, especially in endothermic newborns with yet developing physiological systems. To investigate, I recorded the skin temperature of altricial nestling wading birds at two levels of researcher disturbance in heat index conditions (T_a) that were in and above the TNZ of the species. Underwing temperature was used to approximate T_b , and ankle temperature represented the temperature of extremities where heat-offloading is known to occur in long-legged birds. Data were used to assess two alternate hypotheses: that nestlings would be able to accommodate the increased stress load to maintain a stable T_b , or that adding a disturbance event (an acute stressor) to a hot environment would overwhelm the nestlings' ability to effectively thermoregulate. In all, I found that nestlings of all ages (1-7 wks) were able to thermoregulate effectively in T_a up to 42°C in low- and high-disturbance conditions. I observed that three factors independently increase stress on the thermoregulatory functions in nestling storks, including the level of disturbance, habitat, and body condition, and additionally note that late-season nest initiators will encounter T_a

above the TNZ more frequently than those that begin nesting early in year. Combinations of these stressors increase the metabolic cost of thermoregulation, increasing the likelihood that the thermoregulatory function will trade off with other functions such as growth or immunity, and ultimately survival.

2.2 INTRODUCTION

In endotherms, core body temperature (T_b) is maintained within a narrow range to maximize metabolic efficiency. This makes it possible for endotherms to sustain essential activities such as feeding, locomotion, and defense in a wide range of environmental conditions. The energetic cost of maintaining a constant T_b is lowest in the thermal neutral zone (TNZ), which is the range of ambient temperatures in which T_b is stable without requiring an increase in metabolic rate to maintain that optimal T_b (Fig. 2.1a). While T_b is quite invariable between species within a clade, the TNZ varies by individual and changes over time, most notably during juvenile development. In birds, the TNZ of intermediate- to large-bodied species is typically assumed to be between 20-30°C for adults (Kendeigh 1939; Crawford and Schmidt-Nielsen 1967; Abraham and Evans 1999; Østnes et al. 2001) and 35-38°C for nestlings (Kendeigh 1939; Dunn 1976; Abraham and Evans 1999; Østnes et al. 2001), both of which are below the average T_b of these species (38.5±1.0°C at rest, 40.0±1.3°C when active; (Prinzinger et al. 1991). At hatch, altricial nestlings are functionally ectothermic and therefore require hotter ambient temperatures for optimal functioning than individuals that have completed their major growth period (Kendeigh 1939; Abraham and Evans 1999; Tortosa and Castro 2003; Østnes et al. 2001).

In ambient temperatures above or below an individual's TNZ, metabolic rate is increased to maintain T_b . In hot environments, birds can increase dry heat loss by dilating superficial blood vessels in non-feathered limbs to shed heat to the environment with greater efficiency (Steen and Steen 1965; Phillips and Sanborn 1994; Galván et al. 2017; Schraft et al. 2019), and may also pant to increase evaporative water loss in climates where water is not a scarce resource (Smith et al. 2017). Morphological adaptations such as increased length of un-feathered limbs, and behavioral adaptations such as shade-seeking behaviors, often supplement these physiological mechanisms, but these adaptations depend on the species and population. Whatever the combination of mechanisms and the energetic cost, maintaining homeostasis is essential for survival: lethal T_b is usually above 47°C (Randall 1943; Arad and Marder 1982).

Acute stressors like disturbance or a threat by a potential predator can significantly affect the thermal profile of an individual (Nord and Folkow 2019). For example, handling by researchers was found to induce hyperthermia in intermediate-sized avian species in environments at or below the TNZ (Cabanac and Aizawa 2000; Cabanac and Guillemette 2001; Nord and Folkow 2019). However, how stress-induced hyperthermia (SIH) interacts with ambient temperatures above the TNZ to affect the thermal profile of birds is unknown. Whereas SIH is understood to be advantageous for thermoregulation in cold environments (Robertson et al. 2020), SIH may compound the stress an animal undergoes in a hot environment. The dynamics of these interacting stressors is especially notable for nestlings that have yet developing physiological systems and little-to-no spare energy reserves, depending on body condition and age. Robertson (2021) suggested there would be a trade-off in responding to an acute stressor,

which poses an immediate threat, and hyperthermia, which can be managed to an intermediate degree (riskier-than-optimal T_b yet sublethal as a short-term condition).

The aim of my study was to investigate the effects of disturbance on the thermoregulation of altricial nestlings at ambient temperature in and above the TNZ, and to identify environmental parameters that significantly influence the thermal profile of these nestlings. I hypothesized that the thermoregulatory performance of nestlings would vary by the level of researcher disturbance. Furthermore, whereas extremity temperatures are always expected to increase above the TNZ, core temperatures were expected to change in one of two ways, captured by the following competing hypotheses (Fig. 2.1b): first, that disturbance will overwhelm the thermoregulatory capabilities of nestlings, or alternatively, that nestlings will have the capacity to maintain thermoregulation despite the added stress from disturbance. In the first hypothesis, increased extremity temperatures for heat offloading would not adequately compensate for the increase in metabolic heat gained during SIH, and I should observe that nestlings that experience the most disturbance would have hotter T_b in ambient conditions above the TNZ than those that are less disturbed. In the alternative hypothesis, increased extremity temperatures would offload heat fast enough to compensate for the increase in metabolic heat gained during SIH, and I should observe that nestlings experiencing the most disturbance maintain the same T_b as less disturbed nestlings above the TNZ. Understanding the development of thermoregulation in nestlings and trade-offs in stress response provides guidance for the protection of waterbirds in subtropical and tropical climates.

2.3 METHODS

2.3.1 Study area

Fieldwork took place at 3 Wood Stork (*Mycteria americana*) colonies in southeastern Florida, USA (Griffin 26.0636333, -80.3664916; BallenIsles 26.830142, -80.109086; and Tamiami West 25.75784, -80.54484), during two breeding seasons (Feb-Jun 2019-2020). In South Florida, the coolest month is Jan (average daily min/max heat index: 13/25°C), and the heat index increase steadily through the breeding season (Jun average daily min/max heat index: 23/44°C; climate normals calculated using 80% relative humidity and 1991-2020 daily temperature data in the heat index equation (Rothfusz and Headquarters 1990; National Oceanic and Atmospheric Administration 2021a; Abtew et al. 2011)). Late-nesting storks encounter daily maximum heat indices that are on average 10°C warmer than those encountered by early nesters, with those initiating in Jan encountering an average daily maximum heat index during the Feb-Apr chick-rearing period of 30°C, and those initiating in Mar encountering an average daily maximum heat index during the Apr-Jun chick-rearing period of 40°C. The latter daily maximum heat index is above the TNZ of most intermediate- to large-sized birds. The foraging condition of local marshes was hydrologically poor in both sampling years, so prey were scarce and nestling health and survival were low overall (Frederick et al. 2021; Cook and Baranski 2020).

2.3.2 Nest monitoring

At each colony, 15-30 nests per season were marked by tying a short piece of flagging tape underneath each nest bowl to aid in identification during weekly monitoring

visits. At the beginning and end of the colony visit, the heat index readings ($^{\circ}\text{C}$) from a weather meter (Kestrel 3000 HS, Nielsen-Kellerman Company, Boothwyn, PA) were taken and the two values were averaged to represent the ambient temperature (hereafter, “ T_a ”) of the visit. At each marked nest, I recorded whether the nest was exposed to full sun or partial shade, the number of eggs and nestlings present, an estimate of each nestling’s age (weeks, where a hatching to ~ 6 days old = Week 0; in accordance with (Evans and Gawlik 2020), and any clear behavioral signs of heat stress (e.g., panting). Next, for one nestling per nest (aged 1 week or older), I used an infrared no-contact thermometer (Raytek BT-1800, D:S=50:1; Raytek Corporation, Santa Cruz, CA) to measure the skin temperature ($^{\circ}\text{C}$) of the ankle and the ventral brachial area (feather-less patch of skin under the wing where the wing meets the torso). Emissivity was set to 0.95 in accordance with past studies on the skin temperature of endotherms (Rowley and Alford 2007; Andreasson et al. 2016). The nestling was then removed from the nest, weighed using a Pesola spring scale (g), measured (length of the tarsus (mm) and keel score (0=hatchling, else scale 1-5 where 1=nestling with no fat on the keel and 5=fat layer thick enough to make the shape of the keel unidentifiable), and re-measured for body temperature at the same two body locations as above. The intensity of the acute stress event was considered “low disturbance” when body temperature was recorded prior to nestling handling and “high disturbance” when body temperature was taken after nestling handling. Time spent at each nest (high disturbance) was <5 min, in the vicinity of a nest (low disturbance) was <30 min, and the maximum time spent in a colony during each visit was 1-2 hrs depending on the colony’s size.

2.3.3 Statistical analysis

All statistical analyses were completed in R version 3.6.3 (R Core Development, 2020). To assess the relatedness of age (wks), body size (g), body shape (SA:Vrel=(nestling tarsus mm/average adult tarsus mm)/(nestling mass g/average adult mass g); average adult measurements from (Coulter et al. 2020), and body condition (keel) variables (Fig. 2.2), I created a correlation matrix using the package *corrplot*. Age and size were highly correlated ($r=0.84$), so I dropped the age variable from subsequent analyses. Shape and size were marginally correlated ($r=-0.72$), but since the biological implications of shape and size on body temperature are different and I was interested in both, I opted to retain both variables in my models. All other pairwise correlations were $r\leq 0.54$ (Table 2.1) so were also retained.

I used published literature of experimental studies of mid- to large-sized avian species to determine the T_a threshold that should cause heat stress in nestling storks of two age classes (Kendeigh 1939; Crawford and Schmidt-Nielsen 1967; Davis and Dunn 1976; Abraham and Evans 1999; Østnes et al. 2001). During the period of fastest growth in storks (≤ 3 weeks; Fig. 2.2; Tortosa and Castro 2003), $T_a > 35^\circ\text{C}$ were classified as hotter than the TNZ and were therefore predicted to induce heat stress. For nestlings of fledging age (≥ 4 weeks; Fig. 2.2), the “Above TNZ” threshold was $T_a \geq 30^\circ\text{C}$. After noting records as being in or above the TNZ based on age class of the nestling, I compared wing and ankle temperatures and reviewed changes in the correlation between wing and ankle temperature based on these conditions using simple linear models ($P_\alpha=0.05$). If thermoregulation is happening as expected in both hypotheses, ankle temperature should increase in “Above TNZ” records as the rate of dry heat loss increases at the birds’

extremities. Furthermore, if there is a change in the efficiency of thermoregulation, the correlation between underwing and ankle temperature will change as the underwing temperature gains heat relative to ankle temperature.

In addition to the frequentist statistical approach used above, which was largely descriptive in nature, I wanted to be able to weigh the influence of multiple predictor variables simultaneously. To do so, I used Akaike's Information Criterion for small sample sizes (AIC_c) to compare competing generalized linear mixed models and make inferences about the most important variables affecting core and extremity nestling temperatures (e.g., Grueber et al. 2011 and Anderson 2008). Hatchlings (0 wks of age) were excluded from the AIC_c analyses since hatchlings were only sampled in T_a conditions within the TNZ (Fig. 2.3). Biologically relevant variables were selected (Table 2) based on my understanding of factors affecting avian thermoregulation and then standardized using the package *arm*. In particular, the parameter 'Size' was rescaled (divided by 100). The candidate model sets were identical for both response variables and were comprised of 140 variations (Tables 3-4) of the following global models analyzed as generalized linear mixed models using the package *lme4*:

Global model (core): Underwing temp ~ Ambient temp + Habitat + Disturbance + Body condition + Size + Shape + Ambient temp x Body condition + Habitat x Body condition + Disturbance x Body condition + (1|ID)

Global model (extremity): Ankle temp ~ Ambient temp + Habitat + Disturbance + Body condition + Size + Shape + Ambient temp x Body condition + Habitat x Body condition + Disturbance x Body condition + (1|ID)

Models within 4 ΔAIC_c of the top model were deemed informative (Grueber et al. 2011). To determine the relative influence of each predictor variable on nestling temperature, I calculated model-averaged parameter estimates and 95% confidence intervals for these estimates using the top model sets in the package *MuMIn* (Grueber et al. 2011).

2.4 RESULTS

My full dataset included 86 low disturbance and 176 high disturbance records from 84 independent nests in T_a that ranged from a heat index of 20°C-42°C (Fig. 2.3). In the low disturbance setting, the average underwing (core body; T_b) temperature was 39.4°C±3.4°C (mean±standard deviation (SD)) and the average ankle (extremity) temperature was 34.5°C±4.8°C. In a high disturbance setting, the average underwing temperature was 38.6°C±3.2°C and the average ankle temperature was 35.4°C±4.4°C (Fig. 2.4).

Age class did not significantly affect T_b or ankle temperature within a T_a condition class (“In TNZ” or “Above TNZ”), so age classes were pooled in the linear regression that modelled body temperature according to T_a class. These simple linear models revealed no significant difference in T_b ($p=0.628$; Fig. 2.5a) or ankle temperature ($p=0.169$; Fig. 2.5b) in the TNZ versus above the TNZ. Furthermore, the relationship between T_b and ankle temperature was not significantly different according to T_a class (Fig. 2.6).

Age class did not significantly affect the relationship between T_b and ankle temperature ($p=0.689$), so age classes were pooled. Over the range of sampled T_a , ankle temperature was positively correlated with T_b , suggesting there was a physiological

response to increase heat offloading (Fig. 2.7). However, the slopes of the relationship between T_b and ankle temperature were different ($p=0.005$) depending on the level of disturbance the nestlings were exposed to. When $T_b > 36.1^\circ\text{C}$, nestlings in the high disturbance condition offloaded heat faster than those in the low disturbance condition (Fig. 2.7), suggesting the metabolic rate of nestlings in the high disturbance condition was higher to maintain a similar T_b .

Among all models describing nestling temperature ($n=140$), there were 34 plausible models for core body ($\Delta\text{AIC} < 4$; cumulative Akaike weight (w_i)=1.0; Table 2.3) and 18 plausible models for extremity temperature ($\Delta\text{AIC} < 4$; cumulative $w_i=0.88$; Table 1.4). No single plausible model had support over $w_i=0.13$ and all predictor variables appeared in both top model sets, indicating that every predictor variable explained a small amount of variation in the response variables. In both analyses, habitat type and the interaction between T_a and body condition were the parameters with the most influence. For habitat type, nestlings that were in nests exposed to full sun had an average T_b that was 1.4°C hotter than nestlings in at least partially shaded nests (Fig. 2.8). The interaction term indicated that nestlings that had a poorer body condition (keel score=1-2) had hotter T_b and ankle temperatures at lower T_a but their body temperatures trended stable or even cooling as T_a increased, whereas nestlings in good body condition (keel score 3-4) started off with cooler T_b and ankle temperatures at low T_a but their body temperatures increased with increasing T_a (Fig. 2.9). For all other parameters in the models, the 95% confidence intervals for the parameter estimates bound zero, suggesting a weaker and/or more variable influence on nestling temperature (Tables 2.3-2.5).

2.5 DISCUSSION

This study investigated the ability of altricial nestlings to thermoregulate during disturbance events in hot, humid environmental conditions. Underwing temperature, which approximated T_b , was comparable to the T_b reported in other Ciconiiformes (Benedict and Fox 1927; Tortosa and Castro 2003) and did not vary significantly by the severity of the disturbance. In all, nestlings of all ages were able to thermoregulate effectively in T_a up to 42°C, which is 5-12°C above the TNZ of these birds (depending on age class). Though not significant, ankle (extremity) temperature increased above the TNZ for nestlings of pooled age classes, indicating that the rate of heat offloading increased enough to maintain homeostasis in birds of both stages of development. This is further supported by the significant change in slope of the relationship between underwing and ankle temperature according to level of disturbance, and the suggestive change in this same relationship according to T_a . In both cases, nestlings measured in the more stressful condition (i.e., high disturbance or T_a above the TNZ) increased heat offloading at the ankle, meaning that these nestlings may have to increase their metabolic rate to maintain a similar T_b in the more stressful condition. This is consistent with successful thermoregulation, but also suggests that stress, whether from extreme disturbance, a prolonged heat wave, or a combination there, is likely to cost nestlings energy. If stressors are prolonged, physiological compensation is likely to trade off with growth, immunity and other functions and may ultimately affect the likelihood of survival (Oswald and Arnold 2012; Elliott et al. 2014). I observed no mortality due to the disturbance caused by my research in even food-poor years, but I did not measure and therefore cannot rule out the possibility of slowed growth, damped immunity, or

decreased post-fledging survival. Therefore, researchers are urged to review their field protocols to minimize the duration and intensity of disturbance whenever possible.

Model averaged variable weights revealed that the level of disturbance and nestling body characteristics had a minor influence on underwing and ankle temperature compared to habitat type and the interaction between body condition and T_a . Habitat type had the largest effect size of all, and I found that nestlings in full sun had an average underwing temperature that was 1.4°C hotter than nestlings in at least partially shaded nests. This emphasizes the importance of a previously unrecognized colony-level attribute, vegetative structure. Whereas storks that nest in the historically active cypress dome colonies in the Everglades system have access to shaded limbs on large trees, those that nest in novel urban colonies more often occupy the tops of dense, often non-native invasive shrubs where no shade is available.

Nestlings in poor condition (keel 1), which are young (0-1 wks old) and/or in poor health, show a negative correlation in underwing and ankle temperature with T_a . Nestlings in good condition (keel 3-4), which are older (>2 weeks old) and in good health, show the opposite pattern of increasing underwing and ankle temperature with T_a . Cooling of poor condition nestlings may suggest a hypothermic reaction to stress (instead of SIH) as has been observed during researcher handling in other species, but that hypothermic response observed in other species is likely due to thermal conductance properties of birds <30 g (Nord and Folkow 2019), which does not apply to storks (minimum mass recorded in this study=40 g). Therefore, the level of disturbance is insufficient to explain the cooling trends in nestlings with a keel score of 1. Young nestlings, including all birds with a keel score of 1, have a hotter TNZ (35-38°C) than

older nestlings, including those with a keel score of 3 or 4 (TNZ 20-30°C). Because I only monitored colonies in T_a up to 42°C, trend lines should be compared cautiously since the frequency and severity of thermally stressful environments encountered by nestlings differs for those with a keel score of 1 versus keel score of 3 or 4. Even so, this finding, which was strongly supported by the AIC_c analyses, suggests that nestlings in poor condition have a hotter average core temperature, live closer to their thermal limits and may not have as much capacity to respond to additional acute stressors as do nestlings in better condition. On the other hand, good-condition nestlings, which have greater energy stores, can afford to allow their core body to heat to deal with a potentially more severe and immediate threat.

Widespread hyperthermia can lead to populations declines through multiple avenues. For breeding adults, prolonged hot weather events may steepen behavior-related opportunity costs that compromises parental care (Cunningham et al. 2021). For example, adjusting foraging times or seeking shade adjacent to a nest site may decrease thermal stress but lead to nest abandonment and decreased hatch success rates as has been observed in other avian species (Amat et al. 2017; Andreasson et al. 2018; Reyna and Burggren 2017; Nilsson and Nord 2018). Heat stress also disrupts the physical development of nestlings, and has been show to decrease nestling growth rates, fledging success rates, post-fledging survival (Rodríguez et al. 2016; Rodríguez and Barba 2016) and lifetime cognitive performance (Soravia et al. 2021).

Climate change is expected to influence bird distributions worldwide as species hit their physiological limits thermoregulating in hotter environments (Wolf 2000; Oswald and Arnold 2012; Riddell et al. 2021). However, the stork population monitored

for this study provides a prime example of how species may encounter their physiological limits in more indirect ways than warming climates. First, if levels of disturbance increase, as has been noted with storks and other species that are beginning to move into urban areas, less energy may be available to individuals to invest in thermoregulation, growth, and health. Moreover, the timing of stork nesting has shifted to later in the year in response to changes in the timing of prey availability (Frederick et al. 2009; Cook and Baranski 2020). So, whether or not the climate of South Florida continues to get hotter as projected (Runkle et al. 2017), storks' shift from Dec-Jan nest initiation to Feb-Mar nest initiation means they now encounter daily maximum heat indices that are on average 10°C warmer than they encountered when they historically nested earlier in the year. The metabolic cost of cooling in ambient conditions above the TNZ may have contributed to the observed declined reproductive performance, especially in years with poor foraging conditions.

2.5.1 Conclusion

My study showed that even young stork nestlings successfully thermoregulate in T_a up to 42°C amidst disturbance events. When T_b exceeded 36.1°C, extremity temperature exceeded T_b , suggesting that active energy-requiring thermoregulation was taking place. Furthermore, there was a suggestive increase in mean extremity temperature in T_a above the TNZ compared to in the TNZ. These joint observations are evidence that nestling storks increase their metabolism to thermoregulate in $T_a > 35^\circ\text{C}$ (for nestlings age 0-3 wks) or $\geq 30^\circ\text{C}$ (for nestlings age ≥ 4 wks), which are T_a frequently encountered during the breeding season in South Florida.

I observed three factors that can independently increase stress on the thermoregulatory functions in nestling storks, including disturbance (low vs. high levels), habitat (shade vs. sun), and body condition (poor vs. healthy), and additionally note that late-season nest initiators will encounter T_a above the TNZ more frequently than those that begin nesting early in year. Combinations of these stressors increase the metabolic cost of thermoregulation, increasing the likelihood that the thermoregulatory function will trade off with other functions such as growth or immunity, and ultimately survival. Because T_b is highly consistent across avian species, and variations in thermoregulatory mechanisms are primarily driven by body size and thermal environment, I expect my findings to be applicable to other intermediate-sized waterbirds that nest in hot, humid climates.

2.6 ACKNOWLEDGEMENTS

I wish to thank BallenIsles Country Club and the City of Weston for granting land access permissions, especially during the COVID-19 pandemic. I also thank Ricardo Zambrano, Rosemarie Moore, and many other volunteers for invaluable assistance in the field. Data collection was conducted in accordance with the conditions stated in the following permits: FAU IACUC A17-33, USFWS TE65550A-2, NPS EVER-2018-SCI-0017, and FFWCC LSSC-18-00027.

Table 2.1. Correlation matrix of the morphometric measurements recorded in this study (n=187, includes repeated measurements of individuals), including nestling shape (surface-area-to-volume ratio relative to an average adult Wood Stork, Coulter et al. 2020), body condition (keel score 1-5), age (wks), and size (mass, g).

	Shape	Condition	Age	Size
Shape	1			
Condition	-0.51	1		
Age	-0.48	0.42	1	
Size	-0.72	0.54	0.84	1

Table 2.2. Description of variables used in the global models of model sets evaluated by an information theoretic approach (AIC_c). Global models were identical except for the response variable (Y) used.

Global model component	Parameter name	Description and level units	Justification
Y1	Underwing	Skin temperature at featherless patch where underwing meets torso Continuous, °C.	Underwing temperature, which is an approximation for core body temperature (T _b), is used to determine whether an individual is in a state of hyperthermia.
Y2	Ankle	Skin temperature at ventral end of tarsus; represents extremity temperature. Continuous, °C.	Heat from the core body is offloaded at the extremities during thermoregulation at ambient temperatures above the thermal neutral zone (TNZ).
X1	Ambient temperature	Average heat index reading (Kestrel 3000 Heat Stress meter) from inside the colony during a monitoring visit. Continuous, °C.	Ambient conditions outside the TNZ require endotherms to thermoregulate to maintain a stable T _b .
X2	Disturbance level	Description of the severity of the disturbance used to elicit an acute stress response. Low = area entered but nestling not handled, High = area entered and nestling handled.	Disturbance, an acute stressor, may disrupt thermoregulation by initiating a “fight or flight” response which involves sending blood (and heat) to the core body.
X3	Body mass	Rescaled body mass. Continuous, g/100	Small masses naturally gain and lose heat faster than larger masses.
X4	Body condition	Description of the amount of muscle overlaying the keel bone. Young and/or poorly fed nestlings with no muscle have a low score (1-2), while healthy, older nestlings that have built muscle will have a higher score (3-5).	Body condition is an indication of the overall health of an animal; those in good condition are expected to have the resources to cope with stress better than those in poor condition.

X5	Body shape	Tarsus (mm) / mass (g) relative to the same measurements from an adult-sized stork. Continuous, unitless.	Animals with a large surface area-to-volume ratio naturally gain and lose heat faster than animals with a small surface-area-to-volume ratio.
X6	Chick age	Age (wks) of the nestling as determined by known hatch dates and assumed nest order where the largest nestling is considered the first hatched. Integers beginning at 1.	Storks hatch as altricial animals and develop feathers and physiological coping mechanisms at the end of their major growth period (Tortosa and Castro 2003); therefore, heat stress is expected to impact young (1-3 wks of age) and older (≥ 4 wks of age) nestlings differently.
Intercept	Nest identity	Unique identification number	Some nests were sampled on a weekly basis; therefore, identity was included in the model to account for the non-independence of these data.

Table 2.3. Full model set for the global model: Underwing temp ~ Ambient temp + Habitat + Disturbance + Body condition + Size + Shape + Ambient temp x Body condition + Habitat x Body condition + Disturbance x Body condition + (1|ID). Models within 4 ΔAIC_c of the top model were deemed informative.

Rank	(Intercept)	Habitat	Handled	Keel	KestrelHI	Mass.bird. scaled	SAVrel	Habitat x Keel	Handled x Keel	Keel x KestrelHI	df	logLik	AIC _c	delta	weight	CumWt
1	39.21	-1.82	NA	-0.08	-0.38	NA	-0.93	NA	NA	2.30	8	-467.68	952.16	0.00	0.07	0.07
2	39.22	-1.83	-0.65	0.00	-0.39	NA	-0.87	NA	NA	2.35	9	-466.65	952.32	0.16	0.07	0.14
3	39.21	-1.78	-0.71	0.45	-0.28	NA	NA	NA	NA	2.24	8	-468.08	952.97	0.81	0.05	0.19
4	39.23	-1.63	NA	NA	NA	NA	-0.80	NA	NA	NA	5	-471.43	953.19	1.02	0.04	0.23
5	39.20	-1.76	NA	0.39	-0.26	NA	NA	NA	NA	2.18	7	-469.30	953.23	1.07	0.04	0.27
6	39.23	-1.83	NA	-0.11	-0.41	NA	-0.93	1.01	NA	2.61	9	-467.16	953.34	1.17	0.04	0.31
7	39.24	-1.64	-0.59	NA	NA	NA	-0.78	NA	NA	NA	6	-470.61	953.69	1.53	0.03	0.34
8	39.24	-1.84	-0.61	-0.03	-0.42	NA	-0.88	0.89	NA	2.62	10	-466.26	953.76	1.60	0.03	0.38
9	39.20	-1.80	-0.62	-0.04	-0.40	NA	-0.88	NA	0.59	2.32	10	-466.47	954.18	2.02	0.03	0.40
10	39.22	-1.62	NA	NA	NA	NA	NA	NA	NA	NA	4	-473.00	954.22	2.05	0.03	0.43
11	39.21	-1.82	-0.69	0.16	-0.33	0.51	NA	NA	NA	2.37	9	-467.61	954.24	2.08	0.03	0.45
12	39.20	-1.80	NA	0.08	-0.32	0.55	NA	NA	NA	2.32	8	-468.77	954.34	2.18	0.02	0.48
13	39.21	-1.81	NA	-0.07	-0.38	-0.06	-0.97	NA	NA	2.29	9	-467.67	954.36	2.20	0.02	0.50
14	39.22	-1.77	NA	0.37	-0.29	NA	NA	1.00	NA	2.49	8	-468.80	954.42	2.25	0.02	0.52
15	39.23	-1.79	-0.68	0.43	-0.30	NA	NA	0.86	NA	2.51	9	-467.71	954.44	2.28	0.02	0.55
16	39.22	-1.82	-0.65	0.02	-0.39	-0.06	-0.91	NA	NA	2.33	10	-466.65	954.55	2.38	0.02	0.57
17	39.23	-1.62	-0.61	NA	NA	NA	NA	NA	NA	NA	5	-472.12	954.57	2.41	0.02	0.59
18	39.20	-1.75	-0.68	0.42	-0.29	NA	NA	NA	0.54	2.22	9	-467.93	954.87	2.71	0.02	0.61
19	39.23	-1.68	NA	NA	-0.26	NA	-0.83	NA	NA	NA	6	-471.28	955.04	2.87	0.02	0.63
20	39.23	-1.63	NA	NA	NA	-0.28	-1.01	NA	NA	NA	6	-471.33	955.13	2.97	0.02	0.64
21	39.23	-1.63	NA	0.03	NA	NA	-0.79	NA	NA	NA	6	-471.43	955.32	3.16	0.01	0.66
22	39.22	-1.64	NA	NA	NA	0.44	NA	NA	NA	NA	5	-472.52	955.37	3.21	0.01	0.67
23	39.22	-1.61	NA	0.43	NA	NA	NA	NA	NA	NA	5	-472.57	955.48	3.32	0.01	0.69
24	39.23	-1.82	NA	-0.07	-0.41	-0.17	-1.03	1.05	NA	2.59	10	-467.13	955.51	3.35	0.01	0.70
25	39.24	-1.69	-0.59	NA	-0.26	NA	-0.81	NA	NA	NA	7	-470.46	955.54	3.38	0.01	0.71

26	39.22	-1.80	-0.57	-0.08	-0.43	NA	-0.89	0.94	0.67	2.61	11	-466.02	955.55	3.39	0.01	0.73
27	39.23	-1.62	-0.65	0.48	NA	NA	NA	NA	NA	NA	6	-471.58	955.62	3.46	0.01	0.74
28	39.24	-1.63	-0.58	NA	NA	-0.26	-0.97	NA	NA	NA	7	-470.53	955.69	3.52	0.01	0.75
29	39.23	-1.64	-0.61	NA	NA	0.43	NA	NA	NA	NA	6	-471.64	955.76	3.59	0.01	0.76
30	39.22	-1.81	NA	0.09	-0.34	0.49	NA	0.90	NA	2.59	9	-468.37	955.76	3.59	0.01	0.77
31	39.24	-1.64	-0.60	0.11	NA	NA	-0.73	NA	NA	NA	7	-470.59	955.81	3.64	0.01	0.79
32	39.23	-1.82	-0.66	0.17	-0.35	0.46	NA	0.77	NA	2.60	10	-467.32	955.90	3.73	0.01	0.80
33	39.24	-1.83	-0.61	0.01	-0.41	-0.15	-0.97	0.92	NA	2.60	11	-466.23	955.97	3.81	0.01	0.81
34	39.20	-1.79	-0.66	0.12	-0.34	0.51	NA	NA	0.55	2.35	10	-467.45	956.16	3.99	0.01	0.82
35	39.23	-1.65	NA	NA	-0.15	NA	NA	NA	NA	NA	5	-472.95	956.22	4.06	0.01	0.83
36	39.21	-1.75	-0.64	0.39	-0.32	NA	NA	0.92	0.61	2.49	10	-467.51	956.28	4.11	0.01	0.84
37	39.20	-1.79	-0.62	-0.03	-0.40	-0.06	-0.92	NA	0.59	2.31	11	-466.46	956.43	4.27	0.01	0.84
38	39.24	-1.66	-0.61	NA	-0.17	NA	NA	NA	NA	NA	6	-472.06	956.59	4.43	0.01	0.85
39	39.24	-1.68	NA	NA	-0.26	-0.28	-1.04	NA	NA	NA	7	-471.19	957.00	4.84	0.01	0.86
40	39.23	-1.68	NA	0.01	-0.25	NA	-0.82	NA	NA	NA	7	-471.28	957.19	5.03	0.01	0.86
41	39.23	-1.62	NA	0.11	NA	-0.32	-0.98	NA	NA	NA	7	-471.31	957.25	5.09	0.01	0.87
42	39.22	-1.62	NA	0.26	NA	0.30	NA	NA	NA	NA	6	-472.41	957.28	5.12	0.01	0.88
43	39.21	-1.58	-0.62	0.44	NA	NA	NA	NA	0.66	NA	7	-471.36	957.34	5.18	0.01	0.88
44	39.22	-1.68	NA	NA	-0.20	0.45	NA	NA	NA	NA	6	-472.44	957.34	5.18	0.01	0.89
45	39.23	-1.63	NA	0.03	NA	NA	-0.79	0.01	NA	NA	7	-471.43	957.48	5.31	0.01	0.89
46	39.22	-1.60	-0.56	0.06	NA	NA	-0.74	NA	0.70	NA	8	-470.34	957.49	5.32	0.01	0.90
47	39.22	-1.64	NA	0.43	-0.15	NA	NA	NA	NA	NA	6	-472.52	957.51	5.35	0.00	0.90
48	39.23	-1.63	-0.64	0.34	NA	0.26	NA	NA	NA	NA	7	-471.45	957.53	5.37	0.00	0.91
49	39.25	-1.69	-0.58	NA	-0.26	-0.26	-1.00	NA	NA	NA	8	-470.38	957.56	5.40	0.00	0.91
50	39.22	-1.61	NA	0.43	NA	NA	NA	0.04	NA	NA	6	-472.57	957.61	5.45	0.00	0.92
51	39.23	-1.65	-0.66	0.49	-0.16	NA	NA	NA	NA	NA	7	-471.52	957.66	5.50	0.00	0.92
52	39.24	-1.69	-0.60	0.09	-0.26	NA	-0.77	NA	NA	NA	8	-470.44	957.70	5.54	0.00	0.92
53	39.24	-1.69	-0.61	NA	-0.21	0.45	NA	NA	NA	NA	7	-471.55	957.73	5.57	0.00	0.93
54	39.24	-1.63	-0.60	0.19	NA	-0.32	-0.93	NA	NA	NA	8	-470.47	957.75	5.59	0.00	0.93
55	39.21	-1.79	-0.62	0.12	-0.36	0.46	NA	0.82	0.61	2.58	11	-467.12	957.76	5.60	0.00	0.94
56	39.23	-1.62	-0.66	0.49	NA	NA	NA	-0.10	NA	NA	7	-471.57	957.77	5.61	0.00	0.94
57	39.22	-1.80	-0.57	-0.04	-0.43	-0.16	-0.99	0.98	0.67	2.59	12	-465.99	957.77	5.61	0.00	0.95
58	39.24	-1.64	-0.60	0.11	NA	NA	-0.73	-0.12	NA	NA	8	-470.58	957.97	5.81	0.00	0.95

