

MOVEMENT ECOLOGY OF THE AMERICAN WHITE IBIS (*EUDOCIMUS ALBUS*)
ACROSS AN URBANIZATION GRADIENT

by

ANJELIKA DOMINIQUE KIDD

(Under the Direction of Jeffrey Hepinstall-Cymerman and Sonia M. Hernandez)

ABSTRACT

The American White Ibis (*Eudocimus albus*) is a medium-sized wading bird commonly found in wetland habitats. Urbanization in wetland areas affects ibis as human modifications of the landscape reduce the overall extent of, fragment, or alter the function of existing wetlands. Since wetland degradation, ibis are increasingly found in urban areas and take advantage of anthropogenic resources. I investigated changes in ibis movement ecology by tracking ibis captured in habitats representing an urbanization gradient with GPS-GSM telemetry to define movement-based seasons and calculate seasonal ranges, site fidelity, and habitat use. Urban ibis non-breeding seasons were longer than average with small ranges, high site fidelity, and use of several urban habitat classes compared to wild ibis. Their breeding seasons were shorter than average, but were otherwise similar to that of wild ibis, showing increased range size, decreased site fidelity, and use of agricultural and wetland habitats.

INDEX WORDS: *Eudocimus albus*; GPS; urbanization; space use; site fidelity; habitat use

MOVEMENT ECOLOGY OF THE AMERICAN WHITE IBIS (*EUDOCIMUS ALBUS*)
ACROSS AN URBANIZATION GRADIENT

by

ANJELIKA DOMINIQUE KIDD

B.S., Mars Hill University, 2015

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2018

© 2018

Anjelika Dominique Kidd

All Rights Reserved

MOVEMENT ECOLOGY OF THE AMERICAN WHITE IBIS (*EUDOCIMUS ALBUS*)
ACROSS AN URBANIZATION GRADIENT

by

ANJELIKA DOMINIQUE KIDD

Major Professors: Jeffrey Hepinstall-Cymerman
Sonia Hernandez
Committee: Robert Cooper
Richard Hall
Maureen Murray

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
May 2018

DEDICATION

To my mother, who has always encouraged me to reach beyond my dreams. Thank you for teaching me that circumstance does not define the outcomes in life and that I can achieve any goal, should I put my mind to it. You have been a light in my journey, for which I will always be thankful.

ACKNOWLEDGEMENTS

First, I would like to thank my funding source and hosting institution. Funding for this project was provided by the National Science Foundation Ecology and Evolution of Infectious Diseases program (DEB-1518611), for which I am very grateful. I am also thankful to the D.B. Warnell School of Forestry and Natural Resources at the University of Georgia for hosting me as a graduate student in their esteemed program.

Next, I would like to thank my thesis advisors, Drs. Jeffrey Hepinstall-Cymerman and Sonia Hernandez. Beyond the academic and professional development that I experienced through this project, I will be forever grateful for this opportunity. The invitation to interview on its own was a light in a darker time of my life. Throughout my time working on this project, my advisors have supported me to realize my potential and have helped me find opportunities to develop my research interests. I would also like to thank my committee members, Dr. Robert Cooper, Richard Hall, and Maureen Murray, who provided expert advice and support throughout my thesis development.

For all the behind the scenes work, I would like to thank the amazing field team and labs that helped to collect data, run tests on birds. Deserving its own line of thanks, I would like to thank you for your patience and your holding of birds while I fit harnesses to the ibis. The core members, Maureen Murray, Taylor Ellison, and Henry Adams, as well as countless volunteers helped to make our field seasons both effective and memorable. I also send thanks to Catie Welch for her work on ibis that preceded mine. Your data and conclusions were pivotal in

launching this iteration of ibis research. Also, thank you to the lab of Dr. Michael Yabsley for running tests on our ibis samples to help us learn about the data.

I also extend a word of thanks to my countless mentors of the past for igniting my passion for conservation, research, and education. Among the many amazing people in my life, Dr. Scott Pearson, Mr. Alan Smith, Dr. Matthew Milnes, and Mark Hopey helped to introduce me to research and guide me to my current path. Dr. Kathy Meacham helped me to find my inner human and lead me on a journey to understand my greater purpose and reason for being. Finally, I send many thanks to the late Dr. Paul Schierhorn, who taught me how to have a conversation with an audience and how to give words greater power.

Last, but certainly not least, I would like to thank all of my labmates, friends, and family for their support through this journey. Thank you for picking me up on my worst days. Wednesday morning analysis group with Becca Cozad and Caroline Cummings, and writing groups with other members of the Hernandez lab were so helpful in that final push. I also thank members of the Hepinstall-Cymerman lab for reading drafts and helping to troubleshoot analyses. Specifically, I would like to thank Betsy Kurimo-Beechuk for your endless support and encouragement. Thank you all for your camaraderie and support as we made this journey together. To my family, thank you for understanding when I was too busy to pick up the phone and for encouraging me along my journey. Finally, I must express my profound gratitude to Nathan Weaver, for meals made, dishes cleaned, dogs cared for, and forcing me to get out every once in a while in my times of being glued to a computer. Without you, my life would not be quite so nice.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	v
LIST OF TABLES	ix
LIST OF FIGURES	x
CHAPTER	
1 INTRODUCTION AND LITERATURE REVIEW	1
The American White Ibis	1
Urbanization and Wetland Loss	2
Impacts of Urbanization on Wildlife	4
Consequences of Urban Habitat Use	7
Rationale and Significance	10
2 DEFINING SEASONS OF THE AMERICAN WHITE IBIS (<i>EUDOCIMUS ALBUS</i>)	
USING MOVEMENT CHARACTERISTICS	14
Abstract	15
Introduction	16
Methods	22
Results	27
Discussion	30
Future Directions	35

3	SPACE USE OF AMERICAN WHITE IBIS (<i>EUDOCIMUS ALBUS</i>) ACROSS AN URBANIZATION GRADIENT	49
	Abstract	50
	Introduction.....	51
	Methods.....	57
	Results.....	63
	Discussion	67
	Future Directions	72
4	CONCLUSIONS.....	87
	Introduction.....	87
	The Wild	88
	The Urban	89
	The Intermediate	90
	Continuing Research	91
	REFERENCES	94
	APPENDICES	
	A A TOTAL LIST OF GPS-TAGGED WHITE IBISES AND CAPTURE CHARACTERISISTICS OCTOBER 2015 TO NOVEMBER 2017.	107

LIST OF TABLES

	Page
Table 3.1: Model average parameters and importance.	82
Table 3.2: Models used in model averaging.	85

LIST OF FIGURES

	Page
Figure 2.1: Map of ibis capture sites in Palm Beach County, Florida.	37
Figure 2.2: Flat summary of the behavioral change point analysis results for ibis “24_LCS01”..	39
Figure 2.3: Duration of each behavioral season for individual ibis fitted with transmitters.	41
Figure 2.4: Distribution of days in each behavioral season (non-breeding-NB, search-and-dispersal-SD, breeding attempt-BA, and post breeding-PB) according to non-breeding season urban habitat use (low, intermediate, high, all combined).	43
Figure 2.5: Distribution of days spent in non-breeding nomadic and non-breeding resident seasons according to non-breeding season urban habitat use (low, intermediate, high). ..	45
Figure 2.6: Distribution of days in each behavioral season (non-breeding, search-and-dispersal, breeding attempt, and post breeding) according to ibis age.....	47
Figure 3.1: Model averaged standardized range size according to non-breeding urban habitat use (horizontal axis) and season (non-breeding blue, breeding red).....	74
Figure 3.2: Model averaged site fidelity according to non-breeding urban habitat use and season	76
Figure 3.3. Proportion of each habitat used within non-breeding and breeding ranges.	78
Figure 3.4. Selection of habitats within seasonal ranges compared to habitat availability in the state of Florida..	80

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The American White Ibis

The American White Ibis (*Eudocimus albus*) is a wading bird species that has been significantly affected by wetland habitat loss (Heath et al. 2009). In the United States, White Ibis are typically found inhabiting freshwater and estuarine wetlands throughout the southeastern states from the Carolinas to Texas. They have specific habitat requirements for foraging, roosting, and breeding that are distributed along a spatial and seasonal gradient throughout the southeastern United States. Ibis are tactile foragers, using touch sensitive sensors in the bill to probe for aquatic prey such as crayfish, fiddler crabs, and small fishes in shallow water where prey occur at high densities. These shallow water habitats are distributed throughout wetland habitats influenced by hydrologic cycles. Ibis have adapted to changing wetland distributions as nomadic foragers moving between wetlands in search of optimal foraging conditions throughout their lifetime (Gawlik 2002, Frederick et al. 2008).

Historically, most of the U.S. White Ibis population moved to Florida during the breeding season where the Everglades ecosystem provided optimal conditions for nesting and raising young. Prior to the 1960s, ibis rookeries in south Florida consisted of up to and sometimes over 100,000 pairs, with such large colonies rarely reported outside of Florida (Frederick et al. 1996). Since the late 1970s, following dramatic wetland degradation in south Florida, more recent surveys of breeding colonies across the species range demonstrate a 90% decline in the south Florida breeding population (Frederick et al. 2008). Simultaneously, breeding populations have

increased in other parts of their range such as in Louisiana, Georgia, and the Carolinas (Frederick et al. 1996, 2002). Similar patterns of population decline, including shifts in the onset of breeding attempts from November to February that were related to reduced reproductive success, have been documented for other wading bird species associated with the Everglades (e.g., Wood Stork (*Mycteria americana*)) (Frederick et al. 2002).

Approximately 20 years ago, ibis have been increasingly found in urban areas, forming recurring flocks in urban habitats. Individuals using urban areas are often foraging on terrestrial invertebrates in irrigated lawns or are fed nutrient-deficient food (e.g., bread) by people, bringing them into close and frequent contact with peri-domestic species, domestic animals, humans, and low-quality resources (Dorn et al. 2011, Hernandez et al. 2016, Murray et al. 2018). White Ibis are known to use alternative food resources such as human food waste during years of environmental stress, particularly related to water depth following years of drought or flooding, yet some do not return to using natural food items when conditions return to normal (Dorn et al. 2011). This failure to return to natural food items suggests that some individuals may continue using urban resources regardless of wetland suitability, and thus, fully rely on urban resources.

Urbanization and Wetland Loss

Around the globe, urbanization in response to human population growth is a profound source of habitat loss impacting ecological systems and wildlife populations (Ehrenfeld 2000, Dahl 2005). Wetland habitats are particularly vulnerable, with one study, Ehrenfeld (2000), reporting that 96% of wetland loss in the United States was attributable to urbanization. In the United States, the rate of wetland loss increased by 140% between 2004 and 2013 as a result of human land use change, pollution, and climate change (NABCI 2016). Dahl (2005) reports that Florida has the greatest percent area of wetland habitat of any conterminous U.S. state at

approximately 11.4 million acres, or 29% of the state's land surface. However, Florida's current wetland extent includes only 56% of the original 20.3 million acres. Florida's wetland habitat is largely concentrated in the southern portion of the peninsula (hereafter South Florida), which also includes the state's three most populous counties and the Everglades ecosystem (Kranzer 2002, Dahl 2005).