59	39.23	-1.67	NA	0.09	-0.25	-0.31	-1.02	NA	NA	NA	8	-471.18	959.16	7.00	0.00	0.95
60	39.21	-1.59	-0.60	0.29	NA	0.27	NA	NA	0.67	NA	8	-471.23	959.26	7.10	0.00	0.95
61	39.22	-1.66	NA	0.25	-0.18	0.32	NA	NA	NA	NA	7	-472.34	959.30	7.13	0.00	0.96
62	39.22	-1.65	-0.56	0.03	-0.28	NA	-0.78	NA	0.73	NA	9	-470.17	959.36	7.20	0.00	0.96
63	39.23	-1.68	NA	0.01	-0.26	NA	-0.82	0.02	NA	NA	8	-471.28	959.38	7.21	0.00	0.96
64	39.22	-1.62	-0.62	0.44	-0.18	NA	NA	NA	0.68	NA	8	-471.29	959.38	7.22	0.00	0.96
65	39.23	-1.62	NA	0.11	NA	-0.33	-0.99	0.10	NA	NA	8	-471.31	959.42	7.26	0.00	0.96
66	39.22	-1.62	NA	0.26	NA	0.31	NA	-0.05	NA	NA	7	-472.41	959.44	7.28	0.00	0.97
67	39.22	-1.59	-0.56	0.14	NA	-0.33	-0.94	NA	0.70	NA	9	-470.22	959.45	7.29	0.00	0.97
68	39.21	-1.58	-0.62	0.44	NA	NA	NA	-0.04	0.66	NA	8	-471.36	959.52	7.36	0.00	0.97
69	39.23	-1.67	-0.64	0.33	-0.19	0.28	NA	NA	NA	NA	8	-471.38	959.56	7.40	0.00	0.97
70	39.22	-1.64	NA	0.43	-0.15	NA	NA	0.05	NA	NA	7	-472.52	959.67	7.51	0.00	0.97
71	39.24	-1.68	-0.60	0.17	-0.25	-0.32	-0.96	NA	NA	NA	9	-470.33	959.68	7.52	0.00	0.98
72	39.23	-1.63	-0.65	0.33	NA	0.28	NA	-0.18	NA	NA	8	-471.44	959.68	7.52	0.00	0.98
73	39.22	-1.60	-0.56	0.06	NA	NA	-0.74	-0.06	0.69	NA	9	-470.34	959.69	7.53	0.00	0.98
74	39.23	-1.65	-0.66	0.49	-0.16	NA	NA	-0.09	NA	NA	8	-471.51	959.84	7.67	0.00	0.98
75	39.24	-1.69	-0.60	0.09	-0.26	NA	-0.77	-0.11	NA	NA	9	-470.44	959.89	7.73	0.00	0.98
76	39.24	-1.63	-0.60	0.19	NA	-0.32	-0.93	-0.04	NA	NA	9	-470.47	959.96	7.80	0.00	0.98
77	39.25	NA	NA	NA	NA	NA	-0.77	NA	NA	NA	4	-476.47	961.15	8.99	0.00	0.98
78	39.22	-1.64	-0.61	0.28	-0.20	0.29	NA	NA	0.69	NA	9	-471.14	961.29	9.13	0.00	0.98
79	39.24	-1.67	NA	0.09	-0.25	-0.33	-1.02	0.10	NA	NA	9	-471.17	961.36	9.19	0.00	0.99
80	39.22	-1.64	-0.56	0.11	-0.27	-0.32	-0.98	NA	0.73	NA	10	-470.06	961.37	9.21	0.00	0.99
81	39.21	-1.60	-0.61	0.29	NA	0.28	NA	-0.12	0.66	NA	9	-471.22	961.46	9.29	0.00	0.99
82	39.22	-1.66	NA	0.25	-0.18	0.33	NA	-0.04	NA	NA	8	-472.33	961.48	9.32	0.00	0.99
83	39.21	-1.62	-0.62	0.44	-0.18	NA	NA	-0.03	0.67	NA	9	-471.29	961.59	9.43	0.00	0.99
84	39.22	-1.65	-0.56	0.03	-0.27	NA	-0.78	-0.04	0.72	NA	10	-470.17	961.59	9.43	0.00	0.99
85	39.22	-1.59	-0.56	0.14	NA	-0.33	-0.94	0.03	0.70	NA	10	-470.22	961.69	9.52	0.00	0.99
86	39.23	-1.67	-0.65	0.32	-0.19	0.30	NA	-0.18	NA	NA	9	-471.36	961.74	9.57	0.00	0.99
87	39.26	NA	-0.57	NA	NA	NA	-0.76	NA	NA	NA	5	-475.71	961.75	9.59	0.00	0.99
88	39.24	NA	NA	NA	NA	NA	NA	NA	NA	NA	3	-477.84	961.80	9.64	0.00	0.99
89	39.24	-1.68	-0.60	0.17	-0.25	-0.31	-0.96	-0.03	NA	NA	10	-470.33	961.91	9.75	0.00	0.99
90	39.26	NA	-0.59	NA	NA	NA	NA	NA	NA	NA	4	-477.03	962.27	10.11	0.00	0.99
91	39.23	NA	NA	-0.02	-0.05	NA	-0.83	NA	NA	1.98	7	-473.94	962.51	10.35	0.00	0.99

92	39.21	NA	NA	0.40	0.06	NA	NA	NA	NA	1.88	6	-475.14	962.75	10.58	0.00	0.99
93	39.23	NA	-0.68	0.46	0.05	NA	NA	NA	NA	1.94	7	-474.08	962.79	10.63	0.00	0.99
94	39.24	NA	-0.62	0.05	-0.05	NA	-0.77	NA	NA	2.02	8	-473.03	962.87	10.71	0.00	0.99
95	39.25	NA	NA	NA	NA	-0.39	-1.06	NA	NA	NA	5	-476.29	962.92	10.76	0.00	0.99
96	39.23	NA	NA	0.43	NA	NA	NA	NA	NA	NA	4	-477.44	963.11	10.95	0.00	0.99
97	39.25	NA	NA	0.05	NA	NA	-0.75	NA	NA	NA	5	-476.46	963.26	11.09	0.00	0.99
98	39.25	NA	NA	NA	0.03	NA	-0.77	NA	NA	NA	5	-476.46	963.26	11.10	0.00	0.99
99	39.24	NA	NA	NA	NA	0.36	NA	NA	NA	NA	4	-477.53	963.27	11.11	0.00	1.00
100	39.25	NA	-0.63	0.48	NA	NA	NA	NA	NA	NA	5	-476.54	963.41	11.25	0.00	1.00
101	39.21	-1.64	-0.61	0.27	-0.20	0.30	NA	-0.11	0.67	NA	10	-471.13	963.51	11.35	0.00	1.00
102	39.27	NA	-0.57	NA	NA	-0.37	-1.03	NA	NA	NA	6	-475.55	963.57	11.41	0.00	1.00
103	39.23	-1.64	-0.56	0.11	-0.27	-0.32	-0.98	0.04	0.73	NA	11	-470.06	963.63	11.46	0.00	1.00
104	39.25	NA	-0.59	NA	NA	0.36	NA	NA	NA	NA	5	-476.72	963.78	11.61	0.00	1.00
105	39.24	NA	NA	NA	0.12	NA	NA	NA	NA	NA	4	-477.81	963.83	11.67	0.00	1.00
106	39.26	NA	-0.58	0.12	NA	NA	-0.70	NA	NA	NA	6	-475.69	963.84	11.68	0.00	1.00
107	39.26	NA	-0.57	NA	0.03	NA	-0.75	NA	NA	NA	6	-475.71	963.88	11.72	0.00	1.00
108	39.21	NA	-0.57	-0.02	-0.09	NA	-0.79	NA	0.92	1.99	9	-472.59	964.21	12.04	0.00	1.00
109	39.20	NA	-0.63	0.40	0.02	NA	NA	NA	0.86	1.90	8	-473.70	964.21	12.04	0.00	1.00
110	39.25	NA	-0.59	NA	0.12	NA	NA	NA	NA	NA	5	-477.00	964.33	12.17	0.00	1.00
111	39.21	NA	NA	0.19	0.02	0.38	NA	NA	NA	1.98	7	-474.89	964.42	12.25	0.00	1.00
112	39.23	NA	-0.66	0.26	0.02	0.34	NA	NA	NA	2.02	8	-473.88	964.57	12.41	0.00	1.00
113	39.23	NA	NA	0.04	-0.05	-0.22	-0.96	NA	NA	1.93	8	-473.89	964.59	12.43	0.00	1.00
114	39.22	NA	-0.58	0.41	NA	NA	NA	NA	0.97	NA	6	-476.06	964.59	12.43	0.00	1.00
115	39.23	NA	-0.52	0.04	NA	NA	-0.72	NA	1.01	NA	7	-475.16	964.95	12.79	0.00	1.00
116	39.24	NA	-0.62	0.11	-0.05	-0.22	-0.91	NA	NA	1.98	9	-472.98	964.97	12.81	0.00	1.00
117	39.25	NA	NA	0.16	NA	-0.44	-1.02	NA	NA	NA	6	-476.26	964.98	12.82	0.00	1.00
118	39.25	NA	NA	NA	0.03	-0.38	-1.05	NA	NA	NA	6	-476.29	965.05	12.89	0.00	1.00
119	39.23	NA	NA	0.31	NA	0.20	NA	NA	NA	NA	5	-477.37	965.08	12.92	0.00	1.00
120	39.23	NA	NA	0.43	0.13	NA	NA	NA	NA	NA	5	-477.41	965.15	12.98	0.00	1.00
121	39.24	NA	NA	NA	0.10	0.35	NA	NA	NA	NA	5	-477.51	965.35	13.18	0.00	1.00
122	39.25	NA	NA	0.05	0.04	NA	-0.74	NA	NA	NA	6	-476.46	965.39	13.22	0.00	1.00
123	39.25	NA	-0.62	0.39	NA	0.16	NA	NA	NA	NA	6	-476.49	965.46	13.29	0.00	1.00
124	39.25	NA	-0.63	0.48	0.13	NA	NA	NA	NA	NA	6	-476.50	965.48	13.31	0.00	1.00

125	39.26	NA	-0.58	0.23	NA	-0.45	-0.98	NA	NA	NA	7	-475.47	965.57	13.41	0.00	1.00
126	39.27	NA	-0.57	NA	0.02	-0.37	-1.02	NA	NA	NA	7	-475.55	965.72	13.56	0.00	1.00
127	39.25	NA	-0.59	NA	0.09	0.35	NA	NA	NA	NA	6	-476.70	965.87	13.71	0.00	1.00
128	39.20	NA	-0.61	0.19	-0.01	0.35	NA	NA	0.88	1.99	9	-473.48	965.98	13.82	0.00	1.00
129	39.26	NA	-0.58	0.12	0.04	NA	-0.69	NA	NA	NA	7	-475.68	965.99	13.83	0.00	1.00
130	39.22	NA	-0.57	0.04	-0.08	-0.22	-0.93	NA	0.92	1.94	10	-472.54	966.33	14.17	0.00	1.00
131	39.22	NA	-0.57	0.31	NA	0.18	NA	NA	0.98	NA	7	-476.01	966.65	14.48	0.00	1.00
132	39.22	NA	-0.58	0.41	0.10	NA	NA	NA	0.96	NA	7	-476.04	966.71	14.55	0.00	1.00
133	39.23	NA	-0.53	0.15	NA	-0.44	-0.99	NA	1.01	NA	8	-474.95	966.71	14.55	0.00	1.00
134	39.25	NA	NA	0.16	0.04	-0.44	-1.02	NA	NA	NA	7	-476.25	967.13	14.97	0.00	1.00
135	39.23	NA	-0.52	0.04	0.00	NA	-0.71	NA	1.01	NA	8	-475.16	967.14	14.97	0.00	1.00
136	39.23	NA	NA	0.32	0.12	0.19	NA	NA	NA	NA	6	-477.35	967.16	15.00	0.00	1.00
137	39.25	NA	-0.62	0.40	0.12	0.15	NA	NA	NA	NA	7	-476.47	967.56	15.39	0.00	1.00
138	39.26	NA	-0.58	0.23	0.04	-0.45	-0.97	NA	NA	NA	8	-475.47	967.75	15.58	0.00	1.00
139	39.22	NA	-0.57	0.32	0.08	0.17	NA	NA	0.97	NA	8	-476.00	968.80	16.64	0.00	1.00
140	39.23	NA	-0.53	0.15	0.01	-0.44	-0.99	NA	1.00	NA	9	-474.95	968.92	16.76	0.00	1.00

Table 2.4. Full model set for the global model: Ankle temp ~ Ambient temp + Habitat + Disturbance + Body condition + Size + Shape + Ambient temp x Body condition + Habitat x Body condition + Disturbance x Body condition + (1|ID). Models within 4 ΔAIC_c of the top model were deemed informative.

Rank	(Intercept)	Habitat	Handled	Keel	KestrelHI	Mass.bird.s caled	SAVrel	Habitat x Keel	Handled x Keel	Keel x KestrelHI	df	logLik	AIC _c	delta	weight	CumWt
1	35.35	-3.25	NA	-0.85	0.73	NA	NA	NA	NA	4.02	7	-566.02	1146.63	0.00	0.13	0.13
2	35.36	-3.21	NA	-0.71	0.74	-1.63	-1.47	NA	NA	3.83	9	-564.17	1147.29	0.66	0.09	0.22
3	35.35	-3.22	0.70	-0.89	0.78	NA	NA	NA	NA	4.04	8	-565.38	1147.52	0.89	0.08	0.30
4	35.36	-3.18	NA	-0.46	0.79	-0.72	NA	NA	NA	3.86	8	-565.54	1147.83	1.20	0.07	0.37
5	35.35	-3.18	0.76	-0.78	0.78	-1.65	-1.54	NA	NA	3.85	10	-563.41	1148.00	1.36	0.06	0.43
6	35.35	-3.28	NA	-1.11	0.69	NA	-0.50	NA	NA	4.09	8	-565.77	1148.31	1.67	0.06	0.49
7	35.37	-3.27	0.67	-0.85	0.76	NA	NA	NA	-1.37	3.92	9	-564.80	1148.55	1.91	0.05	0.54
8	35.36	-3.25	NA	-0.86	0.72	NA	NA	0.34	NA	4.13	8	-565.99	1148.75	2.11	0.04	0.58
9	35.35	-3.16	0.68	-0.51	0.83	-0.69	NA	NA	NA	3.88	9	-564.93	1148.81	2.18	0.04	0.62
10	35.38	-3.23	0.73	-0.72	0.77	-1.67	-1.55	NA	-1.41	3.72	11	-562.78	1148.97	2.34	0.04	0.66
11	35.35	-3.26	0.74	-1.19	0.74	NA	-0.57	NA	NA	4.11	9	-565.06	1149.08	2.45	0.04	0.70
12	35.37	-3.20	NA	-0.71	0.72	-1.72	-1.52	0.79	NA	4.07	10	-564.01	1149.20	2.56	0.04	0.74
13	35.35	-3.22	0.72	-0.91	0.77	NA	NA	0.46	NA	4.19	9	-565.33	1149.61	2.98	0.03	0.76
14	35.37	-3.17	0.79	-0.78	0.76	-1.75	-1.61	0.92	NA	4.13	11	-563.19	1149.81	3.17	0.03	0.79
15	35.37	-3.21	0.65	-0.45	0.82	-0.71	NA	NA	-1.40	3.75	10	-564.32	1149.81	3.17	0.03	0.82
16	35.36	-3.18	NA	-0.45	0.78	-0.75	NA	0.54	NA	4.02	9	-565.46	1149.88	3.25	0.03	0.84
17	35.37	-3.30	0.71	-1.14	0.72	NA	-0.56	NA	-1.36	3.99	10	-564.48	1150.14	3.50	0.02	0.86
18	35.36	-3.28	NA	-1.12	0.69	NA	-0.50	0.34	NA	4.20	9	-565.74	1150.44	3.81	0.02	0.88
19	35.37	-3.26	0.69	-0.86	0.76	NA	NA	0.35	-1.35	4.03	10	-564.76	1150.71	4.07	0.02	0.90
20	35.36	-3.16	0.70	-0.51	0.82	-0.74	NA	0.65	NA	4.07	10	-564.82	1150.82	4.18	0.02	0.91
21	35.39	-3.22	0.75	-0.73	0.75	-1.76	-1.60	0.81	-1.36	3.97	12	-562.61	1150.90	4.27	0.02	0.93
22	35.35	-3.26	0.75	-1.20	0.73	NA	-0.57	0.47	NA	4.26	10	-565.01	1151.19	4.55	0.01	0.94
23	35.38	-3.20	0.67	-0.45	0.81	-0.75	NA	0.54	-1.36	3.91	11	-564.24	1151.90	5.27	0.01	0.95
24	35.37	-3.30	0.72	-1.15	0.71	NA	-0.56	0.35	-1.34	4.10	11	-564.45	1152.32	5.68	0.01	0.96
25	35.42	-2.98	NA	NA	1.06	-2.21	-1.47	NA	NA	NA	7	-569.67	1153.94	7.30	0.00	0.96

26	35.43	-3.22	NA	NA	NA	-2.20	-1.56	NA	NA	NA	6	-570.93	1154.31	7.67	0.00	0.97
27	35.42	-3.00	NA	NA	1.12	-1.17	NA	NA	NA	NA	6	-571.00	1154.44	7.80	0.00	0.97
28	35.42	-2.95	0.70	NA	1.10	-2.25	-1.52	NA	NA	NA	8	-569.05	1154.86	8.22	0.00	0.97
29	35.43	-3.25	NA	NA	NA	-1.09	NA	NA	NA	NA	5	-572.40	1155.12	8.48	0.00	0.97
30	35.43	-3.20	0.65	NA	NA	-2.24	-1.61	NA	NA	NA	7	-570.40	1155.39	8.75	0.00	0.97
31	35.41	-2.97	0.64	NA	1.16	-1.18	NA	NA	NA	NA	7	-570.48	1155.54	8.91	0.00	0.97
32	35.42	-3.05	NA	NA	1.01	NA	NA	NA	NA	NA	5	-572.72	1155.75	9.11	0.00	0.98
33	35.43	-3.01	NA	-0.38	1.06	-2.08	-1.55	NA	NA	NA	8	-569.55	1155.87	9.23	0.00	0.98
34	35.43	-3.28	NA	NA	NA	NA	NA	NA	NA	NA	4	-573.87	1155.95	9.32	0.00	0.98
35	35.44	-3.25	NA	-0.41	NA	-2.06	-1.65	NA	NA	NA	7	-570.79	1156.18	9.54	0.00	0.98
36	35.42	-3.23	0.59	NA	NA	-1.09	NA	NA	NA	NA	6	-571.98	1156.39	9.76	0.00	0.98
37	35.42	-3.01	NA	-0.12	1.12	-1.11	NA	NA	NA	NA	7	-570.99	1156.56	9.93	0.00	0.98
38	35.42	-3.10	NA	-0.72	1.05	NA	NA	NA	NA	NA	6	-572.10	1156.65	10.01	0.00	0.98
39	35.42	-2.99	0.72	-0.44	1.09	-2.10	-1.62	NA	NA	NA	9	-568.88	1156.72	10.08	0.00	0.98
40	35.41	-3.02	0.64	NA	1.05	NA	NA	NA	NA	NA	6	-572.21	1156.87	10.23	0.00	0.98
41	35.44	-3.06	0.69	-0.38	1.07	-2.10	-1.63	NA	-1.79	NA	10	-567.88	1156.93	10.30	0.00	0.98
42	35.43	-3.34	NA	-0.68	NA	NA	NA	NA	NA	NA	5	-573.33	1156.97	10.34	0.00	0.99
43	35.43	-3.24	0.68	-0.47	NA	-2.08	-1.73	NA	NA	NA	8	-570.21	1157.19	10.55	0.00	0.99
44	35.43	-3.26	NA	-0.13	NA	-1.02	NA	NA	NA	NA	6	-572.39	1157.22	10.58	0.00	0.99
45	35.42	-3.27	0.58	NA	NA	NA	NA	NA	NA	NA	5	-573.46	1157.23	10.60	0.00	0.99
46	35.45	-3.30	0.64	-0.41	NA	-2.08	-1.73	NA	-1.84	NA	9	-569.16	1157.28	10.64	0.00	0.99
47	35.41	-3.08	0.68	-0.76	1.09	NA	NA	NA	NA	NA	7	-571.53	1157.65	11.01	0.00	0.99
48	35.41	-2.99	0.65	-0.17	1.16	-1.09	NA	NA	NA	NA	8	-570.45	1157.66	11.03	0.00	0.99
49	35.41	-3.04	NA	-0.40	1.05	-1.96	-1.50	-0.78	NA	NA	9	-569.39	1157.74	11.11	0.00	0.99
50	35.39	-3.13	NA	-0.69	1.05	NA	NA	-1.37	NA	NA	7	-571.59	1157.77	11.14	0.00	0.99
51	35.42	-3.05	NA	NA	1.02	NA	0.12	NA	NA	NA	6	-572.70	1157.84	11.20	0.00	0.99
52	35.43	-3.05	0.62	-0.10	1.13	-1.09	NA	NA	-1.79	NA	9	-569.47	1157.91	11.27	0.00	0.99
53	35.44	-3.14	0.64	-0.70	1.06	NA	NA	NA	-1.78	NA	8	-570.57	1157.91	11.27	0.00	0.99
54	35.42	-3.27	NA	-0.43	NA	-1.94	-1.59	-0.77	NA	NA	8	-570.64	1158.04	11.40	0.00	0.99
55	35.43	-3.28	NA	NA	NA	NA	0.03	NA	NA	NA	5	-573.87	1158.06	11.42	0.00	0.99
56	35.39	-3.36	NA	-0.66	NA	NA	NA	-1.35	NA	NA	6	-572.83	1158.11	11.47	0.00	0.99
57	35.42	-3.32	0.62	-0.72	NA	NA	NA	NA	NA	NA	6	-572.85	1158.15	11.51	0.00	0.99
58	35.39	-3.04	NA	-0.16	1.11	-1.00	NA	-1.02	NA	NA	8	-570.71	1158.18	11.55	0.00	0.99

59	35.45	-3.38	0.59	-0.66	NA	NA	NA	NA	-1.84	NA	7	-571.84	1158.28	11.64	0.00	0.99
60	35.42	-3.25	0.59	-0.17	NA	-1.00	NA	NA	NA	NA	7	-571.95	1158.49	11.85	0.00	0.99
61	35.44	-3.31	0.56	-0.11	NA	-1.01	NA	NA	-1.85	NA	8	-570.92	1158.60	11.96	0.00	0.99
62	35.42	-3.12	NA	-0.87	1.02	NA	-0.30	NA	NA	NA	7	-572.02	1158.62	11.99	0.00	0.99
63	35.40	-3.01	0.70	-0.46	1.09	-1.99	-1.57	-0.68	NA	NA	10	-568.76	1158.70	12.06	0.00	1.00
64	35.43	-3.35	NA	-0.89	NA	NA	-0.41	NA	NA	NA	6	-573.18	1158.80	12.16	0.00	1.00
65	35.40	-3.29	NA	-0.17	NA	-0.91	NA	-1.04	NA	NA	7	-572.11	1158.80	12.17	0.00	1.00
66	35.42	-3.08	0.67	-0.40	1.06	-1.99	-1.57	-0.75	-1.82	NA	11	-567.73	1158.88	12.24	0.00	1.00
67	35.38	-3.10	0.64	-0.73	1.09	NA	NA	-1.28	NA	NA	8	-571.08	1158.92	12.29	0.00	1.00
68	35.41	-3.02	0.64	NA	1.06	NA	0.10	NA	NA	NA	7	-572.20	1158.99	12.36	0.00	1.00
69	35.41	-3.17	0.60	-0.67	1.06	NA	NA	-1.35	-1.83	NA	9	-570.07	1159.10	12.46	0.00	1.00
70	35.41	-3.26	0.66	-0.49	NA	-1.97	-1.67	-0.67	NA	NA	9	-570.09	1159.15	12.51	0.00	1.00
71	35.43	-3.32	0.62	-0.42	NA	-1.97	-1.67	-0.75	-1.87	NA	10	-569.01	1159.20	12.57	0.00	1.00
72	35.42	-3.26	0.58	NA	NA	NA	0.01	NA	NA	NA	6	-573.46	1159.36	12.72	0.00	1.00
73	35.39	-3.01	0.63	-0.20	1.15	-0.99	NA	-0.94	NA	NA	9	-570.22	1159.39	12.76	0.00	1.00
74	35.39	-3.35	0.58	-0.69	NA	NA	NA	-1.27	NA	NA	7	-572.42	1159.43	12.79	0.00	1.00
75	35.42	-3.41	0.54	-0.62	NA	NA	NA	-1.35	-1.90	NA	8	-571.35	1159.46	12.83	0.00	1.00
76	35.41	-3.10	0.70	-0.94	1.06	NA	-0.36	NA	NA	NA	8	-571.41	1159.57	12.94	0.00	1.00
77	35.41	-3.08	0.59	-0.14	1.12	-0.99	NA	-1.01	-1.83	NA	10	-569.20	1159.58	12.95	0.00	1.00
78	35.39	-3.15	NA	-0.86	1.02	NA	-0.33	-1.39	NA	NA	8	-571.49	1159.74	13.11	0.00	1.00
79	35.44	-3.16	0.67	-0.88	1.03	NA	-0.36	NA	-1.78	NA	9	-570.45	1159.86	13.22	0.00	1.00
80	35.42	-3.34	0.65	-0.96	NA	NA	-0.46	NA	NA	NA	7	-572.66	1159.90	13.26	0.00	1.00
81	35.40	-3.38	NA	-0.88	NA	NA	-0.42	-1.38	NA	NA	7	-572.67	1159.92	13.29	0.00	1.00
82	35.45	-3.40	0.62	-0.89	NA	NA	-0.46	NA	-1.84	NA	8	-571.65	1160.06	13.42	0.00	1.00
83	35.39	-3.28	0.57	-0.21	NA	-0.90	NA	-0.97	NA	NA	8	-571.71	1160.18	13.54	0.00	1.00
84	35.42	-3.34	0.53	-0.14	NA	-0.90	NA	-1.04	-1.89	NA	9	-570.63	1160.22	13.59	0.00	1.00
85	35.38	-3.13	0.67	-0.93	1.06	NA	-0.38	-1.30	NA	NA	9	-570.94	1160.85	14.21	0.00	1.00
86	35.41	-3.19	0.63	-0.86	1.03	NA	-0.38	-1.37	-1.83	NA	10	-569.93	1161.04	14.40	0.00	1.00
87	35.39	-3.37	0.61	-0.94	NA	NA	-0.48	-1.29	NA	NA	8	-572.20	1161.17	14.54	0.00	1.00
88	35.42	-3.43	0.57	-0.87	NA	NA	-0.48	-1.37	-1.89	NA	9	-571.14	1161.23	14.60	0.00	1.00
89	35.39	NA	NA	-0.37	1.45	-2.02	-1.49	NA	NA	3.24	8	-574.91	1166.59	19.95	0.00	1.00
90	35.37	NA	NA	-0.71	1.44	NA	NA	NA	NA	3.59	6	-577.15	1166.74	20.10	0.00	1.00
91	35.37	NA	NA	-0.12	1.51	-1.09	NA	NA	NA	3.32	7	-576.15	1166.88	20.25	0.00	1.00

92	35.37	NA	0.83	-0.44	1.49	-2.04	-1.56	NA	NA	3.27	9	-574.07	1167.11	20.47	0.00	1.00
93	35.36	NA	0.80	-0.75	1.48	NA	NA	NA	NA	3.61	7	-576.39	1167.38	20.74	0.00	1.00
94	35.36	NA	0.77	-0.18	1.54	-1.06	NA	NA	NA	3.34	8	-575.45	1167.65	21.02	0.00	1.00
95	35.39	NA	0.81	-0.40	1.48	-2.06	-1.57	NA	-1.07	3.16	10	-573.74	1168.65	22.02	0.00	1.00
96	35.37	NA	NA	-0.85	1.42	NA	-0.27	NA	NA	3.63	7	-577.08	1168.76	22.12	0.00	1.00
97	35.38	NA	0.78	-0.71	1.48	NA	NA	NA	-1.00	3.52	8	-576.11	1168.98	22.35	0.00	1.00
98	35.45	NA	NA	NA	1.67	-2.49	-1.59	NA	NA	NA	6	-578.29	1169.02	22.38	0.00	1.00
99	35.38	NA	0.74	-0.13	1.54	-1.07	NA	NA	-1.05	3.24	9	-575.13	1169.21	22.58	0.00	1.00
100	35.36	NA	0.82	-0.93	1.46	NA	-0.34	NA	NA	3.65	8	-576.29	1169.34	22.71	0.00	1.00
101	35.43	NA	0.78	NA	1.70	-2.53	-1.64	NA	NA	NA	7	-577.55	1169.68	23.05	0.00	1.00
102	35.43	NA	NA	NA	1.75	-1.37	NA	NA	NA	NA	5	-579.69	1169.69	23.06	0.00	1.00
103	35.42	NA	0.73	NA	1.79	-1.37	NA	NA	NA	NA	6	-579.05	1170.55	23.91	0.00	1.00
104	35.38	NA	0.80	-0.89	1.45	NA	-0.33	NA	-0.99	3.56	9	-576.01	1170.98	24.34	0.00	1.00
105	35.45	NA	NA	-0.11	1.67	-2.45	-1.61	NA	NA	NA	7	-578.28	1171.15	24.51	0.00	1.00
106	35.43	NA	NA	0.16	1.75	-1.45	NA	NA	NA	NA	6	-579.67	1171.78	25.14	0.00	1.00
107	35.44	NA	0.79	-0.17	1.70	-2.47	-1.68	NA	NA	NA	8	-577.52	1171.81	25.17	0.00	1.00
108	35.43	NA	NA	NA	1.65	NA	NA	NA	NA	NA	4	-581.80	1171.82	25.18	0.00	1.00
109	35.48	NA	NA	NA	NA	-2.55	-1.79	NA	NA	NA	5	-581.08	1172.48	25.85	0.00	1.00
110	35.42	NA	0.73	0.11	1.79	-1.42	NA	NA	NA	NA	7	-579.04	1172.68	26.04	0.00	1.00
111	35.42	NA	0.74	NA	1.69	NA	NA	NA	NA	NA	5	-581.18	1172.68	26.05	0.00	1.00
112	35.46	NA	0.76	-0.12	1.69	-2.48	-1.69	NA	-1.40	NA	9	-576.95	1172.85	26.22	0.00	1.00
113	35.43	NA	NA	-0.61	1.68	NA	NA	NA	NA	NA	5	-581.41	1173.13	26.49	0.00	1.00
114	35.47	NA	0.73	NA	NA	-2.59	-1.85	NA	NA	NA	6	-580.45	1173.34	26.71	0.00	1.00
115	35.44	NA	0.70	0.17	1.78	-1.43	NA	NA	-1.39	NA	8	-578.49	1173.74	27.10	0.00	1.00
116	35.43	NA	NA	NA	1.67	NA	0.21	NA	NA	NA	5	-581.76	1173.82	27.19	0.00	1.00
117	35.46	NA	NA	NA	NA	-1.27	NA	NA	NA	NA	4	-582.81	1173.83	27.20	0.00	1.00
118	35.42	NA	0.77	-0.65	1.72	NA	NA	NA	NA	NA	6	-580.73	1173.90	27.26	0.00	1.00
119	35.48	NA	NA	-0.16	NA	-2.50	-1.83	NA	NA	NA	6	-581.07	1174.57	27.94	0.00	1.00
120	35.42	NA	0.73	NA	1.70	NA	0.18	NA	NA	NA	6	-581.15	1174.73	28.10	0.00	1.00
121	35.45	NA	0.67	NA	NA	-1.27	NA	NA	NA	NA	5	-582.30	1174.91	28.28	0.00	1.00
122	35.44	NA	0.74	-0.60	1.71	NA	NA	NA	-1.37	NA	7	-580.20	1175.00	28.36	0.00	1.00
123	35.44	NA	NA	-0.67	1.67	NA	-0.11	NA	NA	NA	6	-581.40	1175.23	28.60	0.00	1.00
124	35.45	NA	NA	NA	NA	NA	NA	NA	NA	NA	3	-584.60	1175.31	28.68	0.00	1.00

125	35.47	NA	0.74	-0.23	NA	-2.51	-1.91	NA	NA	NA	7	-580.41	1175.41	28.78	0.00	1.00
126	35.46	NA	NA	0.16	NA	-1.35	NA	NA	NA	NA	5	-582.80	1175.90	29.27	0.00	1.00
127	35.42	NA	0.78	-0.74	1.70	NA	-0.18	NA	NA	NA	7	-580.70	1175.99	29.36	0.00	1.00
128	35.44	NA	0.67	NA	NA	NA	NA	NA	NA	NA	4	-584.10	1176.41	29.77	0.00	1.00
129	35.49	NA	0.71	-0.17	NA	-2.53	-1.91	NA	-1.41	NA	8	-579.83	1176.42	29.79	0.00	1.00
130	35.46	NA	NA	-0.57	NA	NA	NA	NA	NA	NA	4	-584.27	1176.74	30.11	0.00	1.00
131	35.45	NA	0.66	0.10	NA	-1.33	NA	NA	NA	NA	6	-582.29	1177.02	30.39	0.00	1.00
132	35.44	NA	0.75	-0.69	1.69	NA	-0.17	NA	-1.37	NA	8	-580.18	1177.12	30.48	0.00	1.00
133	35.45	NA	NA	NA	NA	NA	0.05	NA	NA	NA	4	-584.59	1177.39	30.76	0.00	1.00
134	35.45	NA	0.70	-0.61	NA	NA	NA	NA	NA	NA	5	-583.72	1177.75	31.12	0.00	1.00
135	35.47	NA	0.63	0.16	NA	-1.34	NA	NA	-1.42	NA	7	-581.73	1178.04	31.41	0.00	1.00
136	35.44	NA	0.66	NA	NA	NA	0.03	NA	NA	NA	5	-584.10	1178.51	31.87	0.00	1.00
137	35.46	NA	NA	-0.72	NA	NA	-0.29	NA	NA	NA	5	-584.20	1178.71	32.07	0.00	1.00
138	35.47	NA	0.67	-0.56	NA	NA	NA	NA	-1.40	NA	6	-583.18	1178.81	32.17	0.00	1.00
139	35.45	NA	0.72	-0.80	NA	NA	-0.36	NA	NA	NA	6	-583.62	1179.67	33.04	0.00	1.00
140	35.47	NA	0.69	-0.74	NA	NA	-0.35	NA	-1.39	NA	7	-583.08	1180.75	34.12	0.00	1.00

Table 2.5. Average parameter estimates from the top model set ($\Delta AIC_c < 4$) for a) Underwing (n=34 models) and b) Ankle (n=18 models) identified using an information theoretic approach (AIC_c). Bolded parameters are those with 95% confidence intervals that do not overlap 0. The cumulative weight (w_i) for the Underwing top model set was 1.0 and for the Ankle model set was 0.88.

a)

Parameter (Underwing model)	Number of top models in which parameter appears	Average estimate (model subset)	Confidence Interval	
			2.5%	97.5%
Habitat	34	-1.75	-2.74	-0.76
Body condition	24	0.12	-0.96	1.20
Ambient temperature	22	-0.35	-1.29	0.58
Ambient Temperature x Body condition	20	2.38	0.65	4.12
Disturbance level	19	-0.64	-1.54	0.26
Body shape	18	-0.89	-1.94	0.17
Body size	13	0.19	-1.13	1.50
Habitat x Body condition	9	0.94	-1.04	2.92
Disturbance x Body condition	9	0.59	-1.33	2.50

b)

Parameter (Ankle model)	Number of top models in which parameter appears	Average estimate (model subset)	Confidence Interval	
			2.5%	97.5%
Habitat	18	-3.22	-4.54	-1.91
Ambient temperature	18	0.76	-0.51	2.02
Body condition	18	-1.39	-2.22	0.63
Ambient Temperature x Body condition	18	3.07	1.70	6.24
Disturbance level	10	0.72	-0.50	1.93
Body shape	9	-1.18	-3.05	0.69
Body size	9	-1.30	-3.19	0.60
Habitat x Body condition	6	0.56	-2.22	3.34
Disturbance x Body condition	4	-1.39	-3.87	1.10

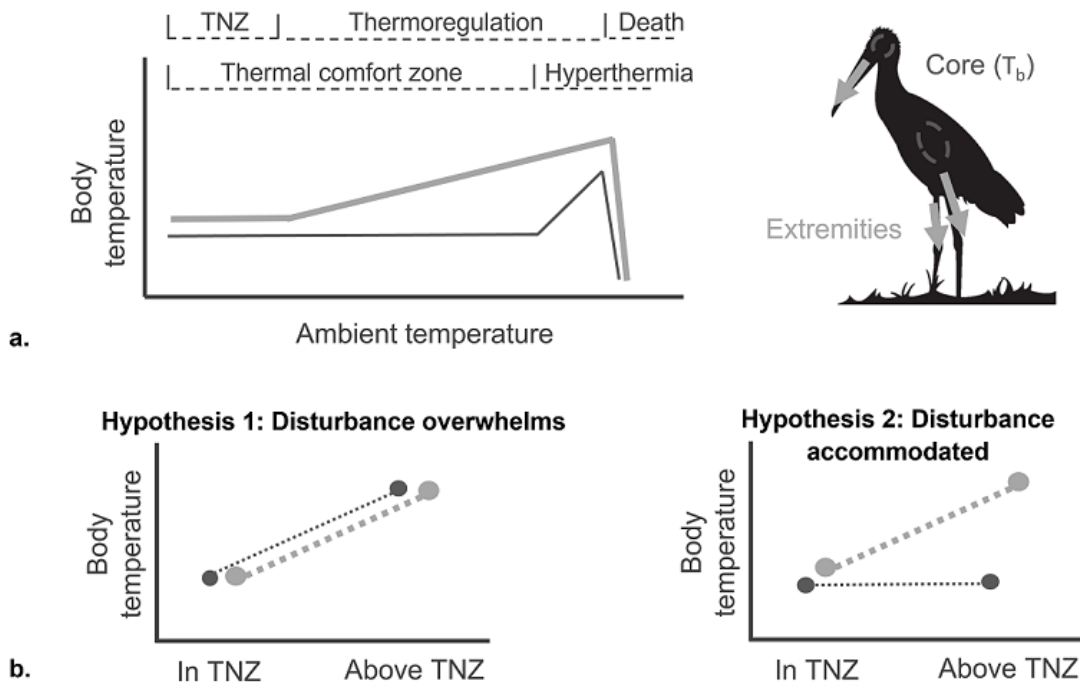


Figure 2.1. a) Thermal profile of the core (T_b) and extremities at ambient temperatures that are in and above the thermal neutral zone (TNZ) of a bird whose metabolic heat gets offloaded at the feet. b) Competing hypotheses and predictions regarding the thermal profile of birds immediately following an acute stressor in ambient temperatures that are in and above the TNZ.

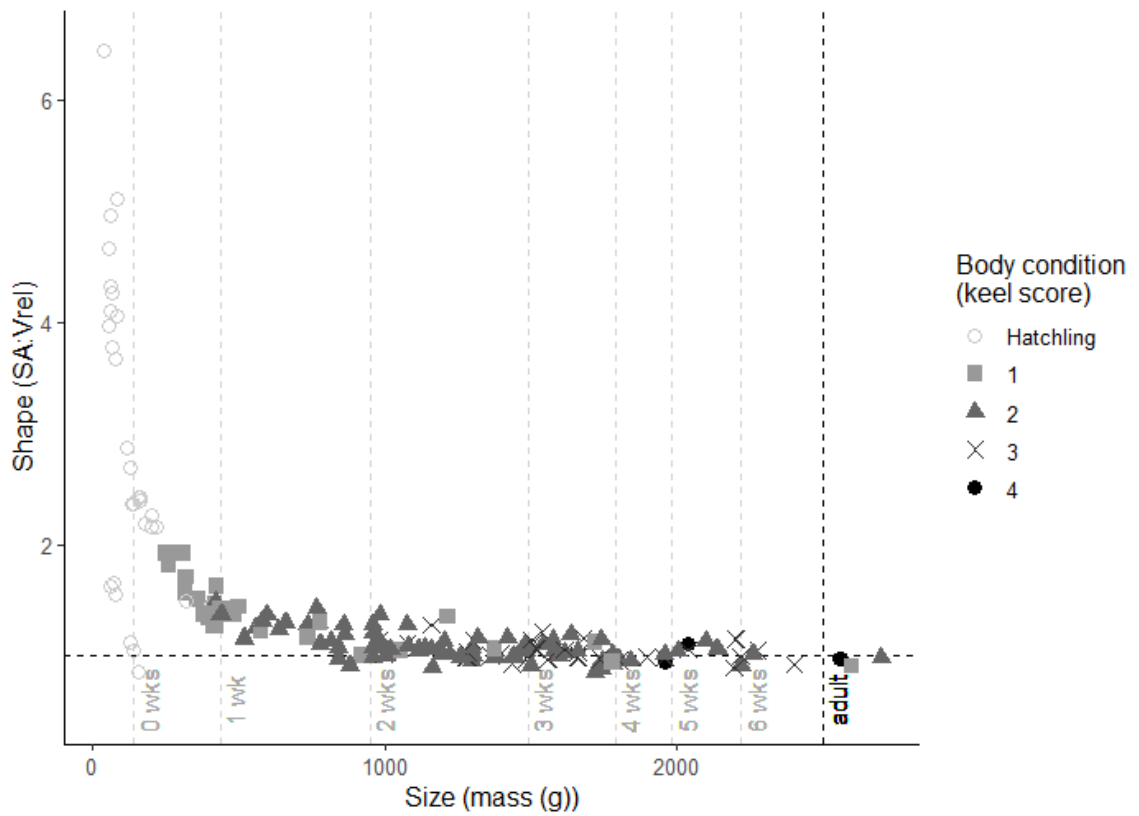


Figure 2.2. Relationship between the age (wks), size (mass, g), shape (surface-area-to-volume ratio relative to that of an average adult stork), and body condition (keel score) of stork nestlings modelled in this study. The black dashed lines indicate the mean shape and size of an adult stork (Coulter et al. 2020). Gray vertical lines indicate the mean size of nestlings of an age group in this study.

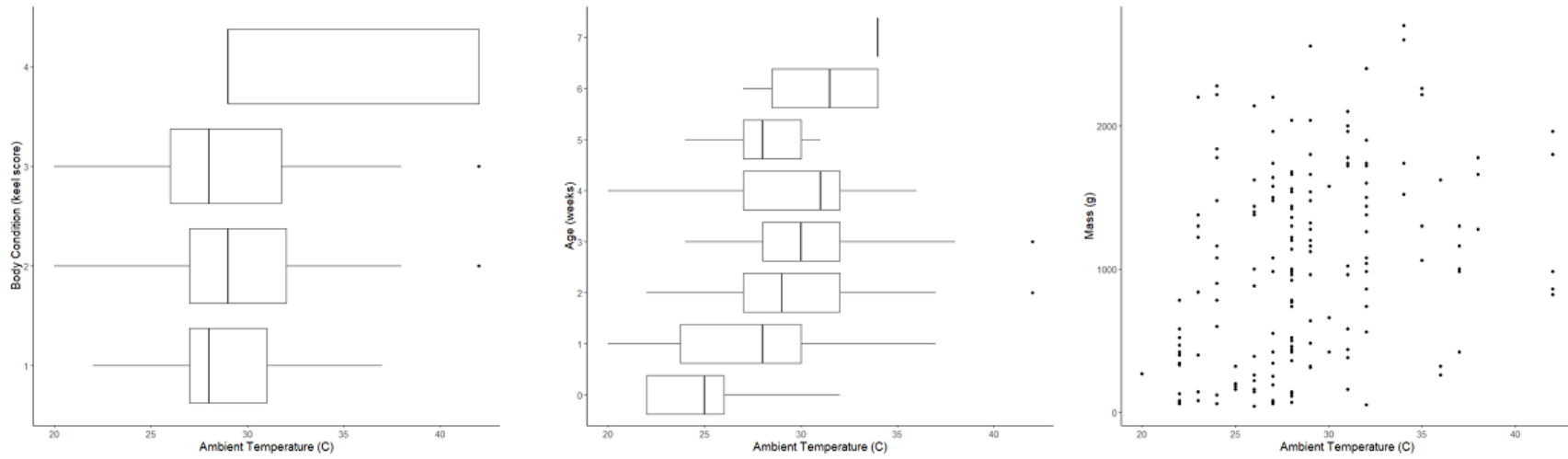
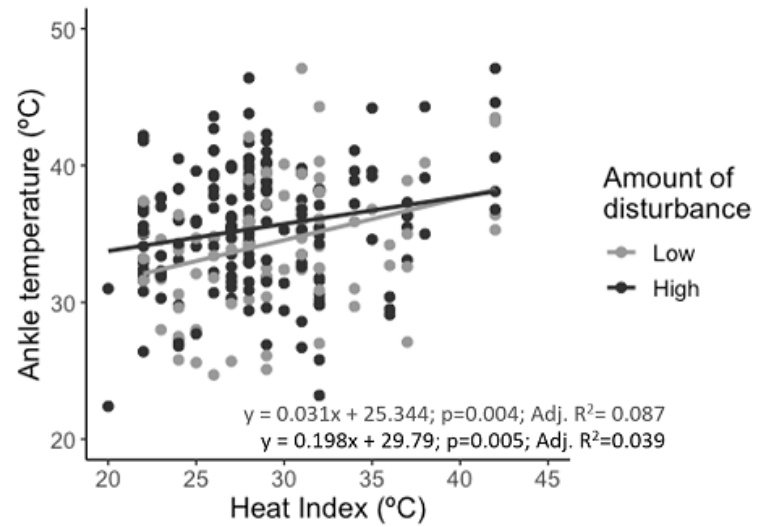
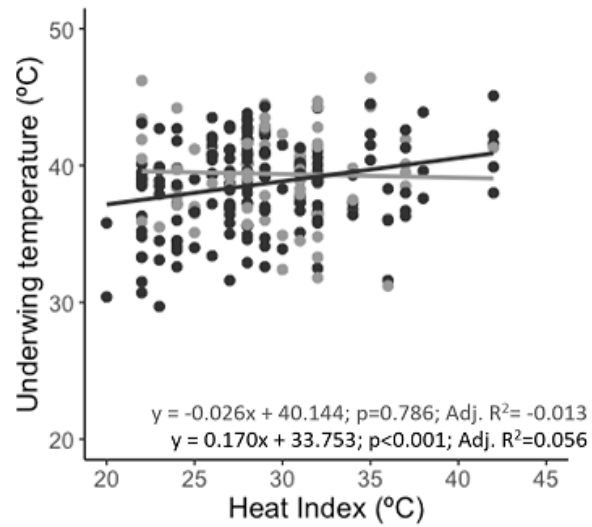


Figure 2.3. Sampling effort as shown by the range of ambient temperatures encountered versus the body temperature (keel score), age (wks), and mass (g) of measured nestling storks.



43

a.

b.

Figure 2.4. Nestling temperature (a. underwing (core) temperature; b. ankle (extremity) temperature) at a range of ambient temperatures (heat index) at two different disturbance levels, low (researchers in proximity but not handling nestling) and high (researchers handling nestling).

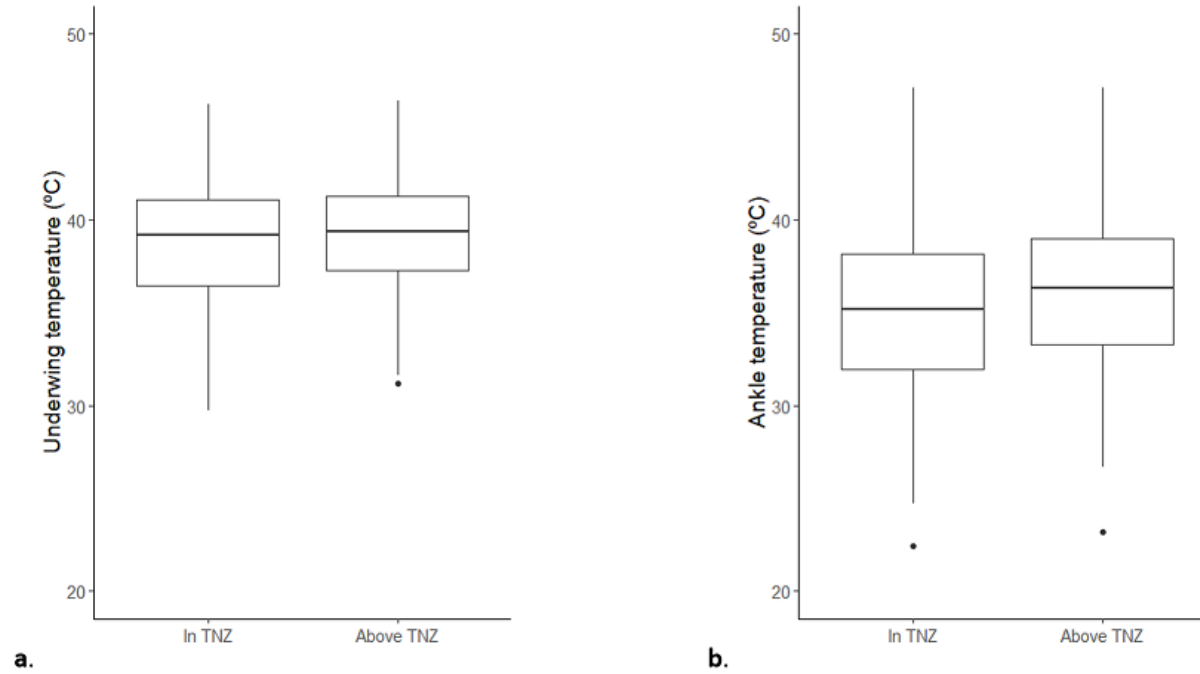


Figure 2.5. a) Underwing and b) ankle temperatures in ambient conditions (heat index °C) that are in or above the TNZ of storks. Within boxplots, the central horizontal line represents the median value (50%), the box represents the interquartile range (25-75%), the whiskers represent the largest value beyond 1.5x the interquartile range, and dots beyond the whiskers represent outliers.

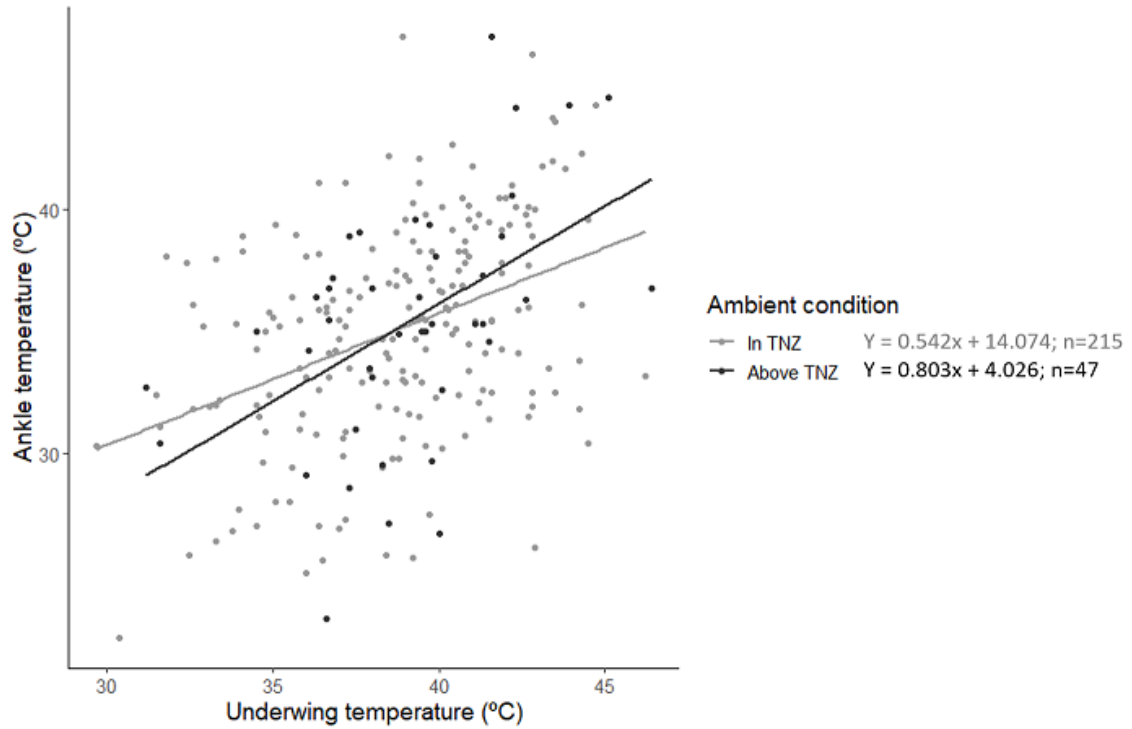


Figure 2.6. Underwing (core) versus ankle (extremity) temperature measured when nestlings are in an environment that is within their thermal neutral zone (TNZ) versus hotter than their TNZ. Theoretically, nestlings should be actively thermoregulating above the TNZ. Note that the temperature range for 'In TNZ' versus 'Above TNZ' has been adjusted to factor in age.

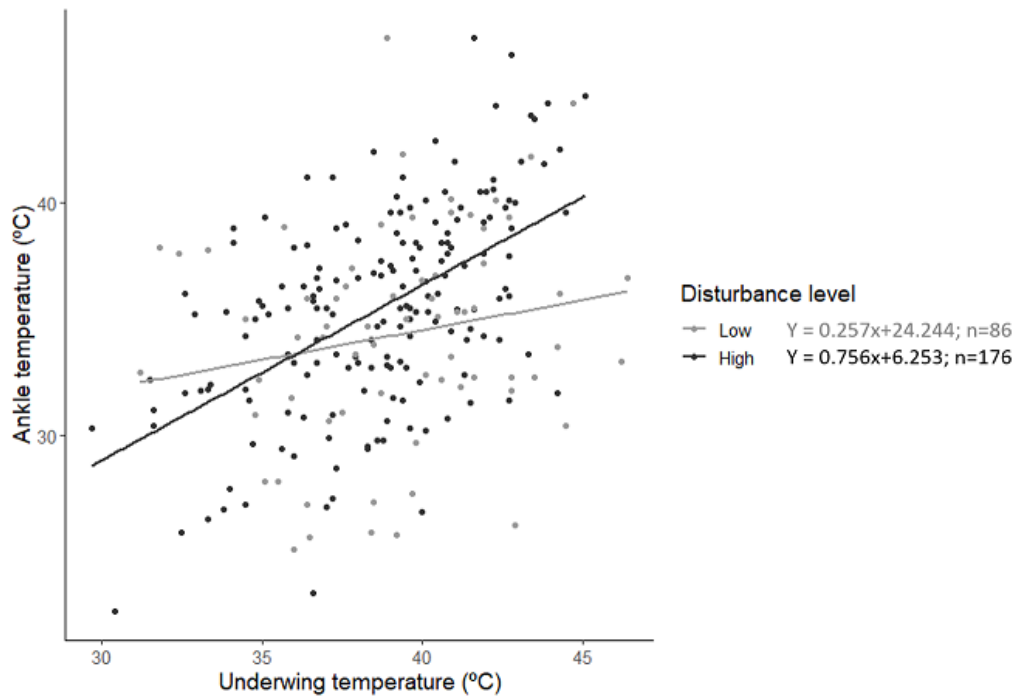


Figure 2.7. Underwing (core) and ankle (extremity) nestling temperature at low and high levels of disturbance. The ‘low’ disturbance condition was when researchers were in proximity to the nest but were not handling the nestling being measured. The ‘high’ disturbance condition was when the nestling was being handled by researchers.

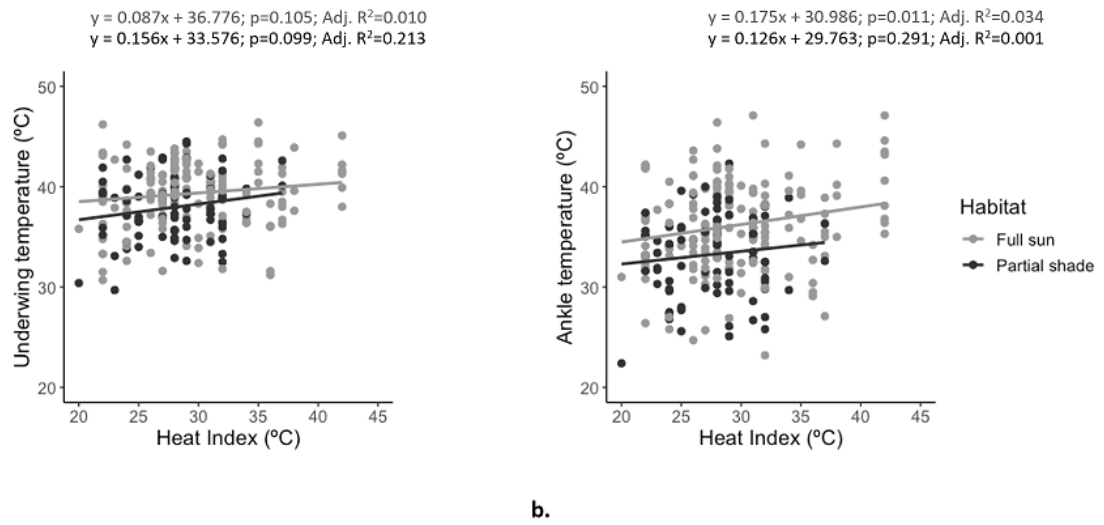


Figure 2.8. Effect of habitat type (whether the nest was in full sun or partial shade) on a) underwing (n=240) and b) ankle (n=252) temperature of stork nestlings at a range of T_a (heat index °C) within or above the known thermal neutral zone of other avian species that live in hot climates.

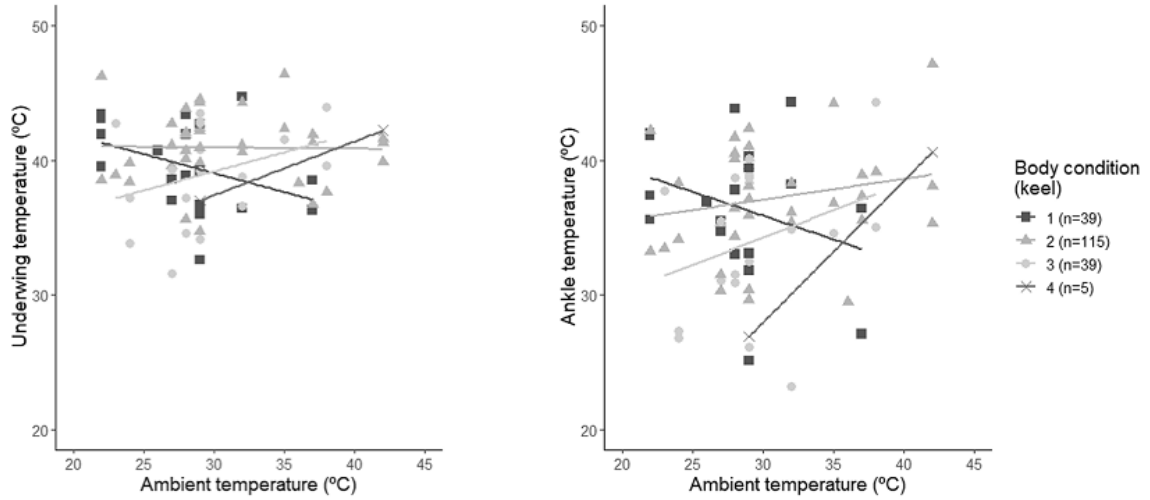


Figure 2.9. Interaction between T_a (heat index °C) and body condition on a) core (n=187) and b) extremity (n=198) temperatures of nestlings. Low keel scores indicate nestlings in poor condition (little-to-no muscle overlaying the keel bone); high keel scores indicate nestlings in good condition (thicker layer of muscle overlaying the keel bone).

3 COMMUTERS: A NEW VIEW OF HOW WIDE-RANGING SPECIES UTILIZE URBAN ENVIRONMENTS

3.1 ABSTRACT

Species are commonly classified as an “urban exploiter”, “urban avoider”, or “suburban adapter” based on their response to urban environments. However, species with large home ranges may within a single day utilize a variety of habitats along the urban-wildland gradient. Therefore, the traditional classification of species fails to capture the behavior of those that rely on both urban and wildland resources for population persistence. Here, I use the Wood Stork (*Mycteria americana*), a species that makes daily foraging trips up to 74 km away from its nesting colony, as an example of a fourth type of response to urbanization, the “urban commuter.” I monitored nests and sampled diet at stork colonies in South Florida, USA 2014-2020, and compiled nesting records from the entirety of the stork’s U.S. breeding range 2002-2019, to investigate whether storks use (or avoid) urban habitats. I found that urban development now comprises up to 38.9% regionally of the land cover within the 10-km core foraging area surrounding colonies, and that storks access alternative prey types within these urban areas. My results also showed that urban-nesting storks outperformed wildland-nesting storks when the hydrologic condition of the wetlands were suboptimal. I conclude that, whereas the Wood Stork still requires healthy wetlands and coastal systems for population persistence, the availability of urban habitat benefits storks when hydrologic patterns are not ideal for the concentration of prey in wildland habitats. This “commuter”

response to urbanization, where individuals utilize both highly urban and wildland resources over short time periods, likely applies to many waterbirds and other animals with large home ranges.

3.2 INTRODUCTION

The field of urban ecology, which is concerned with the study of urban ecosystems, generously includes suburban surroundings and even isolated towns or villages in addition to the expected core city environments (Pickett et al. 2011). This definition of urban ecology is broad in that it allows for the study of rural habitats surrounding urban centers. However, it notably assumes that wildland habitats are unavailable to urban-dwelling species. Many avian species have the locomotive advantage of efficient flight and therefore have large home ranges which could allow individuals to fluidly utilize resources from a range of habitat types along the complete urban-wildland gradient. Even species with smaller ranges may be able to move readily between urban and non-urban habitats as the urban-wildland interface expands (Radeloff et al. 2005).

Foundational studies in urban bird ecology have focused on species-level tolerances of urbanization (Blair 1996; Shochat et al. 2004; Kettel et al. 2017; Seress et al. 2020) and community assemblages (Crooks et al. 2004; Shochat et al. 2004), categorizing species as “urban avoiders,” “urban exploiters,” or “suburban adaptable” (Blair 1996; Pennington and Blair 2012). Far fewer studies have explored the occurrence of individuals that rely on resources from both urban and wildland habitat types, which I

will refer to as “urban commuters.” The extent to which concurrent use of urban and wildland resources may improve individual fitness is unknown.

Waterbirds are found to be the avian clade that is most able to persist in urban environments by adaptation (Callaghan et al. 2019); these wide-ranging species may have the ability to access both wildland and urban resources. Among waterbird species, the Wood Stork (*Mycteria americana*; hereafter, “stork”) is an ideal subject to examine the commuter response because individuals of this species are known to make daily foraging flights up to 74 km away from their nest location (Herring et al. 2015) and they nest in both marsh (wildland) and urban habitats. In South Florida, USA, urban/wildland land cover types are sharply contrasted because Everglades National Park and other protected lands in the Everglades system are directly adjacent to the Miami metropolitan area. Hence, to address the gap in the urban ecology literature, I investigated the effect of concurrent urban/wildland resource use on nest-level productivity by monitoring 6 stork colonies located along the Everglades—Miami metropolitan interface from 2014-2020.

The Miami metropolitan area stretches from Miami to West Palm Beach in southeastern Florida, and is positioned between the Atlantic Ocean to the east and the protected Everglades wetlands to the west. The current population in this coastal corridor is approximately 6 million people (South Florida Regional Planning Council 2021) and is expected to continue growing through the remainder of the century (Carr and Zwick 2016). This metropolis is also relatively young, having grown to its current size from a population of under 100,000 people in 1940 (South Florida Regional Planning Council 2021).

Occurring alongside urbanization were two important behavioral changes in storks beginning in the 1990s: the novel use of urban habitats for foraging and nesting, and the novel consumption of non-native prey species. Urban nesting colonies started forming in the late 1990s and are continuing to grow (Cook and Baranski 2021). In years when the hydrological condition of the Everglades marsh is poor for foraging, the number of storks nesting in urban colonies has even exceeded the number of nests in nearby natural colonies (Cook and Baranski 2021). Urban-nesting storks may benefit from the ability to access foraging areas outside the natural system (Evans and Gawlik 2020; Evans et al. 2021). This benefit could be significant since storks are a food-limited species (Frederick et al. 2009).

Non-native fish, which are prey for storks, have been colonizing South Florida since the 1950s but notably increased after changes to water management regimes in the 1990s (Kline et al. 2014). Because the native ranges of many of these species are tropical, cold tolerance appears to be the primary barrier to range expansion (Rehage and Trexler 2006). Therefore, non-native fishes are primarily found in the far southern estuaries of the Everglades, where freezing temperature almost never occur, and in the 1,400-mile network of canals that are deep enough to be year-round thermal refuges (Rehage and Trexler 2006; Trexler et al. 2000).

Storks nesting in both urban and marsh colony types now consume non-native fishes, which is a change from the stork's diet prior to the 1980s (Klassen and Gawlik 2018). Diet is a key mechanism of demographic change for food-limited species, so changes in diet like the ones observed by Klassen and Gawlik (2018a) and Evans and Gawlik (2020) could have significant impacts on productivity and survival. The presence

of non-native fish may affect storks positively or negatively, possibly in a complex manner.

I propose two testable hypotheses regarding the urbanization of storks breeding in South Florida. First, I hypothesize that urban resource use affects nest-level productivity. Second, I hypothesize that the consumption of non-native prey affects nest-level productivity. If use of urban colony sites, urban prey items, and/or the amount of non-native fish biomass found in the diet are associated with increased or decreased productivity metrics, I will conclude that one or more of these documented behavioral shifts have demographic consequences. Identifying whether these are mechanisms of demographic change could help us predict future trends in the South Florida population. Therefore, this study is foundational to assessing the health and longevity of the U.S. breeding population. More broadly, storks serve as a case study to explore the dynamics of species which have individuals concurrently utilizing urban and ex-urban resources along urban-wildland interfaces.

3.3 METHODS

3.3.1 Colony monitoring

6 stork colonies in southeastern Florida—3 located in the natural Everglades system (Tamiami West 25.75784, -80.54484, Paurotis Pond 25.2815, -80.803, and Jetport South 25.8051, -80.84902), and 3 located in urban areas (Griffin 26.0636333, -80.3664916, BallenIsles 26.830142, -80.109086, and Sawgrass 26.149802, -80.337681)—were each visited during the cool morning hours 1-2 times per week during the breeding season (Jan-Jun) 2014-2020 (Fig. 3.1). After the mid-point of incubation,

each colony was entered and a short strip of numbered flagging tape was tied beneath nest bowls for identification. Total clutch size, hatch dates, and the number, estimated age, and keel score of chicks were recorded during every subsequent visit. Keel score, a proxy for body condition, ranged from 1 to 5, where 1 is a protruding keel bone with no overlaid muscle and 5 is a muscle layer thick enough to hide the shape of the keel bone entirely (after Evans and Gawlik 2020).

3.3.2 Diet sampling

During nest checks, one or more chicks per nest was handled for bolus collection. Many chicks voluntarily regurgitate when pick up, so this sample was collected. If a chick did not voluntarily regurgitate but food could be felt in the crop, the trachea of the bird was gently massaged to induce regurgitation. The chick was then returned to the nest and provided with purchased bait fish, Atlantic Silversides *Menidia menidia*, which the storks readily consumed, to compensate for their lost meal. Boluses were stored in plastic bags on ice in the field, and frozen upon return. In the lab, boluses were thawed, rinsed, weighed, measured (standard length, mm) and identified to the lowest possible taxonomic level, which was usually species. In the database, prey species were grouped into native, non-native, and trash (discarded human food and other refuse) categories.

3.3.3 Statistical analysis

Land cover types available to storks within core foraging areas (CFAs), i.e., all land within a 30-km radius of each monitored colony site (Brooks and Dean 2008), was

compared. First, a land cover classification system (Kawula and Redner 2018) was imported to ArcGlobe 10.8 as a raster, clipped to the buffer edges, summed by land cover type based on the number of pixels per CFA, and then exported to a text file. Then, in Excel, land cover types were manually reclassified as “urban,” “rural,” or “marsh” based on their descriptions (Kawula and Redner 2018). Finally, the proportion of urban, rural, and marsh habitats found within the CFA was calculated for each colony (Fig. 3.1).

Stork productivity and diet were analyzed in R version 4.0.2 (R Core Development Team 2020). Productivity and diet, which were recorded at the nest-level in the field, were summarized as the mean±standard deviation (SD) at the levels of colony and colony type (urban or marsh). Nest success (%) was based on the proportion of nests that successfully fledged (age ≥ 4 weeks after Evans and Gawlik 2020) at least one chick. Keel score was reported as the average score of chicks at fledge (age=4 weeks). For diet, the biomass (g) of non-native prey and trash were calculated and then divided by the total biomass of each nest to be represented as a proportion of the diet (%). In preparation for a generalized linear mixed model (GLMM), the proportion of non-native prey and trash at the nest-level were binned into nests that consumed relatively low, medium, or high amounts of each. For non-native prey, most nests (130 of 234) consumed $< 1\%$, so these were binned into the “Low” category. Of the nests that consumed $\geq 1\%$ non-native prey by biomass, the number of nests was divided in half to preserve sample size in the analysis, and the % non-native biomass at that divide was used as the cutoff. In doing so, 1-22% non-native prey was considered a “Medium” level of consumption (n=51) and 22-100% non-native prey was considered a “High” level of consumption (n=53). Similarly, most storks (213 of 234 nests) consumed no trash, so 0% was considered the “Low”

consumption. The number of nests that did eat trash were divided in half, so that “Medium” consumption ranged from 0.1-20.0% (n=10) and “High” consumption included those nests that consumed >20% trash (n=11).

I used Akaike’s Information Criterion for small sample sizes (AIC_c; Anderson 2008) to compare competing GLMMs explaining the number of fledglings per nest and then averaged the top model set following the method described in (Grueber et al. 2011). Biologically relevant variables and interaction terms were selected (Table 3.1) and standardized to a mean of 0 and a SD of 0.5 using the package *arm*. In addition to the diet and colony type (urban or marsh) parameters related to our hypotheses, I included a variable summarizing the hydrological condition of the natural marsh during the breeding season (suboptimal, moderate, optimal) as that is known to have a strong influence on breeding success via prey availability (Frederick et al. 2009; Evans and Gawlik 2020). Twenty-six candidate models were analyzed using the package *lme4* based on the follow global model:

$$\begin{aligned} \text{Productivity} \sim & \text{Nonnatives} + \text{Trash} + \text{Colony Type} + \text{Hydro Year} + \text{Nonnatives} \times \\ & \text{Colony Type} + \text{Nonnatives} \times \text{Hydro Year} + \text{Colony Type} \times \text{Hydro Year} + \\ & (1|\text{ColonyID}) \end{aligned}$$

Models within 4 ΔAIC_c of the top model were deemed informative. To determine the relative influence of each predictor variable on nestling temperature, I calculated model-averaged parameter estimates and 95% confidence intervals for these estimates using the top model sets in the package *MuMIn*.

I was specifically concerned that ‘Trash’ might be an uninformative parameter since no marsh-nesting storks consumed any amount of trash, and therefore ‘Trash’

aligned in pattern with ‘Colony Type.’ To test this, I followed the protocol described by (Leroux 2019), re-running the models in the top model set that contained ‘Trash’ without that variable. Next, I compared the results of the paired models to determine whether ‘Trash’ contributed information to the model in the top set by comparing the paired models’ log likelihood and AIC_c values (Table 3.2). 1 of 5 of the models in the top model set that contained ‘Trash’ likely contains an uninformative parameter, so this is labeled as such in the results.

3.4 RESULTS

Over our sampling years (2014-2020), storks experienced a broad range of hydrological conditions in the natural marsh system, relatedly experiencing very productive breeding years as well as years of high nest failure (Cook and Baranski 2021). Storks nested in all urban colonies in all years of record (2015-2020), but not in all marsh colonies in all years (2014-2020). Specifically, storks did not nest in Tamiami West in 2016 or 2018, Jetport South in 2015, 2016, or 2019, and initiated very late and in low numbers in Tamiami West in 2019. The number of nests in each urban colony was small and consistent between years (mean±SD: 55±39 nests/colony/year, range: 10-150 nests/colony/year; Tables 3.3-3.4), while the number of nests in each marsh colony was boom-or-bust (mean±SD excluding non-nesting events: 328±274 nests/colony/year, range: 0-953/colony/year; Table 3.2, Table 3.4). Over our 6 years of study, in all known stork colonies in South Florida, nesting in 7 urban colonies accounted for 26±7% (mean±SD; range: 18-37%) of all nesting in South Florida each year (Table 3.4).

Storks nesting in urban colonies could readily access both urban (mean 46.9%, range 41.5-51.6%) and marsh (mean 49.4%, range 48.3-51.4%) land cover types within their CFAs, while storks nesting in marsh colonies had little access to urban habitats (mean 9.2%, range 0.2-26.8%) and increased access to marsh (mean 88.3%, range 66.2-99.6%) land cover types within their CFAs (Table 3.5; Fig. 3.1).

Averaged over all years, storks in urban colonies experienced a nest success rate of $88.1 \pm 32.5\%$ compared to the marsh colony average of $83.0 \pm 37.6\%$. The number of fledglings produced per successful nest and the average keel score of those fledglings did not differ by colony type (Table 3.3). Diet was highly variable at the nest level, though storks from marsh colonies tended to consume more non-native prey ($24.7 \pm 55.3\%$ biomass) and ate no trash in comparison to urban-nesting storks that ate $15.7 \pm 37.8\%$ non-native prey and $7.0 \pm 24.0\%$ trash as proportions of their dietary biomass (Table 3.6, Figs. 3.2-3.3).

Of the 26 GLMMs in the candidate model set, 10 were considered informative having scored within $4 \Delta AIC_c$ of the top-ranked model (top model $w_i=0.263$; cumulative $w_i=1.0$; Table 3.2). All parameters except for Colony Type \times Hydro Year appeared in this top model set, and the Hydro Year parameter appeared in all 10 models. Three parameters—Hydro Year (Optimal), Trash (High), and Colony Type \times Nonnatives (High)—had coefficient estimates with 95% confidence intervals that did not bound 0, indicating that these had the most influence on stork productivity (Table 3.7, Figs. 3.4-3.6).

3.5 DISCUSSION

This study considered the case of the Wood Stork in South Florida where individuals have the opportunity to use resources from both urban and ex-urban environments during the breeding season. By examining productivity and diet at the nest level in both urban and marsh colony sites, I was able to assess the range of concurrent urban/ex-urban resource use by breeding storks and the potential effects these choices may have on the population demographics of this protected species.