As the human population in South Florida grew from approximately 30,000 in the late 1800s to over 7 million by the year 2000, approximately 40% of South Florida's natural land, including wetland habitats, was replaced by agricultural lands and urban development (Kranzer 2002). More specifically, major wetland loss occurred between the 1950s and 1970s, estimated at 7,200 acres per year, and declined to 5,000 acres per year from 1985 to 1996 (Dahl 2005). Between 1845 and 1996 alone, 72% of the wetland loss was due to rural and urban development and 28% to agriculture (Kranzer 2002, Dahl 2005). Although the current rate of wetland loss in Florida has been greatly reduced due to federal and state level protections, the landscape and its wildlife remain impacted by the environmental changes which occurred as a result of rapid urbanization in the last several decades (Dahl 2005).

As human populations and the percentage of land used for urban living increases, the amount of wildland habitat, such as unaltered wetlands, decreases and becomes more patchily distributed across the landscape (Ogden et al. 2005). To make wetlands more hospitable for human living, natural wetland drainage networks are channelized and artificial drainage systems are implemented, controlling the flow of water between wetlands and ocean outputs. This type of water management system prevents flooding of residential and agricultural areas and provides a controlled source of water for urban living (Kranzer 2002, Ogden et al. 2005, Frederick et al. 2008). However, it also creates uncharacteristic wetland conditions such as permanently flooded,

deep water areas and permanently dry areas, which disrupts the dynamic nature of wetland ecosystems including the the natural hydrological system of the wetland on which the native biota are dependent, resulting in reduction and fragmentation of overall wetland habitat (Frederick and Mcgehee 1994, Ehrenfeld 2000, Kranzer 2002, DeAngelis et al. 2005, Ogden et al. 2005, Frederick et al. 2008).

Impacts of Urbanization on Wildlife

The distribution of suitable habitat across the landscape affects the abundance, distribution and movement of wildlife, particularly for wetland-associated species (Frederick et al. 1996, Bancroft et al. 2002). The Everglades and similar ecosystems around the world have experienced dramatic declines in native wildlife populations in wildland habitats, increases in population size and prevalence of exotic species, and increased use of urban habitats by wildlife in response to loss of wildland habitats (Ogden et al. 2005, Frederick et al. 2008, Martin et al. 2012, Varner et al. 2014).

Large populations of wading birds (e.g., species in the orders Pelecaniformes and Ciconiiformes), dependent on abundant aquatic vertebrate and invertebrate prey, have been identified as defining characteristics of South Florida wetlands (Ogden et al. 2005, Frederick et al. 2008). Wading bird distributions are related to the distribution of foraging opportunities in the landscape, which are influenced by hydrological fluctuations controlling water depth and prey densities. However, altered hydrological cycles limit the abundance and extent of aquatic populations in the wetland system by reducing dispersal opportunities and preventing breeding activities normally stimulated by seasonal variation in water depths (Frederick and Mcgehee 1994, Ogden et al. 2005, Dorn et al. 2011). Therefore, wading bird distributions are also affected

by changes in wetland hydrology (Gawlik 2002, Frederick et al. 2008, Dorn et al. 2011, Herring and Gawlik 2011).

American White Ibis and Wood Stork are wading bird species that flourished in South Florida wetlands prior to human landscape modification, and are considered to be indicator species of wetland restoration (Frederick et al. 2008). Both species are more sensitive to changes in the hydrological cycle than other birds, as they are dependent on shallow water conditions (5-20 cm) with dense prey populations (Frederick and Ogden 1997, Gawlik 2002). These optimal foraging conditions were once reliably created by natural hydrological cycles of the wetland ecosystem and breeding cycles of prey populations, and were distributed along a spatiotemporal gradient based on precipitation, slight elevation gradients, and other climatic or landscape features (Frederick et al. 2008). White Ibis and Wood Stork are adapted to these conditions as nomadic species, meaning that they will abandon foraging sites in search of better foraging opportunities when prey densities decrease at their current location (Frederick et al. 2002, Gawlik 2002, Dorn et al. 2011). However, water management strategies in human-modified wetlands do not provide the natural seasonal fluctuations in water depth to which these birds are adapted. Permanent deep water areas can provide roosting or nesting habitat, but are not suitable for foraging and thus cannot be exploited by these tactile foragers (Frederick and McGehee 1994).

The consequences of loss of optimal foraging conditions for wading birds, include reduced population size, altered distribution within their range, and use of novel resources in altered wetlands (Frederick and Ogden 1997, Frederick et al. 2008, Singh and Downs 2016). Wood Storks have experienced reduced nesting success as a result of unreliable food resources near nesting colonies, contributing to their designation as a Threatened species by the U.S. Fish

and Wildlife Service (U.S. Fish and Wildlife Service 2014). The onset of their nesting season is delayed up to 2 months compared to historical records, in response to reduced levels of foraging habitat during the dry seasons, though the overall overlap between times in which prey availability is high and nestlings are present is reduced (Frederick et al. 2008). During the nesting season, adult Wood Storks must search longer and travel further, increasing the energetic cost of raising young and making it difficult for young to learn how to forage (Herring and Gawlik 2011, Borkhataria et al. 2013). Despite their foraging similarities, reduced nesting success is not the primary driver of declines in South Florida White Ibis populations (Frederick et al. 2008).

White Ibis respond more quickly to environmental change, abandoning nesting colonies and foraging sites more readily than Wood Storks (Frederick and Ogden 1997). As a result, White Ibis breeding populations in South Florida have decreased by at least 90% between the 1930s and 1980s while populations in North and South Carolina, Texas, and Louisiana simultaneously increased in the same time period following expansive wetlands drainage efforts (Frederick et al. 1996, Frederick and Ogden 1997). These changes in population distribution may be evidence of movements out of South Florida and into other parts of their range in the southeastern United States. This is not completely unexpected for a nomadic species as they are adapted to searching for resources distributed unpredictably in the landscape (Frederick et al. 1996, 2008). For White Ibis remaining in South Florida, an increasing proportion utilize urban habitats while they are not breeding (Hernandez et al. 2016). Other ibis species that experienced loss of natural habitats or that have learned to exploit human-created habitats, such as the Australian White Ibis (*Threskiornis moluccus*) and the Hadedda Ibis (*Bostrychia hagedash*), have also demonstrated similar shifts into urban habitat (Martin et al. 2011, Singh and Downs 2016).

Human activities, such as constructing water bodies or irrigating lawns, interspersed among urban developments can attract wetland wildlife to find resources necessary for survival. Constructed wetlands, parks with water bodies and other landscapes where active supplemental feeding occurs, as well as landfills that provide food unintentionally and irrigated lawns that provide moist, easy-to-probe substrates, may provide spatially consistent, year-round reliable sources of food (Warren and Lepczyk 2012, Hernandez et al. 2016, Singh and Downs 2016). These alterations may negate the need to search for foraging habitat in natural wetlands that experience environmental fluctuations in suitable foraging habitat availability (Singh and Downs 2016). Dorn *et al.* (2011) found that in the nesting season following a drought, White Ibis increased the amount of “garbage”-- food that the study associated with urban environments and landfills -- fed to nestlings by 22.6% as compared to the previous nesting season. Therefore, White Ibis will seek out and use urban resources when their natural resources are not available (Dorn et al. 2011). However, the effects of consuming of human-provided food are currently unknown regarding successful buffering populations from decline in years of resource scarcity or potential negative long term effects. Originally attracted to wetland-like features, individuals may become dependent on human provided habitats and food resources reducing seasonal variation in habitat use and increasing site fidelity to urban areas (Martin et al. 2011, Varner et al. 2014, Gilbert et al. 2016).

Consequences of Urban Habitat Use

Use of urban resources can alter the health and behaviors of individuals by 1) encouraging individuals to aggregate at higher densities, 2) promoting contact with novel species, including pathogens 3) increasing the rate of direct contact among individuals, 4) consuming contaminated or poor quality food resources (Frederick and Mcgehee 1994, Orams

2002, Brearley et al. 2013, Gilbert et al. 2016). Urbanized populations of several species have demonstrated shifts from wildland to urban landscapes and abandonment of typical migration behaviors primarily because of consistently available urban food resources (e.g., landfills and handouts from humans), promoting sedentary behaviors (Martin et al. 2010, Gilbert et al. 2016). Animals in urban environments can also interact with humans and domestic animals directly or indirectly through feeding by people and common use of infrastructure (e.g., picnic tables, water fountains, sitting areas, etc) (Epstein et al. 2006). These experiences can lead to negative interactions between people and urban wildlife through fecal contamination of infrastructure, animal aggression and the perception or reality of transmission of zoonotic pathogens (Orams 2002, Hall and Saito 2008, Brearley et al. 2013, Poessel et al. 2016).

Animals that forage socially, such as ibis and stork species, may be influenced to forage in denser aggregations in urban settings than in the wild. Increased density during foraging events can increase the transmission of density-dependent transmitted pathogens (Hall and Saito 2008, Brearley et al. 2013). Feeding aggregations may also include common urban and peri-domestic species (e.g., Muscovy Duck (*Cairina moschata*)), which are common reservoirs of pathogens, resulting in pathogen spillover into novel hosts (Hoelzer et al. 2011). Increased reliance on urban resources can exacerbate health concerns for both human and wildlife populations.

As individuals move into urban habitats and come into close and frequent contact with urban stimuli, they may experience behavioral changes associated with habituation to the urban environment. Animals fed by people and living in urban areas may lose their perception of danger to humans, domestic animals, vehicles, and other potential threats, especially if they associate those dangers with non-consequential effects or benefits (Orams 2002, Clucas and

Marzluff 2012, Gravolin et al. 2014, Stewart et al. 2016). As animals become more habituated to the human presence and associate humans with food, the development of aggressive behavior is a concern when animals do not receive expected food (Orams 2002, Maljkovic and Cote 2011). For example, urbanized Australian White Ibis which have been observed exhibiting strong begging behaviors towards people and become aggressive when food is not provided (Martin et al. 2011).

Migratory or nomadic species can exhibit altered movement behaviors and habitat use from their typical natural history when they become dependent on utilizing urban environments (Orams 2002, Martin et al. 2011, Varner et al. 2014, Gilbert et al. 2016). However, species that are adapted to fragmented habitats or systems with periodic disturbance, may adapt more easily to use urban ecosystems (Marzluff 2001). Such species may have behavioral plasticity regarding movement patterns and resource requirements, allowing them to more easily adapt to human-related resources. Species utilizing urban resources have been documented using smaller areas, having fewer foraging locations, and existing in larger aggregations as they exploit a habitat with reliable resources and habitat conditions (Marzluff 2001, Martin et al. 2011, Varner et al. 2014, Poessel et al. 2016). For example, White Stork (*Ciconia ciconia*) and Hadedda Ibis utilizing urban environments have abandoned their migratory behaviors between seasons (Gilbert et al. 2016, Singh and Downs 2016). Movements typically associated with searching for food become unnecessary as individuals exploit human provided refuse areas such as landfills or artificially maintained foraging conditions through processes such as watering lawns (Orams 2002, Gilbert et al. 2016, Singh and Downs 2016). For some species in which migratory or foraging behaviors are passed from parents to offspring by learning, reliance on urban resources may be exacerbated as natural foraging and/or searching behaviors are not learned (Orams 2002).