My results aligned with the bounty of previous Everglades research showing the importance of marsh hydrological conditions on wading bird productivity (Frederick and Ogden 2001; Herring and Gawlik 2011; Evans and Gawlik 2020), but extends the pattern to urban-nesting storks in addition to those that nest in natural marsh colonies. This is noteworthy because it suggests that urban storks, which have ample access to both urban and marsh habitats within their CFAs, are still their most productive when foraging conditions are good in the natural system. Across all years, storks in urban colonies had higher nesting success (i.e, higher proportion of nests that fledged at least 1 chick), but produced a similar number of fledglings per successful nest compared to storks in marsh colonies. This indicates that early nest failures were common in marsh colonies, at least in our years of study. Urban nesters may be less susceptible to abandonment since they have access to alternate food types and foraging habitat types in the urban environment, benefiting urban breeders in years when the marsh hydrological condition was poor. Prey switching, as may be happening in urban storks, has been noted in other South Florida wading bird (Dorn et al. 2011). In our GLMM, colony type had only a moderate influence on productivity in favor of urban breeders (average estimate: -0.38, 95% CI: -

1.01-0.25), but high trash consumption was associated with high productivity of storks at the nest-level as one of the 3 most influential parameters (average estimate: 0.69, 95% CI: 0.02-1.46). In combination, these findings lend strong support to our first hypothesis: urban habitat use increases productivity at the nest level.

My second hypothesis on the effect of non-native prey consumption on productivity is not well supported except for in relation to colony type. In the GLMM, Nonnatives (Med) and Nonnatives (High) both had a moderate influence on productivity, with moderate levels of consumption being associated with increased productivity (average estimate: 0.22, 95% CI: -0.15-0.59) and high levels of consumption being associated with low productivity (average estimate: -0.21, 95% CI: -0.55-0.13). More notably, the interaction term Nonnatives \times Colony Type (High) had a strong influence (average estimate: 0.74, 95% CI: 0.02-1.46), though it only appeared in 2 models in the top model set. Here, urban nesters that consumed high levels of non-native prey paid a bigger penalty in terms of productivity than marsh-nesting storks with a similar level of non-native prey consumption. This interaction was not previously known. The increased penalty to urban breeders could be due to the prey itself (e.g., accessing non-native prey that are low in nutrients, high in parasites or contaminants), or it could be because urban nesters are flying further to access foraging patches where the non-natives are present, thereby gaining less net energy per trip and having less time available for nest defense.

The mechanism by which non-native prey might affect productivity is unclear. Non-native fish could alter the concentration of prey across the landscape. Non-native fishes predominate in the southern mangroves and canals of South Florida (Trexler et al. 2000) as they have unique habitat requirements, being more tolerant to hypoxia

(Schofield et al. 2007) and less tolerant to cold (Trexler et al. 2000; Schofield and Kline 2018) than native fish species. The prevalence of non-natives in canals could be a draw for storks and other wading birds away from marsh foraging habitats to canals near urban areas where non-natives are concentrated. Non-native species can also be aggressive competitors (Kline et al. 2014), and other authors have hypothesized that canals additionally contribute to altered fish community patterns by increasing the habitat available for large fishes to survive the seasonal dry-down; however, evidence supporting this hypothesis is lacking (Rehage and Trexler 2006). Once more, non-natives tend to spawn earlier in the season than native fishes (Faunce and Lorenz 2000), which could change the timing of prey resource pulses for storks in this pulsed system (Frederick and Ogden 2001; Gatto and Trexler 2019,2020).

Alternately, non-native fish could differ in terms of prey quality. Prey fish are known to be variable in lipid, protein, and nutrient content in other systems (Kushlan 1979; Lamb et al. 2017; Scopel and Diamond 2018). In urban water bodies including canals, non-native fish are more prone to parasites (Frederick et al. 1996; Caudill et al. 2014) and contaminants (Francis et al. 2021). Non-natives could also require different handling and/or foraging time due to differing prey size or idiosyncrasies in behavior as has been seen in other avian predators (Cattau et al. 2010). Changes in handling and searching time would impact the net energy gained during foraging bouts and could allow more or less time for nest attendance and defense.

Consumption of non-native fish is already being observed in other wading bird species in South Florida (Gawlik unpub. data). Jackson (2018) found no effect of non-native prey on the productivity of small herons in natural marsh colonies in the

Everglades, though I note the absence of urban-nesting data and the shorter monitoring timeframe (chicks were considered fledged at 2 weeks of age). Little Blue Herons *Egretta caerulea* and Tricolored Herons *E. tricolor* are “exploiter” species that remain local to fully exploit prey patches. Conversely, storks are “searcher” species that are willing to fly further to exploit only the densest prey patches (Gawlik 2002). This contrast in foraging strategies could be a clue that the negative impact I observed on the productivity of storks that consume high amounts of non-native prey may be more related to the effect that non-natives have on foraging behavior than the quality of the non-native prey since small herons, which likely ate non-native prey as they appeared in local prey patches, suffered no consequences.

The impact of trash and other anthropogenic food subsidies on wading bird populations has been debated in the literature. My study found a positive association between trash consumption and productivity. No marsh-nesting storks consumed trash, and only some urban-nesting storks did, primarily in years when the hydrological condition of the marsh was moderate or poor. Hydrologic patterns are known to have an extreme impact on stork productivity in South Florida, and productivity is generally very low in years with poor hydrological conditions (Frederick and Ogden 2001). Therefore, I believe that the positive impact of trash in the birds I observed is due to birds utilizing alternative food resources when preferred food types were extremely scarce, as has been found in other prey-switching studies (Dorn et al. 2011).

Regular consumption of trash from landfills has been observed in other Ciconiiformes including Marabou Storks *Leptoptilos crumenifer* in Botswana (Francis et al. 2021) and White Storks *Ciconia ciconia* in Spain (Peris 2003), and anthropogenic

food, specifically processed meat, comprises notable proportions of the diet of Woolly-necked Storks *Ciconia episcopus* in South Africa (Thabethe et al. 2021) and White Stork diet in Algeria (Chenchouni 2017a). Some trash items like plastic and wire offer no nutritional value and may be dangerous when ingested (Peris 2003), and urban-sourced prey, whether anthropogenic or natural types, may contain high levels of trace metals (Urfi 2011; Francis et al. 2021). Therefore, I expect that trash consumption by storks in South Florida is only beneficial to a certain point.

The urbanization of wading birds, and specifically Ciconiiformes, is a global phenomenon. White Storks in Europe (Chenchouni 2017a), Painted Storks *Mycteria leucocephala* in India (Suryawanshi and Sundar 2019), Marabou Storks in Botswana (Francis et al. 2021) and Woolly-necked Storks in South Africa (Thabethe et al. 2021) are known to nest in urban or suburban habitats. In South Florida, I showed that urban-nesting Wood Storks not only used urban areas for foraging and breeding, but in some years do better than those birds that nested in the natural system. Urban colonies may therefore be key to the future longevity of stork nesting in South Florida. However, I also note that storks from both urban and marsh colonies foraged in the marsh when hydrological conditions were optimal, and optimal hydrological years are the key to high productivity years of both urban and marsh nesters. Only in suboptimal hydrological years did urban-nesting storks take advantage of urban food resources to benefit productivity. These findings are in accordance with Evans and Gawlik (2020) and together suggest that the concurrent use of resources from the urban and ex-urban environments contributes to the success of storks in South Florida.

The commonly cited categorization of species-level urban response types by Blair (1996) and Pennington and Blair (2012) does not adequately describe storks and, I suspect, other species with large foraging ranges that include both natural and urban systems. Storks are not “urban exploiters” as they are not purely urban birds, relying heavily on optimal hydrological conditions of the ex-urban marsh for high productivity. Likewise, they are not “urban avoiders” as they do use urban habitats for both nesting and foraging, and they are not “suburban adaptors” since they seek resources from truly urban and truly ex-urban habitat types concurrently. As such, I believe a fourth category, the “urban commuters” is a more appropriate term to describe storks and other species that thrive in urban matrices such as the urban-wildland interface.

In conclusion, I find that optimal hydrological years are key to high stork productivity in both urban and natural marsh colonies. The use of urban food resources, including anthropogenic food and trash, is beneficial in years when the marsh is in poor hydrological condition. Only urban-nesting storks have access to urban food types, so this may be an important advantage for urban nesters. The consumption of non-native fish does not have a strong influence on stork productivity in South Florida. However, I did find that urban nesters pay a larger reproductive penalty for eating high amounts (>22% of biomass/nest) of non-native prey than marsh nesters, likely because accessing non-natives is more costly to urban nesters. These examples of urban resource use cumulatively suggest that Everglades indicator models and stork species recovery models should be revised to include urban conditions such as urban hydrological conditions or urban prey availability, and that annual stork nesting count protocols should be modified to systematically include urban nesting colonies. Ciconiiformes in the U.S., and perhaps

globally, represent a new type of urban user, the “urban commuters.” This type of use may be more common than is currently discussed, in waterbirds and in other generalist species with large home ranges.

3.6 ACKNOWLEDGEMENTS

I wish to thank BallenIsles Country Club and the City of Weston for granting land access permissions, especially during the COVID-19 pandemic. Data collection was conducted in accordance with the conditions stated in the following permits: FAU IACUC A17-33, USFWS TE65550A-2, NPS EVER-2018-SCI-0017, and FFWCC LSSC-18-00027.

Table 3.1. Description of variables used in the global model of a model set evaluated by an information theoretic approach (AIC_c).

Global model component	Parameter name	Description	Levels	Data source
Y	Productivity	# nestlings survived to 4 wks per nest	0-4 nestlings	Colony monitoring
X1	Nonnatives	Proportion of diet that is non-native prey per nest	Low = 0-1% non-natives by biomass (n=130 nests) Med = 1-22% non-natives by biomass (n=51 nests) High = 22-100% non-natives by biomass (n=53 nests)	Bolus sampling
X2	Trash	Proportion of diet that is trash per nest	Low = 0% trash by biomass (n=213 nests) Med = 0.1-20%. Trash by biomass (n=10 nests) High = 20-100T trash by biomass (n=11 nests)	Bolus sampling
X3	Colony_Type	Colony type	Urban (BallenIsles, Griffin, Sawgrass) Marsh (Jetport South, Tamiami West, Paurotis Pond)	Colony monitoring
X4	Hydro_Year	Marsh hydrological condition based on % marsh habitat that is available for foraging/year (Evans et al. 2020)	Suboptimal (2016, 2019, 2020) Moderate (2015) Optimal (2017, 2018)	FAUNA reports
X5	Nonnatives x Colony_Type	Interacting variables described above		
X6	Nonnatives x Hydro_Year	Interacting variables described above		
Intercept	Colony	Colony	2015-2020 (year of data collection)	Colony monitoring

Table 3.2. Complete AIC_c model set of stork response (Y) to prey choice and hydrological condition of marsh foraging locations. Models in the top set ($\Delta AIC_c < 4$; delineated by horizontal line) were averaged. For those models which included the potential uninformative parameter ‘Trash’, the model was re-run without the parameter (bold rows) for comparison; ‘Trash’ was deemed uninformative if the intercept, logLik, and AIC_c values were identical between the pair of models.

Rank	(Intercept)	ColonyType	Non-natives	HydroYr	Trash	ColonyType x Non-natives	ColonyType x HydroYr	df	logLik	AIC _c	delta	weight	CumWt
1	1.710	NA	NA	+	+	NA	NA	7	-212.905	440.532	0.000	0.245	0.245
2	1.749	NA	+	+	+	NA	NA	9	-211.157	441.491	0.959	0.152	0.397
(2)	1.843	NA	+	+	NA	NA	NA	7	-214.261	443.246			
3	1.731	-0.284	NA	+	+	NA	NA	8	-212.452	441.839	1.307	0.127	0.524
(3)	1.841	-0.360	NA	+	NA	NA	NA	6	-215.839	444.217			
4	1.760	-0.294	+	+	+	NA	NA	10	-210.599	442.645	2.114	0.085	0.609
(4)	1.857	-0.364	+	+	NA	NA	NA	8	-213.509	443.952			
5	1.695	-0.538	+	+	+	+	NA	12	-208.456	442.991	2.459	0.072	0.681
(5)	1.785	-0.604	+	+	NA	+	NA	10	-211.236	443.919			
6	1.843	NA	+	+	NA	NA	NA	7	-214.261	443.246	2.714	0.063	0.744
7	1.815	NA	NA	+	NA	NA	NA	5	-216.470	443.323	2.791	0.061	0.805
(7)	1.815	NA	NA	+	NA	NA	NA	5	-216.470	443.323			
8	1.785	-0.604	+	+	NA	+	NA	10	-211.236	443.919	3.387	0.045	0.850
9	1.857	-0.364	+	+	NA	NA	NA	8	-213.509	443.952	3.420	0.044	0.894
10	1.841	-0.360	NA	+	NA	NA	NA	6	-215.839	444.217	3.685	0.039	0.933
11	1.736	-0.183	NA	+	+	NA	+	10	-212.100	445.648	5.116	0.019	
12	1.767	-0.087	+	+	+	NA	+	12	-209.923	445.926	5.394	0.017	
13	1.701	-0.396	+	+	+	+	+	14	-207.952	446.741	6.209	0.011	
14	1.862	-0.217	+	+	NA	NA	+	10	-212.946	447.338	6.807	0.008	
15	1.788	-0.526	+	+	NA	+	+	12	-210.818	447.716	7.184	0.007	
16	1.842	-0.339	NA	+	NA	NA	+	8	-215.511	447.956	7.424	0.006	
17	2.106	NA	NA	NA	NA	NA	NA	3	-228.530	463.210	22.678	0.000	
18	2.152	NA	+	NA	NA	NA	NA	5	-227.069	464.521	23.989	0.000	
19	2.130	-0.295	NA	NA	NA	NA	NA	4	-228.145	464.544	24.012	0.000	
20	2.073	NA	NA	NA	+	NA	NA	5	-227.164	464.711	24.179	0.000	

21	2.166	-0.283	+	NA	NA	NA	NA	6	-226.662	465.863	25.331	0.000
22	2.093	-0.240	NA	NA	+	NA	NA	6	-226.892	466.322	25.791	0.000
23	2.123	NA	+	NA	+	NA	NA	7	-225.899	466.520	25.988	0.000
24	2.134	-0.233	+	NA	+	NA	NA	8	-225.607	468.148	27.616	0.000
25	2.133	-0.485	+	NA	NA	+	NA	8	-225.683	468.302	27.770	0.000
26	2.103	-0.439	+	NA	+	+	NA	10	-224.717	470.882	30.350	0.000

Table 3.3. Summary of nest-level Wood Stork productivity in urban and marsh colonies in South Florida, 2014-2020. A nest is considered successful if at least one hatched chick survived to fledging age (4 weeks old). Keel Score, a proxy for body condition at the age of fledging, ranges from 1-5, where 1 is a protruding keel bone with no overlaid muscle and 5 is a muscle layer thick enough to hide the shape of the keel bone entirely.

Colony name	Colony type	Nests/yr	Monitored nests (n)	Nest success (%)	Fledglings/nest	Keel score
Griffin	Urban	81 ± 65	77	81.8 ± 38.8	2.2 ± 1.1	2.7 ± 0.5
BallenIsles	Urban	24 ± 10	79	94.9 ± 22.1	2.0 ± 1.2	2.4 ± 0.6
Sawgrass	Urban	72 ± 23	20	85.0 ± 36.6	1.7 ± 1.3	2.5 ± 0.6
<i>Urban colony average</i>		<i>55 ± 39</i>	<i>176</i>	<i>88.1 ± 32.5</i>	<i>2.2 ± 1.1</i>	<i>2.5 ± 0.5</i>
Paurotis Pond	Marsh	290 ± 192	48	58.3 ± 50.0	2.0 ± 1.2	2.6 ± 0.6
Jetport South	Marsh	355 ± 407	3	100.0 ± 0.0	2.2 ± 1.1	NR
Tamiami West	Marsh	105 ± 117	32	90.6 ± 29.6	1.7 ± 1.3	2.5 ± 0.6
<i>Marsh colony average</i>		<i>328 ± 274</i>	<i>83</i>	<i>72.2 ± 45.0</i>	<i>1.7 ± 1.3</i>	<i>2.6 ± 0.6</i>
South Florida average		- ^a	259	83.0 ± 37.6	2.0 ± 1.2	2.6 ± 0.6

Table 3.4. Number of storks per colony during study years (2014-2020) in South Florida. Values are taken from the South Florida Wading Bird Reports, 2015-2020 (Cook and Baranski 2021) and the Wood Stork Working Group Report (USFWS 2021).

Location	2014	2015	2016	2017	2018	2019	2020	Mean	SD
Solid Waste Authority	304	255	NR	155	365	135	100	219	105
BallenIsles	NR	34	28	36	17	10	20	24	10
Sawgrass	NR	74	52	83	80	39	102	72	23
Griffin	NR	NR	NR	NR	150	22	71	81	65
Wakodahatchee	NR	28	59	98	164	82	55	81	47
Bird Island	NR	37	24	44	123	11	78	53	41
Lenore Island	140	69	307	300	473	164	25	211	157
Urban South Florida	444	497	470	716	1372	463	451	630	341
Everglades NP:	1260	648	580	1313	1973	922	912	1087	478
-- <i>Tamiami West</i>	300	75	0	138	0	12	210	105	117
-- <i>Jetport South</i>	400	0	0	857	953	0	275	355	407
-- <i>Paurotis Pond</i>	270	285	230	326	682	170	70	290	192
WCAs+Gator Farm	497	0	63	1058	1642	0	432	527	620
Corkscrew	270	210	651	800	328	17	0	325	302
Marsh South Florida	2027	858	1294	3171	3943	939	1344	1939	1189
Total South Florida	2471	1355	1764	3887	5315	1402	1795		
% Urban	18	37	27	18	26	33	25		

Table 3.5. Percentage of the core foraging area (CFA; 30-km radius surrounding colony site) by land cover type for each of the Wood Stork colonies monitored for this study.

Colony Name	Colony Type	Land Cover Type (%) in CFA (30km buffer)		
		Marsh	Rural	Urban
Griffin	Urban	48.3	0.1	51.6
BallenIsles	Urban	48.5	10.0	41.5
Sawgrass	Urban	51.4	1.0	47.7
<i>Urban Colony Average</i>		<i>49.4</i>	<i>3.7</i>	<i>46.9</i>
Tamiami West	Marsh	66.2	7.0	26.8
Paurotis Pond	Marsh	99.2	0.6	0.2
Jetport South	Marsh	99.6	0.0	0.4
<i>Marsh Colony Average</i>		<i>88.3</i>	<i>2.5</i>	<i>9.2</i>
<i>South Florida Average</i>		<i>68.9</i>	<i>3.1</i>	<i>28.0</i>

Table 3.6. Summary of nest-level biomass of non-native and trash prey types collected from Wood Stork nestlings in South Florida, 2014-2020.

Colony Name	Colony Type	N (nests)	Non-native biomass (%)	Trash biomass (%)
Griffin	Urban	61	13.2 ± 30.0	8.1 ± 23.8
BallenIsles	Urban	56	21.2 ± 48.0	8.0 ± 27.8
Sawgrass	Urban	18	7.2 ± 21.5	0.3 ± 1.1
<i>Urban Colony Average</i>		135	15.7 ± 37.8	7.0 ± 24.0
Paurotis Pond	Marsh	48	29.2 ± 66.8	0.0 ± 0.0
Jetport South	Marsh	11	17.0 ± 35.5	0.0 ± 0.0
Tamiami West	Marsh	40	21.5 ± 48.0	0.0 ± 0.0
<i>Marsh Colony Average</i>		99	24.7 ± 55.3	0.0 ± 0.0
South Florida Average		234	19.5 ± 46.1	4.0 ± 18.6

Table 3.7. Average parameter estimates from the top model set (n=10 models) identified using an information theoretic approach (AIC_c). Bolded parameters are those with 95% confidence intervals that do not overlap 0.

Parameter	Number of top models in which parameter appears	Average estimate (model subset)	Confidence Interval	
			2.5%	97.5%
Hydro_Year_Moderate	10	0.03	-0.33	0.39
Hydro_Year_Optimal	10	0.82	0.48	1.16
Colony_Type	6	-0.38	-1.01	0.25
Nonnatives_Med	6	0.22	-0.15	0.59
Nonnatives_High	6	-0.21	-0.55	0.13
Trash_Med	5 ^a	0.53	-0.10	1.15
Trash_High	5	0.69	0.04	1.33
Colony_Type * Nonnatives_Med	2	0.03	-0.71	0.78
Colony_Type * Nonnatives_High	2	0.74	0.02	1.46
Colony_Type * Hydro_Year	0	N/A	N/A	N/A

^aStrong evidence that Trash_Med was a non-informative parameter in 1 of these top models. See text and Table 3.2 for details.

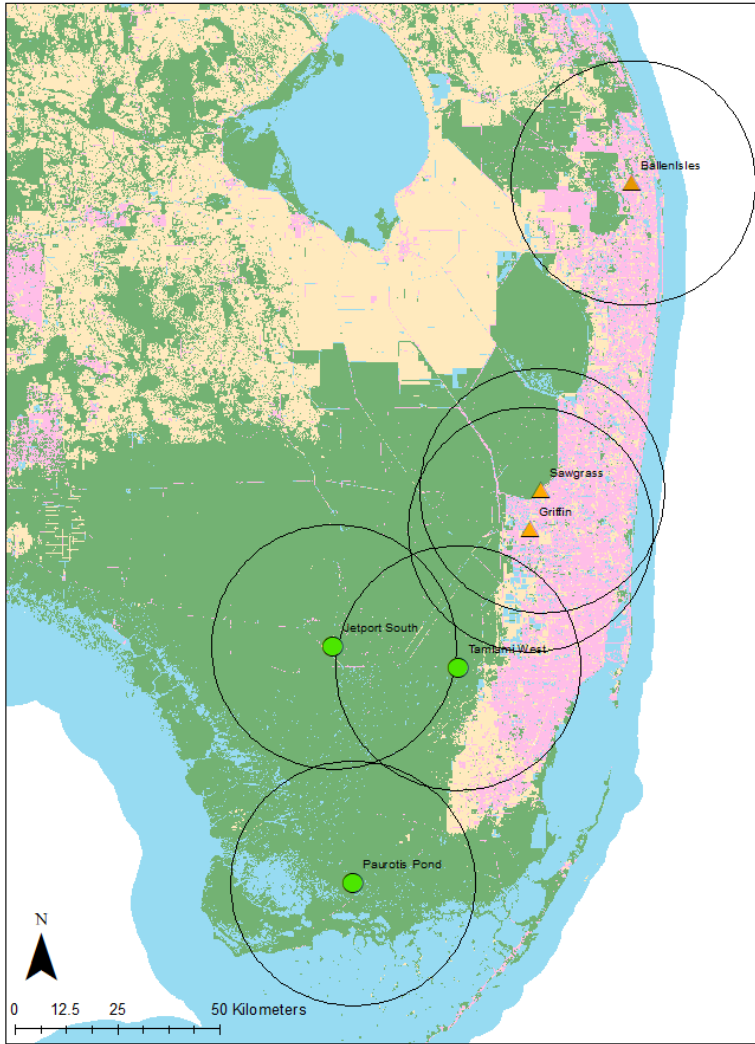


Figure 3.1. Urban (pink), rural (tan), natural (green), and water (blue) land cover types found within the core foraging area (30-km radius) for each of the Wood Stork colonies monitored for this study. Urban colonies are shown as orange triangles, and natural colonies are shown as green circles.

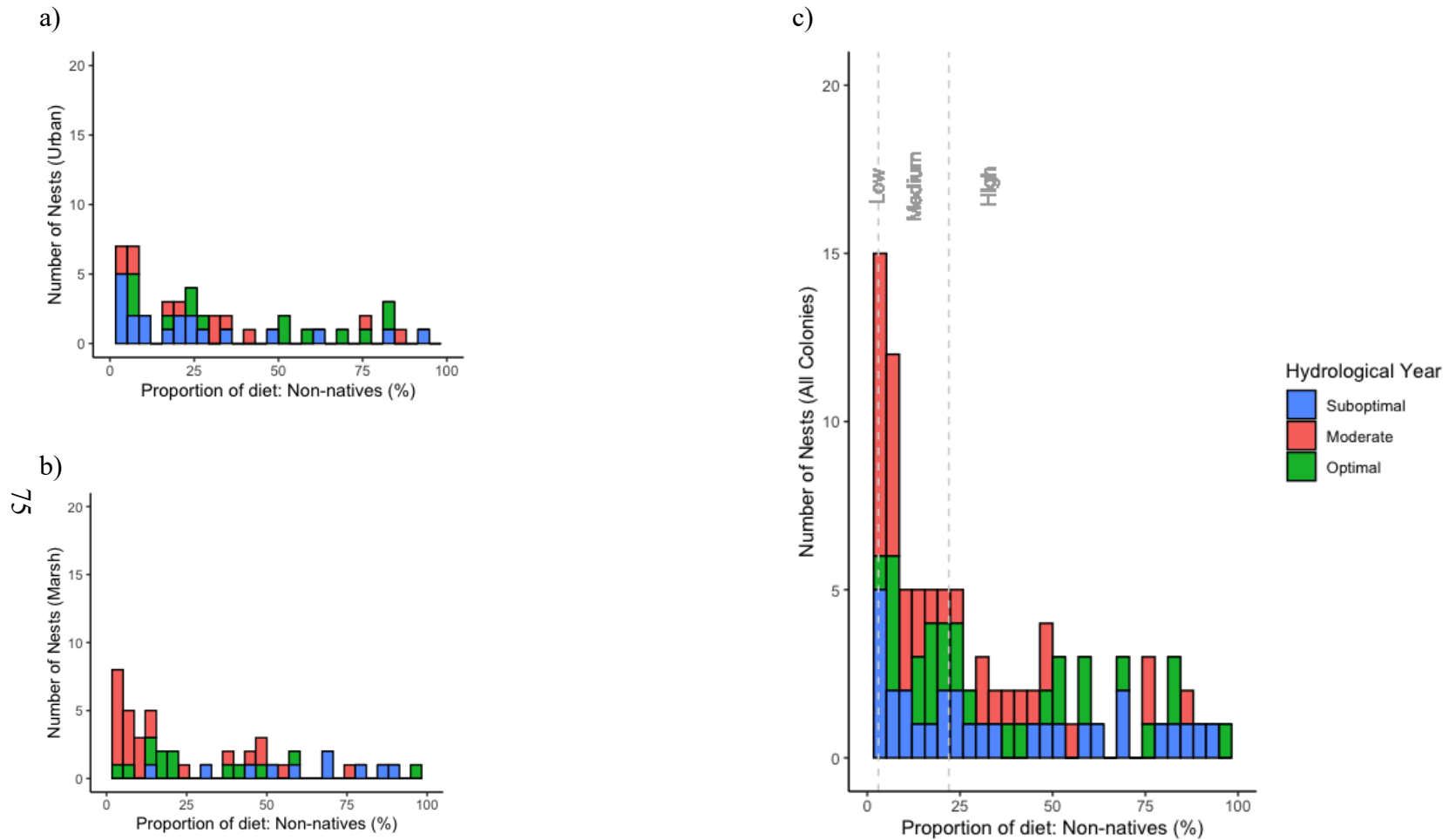


Figure 3.2. Histogram of the number of nests by the proportion of diet that was non-native prey (% biomass) in (a) urban colonies, (b) marsh colonies, and (c) all colonies. The thresholds that were used to define “Low”, “Med”, and “High” consumption of non-native prey in subsequent models are also displayed (see text for details).

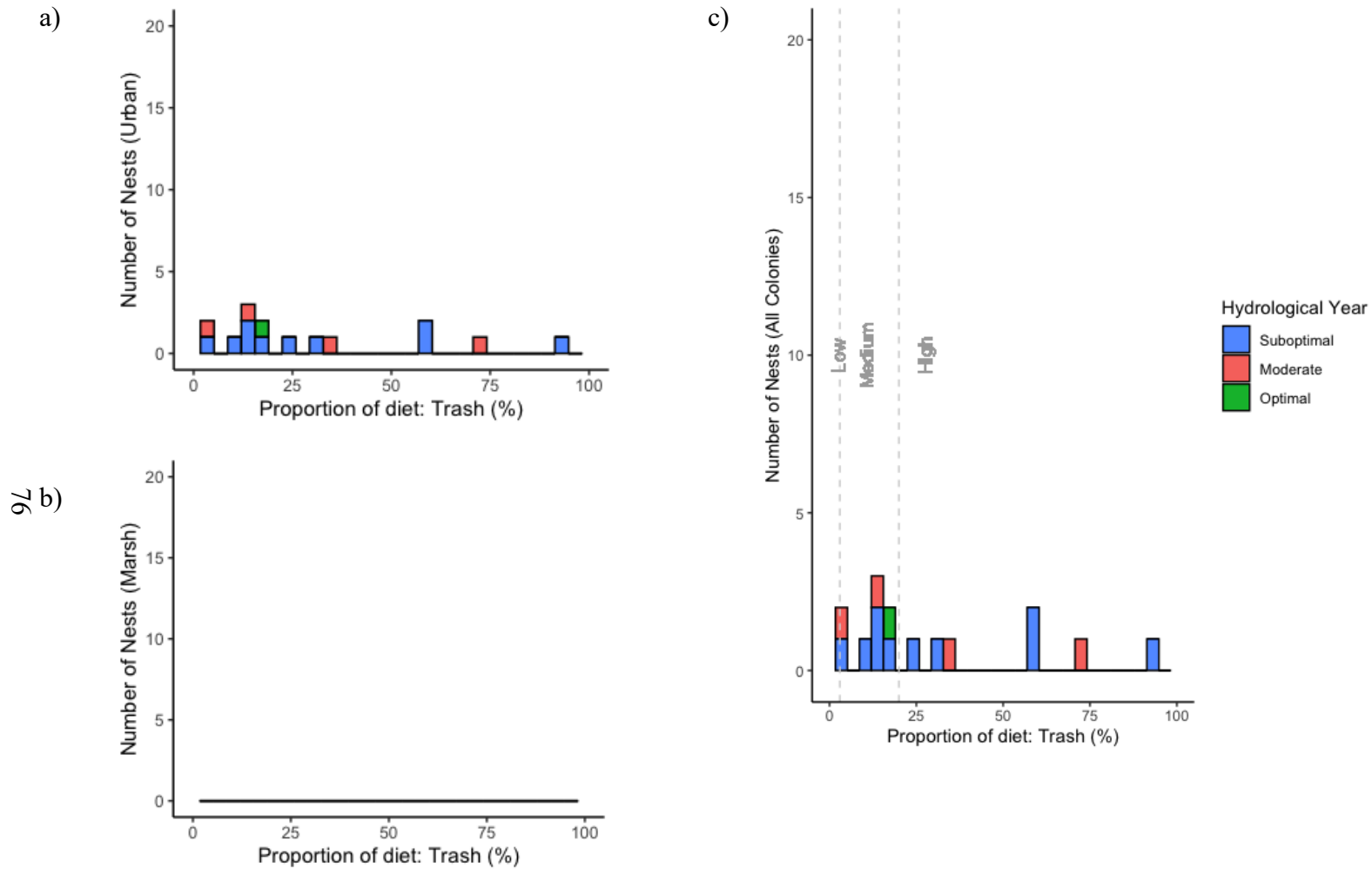
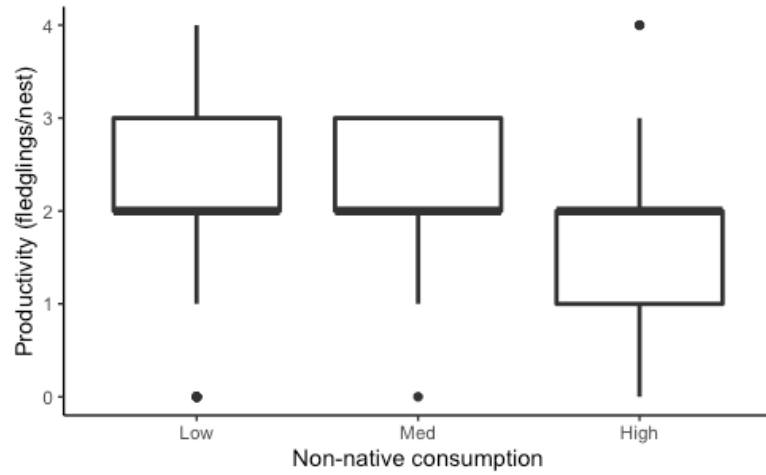


Figure 3.3. Histogram of the number of nests by the proportion of diet that was non-native prey (% biomass) in (a) urban colonies, (b) marsh colonies, and (c) all colonies. The thresholds that were used to define “Low”, “Med”, and “High” consumption of trash in subsequent models are also displayed (see text for details).

a)

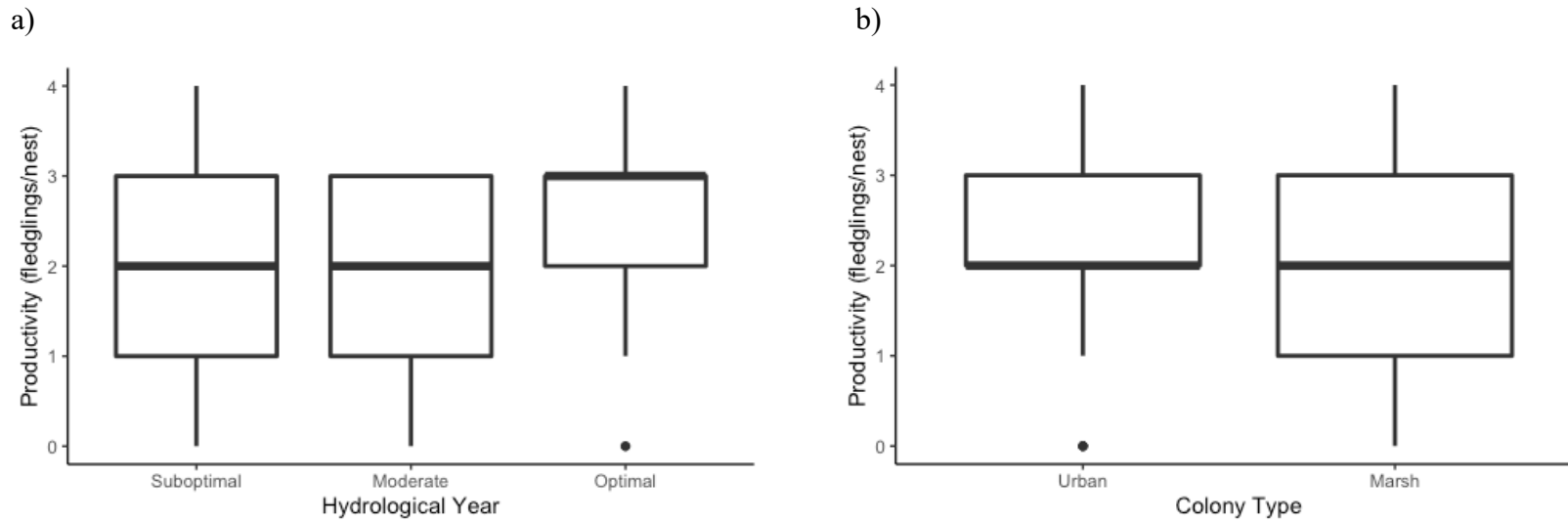


b)



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Figure 3.4. Productivity according to (a) the level of non-native consumption and (b) the level of trash consumption at 6 Wood Stork colonies (n=163 nests) in South Florida, 2015-2020. In the boxplots, the central horizontal line represents the median value (50%), the box represents the IRQ (25-75%), the whiskers represent the largest value beyond 1.5x the IQR, and dots beyond the whiskers represent outliers.



78 Figure 3.5. Productivity according to (a) marsh hydrological condition and (b) colony type at 6 Wood Stork colonies (n=163 nests) in South Florida, 2015-2020. In the boxplots, the central horizontal line represents the median value (50%), the box represents the IRQ (25-75%), the whiskers represent the largest value beyond 1.5x the IQR, and dots beyond the whiskers represent outliers.