Rationale and Significance

As aggregations of wildlife in urban habitats grow larger and the amount of time spent in urban habitats increases, the risk of negative interactions between wildlife and human populations increases (Brearley et al. 2013). For example, populations of Australian White Ibis have successfully colonized urban habitats, but are considered a nuisance species due to their aggressive begging behaviors, damage to public areas, and ability to carry zoonotic pathogens such as *Salmonella* spp. (Martin et al. 2011, Hoque et al. 2012). Although White Ibis in South Florida are increasingly found in urban areas, little is known about how their health and behavior is affected by urban habitat use (Dorn et al. 2011, Hernandez et al. 2016). Hernandez (2016) and Murray et al. (2018) report that White Ibis sampled in urban areas have a higher prevalence of *Salmonella* spp. infection, although adult White Ibis typically do not develop clinical disease, and consume more human-related, nutrient-deficient food than those sampled in wetland areas. Several *Salmonella* strains isolated from urban White Ibis have been matched to cases of human salmonellosis within the same area and year sampling of ibis occurred (Hernandez et al. 2016).

As a nomadic species, White Ibis are expected to disperse across the Southeast U.S. region in response to shifting resource distributions throughout the year. However, it is unknown if White Ibis that use urban habitats will exhibit nomadic movement behaviors characteristic of the species or if they will abandon nomadic movements and adopt a movement pattern more similar to home range residency. Since urban areas do not have the resources required for breeding, it is likely that urban individuals move from urban habitats to wetlands, encountering wild, susceptible individuals.

In this thesis we investigate the movement ecology of ibis across an urbanization gradient to better understand how ibis ecology is altered when using urban habitats. Overall, we

hypothesized that synanthropic ibis, or those associated with humans and human-created habitats (Johnston 2001) at least part of the year, will differ in the timing and extent of movement compared with wild ibis, exhibiting evidence of urban adaptation during the non-breeding season, but that these differences are less apparent during the breeding season when both urban and non-urban birds rely more heavily on natural food resources.

In Chapter 2, we examine changes in the annual cycle of ibis with regards to the amount of time they spend in different behavioral seasons, such as breeding and non-breeding. Ibis typically need 10 weeks for breeding activity between nest initiation and young independence, exhibiting area-restricted movements to nest sites. Non-breeding seasons should encompass majority of the year and be characterized by nomadic movements as ibis are no longer restricted to nest sites. However, as ibis move into urban areas and learn to exploit anthropogenic resources, they may develop synanthropic behaviors and reduce their nomadic movements. We hypothesized that synanthropic ibis will have more restricted movements in non-breeding seasons and that they would have altered annual cycles compared to wild ibis, such as longer pre-breeding seasons as they look for appropriate nesting locations. We found that ibis that exhibit more synanthropic behaviors, measured by their use of urban habitats in the non-breeding season which has been related to increase use of anthropogenic foods (Murray et al. 2018), have longer, resident non-breeding seasons and shorter breeding seasons compared to ibis with less synanthropic behaviors, or those that rarely use urban habitats. These "urban" ibis also often lack intermediate transition periods between breeding and non-breeding seasons. These results suggests that ibis living in urban areas may return directly to non-breeding ranges after breeding, where they center their activities around specific urban habitats.

In Chapter 3, we investigate ibis space use, site fidelity, and habitat use and selection between non-breeding and breeding seasons. Ibis are expected to have more constrained resource selection while breeding than in non-breeding seasons. During the breeding season, they typically restrict their resource use to roost trees that are suitable to nesting and freshwater foraging habitats to support the growth of their young, which cannot efficiently excrete excess salt and will, therefore, not develop properly when fed from estuarine habitats. We hypothesized that synanthropic ibis would have smaller ranges and higher site fidelity in the non-breeding season compared to non-urban ibis. As urban ibis transitioned into breeding seasons, we expected their movements and habitat use to become more similar to non-urban ibis as they moved into wetlands to support their reproductive resource needs. We found that more synanthropic ibis, or those that spend more time in urban areas during the non-breeding season, have smaller ranges and higher site fidelity in non-breeding seasons than less synanthropic ibis, but that their ranges and site fidelity become more similar to less synanthropic ibis in the breeding season. Additionally, an intermediate class of ibis that used urban and wetland habitat types equally consistently had the smallest ranges and highest site fidelity throughout the year. For synanthropic ibis, we also found that they switched their habitat use from urban habitat classes in the non-breeding season to incorporate agricultural and wetland habitat classes within their ranges in breeding seasons. These results suggest that ibis using urban habitats in the non-breeding season alter their movement behaviors in the breeding season to incorporate habitats with resources more suitable for rearing young, and are thus not completely reliant on urban areas throughout their annual cycle.

It is important to understand how White Ibis movement behaviors and habitat selection are affected by their habitat use to better understand the extent of ibis urban habitats and

behavioral change and to predict how their populations might respond to future urbanization and loss of natural foraging habitats. Continued growth of urban development, both in extent and in density, simultaneously removes wildland habitats for wildlife, which may result in wildlife populations encountering human populations at higher rates. For those people who are motivated by environmental concerns and animal welfare, the outcomes of these habitat loss scenarios can provide an opportunity for people to learn how to be better stewards through for the health of wildlife populations and the environment (Warren and Lepczyk 2012). In Chapter 4, I summarize the main findings of this study and discuss the implications of urban foraging for ibis health and conservation, outline new research directions and discuss the wider implications of this research for other species that live in urbanizing environments. This information will inform future conservation and management plans to protect the species and reduce the risks of future human-wildlife conflict. By understanding how these birds are responding to urban development, we may better understand the future of the South Florida ecosystem conservation and management.

CHAPTER 2
DEFINING SEASONS OF THE AMERICAN WHITE IBIS (*EUDOCIMUS ALBUS*) USING
MOVEMENT CHARACTERISTICS¹

¹ Kidd, A. D., J. Hepinstall-Cymerman, and S. M. Hernandez 2018. To be submitted to *Journal of Animal Ecology*.

Abstract

Annual cycles for animals are defined by the transitions between different life stages or behavioral states. During these cycles, animals exhibit changes in their behaviors, resource needs, or spatial locations. As animals adapt to changing environmental conditions, such as climatic shifts and anthropogenic disturbances, conventional methods to define seasons may not accurately characterize the timing of these cycles. The annual cycles of the American White Ibis (*Eudocimus albus*) are typically associated with wet season-dry season hydrologic regimes in wetland habitats and are flexible to accommodate variability between years and across their range. Extensive urbanization has been linked to reduced importance of environmental cues related to seasonality, and altered behaviors across seasons for many species globally. Our objective in this chapter was to determine if birds with greater use of urban habitats during the non-breeding season differ in their seasonality compared to birds with greater use of natural habitats, and whether these differences varied by movement-derived seasons. We used behavioral change point analysis to define seasons of GPS tracked ibis captured in locations that represent a gradient of urbanization. We found that individuals that spent more time in urban habitats in the non-breeding season had longer non-breeding seasons, shorter search-and-dispersal and breeding seasons, and often lacked post-breeding seasons, transitioning directly from breeding to non-breeding seasons, compared to individuals with lower non-breeding urban habitat use. Movement behaviors within non-breeding seasons also differed between ibis with low and high levels of non-breeding urban habitat use. Ibis with low levels of urban habitat use were more likely to have nomadic movement behaviors as compared to ibis with high levels of urban habitat use that had movement behaviors restricted smaller areas. .

Introduction

Animal annual cycles and movements are often related to abiotic environmental conditions such as day length and temperature, temporal and spatial patterns of resource quality and abundance, and the behavioral state of the individual (Ferguson and Elkie 2004, Birkett et al. 2012). As characteristics of an animal's movements change over time in response to shifts in the animal's state and changes in resource requirements, different movement patterns emerge (e.g., migration, nomadism, residency). These movement patterns are subjected to selective pressures as populations evolve to changing environments and landscapes (Partecke and Gwinner 2007, González et al. 2017). Traditionally, research and management efforts have focused on the wildlife ecology of populations during particular phases of the annual cycle, namely the breeding season. However, in the face of changing environments and human landscape modification, it is important to consider the factors affecting individual's behavior and fitness throughout their annual cycle rather than in a single season (e.g., breeding) to better manage populations (Hostetler et al. 2015, Fayet et al. 2016).

Many species exhibit distinct behavioral states in which their movement patterns change due to fluctuating resource availability, mating and breeding requirements, and altered environmental characteristics (Grund et al. 2002, Shephard et al. 2015). These movement patterns can shift from area-restricted movements such as territory or home range establishment, direct or linear movements between two spatially distinct territories or ranges to exploit a temporary resource between the two locations, or nomadic movements that show less clear patterns on the landscape. Resident animals establish home ranges or territories that are maintained throughout the year, rarely changing in spatial location (Harris and Reed 2002, Partecke and Gwinner 2007). Dispersal or migratory movements often emerge as individuals

follow changing resource distributions or move to locations that provide the most optimal resources during a certain time of year (Ferguson and Elkie 2004, Kessel et al. 2014). Migrations are typically direct and cyclical in nature as individuals follow established ecological patterns (e.g., neo-tropical migratory birds travelling directly from the tropics to North America following spring green-up in the northern hemisphere). In contrast, nomadic behaviors are those which are intermediate between resident and migratory behaviors. Nomadic animals move in a series of unidirectional dispersals to exploit resources that are ephemeral, occurring stochastically or vary in abundance seasonally. Some resources are associated with weather patterns; for example, water levels fluctuate through the wet/dry seasons of wetland habitats that affect the availability of food resources which become available through changing water levels for species such as Snail Kites (*Rostrhamus sociabilis*) (Bennetts and Kitchens 2000) and wading birds (Gawlik 2002).

Breeding-related movements often occur in relation to some environmental cue signaling optimal conditions for rearing of young. For species that offer parental care to their young, movements are often restricted to nest or den sites until the young can move independently. Non-breeding ranges are often larger than during the breeding season as individuals are released from the constraints of rearing young. Individuals may expand their territories, switch to nomadic movements around a landscape, move faster, or travel longer distances when no longer restricted to nest and den sites (Harris and Reed 2002, Ferguson and Elkie 2004, Lenz et al. 2015). Non-breeding seasons typically occur in the time of year when resources in the breeding range are scarce, requiring individuals to search more, inhabit lower quality habitats, or to migrate to distinct non-breeding ranges (Lenz et al. 2015).

Behavioral changes in conjunction with seasonal change can be used to define “behavioral seasons” based on the actual state (e.g., reproductive, migratory) of individuals, which may differ from the typical vegetation phenology or wet season-dry season cycle definitions of seasons. Determining behavioral seasons is therefore critical to furthering our understanding of animal ecology and wildlife management decisions (Vander Wal and Rodgers 2009, Singh et al. 2012). Conventional methods to define behavioral seasons rely on the examination of abiotic factors or established annual cycles in the literature to define seasonal change points, or temporal cutoffs between defined seasons. However, climatic variability over large landscapes, human-modified habitats, and individual variation can reduce the effective designation of seasons based on climatic factors and historical records alone (Partecke and Gwinner 2007, Vander Wal and Rodgers 2009, Birkett et al. 2012, Shephard et al. 2015).

The onset of environmental cues which stimulate movements varies across latitudinal gradients and by year; this results in some portions of the population that transition between states at different times (Singh et al. 2012, Kessel et al. 2014). For example, in a study on Moose (*Alces alces*) populations, Singh *et al.* (2012) found that populations living at higher latitudes experienced a higher degree of seasonality than individuals at lower latitudes and thus began their migrations south to better conditions earlier. Populations living at the southernmost latitudes in the study, where environmental conditions were more stable, exhibited nomadic or resident movement behaviors. Individuals living in altered and particularly urban environments can vary in their seasonality as they experience resource variability that differs from that of their wildland counterparts.

In human-altered environments, environmental cues may be reduced in their importance or shifted in time (Partecke and Gwinner 2007, Duckworth et al. 2010, Duckworth and Altwegg

2014). Individuals living in urban environments and exhibiting synanthropic behaviors have been found to alter their seasonal movement behaviors by increasing their site fidelity (i.e., repeated use of a particular location), reducing their range size, giving up migratory movements, or breeding year round rather than in response to environmental cues (Johnston 2001, Martin et al. 2012, Duckworth and Altwegg 2014, Shephard et al. 2015, Gilbert et al. 2016). For example, Haded ibis living in urban areas may breed year round as they forage in irrigated lawns (Duckworth et al. 2010); and European White Storks that live near landfills maintain nesting territories year-round rather than migrating during the winter (Gilbert et al. 2016).

Technological advances in animal tracking such as GPS miniaturization and satellite [Argos] and cellular [GSM] transmission methods have allowed researchers to examine animal behaviors at finer spatial and temporal scales (Cagnacci et al. 2010). By examining animal movement tracks, researchers can identify changes in behaviors related to seasonal changes. This approach is based on the individual's movements rather than using environmental characteristics or relying on seasonal definitions derived from the literature. Additionally, this approach helps identify behavioral variation related to changing environmental conditions, and can identify important areas for conservation (Birkett et al. 2012, Singh et al. 2012, Shephard et al. 2015). However, as technology advances and animal tracking data becomes available at finer scales, difficulties may arise due to complex spatial and temporal autocorrelation in the data and irregular sampling schedules that violate the assumptions of common analytical methods (Edelhoff et al. 2016).

Methods exist which can analyze consecutive points, known as a trajectory or track, which form the basis of understanding of how and where an animal is moving. Location data are samples of a true movement path representing the actual movement and characteristics of an

individual, such as speed and time spent at a particular site. Many techniques and associated metrics have been developed to analyze GPS location data (Gurarie et al. 2016, Edelhoff et al. 2016).

Behavioral change point analysis (BCPA) is a tool that describes animal behaviors and can detect changes in movement characteristics from tracking data that are difficult to interpret visually, or with data structures not suitable for other techniques (Gurarie et al. 2009, Edelhoff et al. 2016). BCPA uses moving window and likelihood methods to examine the time series of movement data to identify points in which the underlying structure (e.g., mean velocity) of the movement track changes. These change points correspond to changes in the individual's behavior. This method has been used to define both large and small-scale movements such as separating migratory segments of animal migrations or identifying foraging versus resting bouts within a single day (Garstang et al. 2014, McEvoy et al. 2015, Mingozi et al. 2016, González et al. 2017, Walden-schreiner et al. 2018).

The American White Ibis (*Eudocimus albus*) is a medium-sized wading bird that primarily lives in freshwater and estuarine wetlands. Considered nomadic, ibis frequently change foraging and roosting sites as they follow variable wetland conditions. Their movement behaviors are most flexible during the non-breeding season, opportunistically moving between wetlands in search of foraging conditions such as shallow water with dense prey populations. While nesting and rearing young, their movements and habitat use are more restricted compared to non-breeding behaviors as they shift their needs to selecting nest habitat and caring for young (Bildstein 1993a, Heath et al. 2009). Nests are often built on tree islands in freshwater wetlands that serve as rookeries for breeding colonies. Freshwater wetlands are selected because young ibis cannot excrete salts as well as adults and, thus, will not develop properly if fed food from

estuarine habitats (e.g., fiddler crabs) (Bildstein 1993a). Therefore, parent ibis restrict their foraging to freshwater habitats near the rookery to support the growth of nestlings and the energetic needs of parents (reviewed in (Bildstein 1993a, Frederick et al. 1996, Heath et al. 2009)).

Ibis living in South Florida are increasing their use of urban habitats in recent decades. This shift from wetland to urban habitat use is likely due to massive wetland loss and degradation. While living in urban habitats, ibis can take advantage of anthropogenic resources and exhibit resident rather than nomadic movement behaviors as they lose their need to search for foraging opportunities (Hernandez et al. 2016, Welch 2016, Murray et al. 2018). Ibis use anthropogenic foods as a foraging resource during years of environmental stress, and also when living in urban habitats (Dorn et al. 2011, Murray et al. 2018). Though urbanized ibis may spend the majority of their time in urban habitats, these areas typically lack the requisite resources for establishing breeding colonies and rearing young, such as protected tree islands. Thus, urbanized ibis are likely to make dispersal or searching movements to locate appropriate breeding locations.

Our objective in this study was to determine if birds with greater use of urban habitats during the non-breeding season exhibit different seasonal patterns from birds with greater use of natural habitats, and whether these differences varied by ibis-derived seasons (e.g., breeding, pre- and post-breeding, non-breeding). Specifically, we analyzed data collected from GPS transmitters using BCPA to define behavioral seasons of GPS tagged ibis. We examined the amount of time ibis spent in each behavioral season in relation to the amount of time they spent using urban habitats. We predicted that: (a) ibis in urban habitats will exhibit more restricted movements during non-breeding seasons compared to ibis in wetland habitats, which will exhibit

more nomadic movements during non-breeding seasons; (b) the duration of time spent in each season will differ according to the degree of non-breeding urban habitat use; and (c) the amount of time spent in breeding and non-breeding seasons will differ based on age because older birds likely have more experience with and memory of their environment.

Methods

Study site: Palm Beach County, Florida

Palm Beach County, FL provides an opportune location to study the effects of urbanization on the American White Ibis because of its relative rapid urbanization and growth. Palm Beach County is Florida's third most populous county, with approximately 1.4 million people (Florida Legislature 2016). Within this county, 55% of the human population lives in only 16.6% of the county's land area, which primarily consists of coastal incorporated urban areas (Palm Beach County 2015). The remaining 83.4% of Palm Beach County's area is unincorporated land, primarily composed of residential areas (15.4%), agricultural lands (40.6%) (USDA 2012), and natural lands (44%) (American Forests 2007). Urbanized, densely populated areas are juxtaposed against natural wetland areas and agricultural lands, which provide ibis with numerous resource options (i.e., foraging and roosting resources) on both a daily and seasonal basis. Within Palm Beach County, we chose 15 capture sites that represented a range of urbanization from urban parks where ibis are actively provisioned by human visitors, to large wetland complexes where ibis have little contact with humans (Figure 2.1). Since all wetlands in this portion of Florida have been modified to control water levels and channelized to permit easy passage of boats, there are no true un-modified wetlands.

Ibis Capture and Transmitter Deployment

To outfit ibis with GPS transmitters, they were captured utilizing two methods: ibises in urban parks were captured using fishing line leg lassos or a manual flip-trap baited with bread (Herring et al. 2008, Parker et al. 2008, Hernandez et al. 2016). Ibises in wetlands were captured with mist nets and decoys, as they could not be baited or approached (Heath and Frederick 2003). All methods were operated by at least two individuals to ensure quick and safe extraction of birds upon capture. Once captured, ibises were aged by plumage, weighed, and fitted with Ecotone GPS-GSM transmitters (North Star Science and Technology, Oakton, VA, USA) using a backpack harness (Bildstein 1993b, Herring and Gawlik 2011, Humphrey and Avery 2014). Transmitters were only applied to ibis for which the transmitter, harness, and identification band were less than 3% of the bird's mass (Casper 2009). All animal handling procedures were reviewed by the University of Georgia's Institutional Animal Care and Use Committee (IACUC # A2016 11-019-Y2-A0). GPS units received up to 12 locations per day at a maximum of 2-hour intervals, primarily during daylight hours. GPS units were allocated among capture sites such that there were 2-4 deployed units per capture site.

Ibis were captured and fitted with transmitters during the following time periods: October - November 2015 (n=15), February - March 2016 (n=17), June - July 2016 (n=5), October - November 2016 (n = 4), and February - March 2017 (n=7). GPS transmissions were monitored until 8 November 2017, or until transmitter failure. As ibis got older through the duration of their deployment, we added one to the ibis's estimated age at capture each summer in the deployment history. For example, an ibis captured in winter 2015 that was aged as a 2 year old was considered a 3 year old in summer 2016 season. Conversely, an adult ibis with all white plumage cannot be reliably aged to a specific year beyond a 3 year old. As such, we recorded all adult ibis as their youngest possible age and similarly added 1 to their age each to each summer (e.g., an

adult ibis captured in winter 2015 that was considered 3, and then aged to 4 in the summer 2016 season).

Urban Habitat Use

Daytime locations for all individuals during non-breeding seasons were used to represent the level of synanthropic association (Johnston 2001). This subset of locations was chosen to represent least constrained habitat use (i.e., can use freshwater wetlands, brackish wetlands, or urban habitats), as opposed to nighttime or breeding locations in which an individual's choices are constrained by specific resource needs. Non-breeding urban habitat use was summarized using the 2016 Cooperative Land Cover (CLC version 3.2) map for the state of Florida (FWC and FNAI 2016) and the C-CAP coastal land cover dataset (NOAA 2010) for coastal regions of southeastern states outside of Florida. The CLC map is a 10-meter resolution raster geospatial layer with 234 land cover classes, while the C-CAP map is a 30-meter resolution layer with 24 land cover classes.

For this chapter, we were primarily interested in differentiating urban versus other habitat use, so we reclassified land cover classes into 6 classes: urban, wetland, agriculture, coastal, open water, and all other terrestrial land cover types (Murray et al. 2018). We defined urban habitat use as the mean proportion of urban land cover within a 650-meter radius of daytime non-breeding locations. The 650-meter radius was derived selected using a first passage time analysis (FPT) to estimate the scale of ibis foraging (Murray et al. 2018). First passage time calculates the time it takes for an individual to leave a circle of fixed radius, representing the scale of different types of movements. We ran FPT for all individuals to find the minimum optimal radius, which we considered the scale of an individual's localized movements, and used the median radius value (650-meters) to represent the minimum scale of habitat selection (Murray et al. 2018). This

buffer was used to account for the urban habitats at ibis GPS point locations and the area around the location, accounting for uncertainty in ibis locations within the 2-hour window of locations, use of edge habitats, and GPS error.