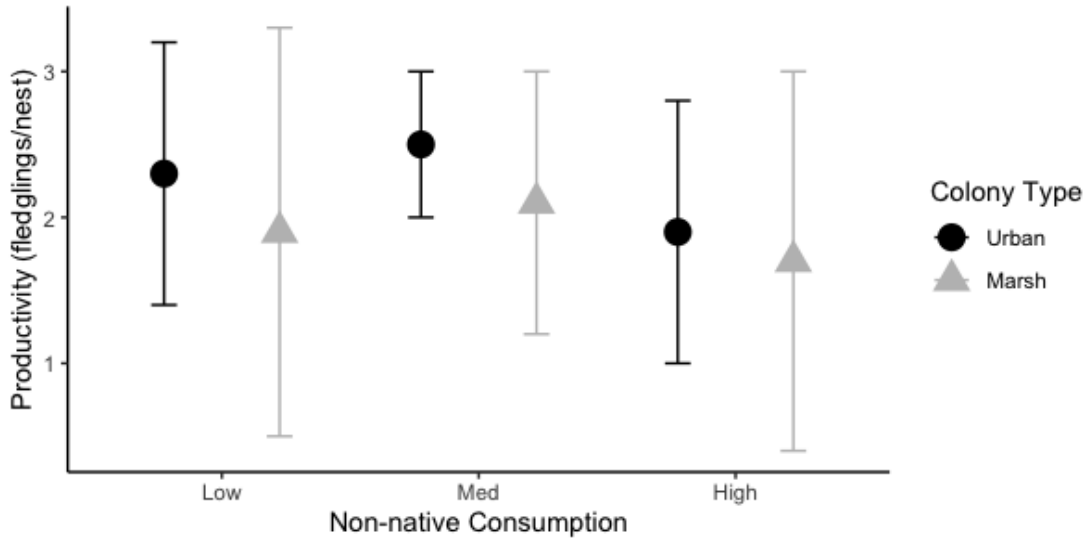


Figure 3.6. Productivity according to the interaction between colony type and the level of non-native prey consumption by Wood Storks at 6 colonies (n=163 nests) in South Florida, 2015-2020. The mean values and standard deviation are shown.

4 RANGE-WIDE IMPACTS OF CLIMATE CHANGE AND URBANIZATION ON THE FUTURE STATUS OF THE WOOD STORK

4.1 ABSTRACT

Climate change and urbanization, two distinct but interacting types of human-induced rapid environmental change, are likely drivers of ongoing changes to the range of the Wood Stork (*Mycteria americana*), a threatened species, in the United States. To model these effects, I collated stork nesting distributions and environmental (weather, land cover type) data from across the stork's U.S. range, 2002-2019. Principle components analysis and cluster analysis were used to define nesting regions, and stork—environmental driver associations for each nesting region were assessed using an information theoretic approach. Lastly, environmental inputs in a complex systems model were manipulated to reflect predicted changes to climate and land cover types by the years 2050 and 2075. I found that, of the four stork nesting regions, south and central Florida colonies are most more sensitive to changes in future rainfall totals. In particular, nesting in the South region is likely to end if the total annual rainfall decreases due to climate change. The predicted outcome for storks in the South regions is less dire if rainfall increases from climate change. Colonies in the Central region are less sensitive to rainfall and/or are buffered by the high availability of urban habitat. Conversely, nesting activity in the two northernmost regions are not strongly associated with the environmental variables I tested here, indicating that sea level rise, local water management schedules, predation, or factors may drive nest abundance and productivity

in Georgia, South Carolina, and North Carolina colonies. A shift of stork nesting away from the Everglades and into urban and temperate regions represents a major shift in the behavior and distribution of this species.

4.2 INTRODUCTION

As a group, waterbirds show tremendous behavioral flexibility and are adept at thriving in naturally stochastic systems. Flight provides efficient locomotion over long distances, allowing species to maintain larger home ranges than most animals, and to migrate or otherwise relocate when local conditions become unfavorable. Displays of plasticity toward environmental fluctuations, including resource pulses, can become so well understood that resource managers can identify the thresholds for water flow to maximize colonial waterbird nesting (Bino et al. 2014), predict how population demographics will change following prolonged droughts or hurricanes (Leberg et al. 2007; Wen et al. 2016; Benscoter et al. 2020), and model changes in avian community composition based on local hydrological conditions (Chin et al. 2014). However, even with plasticity as an advantage, the evidence suggests that many avian species are vulnerable to global changes (Norris et al. 2004; Rosenberg et al. 2019; Bateman et al. 2020). Waterbird habitats, namely freshwater wetlands and coastal estuaries, face unprecedented pressures globally. These pressures include large-scale alterations in weather patterns and sea level rise (SLR), such as increasingly intensive natural resource extraction, increasing urbanization (especially along coasts), and climate change, but also the domino effects that these drivers have on local ecological communities (Romañach et al. 2019). Already, waterbird populations are responding to these pressures by shifting

their ranges (Zhao et al. 2019; Amano et al. 2020) and adopting urban-tolerant behaviors (Minias et al. 2018; Callaghan et al. 2019; Lato et al. 2021).

One species of waterbird which has indeed benefited from behavioral plasticity is the Wood Stork (*Mycteria americana*; hereafter, “stork”). In the Everglades (South Florida, United States (U.S.)), which was historically the core stork nesting region in the U.S. (Kushlan and Frohring 1986), the number of nesting storks declined 78% between 1930 and 2001 following decades of canalization and wetland drainage (Crozier and Gawlik 2003), leading to the stork being listed as an endangered species under the U.S. Endangered Species Act (ESA) in 1984 (Kushlan and Frohring 1986). By the 1990s, however, storks showed signs of expanding their breeding range northward and, for the first time, into urban areas (Cook and Baranski 2021). They have also shifted where they forage and what they prey upon (Klassen and Gawlik 2018; Evans et al. 2021), and demonstrate flexibility in which month they initiate nesting, starting any time between December and April depending on the latitude and the year (Kushlan et al. 1975; Frederick et al. 2009). Evidence of the species’ recovery was strong enough that storks were down-listed from endangered species protections to the status of Threatened in 2014 (U.S. Fish and Wildlife Service 2014). Unfortunately, models that include storks from the entire southeastern U.S. are lacking, with the exception of one preliminary population model by Borkhataria et al. (2008) which was published prior to the down-listing event. The cause of the population increase is not well understood, and source/sink dynamics across the range have not been considered. Further, without the ability to fully describe the current dynamics of this threatened species, I cannot confidently predict its future

status amidst large-scale environmental changes including climate change and urbanization.

The aim of this study was to test the effect of ongoing climate change and urbanization on the future population status of the stork, a recovering, wetland-dependent waterbird, in the US. I hypothesized that the abundance and distribution of nesting storks would change over time to reflect changes in the abiotic conditions within the stork's U.S. range. Specifically, I predicted that 1) the magnitude of a region's predicted change in climate would be reflected in the magnitude of change in the region's stork abundance; and 2) urbanization would be associated with an increase in stork numbers in regions where rainfall is a significant driver of stork abundance and productivity. The latter prediction is based on previous research showing that storks relying on the natural wetlands turn to urban landscapes for alternative prey types when the wetlands are in poor hydrological condition (Evans & Gawlik, 2020; Shlepr Ch. 3). To test these predictions, I collated stork monitoring data from 2002-2019 from the U.S. Fish and Wildlife Service (USFWS) and environmental data from the same time period from the National Oceanic and Atmospheric Administration (NOAA). I modeled the linkages between these components using a complex systems software, and then modified the environmental inputs based on the anticipated effects of climate change and urbanization to measure how stork abundance and distribution are likely to change by comparing mean population size estimates in each region for each environmental scenario. Waterbird studies that project population-level responses to future environmental conditions are rare (Jenouvrier 2013), but my modeling approach closely resembles that of Drever et al. (2012).

4.3 METHODS

4.3.1 Defining nesting regions

Past literature differentiated coastal from inland stork colonies (Kushlan and Frohring 1986; Bryan and Gariboldi 1998; Romanek et al. 2000; Bryan and Robinette 2008), urban from non-urban stork colonies (Evans and Gawlik 2020), and used political boundaries such as state lines to organize reports of monitoring data (U.S. Fish and Wildlife Service 2021a). To improve the objectivity of regional classifications across the full U.S. breeding range, I used landscape-scale environmental and land cover parameters to dictate regional classifications using a bottom-up approach. First, to represent natural hydrological condition, daily weather data were downloaded for 19 rainfall stations and 25 temperature stations across the southeastern US, 2000-2019 (National Oceanic and Atmospheric Administration 2021b). Records were then binned into seasons according to the annual stork life cycle (Table 4.1; Coulter et al., 2020). For each weather station, rainfall was totaled for each season each year, and then the average total rainfall per season per station was calculated (mean±standard deviation (SD)). Similarly, the average maximum daily temperature (TMAX) was calculated for each season for each weather station. Stork colony locations (see *Methods: Stork nesting data*) were used to pair each colony with the nearest weather station for which environmental records were summarized.

In addition to describing the average hydrological condition of each colony, I used two geographic information system (GIS) layers in ArcMap 10 to quantify the amount (km²) of coastal and urban land cover types available to storks within 10, 20, and 30km radii of each colony. These colony buffers represent “core foraging areas”, i.e., the

foraging habitat that is most likely to be used by storks during the breeding season (Bryan et al. 2012). Coastal habitat included all land within 10km of a tidally influenced shoreline (National Oceanic and Atmospheric Administration 2021c). Land located outside this 10km-shoreline buffer was presumed to be inland. A third land cover type that was not mutually exclusive with the inland/coastal classification was urban land cover, which included all medium- to high-density urban land cover at the time of the 2010 U.S. Census.

Hydrological and land cover variables (Table 4.2) were input as the matrix for a principal component analysis (PCA) using the package *factoextra* in R (R Core Development Team 2020). Several rainfall and urban land cover variables strongly co-varied, so were removed from the final PCA (Table 4.2). PCA results were then used in a k-means cluster analysis (CA), and the elbow method was used to determine how many clusters provided the most parsimonious solution. The clusters identified by the CA became the stork nesting regions used in all subsequent analysis.

4.3.2 Stork nesting data

The Wood Stork Working Group, a professional network of researchers that has been organized by the Southeast Ecological Services Office of the USFWS since 2001, provided annual nest monitoring data from 2002-2019. This dataset included two colony-level stork response variables, total nests and productivity. Total nests reflected the highest number of nests observed in each colony per year. Survey methods included state-sponsored aerial surveys (e.g., non-urban greater Everglades region, state of Georgia) and ground counts conducted by foot or boat (e.g., urban South Florida). Nest

numbers were summed by state for each year in my colony-level dataset, and this annual total was compared to the annual nest total reported by the USFWS (U.S. Fish and Wildlife Service 2021a). For years where the colony-level dataset totaled <70% of the USFWS reported total, I assumed colony-level data were missing, and distributed the difference to each region.

The second colony-level stork variable collected was productivity. Productivity is difficult to measure consistently because of field protocols cannot always be standardized and colony-level summary statistics may be calculated in different ways (e.g., “fledging success” could be calculated with or without known failed nests using the number of eggs laid or the number of hatchlings). To circumvent these limitations, I assumed there was consistency in monitoring and reporting methods at the colony level, and used a z score ($z=(x-\mu)/\sigma$, where x is the observation, μ is the colony-level mean, and σ is the colony-level SD) to calculate within-colony relative productivity, discarding any colony that did not have at least 3 years of productivity records in my chosen time period. I then back-transformed these relative annual productivity metrics ($x=z\sigma+\mu$) by using means and standard deviations reported in published studies that were based on standardized protocols (Brooks and Dean 2008; Borkhataria et al. 2008). Finally, standardized productivity was averaged by region on a per-year basis.

4.3.3 Stork response—environmental associations

To link the stork nesting response (total nests, productivity; see *Methods: Stork nesting data*) to environmental drivers (hydrology and land cover type; see *Methods: Defining nesting regions*) in this system, I used Akaike’s Information Criterion corrected

for small sample sizes (AIC_c) to compare the sub-models of the following two global models for each region:

$$\text{Total.nests} \sim \text{Rain.nonbreed} + \text{Rain.early} + \text{Rain.2yr} + \text{TMAX.early}$$

$$\begin{aligned} \text{Stand.prod} \sim & \text{Rain.2yr} + \text{Rain.yr} + \text{Rain.breed} + \text{Rain.late} + \text{TMAX.late} + \\ & \text{Rain.breed} \times \text{Urban} + \text{Rain.breed} \times \text{Shore} \end{aligned}$$

The AIC_c model selection was conducted in R following the protocol outlined by Grueber et al., (2011). Models within 4 AIC_c of each top model were assumed to contribute biologically meaningful information (Grueber et al. 2011), and coefficients from each models' subset were averaged together.

To measure the accuracy of the stork response—environmental driver equations, I compared the predictions of the model averaged equations using the predict function in R with empirical reports to the USFWS over the same time period, 2002-2019. The more closely model predictions match empirical observations, the better the inputted environmental drivers explain observed variability in regional stork numbers. Conversely, if my model does not track closely with empirical observations, the parameters driving a region's stork response were not included in my model.

4.3.4 Simulation model: baseline scenario

All model components—the stork response, environmental drivers, and the equations linking them—were input according to the materials flow diagram sketch into system simulation software (Stella Professional, isee systems, inc, 2021; Fig. 4.1). Because no project has banded or tracked individual storks long-term and range-wide, no empirical data exist to help us model rates of nest relocations between regions. Therefore,

it was not possible to design a simulation model that contained both a timestep feedback loop (which would be necessary to produce a traditional population projection) and the regional structure I aimed to understand. My solution was to use a modeling approach like that of (Drever et al. 2012), where each run of the model selects values from normal distributions of the environmental and stork response variables in my 2002-2019 datasets. The simulation model output, then, is a population prediction for each region (functioning independently) and the U.S. overall (i.e., the sum of regional totals). By averaging the population predictions produced by 10,000 runs, I confidently captured the average population size produced by an average set of environmental conditions in a given climate scenario.

I calibrated the baseline model by running it in stages. First, I ran the core of the model only by replacing the complex environmental driver equations with simple normal distributions based around each parameter's mean by region (see *Methods: Defining nesting regions*) and compared the population predictions produced by the equations with annual empirical observations reported to the USFWS. The equation at the core of the model is as follows:

$$\begin{aligned} \text{Nests}_{\text{US}} = & (\text{Adult.survival} * \text{Nests}_{\text{S}} + \text{Juv.survival} * \text{Prod}_{\text{S}} * \text{Nests}_{\text{S}}) + \\ & (\text{Adult.survival} * \text{Nests}_{\text{C}} + \text{Juv.survival} * \text{Prod}_{\text{C}} * \text{Nests}_{\text{C}}) + \\ & (\text{Adult.survival} * \text{Nests}_{\text{NE}} + \text{Juv.survival} * \text{Prod}_{\text{NE}} * \text{Nests}_{\text{NE}}) + \\ & (\text{Adult.survival} * \text{Nests}_{\text{NW}} + \text{Juv.survival} * \text{Prod}_{\text{NW}} * \text{Nests}_{\text{NW}}) \end{aligned}$$

Here, subscripts indicate whether the metric is in reference to a region (S=South, C=Central, NE=Northeast, NW=Northwest) or the total U.S. population produced by summing all regions. ‘Nests’ refers to nest abundance (number of nests), ‘Prod’ refers to

my standardized productivity metric (fledglings/nest), and ‘Adult.survival’ and ‘Juv.survival’ refer to the annual survival probability in years for adults and the 3-yr cumulative survival probability for first-time breeders, respectively. Mean survival rates were taken from Borkhataria et al. (2008), and SD was estimated to account for variation, with juveniles being more sensitive to hydrological condition than adults (Adult.survival: 0.91 ± 0.03 ; Juv.survival: 0.2 ± 0.1). Two final parameters, ‘Prev.skipped.breeders’ and ‘New.skipped.breeders,’ were added to the model core to account for adults that are alive but choose to skip breeding in a given year, because the phenomenon of skipped breeding is known to happen in storks (Coulter et al. 2020) but cannot be measured during annual nest surveys. Therefore, 500 ± 500 nesting pairs that previously skipped breeding (so were not counted in the previous year’s nest survey) were added to each regions’ annual nest count, and $2,000 \pm 2,000$ nesting pairs (i.e., 500 nesting pairs * 4 regions) that counted as new skipped breeders (so were not going to get counted in the next year’s nest survey) were subtracted from the U.S. population total in each simulation (Appendix 2).

Once I was satisfied that the core of the model was reliable, I added the environmental driver equations (see *Methods: Stork response—environmental associations*) back into the model and checked whether the model produced reasonable population estimates for each region and for the U.S. as a whole. Once the full model was calibrated, I ran the model 10,000 times to determine with high confidence each region’s population size (mean \pm SD) and the total U.S. population size (mean \pm SD). Population numbers after from the final calibration step were considered to be the baseline scenario since they were based on empirical observations.

To measure the accuracy of the simulation model, I compared population predictions produced by the baseline scenario with population predictions from empirical observations to the USFWS over the same time period, 2002-2019. The closer the match between regional and U.S. total population predictions by the model to USFWS reports, the more reliable the model.

4.3.5 Simulation model: future scenarios

I was interested in the changes to the abundance and regional distribution of storks due to climate change and urbanization over a 30 to 60-year timeframe. This timeframe is based on storks' long-lived nature (Coulter et al. 2020) and the timeframe typically associated with the "foreseeable future" mandate of the U.S. Endangered Species Act (Jenouvrier et al. 2021). I identified datasets that summarized changes in the hydrologic condition and urban land cover for each region. For hydrologic condition, I downloaded monthly rainfall and average daily maximum temperature predictions for 2035-2065 (hereafter: '2050') and 2060-2090 (hereafter: '2075') for one county in each stork region (National Environmental Modeling & Analysis Center et al. 2021). I used the month to summarize the total rainfall and average the maximum daily temperature per stage of the storks' annual life cycle, matching the way I handled environmental data in the baseline scenario (see *Methods: Defining nesting regions*). These hydrological predictions included two climate change scenarios: Representative Concentration Pathway (RCP) RCP4.5, which is a conservative prediction based on a small increase in the global temperature, and RCP8.5, which represents a more extreme increase in global

temperature. The Climate Explorer dataset does not report error, so the SD of each hydrologic parameter was assumed to be constant from the baseline scenario.

To predict changes in the amount of urban land cover available to storks within their core foraging areas, I used the conservative end of the predicted range of increase in urbanization per region through 2070 that were reported in published literature (Carr and Zwick 2016; Zhou et al. 2019). Lacking detailed local projections, I assumed urbanization would happen at a linear pace, so added 50% of the gain in urban land cover to the 2050 scenarios, and the remaining gain (full 100%) to the 2075 scenarios.

In the simulation model, I incorporated the above hydrological and land cover changes into four future scenarios representing the two climate change extremes (RCP4.5, RCP8.5) and timeframes (2050, 2075). As with the baseline scenario, I ran each scenario for 10,000 iterations, and summarized the output by calculating the mean \pm SD of each regional population size and the total U.S. population size. These population size metrics allowed us to compare each timeframe and climate change scenario to the baseline scenario to evaluate future population changes.

4.4 RESULTS

4.4.1 Defining nesting regions

A total of 191 independent colonies covering the entire range of U.S.-nesting storks were monitored between 2002-2019. The PCA used to examine the environmental variation underlying these colony locations revealed a first principal component (PC) that accounted for 40.3% of the variance that was composed of seasonal average daily maximum temperature variables. PC2 accounted for an additional 28.7% of the variance

and was comprised of seasonal rainfall totals. Last, PC3, which accounted for 13.6% of the variance (cumulative variance PC1-PC3: 82.6%), captured variation in both urban and coastal land cover availability (Fig. 4.2-4.3).

The CA, which reused the PCA data matrix, indicated that stork colonies could be divided into 4-6 regions based on underlying environmental variation (Fig. 4.4). For simplicity in future modeling steps, and to best serve wildlife managers, I chose to assign each stork colony to one of 4 clusters, hereafter referred to as “regions”. Though explicitly geographic variables, i.e., latitude and longitude, were excluded from the analyses (Table 4.2), spatial gradients in rainfall and temperature shaped the CA results, allowing us to group colonies into South, Central, Northeast, and Northwest regions (Fig. 4.5, Table 4.3). The South region, which includes colonies in Everglades National Park in extreme southern Florida, is defined by a mix of inland and coastal land cover types and gets more rain than any other region during the late breeding season. The Central region includes all colonies in central Florida, and though it also has a wet late breeding season, it has the most urban land cover availability of any region. The Northeast region extends from coastal northern Florida through coastal South Carolina and has a wet early breeding season. Finally, the Northwest region includes colonies in inland Georgia and South Carolina, plus all colonies in North Carolina, and is also characterized by a wet early breeding season (Table 4.3).

4.4.2 Stork nesting data

The average number of stork nests in the U.S. generated from my colony-level dataset was $8,043 \pm 2,934$ per year, and the average standardized productivity was

1.46±0.38 fledglings/nest per year. The Northwest region had the most nests on average (2,629±781 nests), while the South region had the most variable average (1,520±1,269 nests; Table 4.3). In terms of annual standardized productivity, the Northwest was the most productive (1.7±0.5 fledglings/nest), while the Central was the least (1.1±0.4 fledglings/nest; Table 4.3).

4.4.3 Stork response—environmental associations

Evaluation of 8 independent global models (2 response variables x 4 regions) using AIC_c model selection indicated that the strength of the association between stork activity and environmental drivers was highly variable. In the South region, 5 of the 80 possible sub-models for productivity were considered top models, and three predictor variables (Rainfall-previous 2 yrs (+), Rainfall-previous yr (+), and TMAX-late (-)) had confidence intervals that did not overlap 0. Rainfall-previous 2 yrs was also a significant predictor variable (+) of nest abundance in the South, where 6 of the possible 16 models were top models (Fig. 4.6a). In the Central region, 20 of the 80 sub-models were top models, and interactions between rainfall x coastal habitat (-) and rainfall x urban habitat (+) were considered significant drivers of productivity. Nest abundance in this region, however, was associated with TMAX-early (+) and Rainfall-nonbreeding (-), as these were predictor variables that did not overlap 0 in the 7 top models (Fig. 4.6b). In the Northeast region, 21 of 80 possible models were top models, and no predictor variables showed a significant association with productivity. The same was true of nest abundance in the Northeast, which had no significant predictor variables in 9 of 16 possible top models (Fig. 4.6c). Lastly, in the Northwest region, 8 of 80 possible models were top

models, and Rainfall-previous 2 yrs was the only predictor variable (+) with a confidence interval which did not overlap 0. Likewise, nest abundance in the Northwest was associated with Rainfall-previous 2 yrs (+) when the 6 top models of the possible 16 were averaged (Fig. 4.6d). AIC_c and model averaging results from all 8 model evaluations are summarized in Table 4.4 and detailed in Appendix 1.

4.4.4 Simulation model: baseline scenario

The linear trend of the stork population size in the U.S. produced by empirical observations to the USFWS 2002-2019 can be represented by the equation $y=215.9x+7418.1$ (Fig. 4.7). Therefore, when $t_0=7855$ nests (which was the observed U.S. population size in 2002 reported to the USFWS), the predicted population size at the end of the reported era (2019) is $t_{17}=11,088$ nests. For ease of comparison over an extended timescale, the population size predicted using the USFWS trend was also projected to the years 2050 and 2075, at $t_{48}=17,781$ nests and $t_{73}=23,179$ nests, respectively (Fig. 4.7). I validated my simulation model by comparing the population trend produced by my baseline scenario with that of the USFWS. The linear population trend produced by my baseline scenario in the simulation model was $y=420.1x+8042.3$, which equates to 15,337 nests at t_{17} (2019), 28,639 nests at t_{48} (2019), and 39,367 nests at t_{73} (2075; Fig. 4.7). The prediction produced by the USFWS trend line at the end of the empirical observation time period, 11,088 nests, is within the margin of error of the mean produced by the baseline scenario of my simulation model ($15,337 \pm 3,918$ nests) for the same timestep (t_{17}).

4.4.5 Simulation model: future scenarios

Climate models suggested that the total amount and seasonal distribution of rainfall and TMAX will change in each region. The South is the only region where rainfall is expected to decrease in every season, from an average of 1,670 mm/yr in the baseline scenario to 1,272 mm/yr in RCP8.5, the most extreme climate scenario. TMAX is expected to increase in every future period, from a breeding season average of 29.7°C in the baseline scenario to 32.3°C in the most extreme climate scenario (Fig. 4.8a). In the Central region, rainfall is expected to increase in the early breeding season and decrease in the late breeding season, with an annual total remaining approximately constant (baseline: 1,339 mm/yr; RCP8.5: 1,280 mm/yr). TMAX, however, is expected to increase steadily, from a breeding season average of 29.6°C in the baseline scenario to 33.3°C in RCP8.5 (Fig. 4.8b). In the Northeast, rainfall is expected to decrease in the early breeding season but increase overall, from an average of 1,161 mm/yr in the baseline scenario to 1,329 mm/yr in RCP8.5. TMAX is expected to decrease in the early breeding season (baseline: 27.1°C; RCP8.5: 21.2°C) but stay approximately the same in the late breeding season (baseline: 32.7°C; RCP8.5: 33.6°C; Fig. 4.8c). Finally, in the Northwest region, rainfall is expected to increase in the early and late breeding seasons and decrease in the nonbreeding season for a slight annual increase overall, from 1,228 mm/yr in the baseline scenario to 1,302 mm/yr in the most extreme climate scenario. TMAX is expected to decrease in the early breeding season (baseline: 24.7°C; RCP8.5: 23.9°C) and increase in the late breeding season (baseline: 33.0°C; RCP8.5: 36.0°C; Fig 4.8d).

Sources indicated that there will be increasing urbanization pressure range-wide, so the average urban land area within a 20-km buffer of each colony was increased in all

regions through time, from 423.3km² in the baseline scenario to 694.2 km² (+16%) in the Central region, from 173.3 km² to 289.5 km² (+12%) in the Northeast region, and from 189.1 km² to 308.5 km² (+12%) in the Northwest region. Note that land cover variables were not included in the South region module (Appendix 2), as inclusion of these parameters was not supported by the AIC_c analysis (Table 4.4, Appendix 1).

When accounting for these anticipated changes to climate and land cover, I found no significant change in the future U.S. breeding population size compared to the baseline scenario (Fig. 4.9a). However, there was a significant shift in the distribution of nests. Most notably, the South population is expected to collapse under both climate scenarios by 2050, while the number of storks nesting in the Central region is expected to increase in these same scenarios (Fig 4.9b-c). The northern regions show no change in abundance (Fig. 4.9d-e), as is expected since the stork response in those regions is not strongly driven by rainfall or TMAX (see *Results: Stork response—environment associations*).

4.5 DISCUSSION

This study produced the first range-wide population model for storks in the U.S. since 2006, which was before the species was down-listed from Endangered to Threatened status under the U.S. Endangered Species Act (ESA). From 2002-2019, the number of storks in the U.S. increased at a rate of 216 nests per year, and the breeding population expanded into North Carolina—further north than storks were ever previously recorded in North America—and into medium- and high-density urban habitats. As the species approaches benchmark recovery levels set by the USFWS, the need for a range-

wide perspective is of supreme importance, particularly in terms of productivity, which is a health metric that has been notoriously difficult to standardize at broad spatial scales. Nest abundance and productivity will be the keys to monitoring the species' response to climate change and urbanization, two drivers of landscape-scale habitat change which are inevitable in the coming decades.

Four main findings resulted from this study. First, I concluded that stork nesting regions used by the USWFS, which were based on political boundaries for the ease of management discussions, are supported by environmental data. My PCA and CA binned colonies into 4 nesting regions, here named South (very wet late breeding season), Central (most urban, wet late season), Northeast (coastal, wet early breeding season), Northwest (inland, wet early season), which generally correlate with the arrangement used in the USFWS in the latest Species Status Assessment (U.S. Fish and Wildlife Service 2021b).

The second key message is that I showed, empirically, how variable nest abundance and productivity are across the stork's range. This principal has been generally understood (Brooks and Dean 2008), but few studies have reviewed data across the whole US. In terms of abundance, the USFWS reports annual statewide nest number totals, but this is a regional classification that previously had no biological basis and conflated habitat factors than are known to affect nest abundance, including coastal versus inland habitat types (Kushlan and Frohring 1986; Bryan and Gariboldi 1998; Romanek et al. 2000; Bryan and Robinette 2008) and urban versus non-urban habitat types (Evans and Gawlik 2020). Colony-level nesting data are also not regularly collated for comparative purposes. My study did that, gathering and standardizing colony-level

data to calculate annual nesting totals according to the environmentally-based regions that resulted from a PCA and CA.

Likewise, in terms of productivity, standardized range-wide data have been unavailable. Brooks and Dean (2008) reported on productivity at the colony level, but only for colonies in the Central, Northeast, and Northwest regions, and only for 4 years (2003-2006). Borkhataria et al. (2008) reported on productivity at the colony level in South Florida, but also only for 4 years (2002-2005). The data in Borkhataria et al. (2008) are not directly comparable to Brooks and Dean (2008) because field protocols differ (nest checks, 7 weeks used to define fledging versus satellite telemetry, 6-8 weeks used to define fledging success). By comparison, I calculated standardized productivity at the regional level from colony-level data over a 17-yr period (2002-2019).

Having access to range-wide, long-term data on abundance and productivity is necessary to evaluate whether storks have met the recovery criteria stated in the SSA (Brooks and Dean 2008). Additionally, these fundamental demographic data points allow researchers to consider source/sink dynamics. At the time of down-listing (2014), documentation showed that storks had become more abundant in northern and urban locations. However, how productive these colonies were compared to colonies in the historical epicenter of the range was not considered (U.S. Fish and Wildlife Service 2014). Assuming that range expansion is synonymous with an increase in population stability is incautious.

The third research finding of my study resulted from GLM modeling of the association between stork response and environmental variables, which revealed ways in which population drivers vary by region. In South and Central regions, the combination

of rainfall, daily maximum temperature, and land cover type showed a strong association with stork response. By contrast, there was no relationship between these drivers and stork response in the northern regions. Water management, which could override weather as a determinant of local hydrological conditions, is conducted range-wide, but these management practices are implemented on different scales, for different purposes, by different entities. In the South region, nearly all colonies are located on public land where water is managed for the purpose of conservation under the Comprehensive Everglades Restoration Plan (CERP; (Frederick et al. 2009; Cook and Baranski 2021; Bancroft et al. 1992). In the Central region, which is the most urbanized region, flood control infrastructure is likely to have an important influence on local hydrological conditions (Parkos and Trexler 2014). In influence of CERP also extends to the southernmost colonies of this region and into the Kissimmee River Valley (Frederick et al. 2009). This differs markedly from the Northeast, a predominantly coastal region where foraging habitat includes tidal estuaries that vary on a daily timescale with the tide rather than longer-term timescales of rainfall events followed by dry-downs (Bryan and Borkhataria 2013; Gaines et al. 1998; Paulukonis et al. 2021; Tomlinson 2009). Agriculture (rice) is also common here, and water levels will be to the schedule of crop needs except in cases where the schedule is modified for the purpose of wildlife conservation (Folk et al. 2016). The Northwest region is altogether different as it is both inland and rural. There are no large-scale wetland restoration or urban flood control practices that influence the local hydrological condition (Darst and Light 1996; Paulukonis et al. 2021), so annual rainfall and evapotranspiration control the concentration of prey in the landscape (Depkin et al. 1992; Tomlinson 2009).

My results from the South and Central regions imply that rainfall is either such a significant force in determining prey availability that these parameters override the effect of water management actions, or that water management is correlated closely enough to rainfall patterns that rainfall itself is an adequate proxy for water management actions. The former explanation is likeliest in the South region given limited water delivery actions to-date under CERP (Clem and Duever 2019; Boggess et al. 2012). Either explanation may be true for the Central region, which is partly influenced by CERP actions and partly by flood control actions in what is the most urbanized stork region.

In the Northeast and Northwest regions where environmental associations with stork response are not well represented by my model, the suggestion is either that rainfall is not an adequate proxy for annual hydrological conditions and/or prey availability, or that some factor other than prey availability is what drives the stork response in the region. In the Northeast region, which is primarily coastal and tidally influenced, prey availability likely varies on a shorter timescale, i.e., on the order of hours and days (Bryan and Borkhataria 2013; Gaines et al. 1998), rather than in the context of a seasonal dry-down as seen in South Florida. In the Northwest, a factor other than rainfall must be determining prey availability. One possibility is that local water management practices that are not aimed at restoring natural wetland hydrological characteristics are affecting the timing of availability and quality of foraging habitats as they operate out of sync with annual rainfall patterns.

Alternatively or in combination with these mismatches, a non-hydrological factor may be what drives stork dynamics in the northern regions. For example, my GLMs do not account for mass predation events, which could be a primary driver of productivity. It

could also be that hydrological conditions in the South and Central regions are what drive stork abundance in the north regardless of local hydrological conditions so that, in years where early breeding season conditions are optimal in Florida the storks stay, but in years of suboptimal conditions the stork by default move northward. This pattern was observed within Florida by (Larson 2021) and cannot be ruled out at the full spatial range since northern breeders tend to start nesting up to several months later in the year than those in the South and Central regions.

The fourth conclusion of my study is that the South nesting region is the most sensitive to potential changes in rainfall. My population simulations, which were based on two climate models (RCP4.5, RCP 8.5) that projected a decrease in seasonal and annual rainfall totals at two future time steps (2050, 2075), resulted in near-zero annual nest abundance averages. It is worth noting the high level of uncertainty inherent to future climate projections. The dataset I used (National Environmental Modeling & Analysis Center et al. 2021) derived local climate projections (in this case, U.S. counties) from global climate models that are revised regularly for the Intergovernmental Panel on Climate Change (IPCC). These global climate models simulate global climate change based on scenarios of future greenhouse gas emission, concentration, and land-use trajectories (hence the name, RCP; van Vuuren et al., 2011). The regional trends published by (National Environmental Modeling & Analysis Center et al. 2021) are in general alignment with non-IPCC modeling efforts (Ingram et al. 2013; Runkle et al. 2022; Carter et al. 2014), leading us to conclude they are accurate (according to the best available science) if not precise. In South Florida, for example, Abiy et al. (2019) examined trends in monthly rainfall and drought 1906-2016 and found an abrupt

increase in the wet season and annual total rainfall, despite a concurrent lengthening of the dry season after the 1990s. That this trend would reverse between 2016 (the end of Abiy et al.'s analysis) and 2050 (the first future timestep I used from the National Environmental Modeling & Analysis Center et al. dataset) when anthropogenic climate change is already underway is suspect. Nevertheless, the appropriate conclusion from my simulation model is that the South stork nesting region is prone to significant population fluctuations should rainfall patterns change more than anticipated currently.

The loss of the South nesting population, whether due to changing rainfall patterns analyzed here or SLR for which South Florida is particularly vulnerable (Carter et al. 2014), would mark a major change in the distribution of the stork, whose historical stronghold was in coastal southwest Florida. Reconsideration of basic life history characteristics, opportunities, and threats posed to this species in the central and especially northern parts of its current range is of paramount importance. Loss of the South region represents a decline in population redundancy and likely also resiliency, two of the three Rs of endangered species conservation (Smith et al. 2018). For example, a long-term, socioecological examination of the population-level effects of private land ownership on storks is warranted due to the rarity of public lands outside of the Everglades region. Predator dynamics are also likely to be different in the temperate north compared to the subtropical South region, so basic observations of predators and their colony-level effects should be monitored anew.

I made two predictions at the outset of this study. First, I predicted that the magnitude of a region's predicted change in climate would be reflected in the magnitude of change in the region's stork abundance. I found that this prediction held true for the

southern regions, but not the northern ones. Southern regions, especially the South region, are strongly associated with rainfall, so climate change is likely to result in changes in stork abundance and productivity. Indeed, in scenarios that decrease the total rainfall in South Florida, the South region population suffered greatly. Conversely, my models showed that northern regions are not controlled by rainfall and TMAX, so climate change, as I have modeled it, will not drive changes in stork abundance or productivity. One important caution, however, is that a decrease in stork abundance could result directly from SLR (not studied here) if wetland migration does not keep pace with the rate of change (Clausen and Clausen 2014; Gabler et al. 2017; Mitchell et al. 2017). This is especially pertinent in the Northeast (Paulukonis et al. 2021) and South (Carter et al. 2014) regions as they contain significant coastline with low-elevation wetlands that are free of urban infrastructure.

My second prediction was that urbanization would be associated with an increase in stork numbers in regions where the natural hydrological regime is a significant driver of stork abundance and productivity. My rationale was that natural hydrological regimes within my study area typically supply prey resources in pulses (Botson et al. 2016; Kahl 1964), and that storks depending on these pulses might benefit from have the option to switch to a steadier alternative foraging habitats such as anthropogenic water bodies. The benefits of prey switching in general, and related to urban foraging in particular, have been observed in many avian species (Dorn et al.; Chenchouni 2017a; Chard et al. 2018; Burgues et al. 2020) including the stork (Evans et al., 2021; Evans & Gawlik, 2020; Shlepr Ch 3). This prediction was supported by my results from the South and Central regions where the natural hydrological regime was a significant driver of the stork

response. The Central breeding population, which is predicted to experience more urban development than the South region by 2075, is predicted to gain nesting pairs while the South population declines. Though hydrological condition is the ultimate driver of these trends, the positive impact of urban land type availability on stork productivity reinforces these trends rather than negates them.