Behavioral Change Point Analysis

To classify an individual ibis's movement track (i.e., sequential locations) into behavioral seasons, we performed behavioral change point analysis (BCPA) separately for each ibis using two movement patterns: persistence velocity and tortuosity in Program R version 3.4.3 (R Core Team 2016) using the *bcpa* package (Gurarie et al. 2009, Gurarie 2013, 2014). Persistence velocity was calculated from the velocity, angle of the trajectory, and distance moved between successive GPS locations to represent the combination of speed and direction of movement (i.e., is the animal moving straight and fast, or turning slowly). Tortuosity is a summary of the turning angles observed between locations used to describe how many turns and how sharply they were made away from a linear path. For the BCPA analysis of each bird, we used a sub-sampling window size of 120 sequential location observations to reflect a 10-day period in which ibis will locate, exploit, and abandon a new wetland foraging site (Gawlik 2002). Within BCPA, we used a "flat summary" to refine the selection of behavioral change point by selecting the most significant change points from minor change points identified within a new 10-day window. The track segments between change points identified by BCPA are referred to as "bouts" and correspond to segments of the track where the parameter estimates for the movement statistic are stable indicating the individual's movement behavior is consistent.

The output of BCPA is a table of change points with the related mean, standard deviation and temporal autocorrelation of the movement statistic corresponding to the segment of the track before the change point. The BCPA output can be represented graphically showing the change in

the movement statistic over time. The vertical bars indicate the temporal change points, while the line width indicates the number of times the change point was selected within the specified moving window (Figure 2.2a). Minor change points are filtered from the BCPA by selecting significant change points from minor change points within a temporal window (e.g., 10 days) using the “flat” summary in the BCPA method (Figure 2.2b). An example output for ibis 24_LCS01 (Figure 2.2) is an example of the BCPA output showing the unfiltered versus filtered change points and their corresponding movement statistics.

We then determined the number of distinct behaviors exhibited by each ibis by examining the mean, standard deviation, and autocorrelation values for each bout identified by both persistence velocity and tortuosity BCPAs. For example, 24_LCS01 showed 10 bouts in the persistence velocity BCPA (Fig. 2.2b). Unique combinations of these six values were classified into behaviors using hierarchical cluster analysis in the base packages of Program R version 3.4.3 (R Core Team 2016). We evaluated the effective classifications of 6 clusters using a visual analysis of locations in ArcGIS 10.4.1 (ESRI 2016). If the visual analysis implied the classifications were too fine or too coarse, we re-ran the cluster analysis with 4 or 8 clusters, respectively. For example, when evaluating the classifications of 6 clusters, if we consistently found two adjacent bouts that occupied the same space and had the same visual pattern across the landscape, but were identified in separate branches within the same nested hierarchy, we considered the classifications too fine and re-ran the cluster analysis with 4 clusters.

Once we identified the behavior classification associated with each bout, we segmented the location track for each individual by considering the bout identified from the persistence velocity and tortuosity BCPA results, the behavioral classification from the hierarchical cluster analysis, time of year in comparison to the literature (Heath et al. 2009), and amount of time

spent in a particular location. Geographically and temporally adjacent bouts with similar cluster values were combined into one behavioral season. Thus, each bout was assigned a behavioral season by considering a combination of time of year (e.g., non-breeding, breeding) and movement characteristics (e.g., widespread vs. local).

We compared the amount of time individuals spent in each defined behavioral season to determine if birds with greater use of urban habitat during the non-breeding season had: 1) non-breeding behavioral seasons with less movement, and 2) spent different amounts of time in each behavioral season as compared to birds with lower use of urban habitat during the non-breeding season. Finally, we compared age of birds to time spent in each behavioral season to ascertain if experience may alter an ibises' movement behavior.

Results

Ibis Captures and GPS Tracking

Between October 2015 and February 2017, 48 GPS transmitter deployments were made. Ibis captures were equivalently distributed across an urbanization gradient from areas with 0 to 91 % urban land cover within a 650-meter radius around the capture site (Figure 2.1). The mass of individuals ranged from 800 to 1240 grams (mean: 962). The mean transmitter to body weight percentage was 2.67 % [2.05 – 3.29%]; assuming that transmitter weight (vs shape or attachment method) is the predictor for influencing movement, any influence of the transmitter should be minimal (Casper 2009). Due to this mass requirement, most individuals selected for transmitter deployment were adult males (80% age 3 or older at capture; 36 males, 12 females). Estimated ibis age over the sampling duration ranged from 2 to 6 or more years. Deployment from release date until transmitter failure, individual death, or the termination date of 8 November 2017 ranged from 10 days to 757 days (mean: 327 days). Of the transmitter failures, 13 occurred

between 30 December 2016 and 2 January 2017 corresponding to the deactivation of some 2G GSM cellular network towers, which were the method of remote data transmission between the transmitters and the data server. We removed 18 individuals from the analysis due to limited available data (< 3 seasons or < 30 days). See Appendix A for full details of all tagged ibis.

Behavioral Season Definitions

We determined the appropriate number of clusters for the hierarchical cluster analysis to be 4 following visual inspection of 6 and 4 clusters. The 4 clusters included movement behaviors that reflected: (1) local movements with no clear activity center, (2) local movements with one main activity center, (3) widespread movements with an apparent range of movement between many sites or movement between 2 or more activity centers, or (4) long linear dispersal movements or widespread movements with no clear activity center. Movements with no clear activity center were considered nomadic as these patterns suggest an individual's use of several locations across its range without a clear pattern of movement. In combination with time of year, we determined 5 behavioral seasons: (1) non-breeding resident, (2) non-breeding nomadic, which include both local scale and more widespread nomadic movements, (3) breeding search-and-dispersal, (4) potential breeding attempt, and (5) post-breeding movement, where an individual moves from breeding to non-breeding locations or reduces their restriction to nesting areas.

We expected each ibis to exhibit all behavioral seasons sequentially: non-breeding, breeding search-and-dispersal, breeding attempt, post-breeding movement, and return to non-breeding. We calculated the number of expected seasons for each individual by counting the number of expected seasons between the first and last season in the movement track. Skipped seasons were evaluated where a season was missing in the sequence of an individual's movement

track (e.g., an individual exhibits a non-breeding season immediately followed by a breeding season, skipping the intermediate search-and-dispersal season). While all individuals exhibited some form of a non-breeding season when expected, we identified only 28 out of the 33 expected search-and-dispersal seasons, 33 out of 35 expected instances of breeding attempts, and 16 out of 26 expected instances of post-breeding movements across all individuals. Ibis spent on average 102.5 days [22 minimum, 352 maximum] in non-breeding seasons, 79 days [0, 202] in search-and-dispersal seasons, 69 days [0, 129] in breeding seasons, and 34 days [0,115] post-breeding seasons. (Figure 2.3)

Ibis' use of urban habitat classes in the non-breeding season ranged from 1.27% to 95.55% of the area within 650-meter of daytime non-breeding locations. We classified an individual's use of urban habitats during the non-breeding season into three classes based on the values that define 3 quantiles relative to the probability distribution in the data; in other words, we divided the distribution of non-breeding urban habitat use into 3 equal parts. The quantiles were defined by cut points at 0.33 and 0.80. "Low", "intermediate", and "high" urban-use classes were defined as a) non-breeding urban habitat use < 0.33 % of area within 650-meter radius of point locations; b) non-breeding urban habitat use >0.33 % and < 0.80%; and c) non-breeding urban habitat use > 0.80, respectively. Ibis with high non-breeding urban habitat use (hereafter, high urban-use ibis) spent more time in non-breeding seasons than ibis with intermediate and low urban habitat use (hereafter, intermediate urban-use ibis and high urban-use ibis). In contrast, high urban-use ibis spent less time in search-and-dispersal and breeding seasons than the other two groups. Low urban-use ibis spent more time in search-and-dispersal and breeding seasons than the overall median for those seasons when all individuals were pooled; however, they spent less time in post-breeding seasons. Intermediate urban-use ibis were highly variable in their

duration for each season in relation to the overall distribution of locations. For instances where a season was skipped in the expected sequence of behavioral seasons: 3 of the 5 skipped search-and-dispersal seasons were skipped by intermediate urban-use ibis; 2 skipped breeding seasons were by intermediate and high urban-use ibis; and 4 and 5 of the 10 skipped post-breeding seasons were skipped by intermediate and high urban-use ibis, respectively (Figure 2.4).

High urban-use ibis were more likely to exhibit non-breeding resident behaviors with 63% of their non-breeding seasons being considered non-breeding resident. In contrast, 82% of non-breeding seasons for low urban-use ibis were considered non-breeding nomadic, while intermediate urban-use ibis exhibited both non-breeding local and nomadic seasons equally. Non-breeding nomadic seasons tended to be shorter (median = 82 [22, 212]) than non-breeding resident seasons (median = 127 [67, 352])(Figure 2.5).

Ibis seemed to spend more time dedicated to breeding as they get older. The amount of time spent in search-and-dispersal seasons declined with increasing age, while the length of breeding and post-breeding seasons increased with increasing age. The youngest individuals spent the most time in non-breeding seasons while other age classes were highly variable. There was no evident trend in which age class skips particular seasons as all age classes were evenly represented among skipped seasons (Figure 2.6).

Discussion

The American White ibis has a complex annual cycle with flexible non-breeding, migratory, and breeding schedules that are adapted to living in a highly variable wetland environment (Frederick et al. 1996, Heath et al. 2009). Because this species appears to be adapting to urban living, their movements range anywhere from widespread nomadic to local residency. Using BCPA and hierarchical cluster analysis, we defined behavioral seasons for GPS

tracked ibis and described relationships between behavioral seasons, synanthropic association, and age. In support of hypotheses 1 and 2, we found that an ibis's use of urban habitats during the non-breeding season, representing a period of least constrained habitat use and highest potential synanthropic association, is related to the type of movements they exhibit in the non-breeding season, and the length of time they spent in each season. High urban-use ibis tend to have longer non-breeding seasons with restricted movements, and spend less time in breeding seasons than ibis with low and intermediate urban-use ibis. In support of hypothesis 3, we found the length of non-breeding seasons decreases while the length of breeding seasons increased as ibis get older.

Nomadic versus Resident Non-Breeding Seasons

We identified two types of non-breeding seasons for our ibis: those with nomadic movements versus those exhibiting range residency. Of these two non-breeding season types, high urban-use ibis were more likely to engage in longer resident non-breeding seasons where they exhibited activity centers in particular locations. Low urban-use ibis were more likely to have shorter nomadic non-breeding seasons where locations were scattered across the landscape without evidence of a fixed pattern. Local residency has been related to high site fidelity in urban areas for many species (e.g., (Martin et al. 2012, Duckworth and Altwegg 2014, Gilbert et al. 2016)). Urban areas can have plentiful resources that are consistently available in contrast to natural resources that are distributed in space and time, allowing high site fidelity to a particular area rather than requiring nomadic or more widespread movements (Martin et al. 2012, Duckworth and Altwegg 2014, Gilbert et al. 2016, Belton et al. 2016).

Several studies on American White Ibis show evidence of urban adaptation. Murray et al. (2018) found that ibis captured in urban habitats throughout the year have isotopic signatures that

indicate a diet primarily composed of human-associated, carbohydrate-rich foods (e.g., bread) rather than high protein wetland-associated foods (e.g., crayfish). In a similar study, Dorn *et al.* (2011) found that during a breeding season following a drought year ibis were more likely to feed their young human-related foods than wetland-related foods. When normal conditions resumed, many individuals did not return to wetland foraging. In other species, urban adaptation is linked to altered movement behaviors; these are often restricted as individuals use urban habitats as refuge sites or alternate habitats (Grund *et al.* 2002, Partecke and Gwinner 2007, Martin *et al.* 2012, Duckworth and Altwegg 2014, Shephard *et al.* 2015, Gilbert *et al.* 2016, Belton *et al.* 2016). We speculate that the difference in non-breeding resident and non-breeding nomadic seasons was related to high site fidelity and selection of urban over natural wetland resources.

Differences in Season Duration

Ibis spent most of their time outside of breeding seasons. Studies on ibis annual cycles report that there are about 10 weeks between incubation and young independence, though some studies find breeding activities ranging from 8 weeks to 6 months (Heath *et al.* 2009). Post-breeding, non-breeding, and pre-breeding behaviors dominate the remaining portion of the annual cycle, and are the least studied (Bildstein 1993b, Heath *et al.* 2009). Supporting previous studies, we found that ibis spent 10 weeks on average in breeding attempts with a maximum of 18 weeks, about 4 months. The length of breeding attempts declined with increasing use of urban habitats in the non-breeding season such that high urban-use ibis had the shortest breeding seasons. Contrary to our results, many studies on breeding populations in urban environments find that breeding seasons are often initiated earlier and last longer than those in rural or wild environments (Møller *et al.* 2015, Rose *et al.* 2017). However, the breeding requirements of the

species in the aforementioned studies often are present in urban habitats, as opposed to the breeding resource requirements of ibis, which are not typically found in the urban habitats ibis, such as tree island rookeries.

Ibis spend most of their annual cycle in non-breeding seasons; however, our estimate of the amount of time spent in non-breeding seasons may be lower than the actual value. In our sampling effort, 80% of captures and 53% of transmitter failures occurred during non-breeding seasons. Overall, 87% of the reported non-breeding seasons were truncated due to the timing of transmitter deployment or failure. Nevertheless, our finding that ibis spent most of their time in non-breeding seasons is not unexpected since only a small portion of the year is required for breeding and ibis are not known to have long migratory periods.

Search-and-dispersal seasons, in which ibis may be looking for active rookeries and mates, and post-breeding seasons, observed as ibis relax their constraint to the nest location or move from breeding to non-breeding ranges, were variable in duration across ibis and the most frequently skipped season (Heath et al. 2009). Counterintuitively, ibis with low urban-use during the non-breeding season spent more time in search-and-dispersal seasons than ibis with high urban-use. We would expect that their nomadic non-breeding activity would relate to greater knowledge of the landscape, thus finding suitable active rookeries sooner, as opposed to high urban-use ibis with ranges restricted to urban areas that must leave their range to find suitable breeding habitat in a potentially unfamiliar landscape. However, it may be that wild, nomadic ibis are more selective of breeding ranges, resulting in a sampling of several places before deciding the most appropriate breeding location. In other urbanizing populations, animals establish breeding activities in urban areas that resemble native habitats and provide abundant resources reducing their need to search for breeding habitats (e.g., landfills, constructed

rookeries) (Duckworth and Altwegg 2014, Shephard et al. 2015, Gilbert et al. 2016). Thus, urban ibis may have shorter search-and-dispersal seasons because they are already living closer to a breeding colony than nomadic wetland ibis. This hypothesis could also be consistent with our evidence of shorter breeding attempts and a lack of post-breeding seasons for high urban ibis, compared to those of low urban-use ibis, as high urban ibis quickly return to reliable urban foraging resources after breeding ends. We could investigate this hypothesis further by examining the timing of season initiations between ibis.

Length of Seasons Related to Age

We also found interesting relationships between the duration of the different seasons as ibis age that may be a reflection of ibis learning over time. The youngest ibis had the longest non-breeding seasons, while all ibis over 3 years were relatively consistent in duration. The duration of search-and-dispersal seasons also decreases with increasing age, while breeding seasons increased in duration.

The long non-breeding and search-and-dispersal seasons of young ibis may be explained by these young ibis learning how to forage efficiently and gaining breeding experience at active colonies. In the first few years of an ibis's life, young ibis spend much of their time learning from older birds. For example, first year juveniles will form juvenile flocks that follow adults to and from the colony to foraging grounds after fledging. While following adults, young ibis have the opportunity to learn foraging skills and how to fly in flight formations (Bildstein 1993b). Juvenile ibis have also been documented visiting active colonies acting as "helpers" to active nests. This helping behavior is thought to be inexperienced ibis practicing parenting skills. Helping ibis do not restrict their help to a single nest, but move around the colony (Bildstein 1993b). These long seasons, especially in the absence of a breeding season, could be evidence of

young ibis foregoing breeding seasons due to immaturity or moving between colonies visiting or helping active nests. Similarly, shorter breeding seasons could be evidence of extended visits at active nests or breeding attempts that were initiated, but failed. As ibis age and become more successful in their own nesting attempts, their searches may become shorter as their breeding efforts to their own nests become more successful. However, there seems to be little information about ibis breeding success over time as ibis are difficult to age after they reach adulthood (Heath et al. 2009).

Future Directions

The relationships between different behavioral seasons, synanthropic associations, and ibis age, emerging from this study motivate additional questions and hypotheses relating to ibis ecology throughout the annual cycle. Most studies of ibis tend to focus on their ecology while on breeding grounds, providing little information about non-breeding and inter-seasonal ecology (e.g., movement patterns, population status, habitat needs, management concerns) (Heath et al. 2009, Hostetler et al. 2015). The differences seen in the duration of season across a range of urban habitat use and ibis age provide evidence that other aspects of ibis ecology such as space use, movement patterns, and resource selection may also differ with varying degrees of synanthropic behaviors and across seasons.

Our estimates of urban habitat use were restricted to non-breeding seasons to reflect synanthropic associations while ibis are least constrained. To better understand the trend between ibis synanthropic associations and breeding behavior, future studies should investigate ibis site selection and behaviors in the breeding season to compare the distance between seasonal ranges and habitats used between non-breeding and breeding seasons. Future studies could monitor nest success and foraging switching behaviors between non-breeding and breeding seasons across

urbanization gradients to understand which habitat features are most limiting (i.e., do breeding ibis switch to wetland rookeries, but still forage in urban habitats?) and to find if breeding seasons are shorter due to earlier fledging, nest failures, or some other mechanism.

Figure 2.1. Map of ibis capture sites in Palm Beach County, Florida. (A) Raster layer shows land use categories classified from the Cooperative Land Cover (CLC) layer. Icons show capture locations from least to most urban land cover within a 650-meter radius (depicted as the black circles in panels B and C). Our capture sites ranged from 91% urban land use within 650-meter radius (B) to 0% urban land use within 650-meter radius (C).

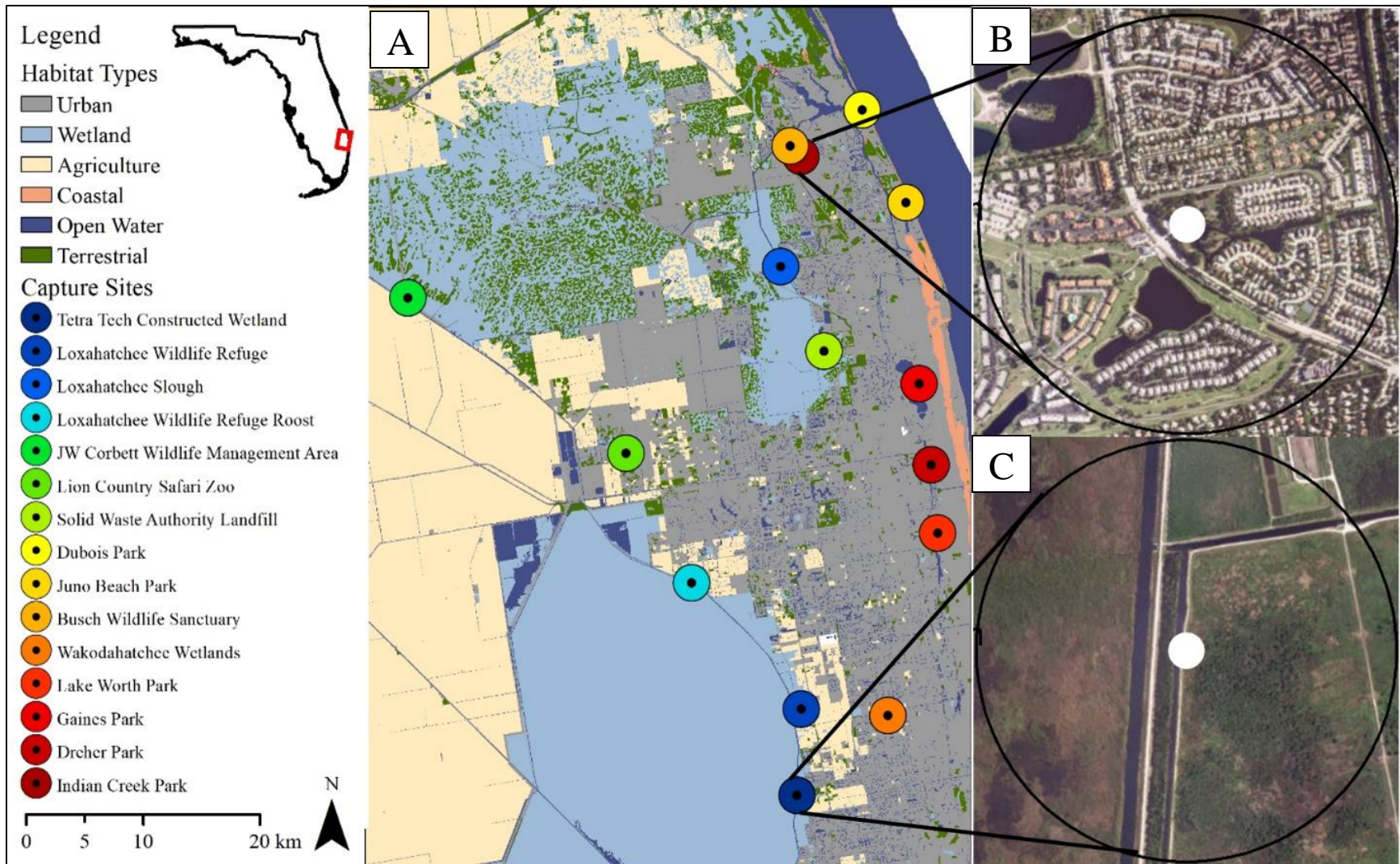


Figure 2.2. Flat summary of the behavioral change point analysis (BCPA) results for ibis “24_LCS01”. The persistence velocity (y-axis) between consecutive locations is calculated with the BCPA and plotted over time. Vertical lines indicate the significant change points with the width of the lines proportional to the number of times that change point was selected in the moving window analysis. The black and red lines show the mean and standard deviation estimate of the persistence velocity. The colored circles ($\hat{\rho}$ in the legend) reflect the autocorrelation time scale (Gurarie 2013). Panel (A) shows the unfiltered BCPA output depicting every change point selected in the moving window analysis. Panel (B) shows the filtered BCPA output that selects significant change points from the neighboring change points within 10 days. Hierarchical clustering, which is based on the mean, standard deviation, and autocorrelation, is used to group bouts with similar behaviors.