4.5.1 Waterbirds in a changing world

Climate change has been identified as a driver of waterbird range shifts globally (Amano et al. 2020; Jenouvrier 2013). The stork provides a good template to study the mechanisms and demographic consequences of a range shift because it has been heavily observed and documented in the U.S. since its ESA listing in 1984. The first lesson learned from storks is to consider not just the new boundaries of a species or its regional abundance, but the productivity of the birds in regions across their range. In some cases, expansion into novel habitat types could represent an ecological trap, making the range shift maladaptive.

Next, the past trajectory of the stork reminds us of the great plasticity and/or adaptive potential of some species, especially waterbirds. Though storks initially responded to wetland drainage and urbanization by declining sharply in number, their population trajectory has since changed course. In addition to a shift in their breeding range, storks have begun utilizing urban water bodies as alternative foraging habitats in years when natural wetland conditions are suboptimal (Evans and Gawlik 2020; Evans et al. 2021), and even prosper from nesting in high-density urban areas where they can more readily access these foraging areas (Evans and Gawlik 2020). So, whereas many of

population models demand static relationships between the species and its environmental drivers (including mine), the potential for adaptation should be considered. New tools to quantify levels of phenotypic plasticity and microevolutionary change, which determine adaptive capacity, are available (Ofori et al. 2017; Berry et al. 2013; Charmantier et al. 2008).

Finally, storks illustrate that range expansion could lead to a significant rewrite in the basic characteristics of a species. Storks are understood to be a primarily coastal species whose populations are controlled by hydrological conditions as related to food availability (Kahl 1964; Kushlan et al. 1975; Ramo and Busto 1992). Prior to the 1960s, most U.S. breeding storks were located in South Florida, predominately in the southwestern Everglades where the estuaries met freshwater flows (Kushlan and Frohring 1986; Ogden and Nesbitt 1979). This region of the Everglades was characterized by long hydroperiod wetlands that received heavy rains during the wet season, providing ample habitat for prey production, followed by a steady dry-down as water levels receded over the course of the dry season, which was a mechanism of prey concentration (Kahl 1964; Kushlan et al. 1975). However, these seasonal dynamics are lost in the temperate parts of the stork's modern-day range, and the mechanisms of prey concentration therefore differ outside the southernmost region. Whether northern storks are even limited by food availability has been called into question, as non-hydrological factors like predation or human land-use practices may have a stronger influence instead.

4.6 ACKNOWLEDGEMENTS

Support for this research was provided by the James A. Kushlan Research Award of the Waterbird Society and the Crutchfield Fellowship of the Harte Research Institute for Gulf of Mexico Studies. I express sincere thanks to members of the Wood Stork Working Group past and present for providing data, expert knowledge, and feedback; this study would not have been possible without the help of Billy Brooks, Larry Bryan, Kristina Ramstad, Christy Hand, Lindsey Garner, Lori Oberhofer, Mark Cook, Peter Frederick, Ricardo Zambrano, Shawn Clem, Tim Keyes, Gen Anderson, Carmen Johnson, Ann Paul, Donna Beard, Mark Sees, Mark Rachal, Chuck Hayes, and Monica Folk.

Table 4.1. Months used to represent stork seasons by colony location. The months used were based on *Birds of the World* (Coulter et al., 2020) and local observations by researchers who contributed colony monitoring data. Generally, early breeding season activity includes nest initiation, egg laying, incubation, and hatching; late breeding season activity includes chick rearing and fledging; and the nonbreeding season denotes when adults are not involved in breeding behaviors and young-of-the-year are independent.

Colony location	Stork season	Months used
Latitude < 27.8° (~South Florida)	Early breeding	Jan 1-Apr 30
	Late breeding	May 1-Jul 31
	Nonbreeding	Aug 1-Dec 31
Latitude 27.8-29.6° (~Central Florida)	Early breeding	Feb 1-May 31
	Late breeding	Jun 1-Aug 31
	Nonbreeding	Sep 1-Jan 31
Latitude > 29.6° (~North Florida, Georgia, South Carolina, North Carolina)	Early breeding	Mar 1-Jun 30
	Late breeding	Jul 1-Aug 31
	Nonbreeding	Sep 1-Feb 28/29

Table 4.2. Colony-level variables considered in the principal components analysis (PCA) matrix describing stork colonies (n=191) in the southeastern United States (US). Averages are based on daily observations from local weather stations (rainfall, daily maximum temperature (TMAX)) and 2010 U.S. Census data (land cover type).

Variable	Included in final PCA?
Colony latitude (°)	No- did not want geography to influence the regional classification
Colony longitude (°)	No- did not want geography to influence the regional classification
Average rainfall-early breeding season (mm)	Yes
Average rainfall-late breeding season (mm)	Yes
Average rainfall-full breeding season (mm)	No- high covariance with ‘average rainfall-previous year’
Average rainfall-previous year (mm)	Yes
Average rainfall-previous 2 years (mm)	No- high covariance with ‘average rainfall-previous year’
Average TMAX-early breeding season (°C)	Yes
Average TMAX-late breeding season (°C)	Yes
Average TMAX-full breeding season (°C)	Yes
Urban land cover-10km radius (km ²)	Yes
Urban land cover-20km radius (km ²)	No- high covariance with ‘urban land cover-10km radius’
Urban land cover-30km radius (km ²)	No- high covariance with ‘urban land cover-10km radius’
Coastal land cover-10km radius (km ²)	Yes

Table 4.3. Summary of average annual environment and stork activity (mean±SD), 2002-2019, within nesting regions (South, Central, Northeast, Northwest) in the US. Regions were identified by a cluster analysis.

	South	Central	Northeast	Northwest
<i>Environmental metric</i>				
Rainfall-early breeding season (mm)	246.6±13.1	259.0±47.3	398.9±50.5	396.0±56.5
Rainfall-late breeding season (mm)	658.8±32.9	613.4±66.2	291.8±34.0	307.6±46.9
Rainfall-previous year (mm)	1670.9±32.6	1339.4±68.8	1155.5±120.1	1229.5±151.6
TMAX-early breeding season (°C)	27.2±0.4	26.8±0.5	27.0±1.2	27.4±1.7
TMAX-late breeding season (°C)	32.3±0.5	32.4±0.5	32.7±0.8	33.0±1.1
TMAX-full breeding season (°C)	29.4±0.4	29.2±0.4	29.0±1.0	29.3±1.4
Urban land cover-10km radius (km ²)	29.0±62.5	122.8±77.3	51.4±49.9	20.5±25.7
Coastal land cover-10km radius (km ²)	127.8±127.9	159.4±143.4	305.6±26.2	21.8±48.2
<i>Stork activity metric</i>				
Stork abundance (number of nests)	1,520±1,269	2,036±1,242	1,857±504	2,629±781
Stork productivity (fledglings/nest)	1.5±0.5	1.1±0.4	1.6±0.4	1.7±0.5

Table 4.4. Summary of AIC_c results for models that describe the relationship between environmental drivers and stork nesting response (nest abundance, standardized productivity as separate models) in each region (Appendix 1). For each model, the top models ($\Delta AIC_c < 4$) were averaged, and a back-transformed version of each model-averaged equation was input into the simulation model (Appendix 2). Bolded rows are predictor variables with 95% confidence intervals that do not overlap 0.

Region	Response variable	Predictor variable	Proportion top models that included predictor	Est.	Adjusted SE	95% Confidence Interval	
South	Nest abundance	(Intercept)	-	1520.0	249.3	1031.4, 2008.6	
		TMAX.early	1/6	-945.4	594.9	-2111.4, 220.5	
		Rain.2yr	4/6	1143.7	551.0	63.8, 2223.6	
		Rain.early	3/6	-1613.3	561.8	-2714.5, -512.2	
		Rain.nonbreed	1/6	-315.6	565.5	-1423.9, 792.8	
		Productivity	(Intercept)	-	1.5	0.1	1.3, 1.9
	Rain.2yr	4/5	1.0	0.3	0.3, 1.7		
	Rain.yr	1/5	-0.7	0.3	-1.3, -0.2		
	Rain.breed	2/5	-0.9	0.5	-1.8, 0.1		
	Rain.late	1/5	0.9	0.5	-0.1, 2.0		
	TMAX.late	1/5	-0.7	0.3	-1.2, -0.1		
	Central	Nest abundance	(Intercept)	-	2036.2	266.0	1514.9, 2557.5
			TMAX.early	5/7	1457.2	637.4	208.0, 2706.4
Rain.2yr			2/7	883.5	591.7	-276.3, 2043.3	
Rain.early			2/7	831.9	621.6	-386.4, 2050.1	
Rain.nonbreed			5/7	-1571.0	646.0	-2937.0, -305.1	
Productivity		(Intercept)	-	1.1	0.1	0.9, 1.3	
Rain.2yr		12/20	0.5	0.3	-0.1, 1.1		
Rain.yr		4/20	-0.4	0.3	-1.0, 0.3		

		Rain.breed	9/20	-0.4	0.3	-1.0, 0.2
		Rain.late	4/20	-0.2	0.3	-0.8, 0.4
		TMAX.late	9/20	0.4	0.2	-0.0, 0.8
		Rain.breed x Shore.10km	3/20	-0.9	0.4	-1.6, -0.1
		Rain.breed x Urban.20km	5/20	0.7	0.4	0.0, 1.4
Northeast	Nest abundance	(Intercept)	-	1857.4	127.6	1607.3, 2107.5
		TMAX.early	3/9	202.6	267.2	-321.1, 726.3
		Rain.2yr	4/9	307.4	277.7	-236.9, 851.7
		Rain.early	2/9	-113.1	292.8	-687.0, 460.9
		Rain.nonbreed	3/9	311.6	267.9	-213.5, 836.6
	Productivity	(Intercept)	-	1.6	0.1	1.4, 1.8
		Rain.2yr	6/21	0.3	0.2	-0.2, 0.7
		Rain.yr	6/21	0.3	0.3	-0.4, 0.9
		Rain.breed	13/21	-0.3	0.3	-0.9, 0.2
		Rain.late	2/21	0.0	0.3	-0.5, 0.5
		TMAX.late	5/21	0.3	0.2	-0.2, 0.8
		Rain.breed x Shore.10km	6/21	-1.6	1.0	-3.5, 0.4
		Rain.breed x Urban.20km	3/21	0.4	0.2	-0.1, 0.8
Northwest	Nest abundance	(Intercept)	-	2629.1	183.3	2269.9, 2988.3
		TMAX.early	1/6	309.1	389.4	-454.1, 1072.3
		Rain.2yr	4/6	807.4	391.4	40.2, 1574.7
		Rain.early	1/6	-242.6	408.6	-1043.3, 558.2
		Rain.nonbreed	2/6	319.5	482.4	-626.0, 1265.0
	Productivity	(Intercept)	-	1.7	0.1	1.5, 1.9
		Rain.2yr	8/8	0.7	0.3	0.1, 1.2

Rain.yr	1/8	-0.4	0.3	-1.0, 0.2
Rain.breed	4/8	-0.2	0.2	-0.7, 0.2
Rain.late	1/8	-0.2	0.2	-0.7, 0.2
TMAX.late	1/8	0.1	0.2	-0.4, 0.5
Rain.breed x Shore.10km	2/8	0.4	0.3	-0.2, 1.0
Rain.breed x Urban.20km	1/8	-0.3	0.2	-0.7, 0.1

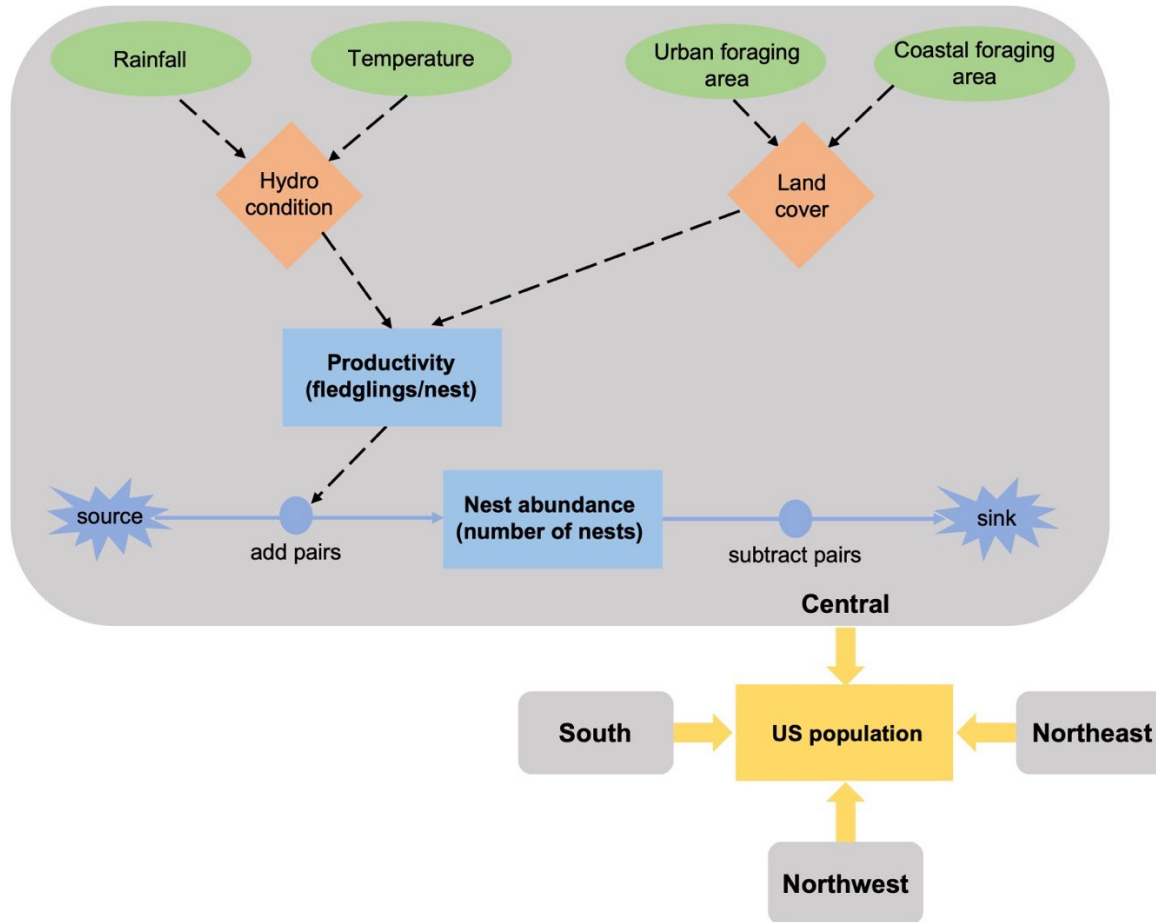


Figure 4.1. Materials flow diagram of stork activity and environmental drivers in the US. This diagram served as the structure for mathematical inputs into STELLA, a complex systems simulation software.

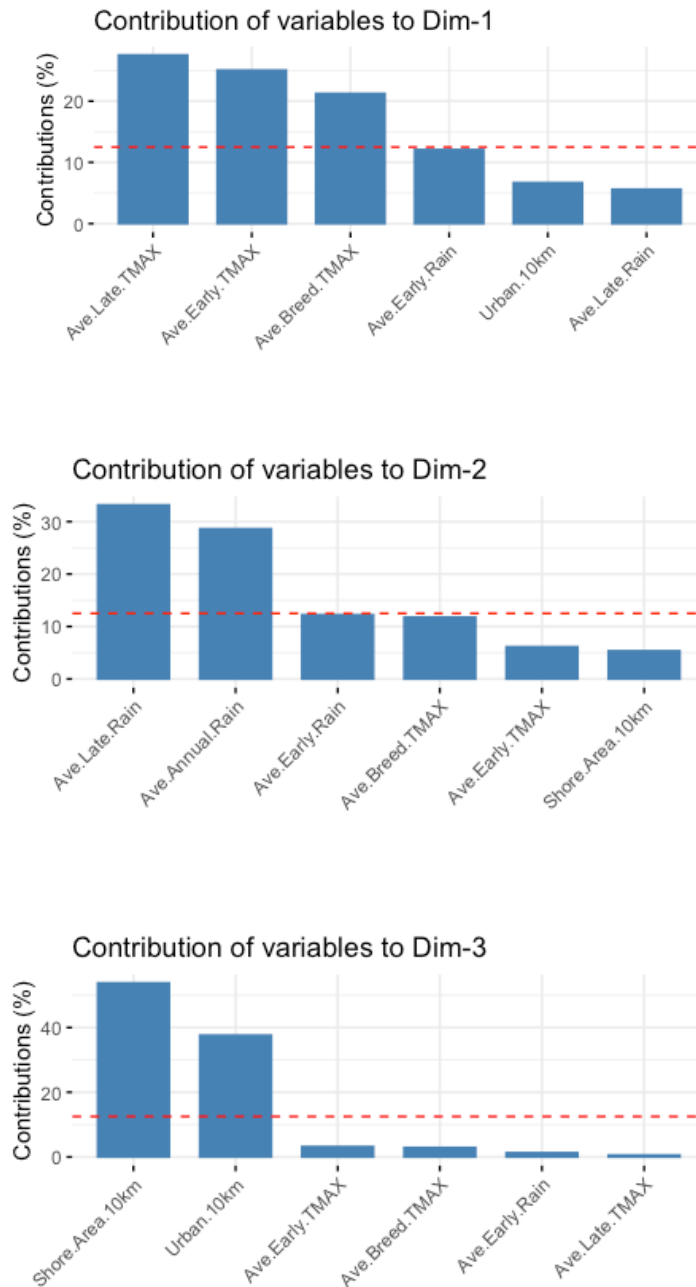


Figure 4.3. Contributions of each variable to principal component (PC)1 (proportion of variance: 40.3%), PC2 (28.7%), and PC3 (13.6%; cumulative proportion of variance, PC1-PC3: 82.6%) of a PCA of the environmental variables underlying stork colony locations (n=191) in the southeastern US. The dashed reference line is the expected value if contributions by all variables were uniform.

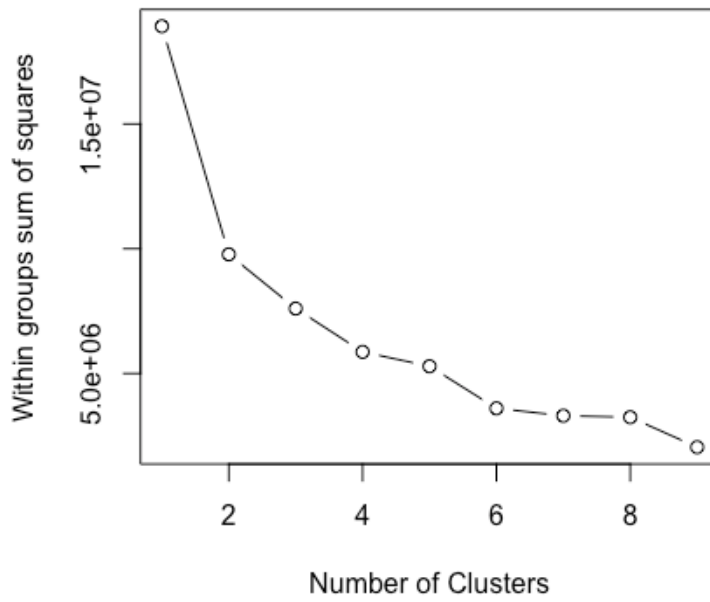


Figure 4.4. Within-group sum of squares for each possible number of clusters, 1-9. Ideally, a distinct “elbow” in the plot would be used to determine the number of clusters that should be chosen.

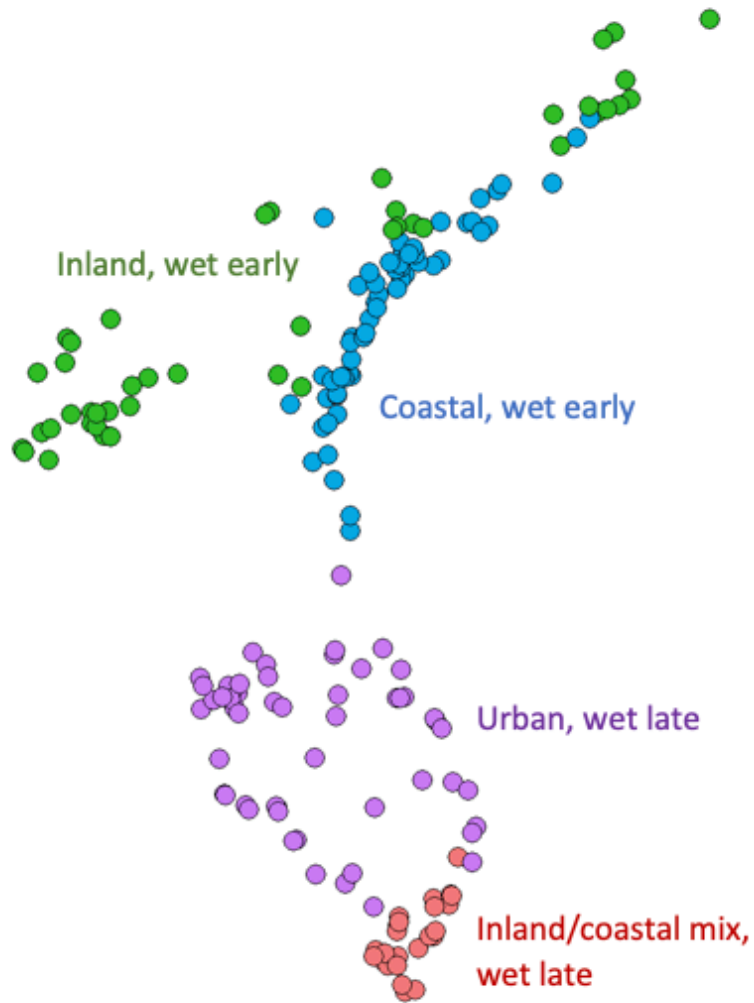
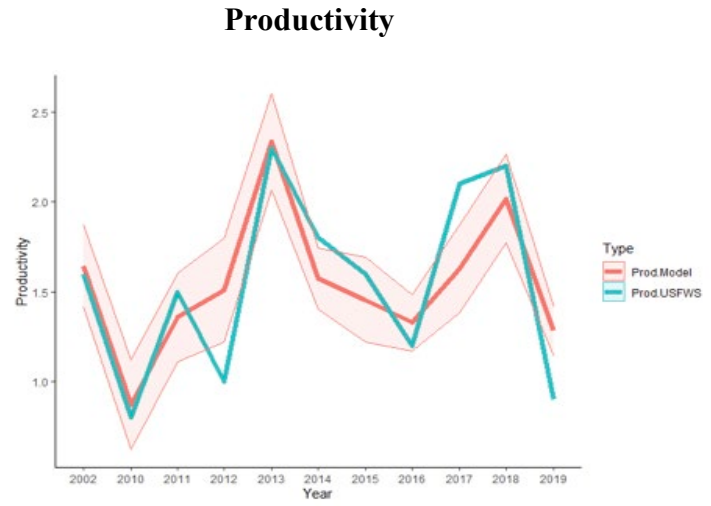
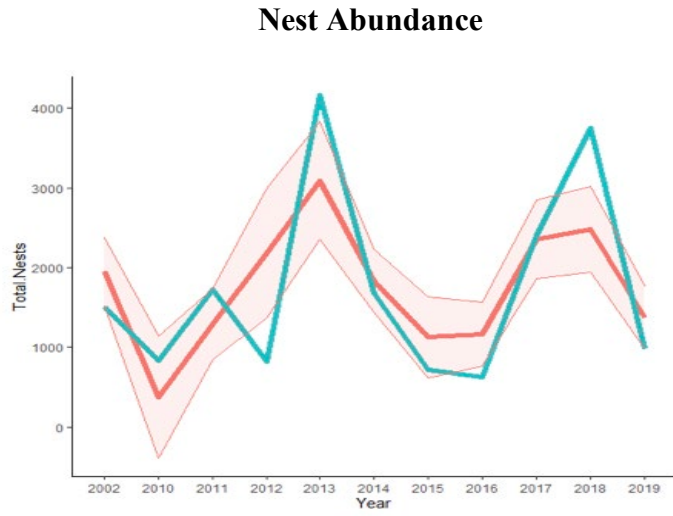
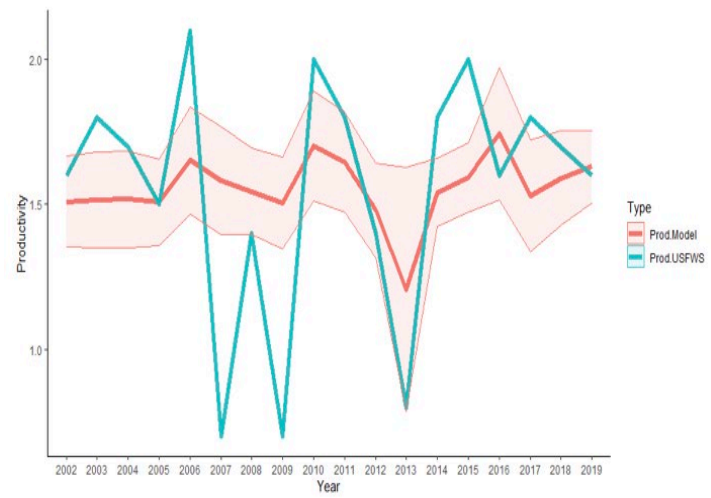
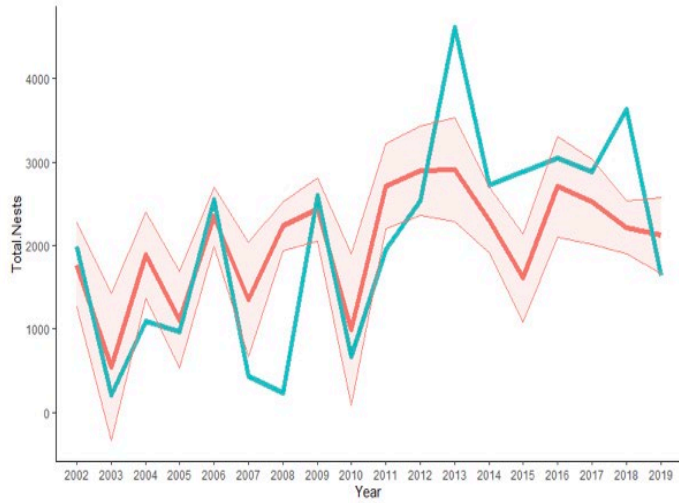


Figure 4.5. Map of stork colony locations (n=191) in the southeastern US colored by their assigned region.

a)



118
b)



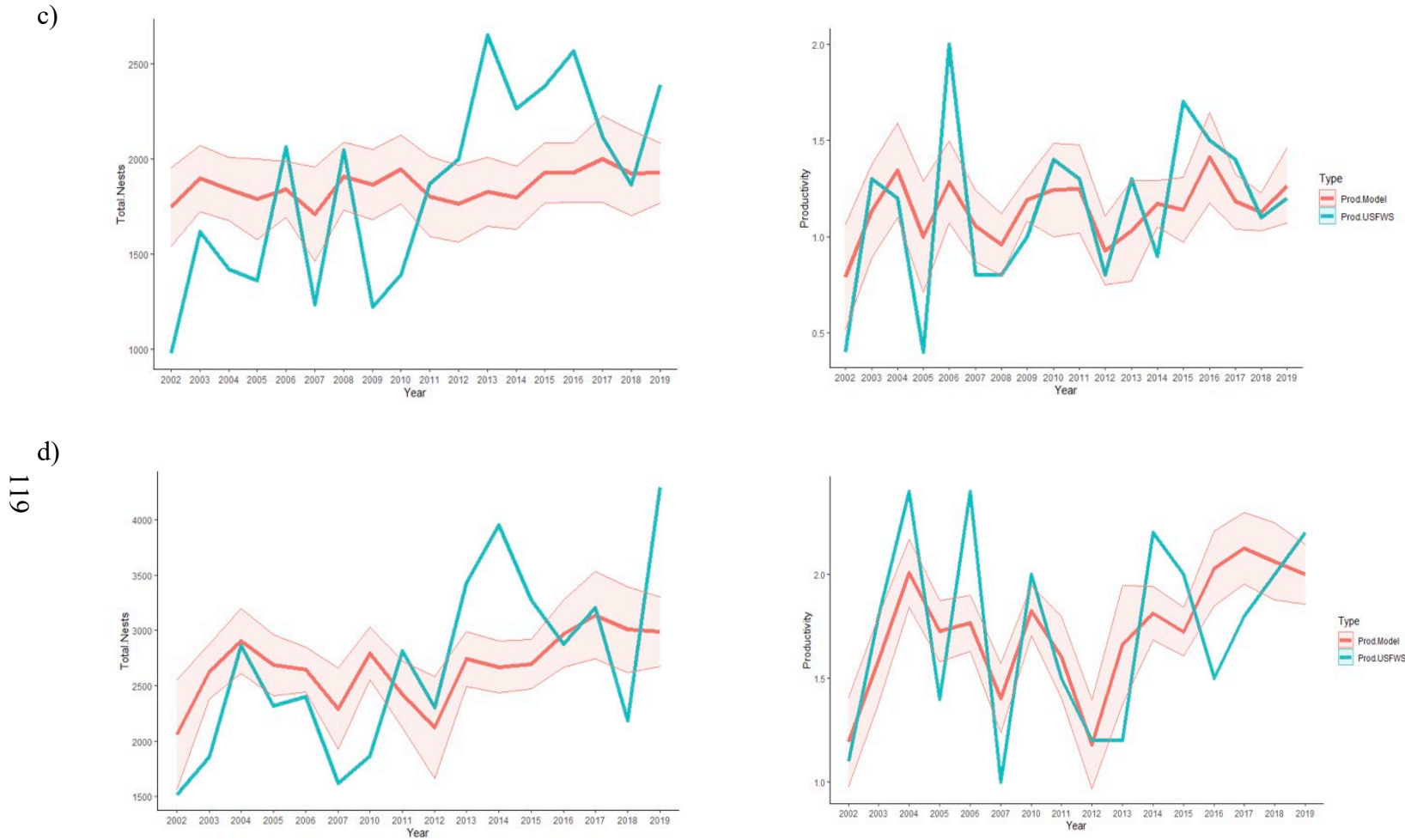


Figure 4.6. Assessment of GLM equations representing Wood Stork responses (nest abundance, productivity) to environmental conditions in each region, a) South, b) Central, c) Northeast, and d) Northwest. The equations were incorporated into a simulation model of population dynamics under changing environmental conditions.

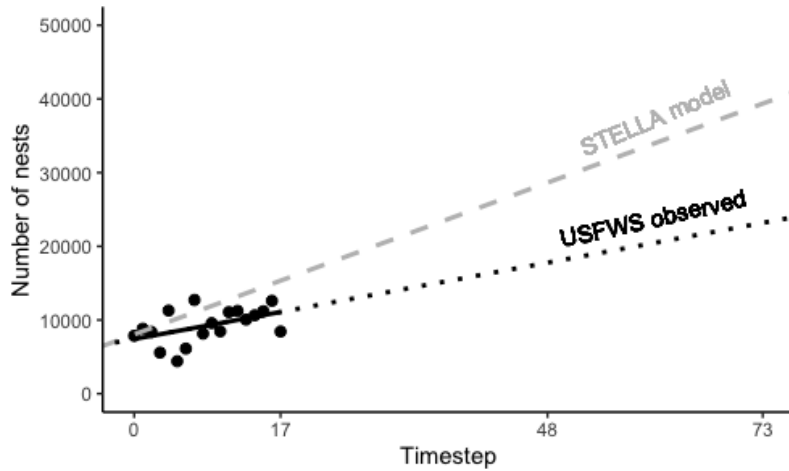
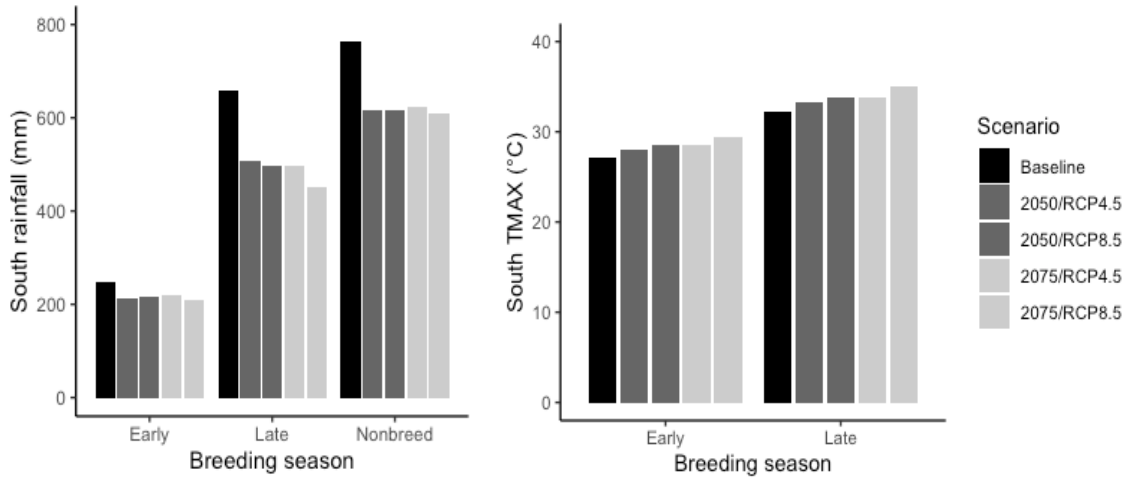
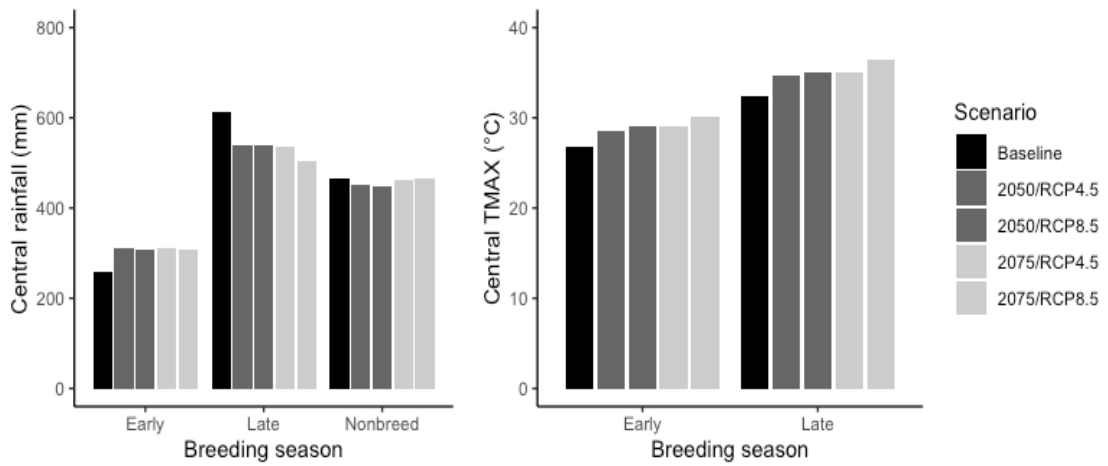


Figure 4.7. Stork population size (number of nests) in the U.S. based on the linear trend derived from empirical observations (U.S. Fish and Wildlife Service 2021a), 2002 (timestep 0) to 2019 (timestep 17), versus the trend produced by the baseline scenario of my simulation model. The USFWS trend line is represented by the equation $y=215.9x+7418.1$. The simulation model trend line is represented by the equation $y=429.1x+8042.3$. Projections for 2050 (timestep 48) and 2075 (timestep 73) are highlighted to illustrate the magnitude of the divergence in each trend over the “foreseeable future” (Jenouvrier et al. 2021).

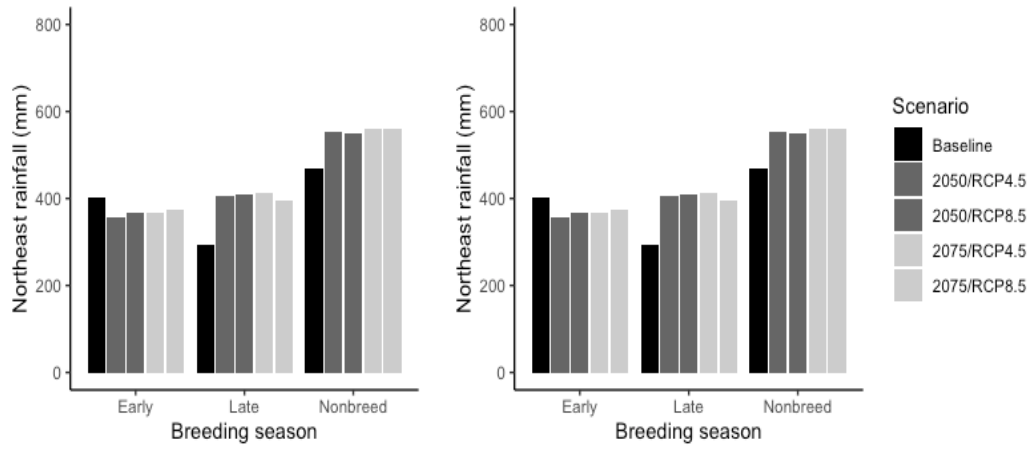
a)



b)



c)



d)

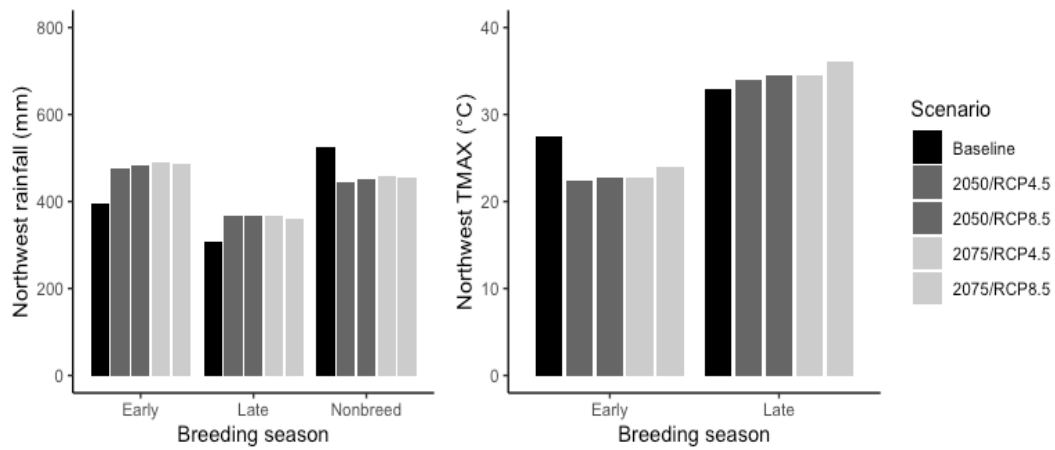
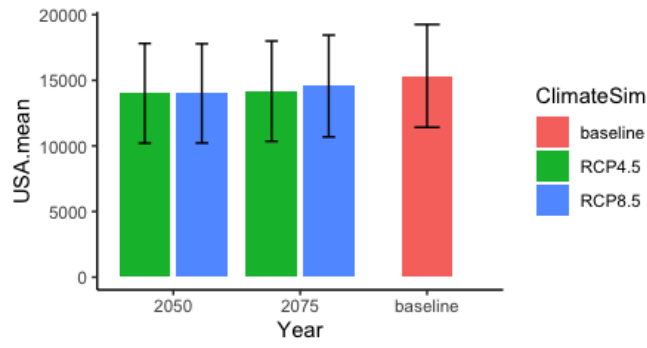
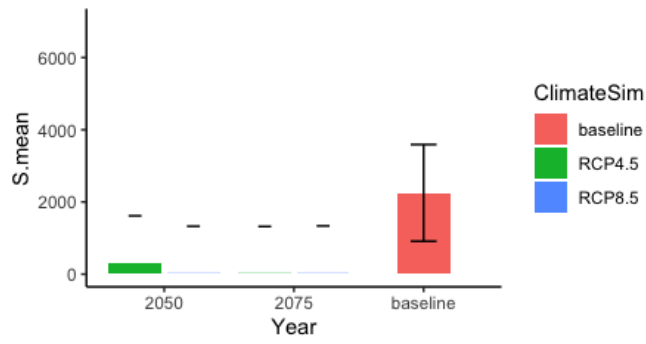


Figure 4.8. Adjustments to seasonal rainfall and average daily maximum temperature (TMAX) in each stork nesting region, a) South, b) Central, c) Northeast, d) Northwest, for five simulation modeling scenarios.

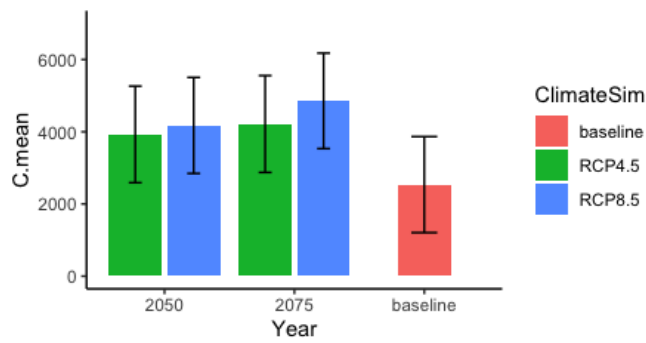
a)



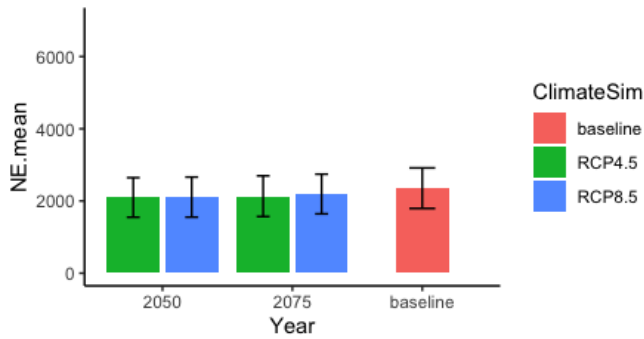
b)



c)



d)



e)

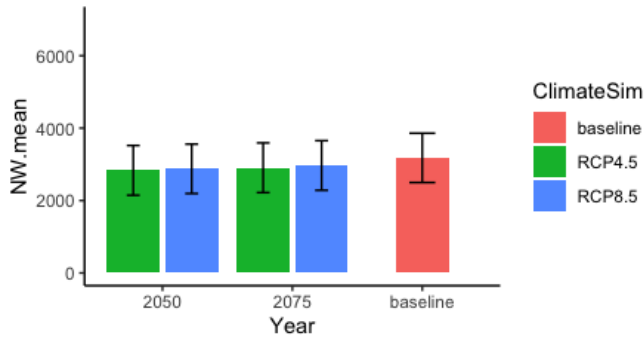


Figure 4.9. Mean population size (\pm SD, number of breeding pairs) of the Wood Stork resulting from 10,000 STELLA simulation runs for a) the total USA, which encompasses regions b) South, c) Central, d) Northeast, and e) Northwest, under current (baseline; 2002-2019) and future (2050, 2075) environmental conditions. Future conditions reflect the anticipated increase in the amount of urban land cover within foraging areas surrounding stork colonies, as well as hydrological changes due to global climate change (RCP4.5, conservative scenario, and RCP8.5, more extreme scenario). Bars that appear to be missing are scenarios where the mean population size is 0.

5 SYNTHESIS

Scientists have paid increasing attention to the interactions of various stork species with the urban environment over the last decade. Globally, research has examined the effects of anthropogenic factors on the stork (Bouton et al. 2005) and other Ciconiiformes (Thabethe et al. 2021; Tortosa et al. 2002; Hilgartner et al. 2014; Jagiello et al. 2018; Chenchouni 2017a) as these factors become more prevalent due to the ever-expanding urban footprint. The number of Wood Storks nesting in urban habitats is also being surveyed more regularly as awareness of the effects on urbanization on avian species in general has increased. This is true in the US, as annual nest counts at the Jacksonville Zoo (Jacksonville, Florida), St. Augustine Alligator Farm (St. Augustine, Florida), Solid Waste Authority (West Palm Beach, Florida), and numerous county parks and residential properties in central and southeastern Florida have become incorporated into annual nesting reports to the South Florida Water Management District and the Southeast Ecological Services Office of the U.S. Fish and Wildlife Service. Reporting on urban colony size is new because the storks' colonization of these locations is new, but also because biologists' understanding of what constitutes "good" stork habitat, i.e., locations that are worth monitoring, is starting to broaden in definition.

Nearly all the foundational literature describing the life history of the stork in the U.S. came from the Everglades system, particularly the southwest portion, where boom nesting years occurred prior to the drainage of the wetland (Kahl 1964; Kushlan et al. 1975; Ogden 1994). This habitat, full of tall Bald Cypress trees, and positioned between a

productive estuarine coastline and long hydroperiod freshwater wetlands, is described as critical breeding habitat (Ogden 1994). The idea that storks need such a habitat to thrive has been reinforced using the stork as an ecosystem indicator in the Comprehensive Everglades Restoration Plan (RECOVER 2005), because it implies that, given the choice between a pristine, restored Everglades and alternative locations (i.e., urban habitat, temperate wetlands), storks will choose the Everglades. While these ideas are well rooted in scientific knowledge, the stork's ability to capitalize on urban resources, and the possibility that habitat in the northern extent of the stork's range is now preferred over the boom-and-bust Everglades by at least some individuals, are ideas that cannot be ignored when considering the conservation of the stork and the health of the Everglades ecosystem at-large.

Rena Borkhataria and Peter Frederick (Department of Wildlife and Ecology, University of Florida), Simona Picardi and Mathieu Basille (Fort Lauderdale Research and Education Center, University of Florida), Betsy Evans and Dale Gawlik (Department of Biological Sciences, Florida Atlantic University), and their university and agency collaborators provided the first detailed studies on stork behavior at urban colonies, spanning from social and foraging behaviors to key demographic metrics like nest success and survival probability.

In my dissertation, I built on these works to test multiple ways in which urban habitats positively or negatively impact the resiliency of the U.S. stork population. In Chapter 2, "Effect of researcher disturbance and environmental variables on the thermoregulatory response of Wood Stork (*Mycteria americana*) nestlings in subtropical South Florida, USA", I measured the skin temperature of nestlings that encounter

different amounts of stress and found that nestlings at urban colonies contend with more stress on average than those in marsh colonies; level of disturbance and body condition of the nestling also affected its thermoregulatory performance.

In Chapter 3, “Commuters: A new view of how wide-ranging species utilize urban environments”, I extended the nest monitoring and diet datasets initiated by Evans and Gawlik to compare the reproductive success and diet of storks nesting in urban versus natural marsh colonies in South Florida. Consistent with Evans and Gawlik (2020) and Evans et al. (2021), I found that storks nesting in urban colonies have access to a wider breadth of resources, and benefit from this access in years when the marsh is in poor hydrological condition. I also tested whether the consumption of non-native fish, which are more commonly encountered by marsh nesters, affects nest-level productivity, and found that urban-nesting storks that consume a high level of non-native prey (>22% of their diet) face a reproductive penalty.

Finally, in Chapter 4, “Range-wide impacts of climate change and urbanization on the future status of a recovering waterbird”, I collated nest monitoring data from across the stork’s U.S. range, 2002-2019, and paired it with environmental data from the same period. I modelled the association between the stork response and environmental drivers, and then manipulated environmental driver inputs in a complete systems model to project the future population size of the stork under two climate change and urbanization scenarios. I found that, of the 4 nesting regions in the US, the southern two showed a strong relationship between climate and stork response, while the northern two regions showed almost no relationship between these same variables. Therefore, when climate variables were manipulated to simulate future climate conditions, the southern regions

notably changed while the northern regions did not. These regional differences suggest that some factor other than hydrological condition (via rainfall) must be driving the response of stork in the north. In the context of this discussion about the impacts of urbanization on the resiliency of the stork population, I note that my finding from Chapter 3, that storks benefited from nesting in urban colonies due to the availability of alternative prey in years when the marsh was in poor condition, was a pattern I also found in Chapter 4 where the stork response—environmental association model for the Central region, which is the most urban of the four stork nesting regions in the US, produced significant interactions between habitat (urban, coastal) availability and total rainfall.

6 APPENDICES

Appendix 1. Complete AIC_c model set of stork response (a-d: total nests, e-h: productivity) to climate and land cover type for each stork nesting region in the U.S. Models in the top set ($\Delta AIC_c < 4$; delineated by horizontal line) were averaged using the subset of models containing each parameter.

a) Stork response=Total nests, Region=South

Rank	(Intercept)	TMAX.early	Rain.2yr	Rain.early	Rain.nonbreed	df	logLik	AIC _c	delta	weight	CumWt
1	1520	-1013.63	1315.67	-1828.75	NA	5	-145.62	306.23	0.00	0.34	0.34
2	1520	NA	939.88	-1456.98	NA	4	-147.85	306.77	0.54	0.26	0.60
3	1520	NA	NA	-1477.01	NA	3	-149.94	307.59	1.36	0.17	0.78
4	1520	-446.47	NA	-1644.29	NA	4	-149.57	310.21	3.98	0.05	0.82
5	1520	NA	1023.39	-1384.87	-315.58	5	-147.61	310.22	3.99	0.05	0.87
6	1520	-986.37	1333.23	-1794.85	-104.57	6	-145.58	310.81	4.57	0.03	
7	1520	NA	NA	-1470.16	-30.75	4	-149.94	310.95	4.72	0.03	
8	1520	NA	NA	NA	NA	2	-153.66	312.11	5.88	0.02	
9	1520	NA	970.93	NA	NA	3	-152.23	312.18	5.95	0.02	
10	1520	-484.91	NA	-1684.41	115.38	5	-149.54	314.09	7.85	0.01	
11	1520	NA	1141.01	NA	-654.75	4	-151.55	314.19	7.95	0.01	
12	1520	NA	NA	NA	-358.37	3	-153.48	314.67	8.43	0.01	
13	1520	169.60	NA	NA	NA	3	-153.62	314.95	8.72	0.00	
14	1520	-231.07	1058.41	NA	NA	4	-152.16	315.39	9.16	0.00	
15	1520	252.71	NA	NA	-409.65	4	-153.39	317.85	11.62	0.00	
16	1520	-153.25	1194.55	NA	-637.57	5	-151.52	318.04	11.81	0.00	

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b) Stork response=Total nests, Region=Central

Rank	(Intercept)	TMAX.early	Rain.2yr	Rain.early	Rain.nonbreed	df	logLik	AIC _c	delta	weight	CumWt
1	2036.22	1319.64	NA	NA	-1401.03	4	-148.71	308.50	0.00	0.27	0.27
2	2036.22	1428.85	922.67	NA	-1848.47	5	-146.92	308.84	0.34	0.23	0.50
3	2036.22	1792.52	NA	889.43	-1617.97	5	-147.16	309.32	0.82	0.18	0.68
4	2036.22	NA	NA	NA	NA	2	-153.27	311.35	2.84	0.07	0.75
5	2036.22	NA	NA	NA	-954.91	3	-151.83	311.38	2.88	0.06	0.81
6	2036.22	846.01	NA	NA	NA	3	-152.16	312.04	3.54	0.05	0.86
7	2036.22	1718.04	680.93	597.75	-1877.04	6	-146.24	312.12	3.62	0.04	0.90
8	2036.22	NA	735.92	NA	-1282.34	4	-151.06	313.20	4.69	0.03	0.93
9	2036.22	NA	165.37	NA	NA	3	-153.23	314.18	5.68	0.02	
10	2036.22	NA	NA	-19.62	NA	3	-153.27	314.26	5.76	0.02	
11	2036.22	NA	NA	41.84	-957.59	4	-151.83	314.74	6.24	0.01	
12	2036.22	1048.83	NA	451.52	NA	4	-151.89	314.86	6.36	0.01	
13	2036.22	840.21	127.07	NA	NA	4	-152.14	315.35	6.85	0.01	
14	2036.22	NA	869.50	-285.64	-1323.44	5	-150.93	316.87	8.36	0.00	
15	2036.22	NA	207.01	-103.18	NA	4	-153.22	317.52	9.01	0.00	
16	2036.22	1072.63	-83.73	496.01	NA	5	-151.88	318.76	10.26	0.00	

c) Stork response=Total nests, Region=Northeast

Rank	(Intercept)	TMAX.early	Rain.2yr	Rain.early	Rain.nonbreed	df	logLik	AIC _c	delta	weight	CumWt
1	1857.39	NA	NA	NA	NA	2	-137.03	278.87	0.00	0.27	0.27
2	1857.39	NA	NA	NA	329.19	3	-136.02	279.75	0.88	0.17	0.44
3	1857.39	NA	304.82	NA	NA	3	-136.17	280.05	1.19	0.15	0.59
4	1857.39	196.32	NA	NA	NA	3	-136.69	281.08	2.22	0.09	0.68
5	1857.39	NA	NA	-45.85	NA	3	-137.01	281.74	2.88	0.06	0.74
6	1857.39	244.02	339.14	NA	NA	4	-135.58	282.24	3.38	0.05	0.79
7	1857.39	NA	193.25	NA	238.97	4	-135.72	282.52	3.66	0.04	0.84
8	1857.39	167.17	NA	NA	313.65	4	-135.74	282.56	3.69	0.04	0.88
9	1857.39	NA	399.30	-218.51	NA	4	-135.78	282.64	3.78	0.04	0.92
10	1857.39	NA	NA	-28.93	327.70	4	-136.01	283.10	4.23	0.03	
11	1857.39	219.82	NA	52.51	NA	4	-136.66	284.41	5.54	0.02	
12	1857.39	212.32	243.22	NA	195.91	5	-135.28	285.55	6.68	0.01	
13	1857.39	194.27	386.67	-126.12	NA	5	-135.47	285.94	7.08	0.01	
14	1857.39	NA	286.76	-160.19	187.05	5	-135.53	286.06	7.19	0.01	
15	1857.39	192.38	NA	56.45	314.23	5	-135.71	286.43	7.56	0.01	
16	1857.39	185.82	280.73	-74.95	176.99	6	-135.24	290.11	11.25	0.00	

d) Stork response=Total nests, Region=Northwest

Rank	(Intercept)	TMAX.early	Rain.2yr	Rain.early	Rain.nonbreed	df	logLik	AIC_c	delta	weight	CumWt
1	2629.06	NA	783.90	NA	NA	3	-142.29	292.30	0.00	0.38	0.38
2	2629.06	NA	NA	NA	NA	2	-144.91	294.61	2.32	0.12	0.50
3	2629.06	309.08	880.19	NA	NA	4	-141.86	294.79	2.49	0.11	0.61
4	2629.06	NA	881.64	-242.56	NA	4	-142.05	295.17	2.87	0.09	0.70
5	2629.06	NA	NA	NA	522.32	3	-143.84	295.39	3.09	0.08	0.78
6	2629.06	NA	728.68	NA	93.93	4	-142.26	295.60	3.31	0.07	0.86
7	2629.06	NA	NA	112.73	NA	3	-144.86	297.43	5.14	0.03	
8	2629.06	34.88	NA	NA	NA	3	-144.90	297.52	5.22	0.03	
9	2629.06	NA	NA	113.16	522.42	4	-143.79	298.65	6.35	0.02	
10	2629.06	264.28	897.33	-77.18	NA	5	-141.84	298.68	6.38	0.02	
11	2629.06	329.00	921.13	NA	-59.09	5	-141.85	298.69	6.39	0.02	
12	2629.06	-28.86	NA	NA	525.82	4	-143.84	298.75	6.45	0.02	
13	2629.06	NA	877.09	-240.72	6.48	5	-142.05	299.09	6.79	0.01	
14	2629.06	187.09	NA	234.28	NA	4	-144.78	300.65	8.35	0.01	
15	2629.06	80.01	NA	165.14	512.76	5	-143.77	302.54	10.24	0.00	
16	2629.06	282.82	946.54	-85.02	-68.50	6	-141.83	303.29	10.99	0.00	

e) Stork response=Productivity, Region=South

Rank	(Intercept)	TMAX.late	Rain.2yr	Rain.breed	Rain.late	Rain.yr	Rain.breed x Coastal.10km	Rain.breed x Urban.30km	df	logLik	AIC _c	delta	weight	Cum Wt
1	1.55	NA	1.12	NA	NA	-0.74	NA	NA	4	-1.15	16.97	0.00	0.35	0.35
2	1.55	-0.70	NA	NA	NA	NA	NA	NA	3	-4.75	18.92	1.95	0.13	0.48
3	1.55	NA	1.08	-0.67	NA	NA	NA	NA	4	-2.18	19.02	2.05	0.13	0.61
4	1.55	NA	0.67	NA	NA	NA	NA	NA	3	-5.19	19.81	2.84	0.08	0.69
5	1.55	NA	0.83	-1.35	0.95	NA	NA	NA	5	0.69	20.62	3.65	0.06	0.75
6	1.55	NA	1.25	-0.40	NA	-0.54	NA	NA	5	0.38	21.23	4.26	0.04	
7	1.55	NA	NA	NA	NA	NA	NA	NA	2	-8.02	21.54	4.57	0.04	
8	1.55	-0.86	NA	-0.37	NA	NA	NA	NA	4	-3.65	21.96	4.99	0.03	
9	1.55	NA	1.31	NA	-0.27	-0.74	NA	NA	5	-0.48	22.96	5.99	0.02	
10	1.55	NA	NA	-1.40	1.57	NA	NA	NA	4	-4.36	23.39	6.42	0.01	
11	1.55	-0.47	0.30	NA	NA	NA	NA	NA	4	-4.44	23.54	6.57	0.01	
12	1.55	-0.73	NA	NA	NA	-0.18	NA	NA	4	-4.45	23.56	6.59	0.01	
13	1.55	-0.82	NA	NA	-0.18	NA	NA	NA	4	-4.57	23.81	6.84	0.01	
14	1.55	0.22	1.35	NA	NA	-0.85	NA	NA	5	-0.96	23.92	6.95	0.01	
15	1.55	NA	NA	NA	0.34	NA	NA	NA	3	-7.42	24.28	7.31	0.01	
16	1.55	NA	0.86	NA	-0.27	NA	NA	NA	4	-4.87	24.41	7.44	0.01	
17	1.55	-0.37	0.77	-0.63	NA	NA	NA	NA	5	-1.40	24.79	7.82	0.01	
18	1.55	NA	NA	NA	NA	-0.06	NA	NA	3	-8.00	25.43	8.46	0.01	
19	1.55	NA	NA	-0.01	NA	NA	NA	NA	3	-8.02	25.46	8.50	0.00	
20	1.57	NA	1.22	-1.00	NA	NA	NA	0.05	5	-1.98	25.96	9.00	0.00	
21	1.57	NA	1.22	-1.00	NA	NA	-0.18	NA	5	-1.98	25.96	9.00	0.00	
22	1.57	NA	1.22	-1.00	NA	NA	-0.18	NA	5	-1.98	25.96	9.00	0.00	
23	1.55	-0.58	NA	-1.03	0.88	NA	NA	NA	5	-2.33	26.66	9.69	0.00	
24	1.49	NA	NA	-0.67	1.43	NA	0.45	NA	5	-2.77	27.54	10.57	0.00	
25	1.49	NA	NA	-0.67	1.43	NA	0.45	NA	5	-2.77	27.54	10.57	0.00	
26	1.49	NA	NA	-0.67	1.43	NA	NA	-0.11	5	-2.77	27.54	10.57	0.00	
27	1.47	NA	NA	0.77	NA	NA	0.58	NA	4	-6.60	27.86	10.89	0.00	
28	1.47	NA	NA	0.77	NA	NA	NA	-0.14	4	-6.60	27.86	10.89	0.00	
29	1.47	NA	NA	0.77	NA	NA	0.58	NA	4	-6.60	27.86	10.89	0.00	

30	1.55	NA	NA	-2.09	1.97	0.51	NA	NA	5	-3.24	28.48	11.52	0.00
31	1.55	NA	NA	NA	0.45	-0.25	NA	NA	4	-7.13	28.92	11.95	0.00
32	1.55	-0.87	NA	-0.43	NA	0.09	NA	NA	5	-3.60	29.20	12.23	0.00
33	1.54	-0.82	NA	-0.27	NA	NA	0.06	NA	5	-3.63	29.25	12.28	0.00
34	1.54	-0.82	NA	-0.27	NA	NA	0.06	NA	5	-3.63	29.25	12.28	0.00
35	1.54	-0.82	NA	-0.27	NA	NA	NA	-0.01	5	-3.63	29.25	12.28	0.00
36	1.55	-0.54	0.49	NA	-0.35	NA	NA	NA	5	-3.83	29.66	12.69	0.00
37	1.59	NA	1.53	-1.00	NA	-0.62	-0.35	NA	6	1.53	29.94	12.97	0.00
38	1.59	NA	1.53	-1.00	NA	-0.62	NA	0.09	6	1.53	29.94	12.97	0.00
39	1.59	NA	1.53	-1.00	NA	-0.62	-0.35	NA	6	1.53	29.94	12.97	0.00
40	1.55	NA	NA	0.07	NA	-0.10	NA	NA	4	-7.99	30.64	13.68	0.00
41	1.55	-0.79	NA	NA	-0.10	-0.15	NA	NA	5	-4.40	30.81	13.84	0.00
42	1.55	NA	1.00	-0.98	0.61	-0.27	NA	NA	6	1.06	30.87	13.90	0.00
43	1.55	-0.09	0.77	-1.30	0.89	NA	NA	NA	6	0.75	31.50	14.53	0.00
44	1.55	NA	0.88	-1.45	0.93	NA	-0.06	NA	6	0.72	31.55	14.58	0.00
45	1.55	NA	0.88	-1.45	0.93	NA	NA	0.01	6	0.72	31.55	14.58	0.00
46	1.55	NA	0.88	-1.45	0.93	NA	-0.06	NA	6	0.72	31.55	14.58	0.00
47	1.55	0.07	1.32	-0.39	NA	-0.58	NA	NA	6	0.41	32.19	15.22	0.00
48	1.55	0.14	1.44	NA	-0.25	-0.81	NA	NA	6	-0.40	33.79	16.82	0.00
49	1.58	-0.42	0.92	-1.10	NA	NA	-0.26	NA	6	-0.94	34.89	17.92	0.00
50	1.58	-0.42	0.92	-1.10	NA	NA	NA	0.06	6	-0.94	34.89	17.92	0.00
51	1.58	-0.42	0.92	-1.10	NA	NA	-0.26	NA	6	-0.94	34.89	17.92	0.00
52	1.47	NA	NA	0.88	NA	-0.15	0.59	NA	5	-6.52	35.05	18.08	0.00
53	1.47	NA	NA	0.88	NA	-0.15	NA	-0.15	5	-6.52	35.05	18.08	0.00
54	1.47	NA	NA	0.88	NA	-0.15	0.59	NA	5	-6.52	35.05	18.08	0.00
55	1.55	-0.52	NA	-1.62	1.27	0.41	NA	NA	6	-1.33	35.66	18.69	0.00
56	1.49	NA	NA	-1.33	1.77	0.42	0.39	NA	6	-1.80	36.59	19.62	0.00
57	1.49	NA	NA	-1.33	1.77	0.42	NA	-0.10	6	-1.80	36.59	19.62	0.00
58	1.49	NA	NA	-1.33	1.77	0.42	0.39	NA	6	-1.80	36.59	19.62	0.00
59	1.52	-0.42	NA	-0.78	1.01	NA	0.22	NA	6	-2.02	37.05	20.08	0.00
60	1.52	-0.42	NA	-0.78	1.01	NA	NA	-0.05	6	-2.02	37.05	20.08	0.00
61	1.52	-0.42	NA	-0.78	1.01	NA	0.22	NA	6	-2.02	37.05	20.08	0.00
62	1.54	-0.85	NA	-0.36	NA	0.08	0.04	NA	6	-3.59	40.18	23.21	0.00
63	1.54	-0.85	NA	-0.36	NA	0.08	NA	-0.01	6	-3.59	40.18	23.21	0.00
64	1.54	-0.85	NA	-0.36	NA	0.08	0.04	NA	6	-3.59	40.18	23.21	0.00
65	1.58	NA	1.39	-1.11	0.23	-0.50	-0.29	NA	7	1.60	48.14	31.17	0.00
66	1.58	NA	1.39	-1.11	0.23	-0.50	NA	0.07	7	1.60	48.14	31.17	0.00

67	1.58	NA	1.39	-1.11	0.23	-0.50	-0.29	NA	7	1.60	48.14	31.17	0.00
68	1.59	0.05	1.58	-0.99	NA	-0.65	-0.35	NA	7	1.54	48.25	31.28	0.00
69	1.59	0.05	1.58	-0.99	NA	-0.65	-0.35	NA	7	1.54	48.25	31.28	0.00
70	1.59	0.05	1.58	-0.99	NA	-0.65	NA	0.09	7	1.54	48.25	31.28	0.00
71	1.55	0.04	1.05	-0.97	0.61	-0.30	NA	NA	7	1.07	49.18	32.21	0.00
72	1.56	-0.12	0.83	-1.43	0.83	NA	-0.10	NA	7	0.82	49.68	32.72	0.00
73	1.56	-0.12	0.83	-1.43	0.83	NA	NA	0.02	7	0.82	49.68	32.72	0.00
74	1.56	-0.12	0.83	-1.43	0.83	NA	-0.10	NA	7	0.82	49.68	32.72	0.00
75	1.52	-0.38	NA	-1.38	1.36	0.39	0.19	NA	7	-1.06	53.46	36.49	0.00
76	1.52	-0.38	NA	-1.38	1.36	0.39	NA	-0.05	7	-1.06	53.46	36.49	0.00
77	1.52	-0.38	NA	-1.38	1.36	0.39	0.19	NA	7	-1.06	53.46	36.49	0.00
78	1.58	0.04	1.44	-1.09	0.22	-0.53	-0.29	NA	8	1.61	84.78	67.81	0.00
79	1.58	0.04	1.44	-1.09	0.22	-0.53	NA	0.07	8	1.61	84.78	67.81	0.00
80	1.58	0.04	1.44	-1.09	0.22	-0.53	-0.29	NA	8	1.61	84.78	67.81	0.00

f) Stork response=Productivity, Region=Central

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Rank	(Intercept)	TMAX.late	Rain.2yr	Rain.breed	Rain.late	Rain.yr	Rain.breed x Coastal.10km	Rain.breed x Urban.20km	df	logLik	AIC _c	delta	weight	CumWt
1	1.14	0.37	NA	NA	NA	NA	NA	NA	3	-7.13	21.97	0.00	0.13	0.13
2	1.14	NA	0.62	NA	NA	-0.54	NA	NA	4	-5.92	22.92	0.96	0.08	0.21
3	1.14	0.39	0.26	NA	NA	NA	NA	NA	4	-5.95	22.98	1.02	0.08	0.28
4	1.14	NA	NA	NA	NA	NA	NA	NA	2	-9.18	23.16	1.20	0.07	0.35
5	1.14	NA	0.56	-0.47	NA	NA	NA	NA	4	-6.48	24.03	2.07	0.05	0.40
6	1.16	NA	0.68	-0.59	NA	NA	-0.87	0.72	6	-2.27	24.18	2.21	0.04	0.44
7	1.14	0.33	0.61	-0.46	NA	NA	-0.76	0.81	7	0.48	24.23	2.27	0.04	0.48
8	1.14	0.27	0.52	NA	NA	-0.39	NA	NA	5	-4.66	24.31	2.35	0.04	0.52
9	1.14	NA	0.24	NA	NA	NA	NA	NA	3	-8.40	24.51	2.54	0.04	0.55
10	1.14	NA	0.38	NA	-0.35	NA	NA	NA	4	-6.85	24.77	2.81	0.03	0.58
11	1.10	0.38	0.58	-0.42	NA	NA	NA	0.56	6	-2.68	24.99	3.02	0.03	0.61
12	1.14	0.30	0.47	-0.32	NA	NA	NA	NA	5	-5.00	25.00	3.04	0.03	0.64
13	1.14	NA	NA	NA	-0.19	NA	NA	NA	3	-8.69	25.10	3.14	0.03	0.67
14	1.14	0.44	NA	NA	0.10	NA	NA	NA	4	-7.02	25.13	3.16	0.03	0.69
15	1.14	0.38	NA	0.02	NA	NA	NA	NA	4	-7.12	25.31	3.35	0.02	0.72
16	1.14	0.38	NA	NA	NA	0.01	NA	NA	4	-7.12	25.32	3.36	0.02	0.74
17	1.16	NA	0.68	-0.37	-0.35	NA	-0.99	0.83	7	-0.18	25.57	3.60	0.02	0.76
18	1.14	NA	NA	NA	NA	-0.11	NA	NA	3	-9.01	25.74	3.77	0.02	0.78
19	1.14	NA	NA	-0.09	NA	NA	NA	NA	3	-9.06	25.84	3.88	0.02	0.80
20	1.11	NA	0.65	-0.58	NA	NA	NA	0.41	5	-5.43	25.86	3.90	0.02	0.82
21	1.18	NA	0.53	-0.43	NA	NA	-0.49	NA	5	-5.51	26.02	4.05	0.02	
22	1.14	NA	0.61	NA	-0.17	-0.43	NA	NA	5	-5.58	26.15	4.19	0.02	
23	1.14	NA	0.64	-0.18	NA	-0.41	NA	NA	5	-5.77	26.54	4.58	0.01	
24	1.14	0.33	0.29	NA	-0.09	NA	NA	NA	5	-5.88	26.77	4.80	0.01	
25	1.14	NA	0.55	-0.34	-0.19	NA	NA	NA	5	-6.08	27.16	5.19	0.01	
26	1.19	NA	NA	-0.07	NA	NA	-0.56	NA	4	-8.10	27.27	5.31	0.01	
27	1.11	0.45	NA	0.00	NA	NA	NA	0.39	5	-6.23	27.47	5.50	0.01	
28	1.17	0.33	NA	0.02	NA	NA	-0.39	NA	5	-6.60	28.21	6.24	0.01	
29	1.19	NA	0.63	-0.07	NA	-0.50	-0.58	NA	6	-4.33	28.30	6.34	0.01	

30	1.14	NA	NA	0.05	-0.22	NA	NA	NA	4	-8.67	28.43	6.46	0.01
31	1.14	NA	NA	NA	-0.20	0.01	NA	NA	4	-8.69	28.46	6.50	0.00
32	1.17	0.25	0.46	-0.32	NA	NA	-0.36	NA	6	-4.42	28.48	6.52	0.00
33	1.14	0.27	0.54	-0.12	NA	-0.30	NA	NA	6	-4.58	28.79	6.83	0.00
34	1.15	0.41	NA	0.00	NA	NA	-0.69	0.61	6	-4.61	28.86	6.90	0.00
35	1.12	NA	NA	-0.11	NA	NA	NA	0.18	4	-8.90	28.88	6.91	0.00
36	1.14	0.30	0.51	NA	0.05	-0.40	NA	NA	6	-4.63	28.90	6.94	0.00
37	1.14	0.45	NA	NA	0.14	-0.06	NA	NA	5	-6.99	28.99	7.02	0.00
38	1.14	0.45	NA	-0.05	0.14	NA	NA	NA	5	-7.00	29.01	7.04	0.00
39	1.10	NA	0.65	-0.42	-0.25	NA	NA	0.46	6	-4.72	29.07	7.10	0.00
40	1.14	NA	NA	0.01	NA	-0.12	NA	NA	4	-9.01	29.10	7.13	0.00
41	1.14	0.38	NA	0.05	NA	-0.03	NA	NA	5	-7.11	29.23	7.26	0.00
42	1.17	NA	NA	-0.11	NA	NA	-0.83	0.47	5	-7.12	29.24	7.27	0.00
43	1.18	NA	0.52	-0.28	-0.23	NA	-0.53	NA	6	-4.91	29.46	7.50	0.00
44	1.12	0.41	0.56	-0.77	NA	0.41	-0.79	1.06	8	1.23	29.55	7.58	0.00
45	1.14	0.34	0.46	-0.35	0.07	NA	NA	NA	6	-4.97	29.57	7.61	0.00
46	1.16	NA	0.68	-0.56	NA	-0.03	-0.87	0.70	7	-2.27	29.74	7.77	0.00
47	1.08	0.45	0.53	-0.68	NA	0.33	NA	0.76	7	-2.33	29.87	7.90	0.00
48	1.19	NA	NA	0.10	-0.26	NA	-0.60	NA	5	-7.52	30.05	8.08	0.00
49	1.11	NA	0.67	-0.43	NA	-0.17	NA	0.32	6	-5.35	30.34	8.37	0.00
50	1.08	0.57	NA	-0.52	NA	0.61	NA	0.78	6	-5.38	30.40	8.43	0.00
51	1.10	0.42	0.57	-0.45	0.08	NA	NA	0.56	7	-2.62	30.45	8.48	0.00
52	1.15	0.24	0.63	-0.40	-0.15	NA	-0.84	0.83	8	0.73	30.54	8.57	0.00
53	1.14	NA	0.63	-0.11	-0.15	-0.36	NA	NA	6	-5.52	30.68	8.72	0.00
54	1.19	NA	NA	0.12	NA	-0.23	-0.61	NA	5	-7.91	30.82	8.85	0.00
55	1.17	NA	NA	0.11	-0.35	NA	-0.94	0.57	6	-5.97	31.57	9.60	0.00
56	1.15	NA	0.65	-0.58	-0.41	0.29	-1.05	1.01	8	0.18	31.64	9.68	0.00
57	1.12	0.53	NA	-0.60	NA	0.69	-0.74	1.06	7	-3.28	31.75	9.79	0.00
58	1.11	0.54	NA	-0.07	0.16	NA	NA	0.40	6	-6.08	31.80	9.83	0.00
59	1.12	NA	NA	0.04	-0.25	NA	NA	0.23	5	-8.40	31.81	9.84	0.00
60	1.14	NA	NA	0.10	-0.21	-0.07	NA	NA	5	-8.66	32.31	10.35	0.00
61	1.18	0.20	0.56	-0.05	NA	-0.40	-0.46	NA	7	-3.64	32.49	10.52	0.00
62	1.17	0.32	NA	0.12	NA	-0.12	-0.42	NA	6	-6.55	32.73	10.76	0.00
63	1.12	NA	NA	-0.14	NA	0.03	NA	0.20	5	-8.90	32.80	10.83	0.00
64	1.17	0.36	NA	0.00	0.04	NA	-0.37	NA	6	-6.59	32.83	10.86	0.00
65	1.19	NA	0.61	0.02	-0.18	-0.45	-0.59	NA	7	-3.94	33.08	11.11	0.00
66	1.14	0.45	NA	0.00	0.15	-0.05	NA	NA	6	-6.99	33.62	11.66	0.00