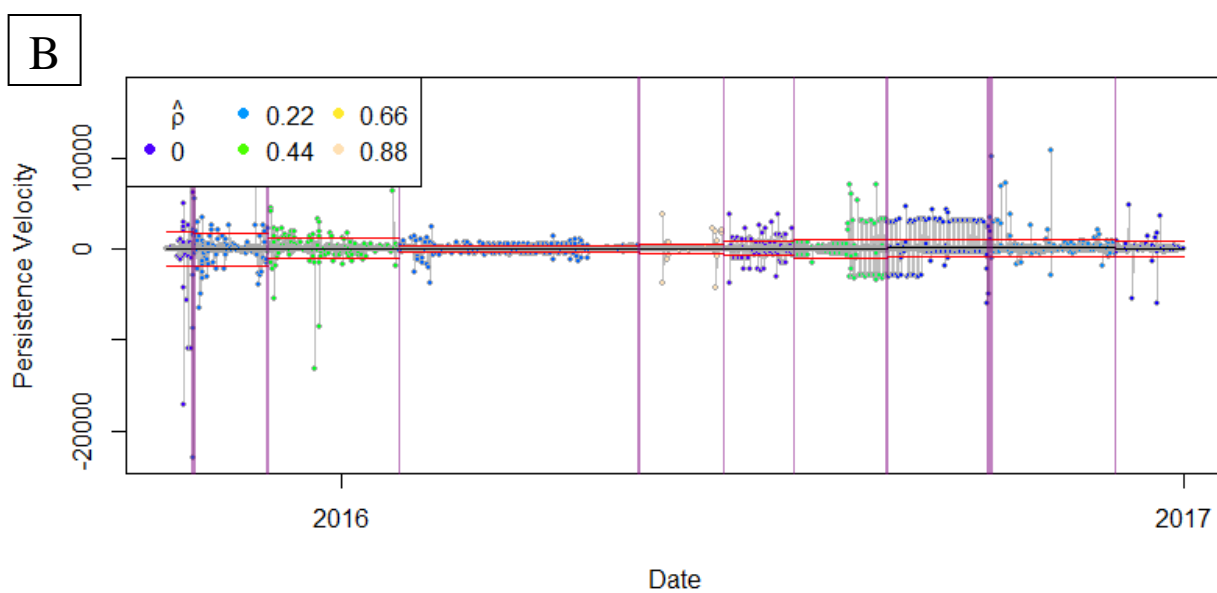
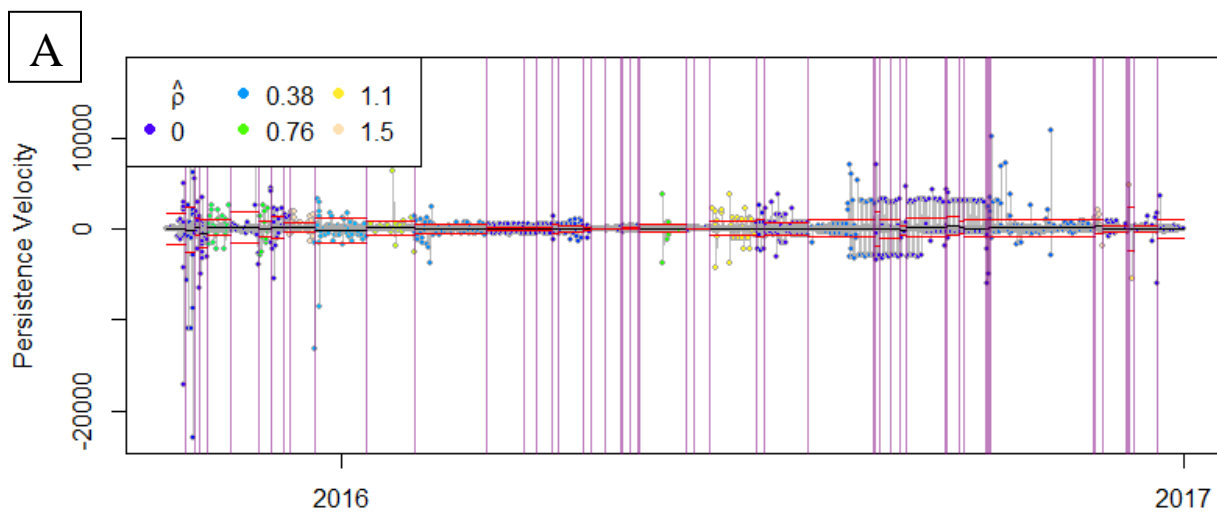


Figure 2.3. Duration of each behavioral season for individual ibis fitted with transmitters (vertical bars). Spaces (white sections) are added to account for delays in deployment after the first deployed transmitter. Horizontal bars show the approximate beginning (thin line) and end (thick line) of the ibis breeding seasons from observational studies of colonies (Heath et al. 2009).

Figure 2.4. Distribution of days in each behavioral season (non-breeding-NB, search-and-dispersal-SD, breeding attempt-BA, and post breeding-PB) according to non-breeding season urban habitat use (low, intermediate, high, all combined). Grey plot in the background indicates the overall values for all individuals. Colored boxplots in the foreground show the different non-breeding urban habitat use class. Numbers below plots indicate the observed sample size in each urban habitat use class. The bold line in each distribution refers to the median, while the horizontal edges of boxes and the end of tails represent the quartiles in the distribution.

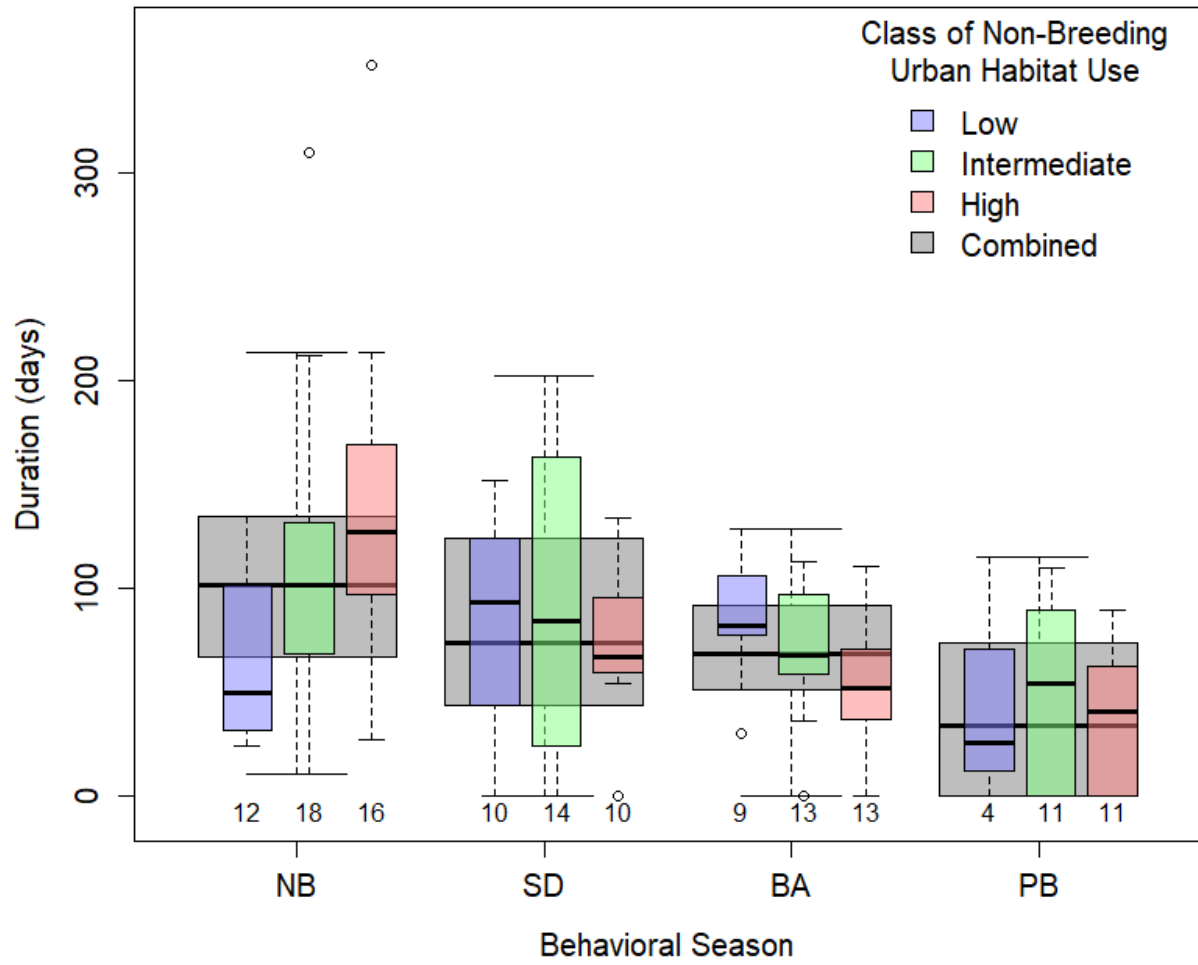


Figure 2.5. Distribution of days spent in non-breeding nomadic and non-breeding resident seasons according to non-breeding season urban habitat use (low, intermediate, high). Grey plot in the background indicates the overall values. Colored boxplots in the foreground show the different non-breeding urban habitat use class. Numbers below plots indicate the sample size in each group. The bold line in each distribution refers to the median, while the horizontal edges of boxes and the end of tails represent the quartiles in the distribution.