67	1.17	NA	NA	-0.26	NA	0.17	-0.85	0.56	6	-7.05	33.74	11.78	0.00
68	1.17	0.24	0.47	-0.30	-0.03	NA	-0.38	NA	7	-4.42	34.03	12.07	0.00
69	1.14	0.31	0.54	-0.15	0.09	-0.31	NA	NA	7	-4.52	34.24	12.27	0.00
70	1.15	0.39	NA	0.01	-0.02	NA	-0.70	0.61	7	-4.61	34.42	12.45	0.00
71	1.19	NA	NA	0.23	-0.24	-0.17	-0.63	NA	6	-7.41	34.46	12.49	0.00
72	1.10	NA	0.65	-0.43	-0.25	0.01	NA	0.47	7	-4.72	34.63	12.67	0.00
73	1.08	0.62	NA	-0.56	0.11	0.58	NA	0.77	7	-5.29	35.79	13.82	0.00
74	1.16	NA	NA	-0.30	-0.45	0.51	-1.04	0.91	7	-5.34	35.88	13.92	0.00
75	1.11	NA	NA	-0.14	-0.29	0.23	NA	0.37	6	-8.30	36.24	14.27	0.00
76	1.08	0.48	0.53	-0.70	0.06	0.32	NA	0.76	8	-2.30	36.60	14.64	0.00
77	1.13	0.31	0.57	-0.73	-0.19	0.45	-0.89	1.11	9	1.64	37.21	15.25	0.00
78	1.17	0.35	NA	0.10	0.05	-0.12	-0.40	NA	7	-6.53	38.27	16.30	0.00
79	1.12	0.48	NA	-0.58	-0.10	0.72	-0.80	1.09	8	-3.20	38.41	16.44	0.00
80	1.18	0.18	0.56	-0.03	-0.03	-0.40	-0.48	NA	8	-3.63	39.27	17.30	0.00

g) Stork response=Productivity, Region=Northeast

Rank	(Intercept)	TMAX.late	Rain.2yr	Rain.breed	Rain.late	Rain.yr	Rain.breed x Coastal.10km	Rain.breed x Urban.20km	df	logLik	AIC _c	delta	weight	CumWt
1	1.56	NA	NA	NA	NA	NA	NA	NA	2	-9.61	24.01	0.00	0.13	0.13
2	1.56	0.29	NA	NA	NA	NA	NA	NA	3	-8.52	24.75	0.74	0.09	0.21
3	1.56	NA	NA	-0.24	NA	NA	NA	NA	3	-8.88	25.47	1.46	0.06	0.28
4	1.60	NA	NA	-0.23	NA	NA	-1.57	NA	4	-7.29	25.66	1.65	0.06	0.33
5	1.60	NA	NA	-0.23	NA	NA	-1.57	NA	4	-7.29	25.66	1.65	0.06	0.39
6	1.60	NA	NA	-0.23	NA	NA	NA	0.36	4	-7.29	25.66	1.65	0.06	0.44
7	1.56	NA	0.12	NA	NA	NA	NA	NA	3	-9.41	26.54	2.52	0.04	0.48
8	1.56	NA	0.31	-0.39	NA	NA	NA	NA	4	-7.82	26.71	2.70	0.03	0.51
9	1.56	NA	NA	NA	-0.07	NA	NA	NA	3	-9.54	26.80	2.78	0.03	0.54
10	1.56	NA	NA	NA	NA	-0.02	NA	NA	3	-9.60	26.92	2.91	0.03	0.57
11	1.56	NA	NA	-0.54	NA	0.40	NA	NA	4	-7.94	26.96	2.95	0.03	0.60
12	1.60	NA	0.31	-0.38	NA	NA	-1.57	NA	5	-6.01	27.03	3.01	0.03	0.63
13	1.60	NA	0.31	-0.38	NA	NA	NA	0.36	5	-6.01	27.03	3.01	0.03	0.66
14	1.60	NA	0.31	-0.38	NA	NA	-1.57	NA	5	-6.01	27.03	3.01	0.03	0.68
15	1.56	0.31	0.17	NA	NA	NA	NA	NA	4	-8.12	27.32	3.30	0.02	0.71
16	1.59	NA	NA	-0.51	NA	0.36	-1.49	NA	5	-6.37	27.75	3.73	0.02	0.73
17	1.59	NA	NA	-0.51	NA	0.36	NA	0.34	5	-6.37	27.75	3.73	0.02	0.75
18	1.59	NA	NA	-0.51	NA	0.36	-1.49	NA	5	-6.37	27.75	3.73	0.02	0.77
19	1.56	0.35	NA	NA	0.12	NA	NA	NA	4	-8.37	27.81	3.80	0.02	0.79
20	1.56	0.32	NA	NA	NA	0.09	NA	NA	4	-8.41	27.89	3.88	0.02	0.80
21	1.56	0.23	NA	-0.09	NA	NA	NA	NA	4	-8.45	27.98	3.97	0.02	0.82
22	1.56	NA	NA	-0.27	0.06	NA	NA	NA	4	-8.84	28.77	4.75	0.01	
23	1.60	NA	NA	-0.29	0.12	NA	-1.66	NA	5	-7.11	29.23	5.22	0.01	
24	1.60	NA	NA	-0.29	0.12	NA	NA	0.38	5	-7.11	29.23	5.22	0.01	
25	1.60	NA	NA	-0.29	0.12	NA	-1.66	NA	5	-7.11	29.23	5.22	0.01	
26	1.59	0.10	NA	-0.16	NA	NA	-1.45	NA	5	-7.21	29.41	5.40	0.01	
27	1.59	0.10	NA	-0.16	NA	NA	NA	0.34	5	-7.21	29.41	5.40	0.01	
28	1.59	0.10	NA	-0.16	NA	NA	-1.45	NA	5	-7.21	29.41	5.40	0.01	
29	1.56	NA	0.23	NA	NA	-0.16	NA	NA	4	-9.20	29.49	5.47	0.01	

30	1.56	NA	0.14	NA	-0.09	NA	NA	NA	4	-9.30	29.68	5.66	0.01
31	1.56	NA	0.22	-0.54	NA	0.26	NA	NA	5	-7.50	30.00	5.99	0.01
32	1.56	NA	NA	NA	-0.08	0.02	NA	NA	4	-9.54	30.15	6.14	0.01
33	1.56	0.15	0.28	-0.27	NA	NA	NA	NA	5	-7.63	30.27	6.26	0.01
34	1.56	NA	0.32	-0.43	0.09	NA	NA	NA	5	-7.72	30.45	6.44	0.01
35	1.56	0.14	NA	-0.41	NA	0.35	NA	NA	5	-7.78	30.57	6.56	0.00
36	1.56	NA	NA	-0.55	0.01	0.40	NA	NA	5	-7.94	30.88	6.87	0.00
37	1.60	NA	0.33	-0.46	0.15	NA	-1.68	NA	6	-5.68	31.00	6.98	0.00
38	1.60	NA	0.33	-0.46	0.15	NA	NA	0.39	6	-5.68	31.00	6.98	0.00
39	1.60	NA	0.33	-0.46	0.15	NA	-1.68	NA	6	-5.68	31.00	6.98	0.00
40	1.56	0.37	0.16	NA	0.10	NA	NA	NA	5	-8.01	31.02	7.00	0.00
41	1.59	NA	0.24	-0.50	NA	0.21	-1.53	NA	6	-5.76	31.16	7.14	0.00
42	1.59	NA	0.24	-0.50	NA	0.21	-1.53	NA	6	-5.76	31.16	7.14	0.00
43	1.59	NA	0.24	-0.50	NA	0.21	NA	0.35	6	-5.76	31.16	7.14	0.00
44	1.56	0.30	0.19	NA	NA	-0.03	NA	NA	5	-8.11	31.22	7.21	0.00
45	1.56	0.29	NA	-0.12	0.15	NA	NA	NA	5	-8.25	31.49	7.48	0.00
46	1.56	0.36	NA	NA	0.10	0.06	NA	NA	5	-8.32	31.65	7.63	0.00
47	1.60	0.00	0.31	-0.38	NA	NA	-1.57	NA	6	-6.01	31.66	7.65	0.00
48	1.60	0.00	0.31	-0.38	NA	NA	NA	0.36	6	-6.01	31.66	7.65	0.00
49	1.60	0.00	0.31	-0.38	NA	NA	-1.57	NA	6	-6.01	31.66	7.65	0.00
50	1.59	NA	NA	-0.53	0.08	0.35	-1.55	NA	6	-6.29	32.23	8.21	0.00
51	1.59	NA	NA	-0.53	0.08	0.35	NA	0.36	6	-6.29	32.23	8.21	0.00
52	1.59	NA	NA	-0.53	0.08	0.35	-1.55	NA	6	-6.29	32.23	8.21	0.00
53	1.59	0.01	NA	-0.50	NA	0.36	-1.48	NA	6	-6.37	32.38	8.37	0.00
54	1.59	0.01	NA	-0.50	NA	0.36	NA	0.34	6	-6.37	32.38	8.37	0.00
55	1.59	0.01	NA	-0.50	NA	0.36	-1.48	NA	6	-6.37	32.38	8.37	0.00
56	1.56	NA	0.22	NA	-0.04	-0.14	NA	NA	5	-9.19	33.37	9.36	0.00
57	1.59	0.16	NA	-0.20	0.17	NA	-1.49	NA	6	-6.90	33.44	9.43	0.00
58	1.59	0.16	NA	-0.20	0.17	NA	NA	0.34	6	-6.90	33.44	9.43	0.00
59	1.59	0.16	NA	-0.20	0.17	NA	-1.49	NA	6	-6.90	33.44	9.43	0.00
60	1.56	0.11	0.21	-0.44	NA	0.22	NA	NA	6	-7.40	34.43	10.42	0.00
61	1.56	0.21	0.28	-0.31	0.15	NA	NA	NA	6	-7.40	34.43	10.42	0.00
62	1.56	NA	0.23	-0.56	0.05	0.24	NA	NA	6	-7.47	34.57	10.56	0.00
63	1.56	0.18	NA	-0.40	0.08	0.32	NA	NA	6	-7.73	35.09	11.08	0.00
64	1.56	0.36	0.21	NA	0.13	-0.09	NA	NA	6	-7.96	35.55	11.53	0.00
65	1.60	NA	0.27	-0.54	0.13	0.16	-1.62	NA	7	-5.54	36.28	12.26	0.00
66	1.60	NA	0.27	-0.54	0.13	0.16	-1.62	NA	7	-5.54	36.28	12.26	0.00

67	1.60	NA	0.27	-0.54	0.13	0.16	NA	0.37	7	-5.54	36.28	12.26	0.00
68	1.60	0.06	0.31	-0.42	0.17	NA	-1.61	NA	7	-5.65	36.49	12.48	0.00
69	1.60	0.06	0.31	-0.42	0.17	NA	NA	0.37	7	-5.65	36.49	12.48	0.00
70	1.60	0.06	0.31	-0.42	0.17	NA	-1.61	NA	7	-5.65	36.49	12.48	0.00
71	1.60	-0.03	0.24	-0.53	NA	0.22	-1.56	NA	7	-5.75	36.70	12.69	0.00
72	1.60	-0.03	0.24	-0.53	NA	0.22	NA	0.36	7	-5.75	36.70	12.69	0.00
73	1.60	-0.03	0.24	-0.53	NA	0.22	-1.56	NA	7	-5.75	36.70	12.69	0.00
74	1.59	0.05	NA	-0.49	0.09	0.33	-1.50	NA	7	-6.27	37.75	13.74	0.00
75	1.59	0.05	NA	-0.49	0.09	0.33	-1.50	NA	7	-6.27	37.75	13.74	0.00
76	1.59	0.05	NA	-0.49	0.09	0.33	NA	0.35	7	-6.27	37.75	13.74	0.00
77	1.56	0.17	0.23	-0.42	0.11	0.17	NA	NA	7	-7.28	39.75	15.74	0.00
78	1.60	0.03	0.27	-0.52	0.14	0.15	-1.60	NA	8	-5.53	43.06	19.05	0.00
79	1.60	0.03	0.27	-0.52	0.14	0.15	NA	0.37	8	-5.53	43.06	19.05	0.00
80	1.60	0.03	0.27	-0.52	0.14	0.15	-1.60	NA	8	-5.53	43.06	19.05	0.00

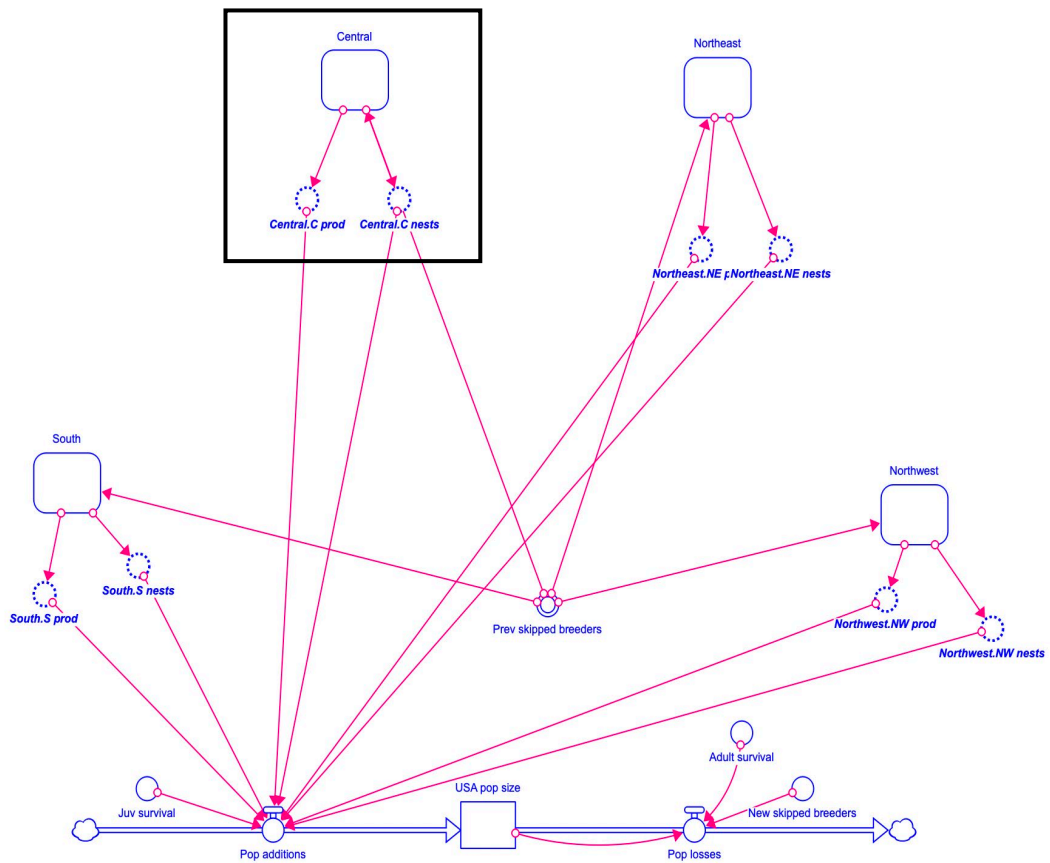
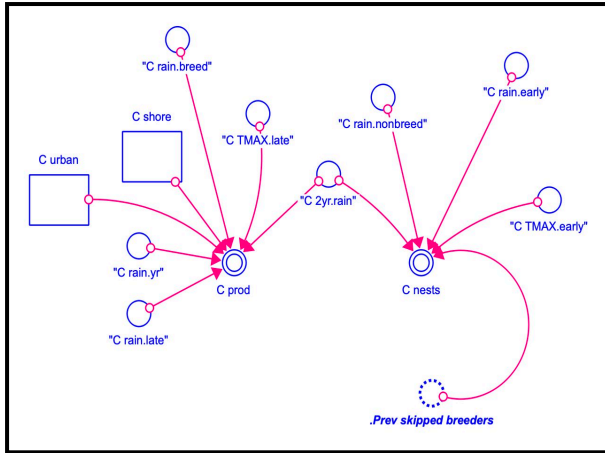
h) Stork response=Productivity, Region=Northwest

Rank	(Intercept)	TMAX.late	Rain.2yr	Rain.breed	Rain.late	Rain.yr	Rain.breed x Coastal.10km	Rain.breed x Urban.20km	df	logLik	AIC _c	delta	weight	CumWt
1	1.73	NA	0.56	NA	NA	NA	NA	NA	3	-6.43	20.87	0.00	0.25	0.25
2	1.73	NA	0.87	NA	NA	-0.42	NA	NA	4	-5.14	21.91	1.05	0.15	0.40
3	1.73	NA	0.68	-0.27	NA	NA	NA	NA	4	-5.56	22.75	1.89	0.10	0.50
4	1.73	NA	0.63	NA	-0.23	NA	NA	NA	4	-5.73	23.10	2.24	0.08	0.58
5	1.73	0.09	0.57	NA	NA	NA	NA	NA	4	-6.33	24.29	3.42	0.05	0.62
6	1.77	NA	0.66	-0.21	NA	NA	0.39	NA	5	-4.30	24.60	3.74	0.04	0.66
7	1.77	NA	0.66	-0.21	NA	NA	NA	-0.26	5	-4.30	24.60	3.74	0.04	0.70
8	1.77	NA	0.66	-0.21	NA	NA	0.39	NA	5	-4.30	24.60	3.74	0.04	0.74
9	1.73	NA	NA	NA	NA	NA	NA	NA	2	-10.01	24.95	4.08	0.03	
10	1.73	NA	0.86	NA	-0.14	-0.36	NA	NA	5	-4.89	25.78	4.91	0.02	
11	1.73	-0.33	0.76	-0.56	NA	NA	NA	NA	5	-4.97	25.94	5.07	0.02	
12	1.73	NA	0.85	-0.10	NA	-0.34	NA	NA	5	-5.07	26.13	5.27	0.02	
13	1.73	-0.04	0.89	NA	NA	-0.45	NA	NA	5	-5.11	26.22	5.35	0.02	
14	1.78	-0.50	0.78	-0.64	NA	NA	0.51	NA	6	-2.72	26.78	5.91	0.01	
15	1.78	-0.50	0.78	-0.64	NA	NA	NA	-0.34	6	-2.72	26.78	5.91	0.01	
16	1.78	-0.50	0.78	-0.64	NA	NA	0.51	NA	6	-2.72	26.78	5.91	0.01	
17	1.73	NA	0.68	-0.19	-0.10	NA	NA	NA	5	-5.48	26.97	6.10	0.01	
18	1.73	-0.16	0.65	NA	-0.35	NA	NA	NA	5	-5.54	27.08	6.22	0.01	
19	1.73	NA	NA	NA	NA	0.21	NA	NA	3	-9.58	27.16	6.29	0.01	
20	1.73	NA	NA	NA	-0.04	NA	NA	NA	3	-10.00	28.00	7.13	0.01	
21	1.73	NA	NA	0.03	NA	NA	NA	NA	3	-10.00	28.01	7.14	0.01	
22	1.73	0.01	NA	NA	NA	NA	NA	NA	3	-10.01	28.02	7.15	0.01	
23	1.77	NA	0.83	-0.04	NA	-0.34	0.39	NA	6	-3.73	28.80	7.94	0.00	
24	1.77	NA	0.83	-0.04	NA	-0.34	NA	-0.26	6	-3.73	28.80	7.94	0.00	
25	1.77	NA	0.83	-0.04	NA	-0.34	0.39	NA	6	-3.73	28.80	7.94	0.00	
26	1.77	NA	NA	0.09	NA	NA	NA	-0.30	4	-9.04	29.71	8.85	0.00	
27	1.77	NA	NA	0.09	NA	NA	0.46	NA	4	-9.04	29.71	8.85	0.00	
28	1.77	NA	NA	0.09	NA	NA	0.46	NA	4	-9.04	29.71	8.85	0.00	
29	1.77	NA	0.66	-0.22	0.01	NA	0.40	NA	6	-4.30	29.93	9.07	0.00	

30	1.77	NA	0.66	-0.22	0.01	NA	NA	-0.26	6	-4.30	29.93	9.07	0.00
31	1.77	NA	0.66	-0.22	0.01	NA	0.40	NA	6	-4.30	29.93	9.07	0.00
32	1.73	-0.26	0.93	NA	-0.32	-0.43	NA	NA	6	-4.36	30.06	9.19	0.00
33	1.73	NA	NA	-0.27	NA	0.41	NA	NA	4	-9.24	30.12	9.26	0.00
34	1.73	NA	NA	NA	-0.17	0.29	NA	NA	4	-9.35	30.34	9.48	0.00
35	1.73	-0.45	0.79	-0.48	-0.25	NA	NA	NA	6	-4.52	30.38	9.52	0.00
36	1.73	0.11	NA	NA	NA	0.26	NA	NA	4	-9.48	30.59	9.73	0.00
37	1.73	-0.27	0.88	-0.38	NA	-0.26	NA	NA	6	-4.69	30.71	9.85	0.00
38	1.73	NA	0.87	0.04	-0.15	-0.38	NA	NA	6	-4.88	31.10	10.23	0.00
39	1.73	NA	NA	0.12	-0.13	NA	NA	NA	4	-9.93	31.50	10.64	0.00
40	1.73	0.09	NA	0.10	NA	NA	NA	NA	4	-9.97	31.58	10.72	0.00
41	1.73	-0.03	NA	NA	-0.06	NA	NA	NA	4	-9.99	31.62	10.76	0.00
42	1.77	NA	NA	-0.20	NA	0.39	0.44	NA	5	-8.27	32.53	11.67	0.00
43	1.77	NA	NA	-0.20	NA	0.39	NA	-0.29	5	-8.27	32.53	11.67	0.00
44	1.77	NA	NA	-0.20	NA	0.39	0.44	NA	5	-8.27	32.53	11.67	0.00
45	1.78	-0.57	0.80	-0.59	-0.16	NA	0.48	NA	7	-2.51	33.01	12.15	0.00
46	1.78	-0.57	0.80	-0.59	-0.16	NA	NA	-0.32	7	-2.51	33.01	12.15	0.00
47	1.78	-0.57	0.80	-0.59	-0.16	NA	0.48	NA	7	-2.51	33.01	12.15	0.00
48	1.78	-0.45	0.87	-0.49	NA	-0.20	0.50	NA	7	-2.51	33.02	12.15	0.00
49	1.78	-0.45	0.87	-0.49	NA	-0.20	NA	-0.33	7	-2.51	33.02	12.15	0.00
50	1.78	-0.45	0.87	-0.49	NA	-0.20	0.50	NA	7	-2.51	33.02	12.15	0.00
51	1.77	-0.06	NA	0.04	NA	NA	0.47	NA	5	-9.03	34.05	13.19	0.00
52	1.77	-0.06	NA	0.04	NA	NA	NA	-0.31	5	-9.03	34.05	13.19	0.00
53	1.77	-0.06	NA	0.04	NA	NA	0.47	NA	5	-9.03	34.05	13.19	0.00
54	1.77	NA	NA	0.09	0.00	NA	NA	-0.30	5	-9.04	34.08	13.21	0.00
55	1.77	NA	NA	0.09	0.00	NA	0.46	NA	5	-9.04	34.08	13.21	0.00
56	1.77	NA	NA	0.09	0.00	NA	0.46	NA	5	-9.04	34.08	13.21	0.00
57	1.73	-0.13	NA	-0.41	NA	0.46	NA	NA	5	-9.19	34.37	13.51	0.00
58	1.73	NA	NA	-0.22	-0.06	0.40	NA	NA	5	-9.23	34.45	13.59	0.00
59	1.73	0.00	NA	NA	-0.17	0.29	NA	NA	5	-9.35	34.71	13.84	0.00
60	1.77	NA	0.83	0.00	-0.04	-0.35	0.38	NA	7	-3.72	35.44	14.57	0.00
61	1.77	NA	0.83	0.00	-0.04	-0.35	NA	-0.25	7	-3.72	35.44	14.57	0.00
62	1.77	NA	0.83	0.00	-0.04	-0.35	0.38	NA	7	-3.72	35.44	14.57	0.00
63	1.73	0.04	NA	0.15	-0.11	NA	NA	NA	5	-9.93	35.86	14.99	0.00
64	1.73	-0.39	0.92	-0.27	-0.28	-0.29	NA	NA	7	-4.15	36.30	15.43	0.00
65	1.78	-0.33	NA	-0.54	NA	0.52	NA	-0.35	6	-7.91	37.16	16.29	0.00
66	1.78	-0.33	NA	-0.54	NA	0.52	0.52	NA	6	-7.91	37.16	16.29	0.00

67	1.78	-0.33	NA	-0.54	NA	0.52	0.52	NA	6	-7.91	37.16	16.29	0.00
68	1.77	NA	NA	-0.26	0.07	0.40	NA	-0.31	6	-8.24	37.82	16.95	0.00
69	1.77	NA	NA	-0.26	0.07	0.40	0.46	NA	6	-8.24	37.82	16.95	0.00
70	1.77	NA	NA	-0.26	0.07	0.40	0.46	NA	6	-8.24	37.82	16.95	0.00
71	1.77	-0.07	NA	0.05	-0.02	NA	NA	-0.31	6	-9.02	39.38	18.52	0.00
72	1.77	-0.07	NA	0.05	-0.02	NA	0.47	NA	6	-9.02	39.38	18.52	0.00
73	1.77	-0.07	NA	0.05	-0.02	NA	0.47	NA	6	-9.02	39.38	18.52	0.00
74	1.73	-0.18	NA	-0.37	-0.11	0.46	NA	NA	6	-9.13	39.60	18.73	0.00
75	1.77	-0.52	0.90	-0.42	-0.18	-0.22	0.47	NA	8	-2.23	41.03	20.16	0.00
76	1.77	-0.52	0.90	-0.42	-0.18	-0.22	NA	-0.31	8	-2.23	41.03	20.16	0.00
77	1.77	-0.52	0.90	-0.42	-0.18	-0.22	0.47	NA	8	-2.23	41.03	20.16	0.00
78	1.78	-0.33	NA	-0.53	-0.01	0.52	0.52	NA	7	-7.91	43.82	22.96	0.00
79	1.78	-0.33	NA	-0.53	-0.01	0.52	NA	-0.34	7	-7.91	43.82	22.96	0.00
80	1.78	-0.33	NA	-0.53	-0.01	0.52	0.52	NA	7	-7.91	43.82	22.96	0.00

Appendix 2. Inputs into the STELLA simulation model for the baseline scenario (empirical data 2002-2019). Four future scenarios were also simulated: 2050/RCP4.5, 2075/RCP4.5, 2050/RCP8.5, 2075/RCP8.5. To do so, all simulation structure and inputs remained constant except rainfall, TMAX, and urban land cover means which were adjusted based on predictions by Climate Explorer (National Environmental Modeling & Analysis Center et al., 2021) and Florida 2070 (Carr & Zwick, 2016).



Variable	Baseline scenario (2002-2019)	Source
USA pop size	NORMAL(8043, 2934)	See Methods: Stork breeding data
Pop additions	(South.S_nests+Central.C_nests+Northeast.NE_nests+Northwest.NW_nests+(0.5*Juv_survival)*(South.S_prod*South.S_nests+Central.C_prod*Central.C_nests+Northeast.NE_prod*Northeast.NE_nests+Northwest.NW_prod*Northwest.NW_nests)	See Methods: Stork breeding data
Pop losses	(Adult_survival*USA_pop_size)-New_skipped_breeders	See Methods: Stork breeding data
Juv survival	NORMAL(0.2, 0.1)	Borkhataria et al. 2008
Adult survival	NORMAL(0.91, 0.03)	Borkhataria et al. 2008
New skipped breeders	NORMAL(2000, 2000)	See Methods: Stork breeding data
Prev skipped breeders	NORMAL(500, 500)	See Methods: Stork breeding data
S nests	1672.41*("S_2yr.rain"-3361.2)/(2*308.3)-1172.10*("S_rain.early"-246.6)/(2*95.9)-1216.79*("S_TMAX.early"-27.1)/(2*1.0)-614.79*("S_rain.nonbreed"-765.5)/(2*154.0))+1747.64+.Prev_skipped_breeders	See Methods: Building Simulation model
S prod	1.02*("S_2yr.rain"-3361.2)/(2*308.3) - 0.74*("S_rain.yr"-1674.5)/(2*207.1) - 0.7*("S_TMAX.late"-32.3)/(2*0.8) - 0.88*("S_rain.breed"-908.3)/(2*177.0) + 0.95*("S_rain.late"-658.8)/(2*178.6) + 1.55	See Methods: Building Simulation model
S rain.yr	NORMAL(1674.5, 207.1)	See Methods: Building Simulation model
S rain.breed	NORMAL(908.3, 177.0)	See Methods: Building Simulation model
S rain.late	NORMAL(658.8, 178.6)	See Methods: Building Simulation model
S TMAX.late	NORMAL(32.3, 0.8)	See Methods: Building Simulation model
S 2yr.rain	NORMAL(3361.2, 308.3)	See Methods: Building Simulation model
S rain.nonbreed	NORMAL(765.5, 154.0)	See Methods: Building Simulation model
S rain.early	NORMAL(246.6, 95.9)	See Methods: Building Simulation model
S TMAX.early	NORMAL(27.1, 1.0)	See Methods: Building Simulation model

S urban	N/a (variable dropped in AIC _c)	See Methods: Building Simulation model
S shore	N/a (variable dropped in AIC _c)	See Methods: Building Simulation model
C nests	1457.2*(("C_TMAX.early"-26.8)/(2*1.1)) - 1571.03*(("C_rain.nonbreed"-467.0)/(2*181.6)) + 883.50*(("C_2yr.rain"-2658.9)/(2*372.4)) + 831.86*(("C_rain.early"-259.0)/(2*111.9)) + 2036.22 + .Prev_skipped_breeders	See Methods: Stork breeding data
C prod	0.36*(("C_TMAX.late"-32.4)/(2*0.7)) + 0.50*(("C_2yr.rain"-2658.9)/(2*372.4)) - 0.37*(("C_rain.yr"-1346.2)/(2*244.7)) - 0.40*(("C_rain.breed"-878.7)/(2*194.5)) - 0.19*(("C_rain.late"-613.4)/(2*160.5)) + 1.14 - 0.85*(("C_rain.breed"-878.7)/(2*194.5))*(C_shore/C_shore) + 0.69*(("C_rain.breed"-878.7)/(2*194.5))*(C_urban/C_urban)	See Methods: Stork breeding data
C rain.late	NORMAL(613.4, 160.5)	See Methods: Building Simulation model
C rain.yr	NORMAL(1346.2, 244.7)	See Methods: Building Simulation model
C urban	423.3	See Methods: Building Simulation model
C shore	159.4	See Methods: Building Simulation model
C rain.breed	NORMAL(878.7, 194.5)	See Methods: Building Simulation model
C TMAX.late	NORMAL(32.4, 0.7)	See Methods: Building Simulation model
C 2yr.rain	NORMAL(2658.9, 372.4)	See Methods: Building Simulation model
C rain.nonbreed	NORMAL(467, 181.6)	See Methods: Building Simulation model
C rain.early	NORMAL(259.0, 111.9)	See Methods: Building Simulation model
C TMAX.early	NORMAL(26.8, 1.1)	See Methods: Building Simulation model
NE nests	311.57*(("NE_rain.nonbreed"-467.5)/(2*163.5)) + 307.42*(("NE_2yr.rain"-2277.7)/(2*450.0)) + 202.59*(("NE_TMAX.early"-27.1)/(2*1.5)) - 113.07*(("NE_rain.early"-401.4)/(2*142.8)) + 1857.39 + .Prev_skipped_breeders	See Methods: Stork breeding data
NE prod	0.30*(("NE_TMAX.late"-32.7)/(2*1.1)) - 0.32*(("NE_rain.breed"-696.7)/(2*180.0))	See Methods: Stork breeding data

	$+0.25*((\text{"NE_2yr.rain"}-2277.7)/(2*450.0))$ $+0.25*((\text{"NE_rain.yr"}-1149.7)/(2*283.1)) + 1.57 -$ $1.56*((\text{"NE_rain.breed"}-$ $696.7)/(2*180.0))*(\text{NE_shore}/\text{NE_shore})$ $+0.36*((\text{"NE_rain.breed"}-$ $696.7)/(2*180.0))*(\text{NE_urban}/\text{NE_urban})$	
NE urban	173.3	See Methods: Building Simulation model
NE shore	305.6	See Methods: Building Simulation model
NE rain.yr	NORMAL(1149.7, 283.1)	See Methods: Building Simulation model
NE rain.breed	NORMAL(696.7, 180.0)	See Methods: Building Simulation model
NE TMAX.late	NORMAL(32.7, 1.1)	See Methods: Building Simulation model
NE 2yr.rain	NORMAL(2277.7, 450.0)	See Methods: Building Simulation model
NE rain.nonbreed	NORMAL(467.5, 163.5)	See Methods: Building Simulation model
NE rain.early	NORMAL(401.4, 142.8)	See Methods: Building Simulation model
NE rain.late	N/a (variable dropped in AIC _c)	See Methods: Building Simulation model
NE TMAX.early	NORMAL(27.1, 1.5)	See Methods: Building Simulation model
NE nests	$850.14*((\text{"NW_2yr.rain"}-2425.2)/(2*479.4))$ $+297.38*((\text{"NW_TMAX.early"}-27.4)/(2*1.9))$ $+274.50*((\text{"NW_rain.nonbreed"}-525.2)/(2*183.9)) -$ $114.07*((\text{"NW_rain.early"}-395.4)/(2*151.0))$ $+2672.56+\text{Prev_skipped_breeders}$	See Methods: Stork breeding data
NW prod	$0.66*((\text{"NW_2yr.rain"}-2425.2)/(2*479.4)) -$ $0.42*((\text{"NW_rain.yr"}-1224.2)/(2*310.3)) -$ $0.24*((\text{"NW_rain.breed"}-707.4)/(2*205.1)) -$ $0.23*((\text{"NW_rain.late"}-307.3)/(2*119.7))$ $+0.09*((\text{"NW_TMAX.late"}-33.0)/(2*1.4)) + 1.74$ $+0.39*((\text{"NW_rain.breed"}-$ $707.4)/(2*205.1))*(\text{NW_shore}/\text{NW_shore}) -$ $0.26*((\text{"NW_rain.breed"}-$ $707.4)/(2*205.1))*(\text{NW_urban}/\text{NW_urban})$	See Methods: Stork breeding data
NW rain.late	NORMAL(307.3, 119.7)	See Methods: Building Simulation model
NW urban	189.1	See Methods: Building Simulation model

NW shore	21.4	See Methods: Building Simulation model
NW rain.yr	NORMAL(1224.2, 310.3)	See Methods: Building Simulation model
NW rain.breed	NORMAL(707.4, 205.1)	See Methods: Building Simulation model
NW TMAX.late	NORMAL(33.0, 1.4)	See Methods: Building Simulation model
NW 2yr.rain	NORMAL(2425.2, 479.4)	See Methods: Building Simulation model
NW rain.nonbreed	NORMAL(525.2, 183.9)	See Methods: Building Simulation model
NW rain.early	NORMAL(395.4, 151.0)	See Methods: Building Simulation model
NW TMAX.early	NORMAL(27.4, 1.9)	See Methods: Building Simulation model

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