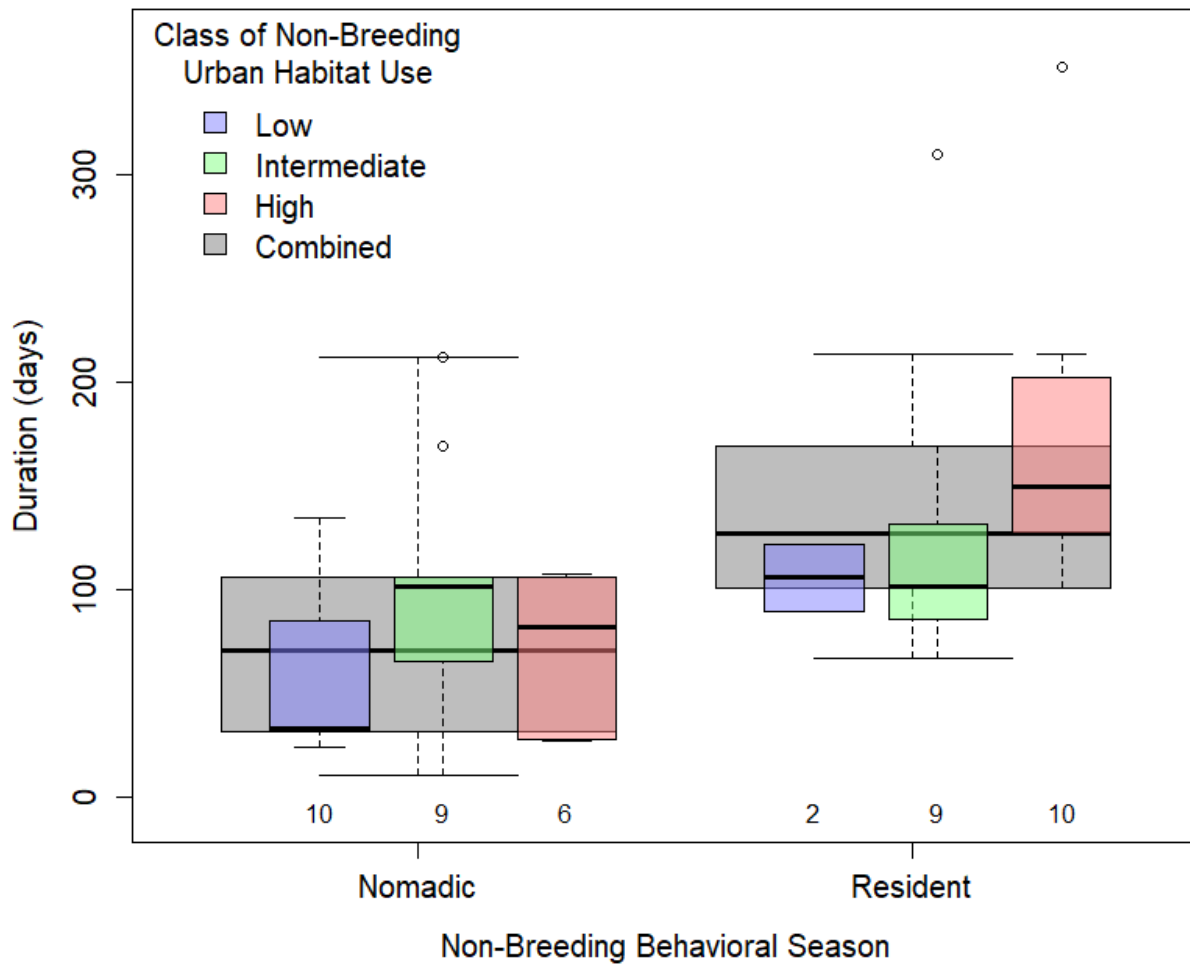
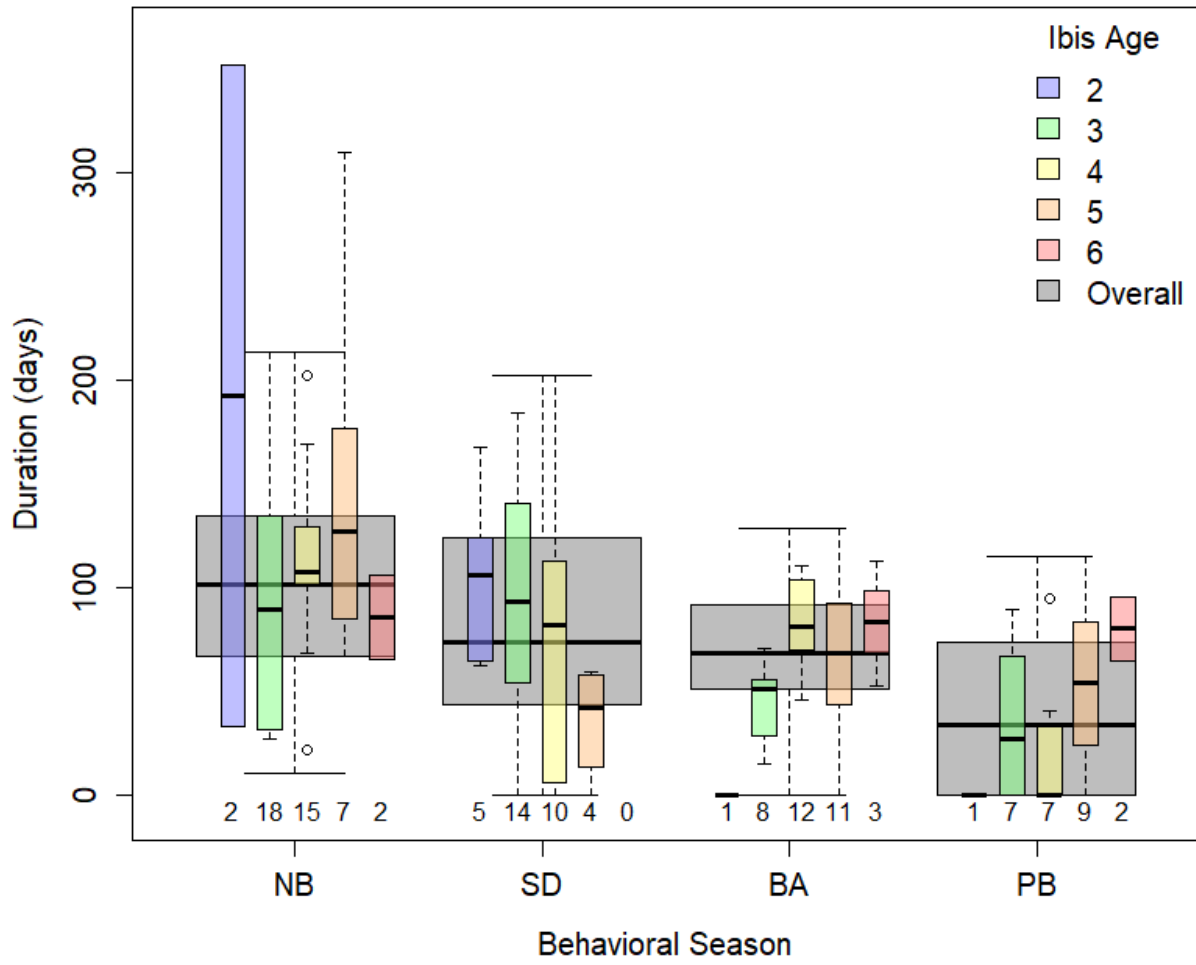


Figure 2.6. Distribution of days in each behavioral season (non-breeding-NB, search-and-dispersal-SD, breeding attempt-BA, and post breeding-PB) according to ibis age. Grey plot in the background indicates the overall values. Colored boxplots in the foreground show the different age class. Numbers below plots indicate the sample size in each urban habitat use class. The bold line in each distribution refers to the median, while the horizontal edges of boxes and the end of tails represent the quartiles in the distribution.



CHAPTER 3
SPACE USE OF AMERICAN WHITE IBIS (*EUDOCIMUS ALBUS*) ACROSS AN
URBANIZATION GRADIENT²

² Kidd, A. D., J. Hepinstall-Cymerman, M. H. Murray, and S. M. Hernandez 2018. To be submitted to *Movement Ecology*.

Abstract

Animal space use is the result of movement patterns related to pursuit of resources required for survival and reproduction. As individuals experience environmental change due to urbanization, their space use can change as they adapt to altered resource distributions. Since urban food resources are often abundant and reliable in space and time, individuals that learn to exploit urban resources may exhibit smaller ranges and greater site fidelity. American White Ibis (*Eudocimus albus*) are a nomadic water birds that typically have large non-breeding ranges as they search for ephemeral foraging opportunities. While breeding, their ranges are smaller and their site fidelity increases as they restrict their movements to rookeries. In urban areas, ibis are increasingly found using urban resources and forming recurring flocks in non-breeding seasons. In this chapter, our objectives were to test if ibis that use more urban areas during their non-breeding season 1) have smaller ranges and higher site fidelity and 2) change their seasonal habitat associations differently than birds using more wildland areas during the non-breeding season. We captured ibis in habitats that represent an urbanization gradient in Florida to track ibis movements with GPS telemetry over time. We found the size of seasonal ranges and site fidelity within those seasonal ranges varied by an individual's reproductive state and their synanthropic associations during the non-breeding season, such that ibis with greater synanthropic associations had much smaller non-breeding ranges, higher use of a variety of urban habitat classes, and higher site fidelity than ibis with lower synanthropic associations. In the breeding season, a shift occurred with high urban-use ibis space use and habitat use becoming more similar to that of low-urban ibis.

Introduction

Animal space use is the result of animal movement patterns that are related to an individual's pursuit of the resources required for survival and reproduction (Börger et al. 2008, Hooten et al. 2017a, 2017b). The spatial scale, or range, of an animal's movements are often smaller than the scale that their mobility would allow. The observed restricted space use is a result of space use limiting behaviors or limited resource distributions that prevent the individual from exercising its full locomotive potential (Börger et al. 2008, Hooten et al. 2017a). However, since space use patterns are the result of a set of interactions between an individual's characteristics, specific behavioral states, and the environment, different patterns are likely to emerge at different stages in an animal's life (e.g., juvenile movements, active breeding, migration) or as individuals respond to their the environment differently (Börger et al. 2008).

Animals exhibit differential space use patterns throughout their lifetime as they transition between life stages or behavioral states (i.e., juvenile to adult, non-reproductive to reproductive), experience variable environmental conditions (e.g., drought, land use modification), and learn how to interact with the environment and other individuals. Many species have adapted to seasonal resource distributions by altering their movement patterns with resource distribution patterns (Singh et al. 2012). Variation in movement patterns exist within a species at both the population and individual levels. Populations that experience dramatic seasonal shifts in resource availability may exhibit migratory periods between two spatially distinct ranges, with the migratory distance decreasing at latitudes closer to the equator due more consistent climates (Singh et al. 2012). Some populations that maintain territories or home ranges through seasonal variation or that live in environments with nearly consistent conditions year-round exhibit space-use patterns of range expansion and contraction between seasons, or switch between home

ranging and nomadic movements between seasons. For example, Trumpeter Hornbills (*Bycanistes bucinator*) maintain territories around nests to care for young in the breeding season, but then exhibit nomadic movements while they utilize fragmented habitats in the non-breeding season (Lenz et al. 2015). Nomadic behaviors are those which are intermediate between resident and migratory behaviors. Nomadic animals frequently move in a series of unidirectional dispersals to exploit resources that are ephemeral or vary in abundance seasonally.

The non-breeding states of nomadic and resident (collectively, non-migratory) populations often occur during seasons with lower and/or more fragmented resource availability. While in non-breeding states, non-migratory populations can expand their territory boundaries or move nomadically to search for scarce resources and to exploit fragmented habitats (Singh et al. 2012, Lenz et al. 2015). As individuals transition into breeding states, the seasonal movements of non-migratory populations are typically more restricted, particularly for species that utilize limited, fixed location resources such as nests or dens. Reproductive activity often coincides with seasons with high resource availability or more densely distributed resources. This allows individuals to have smaller ranges and access to high quality forage as they restrict their movements while rearing young (Harris and Reed 2002, Ferguson and Elkie 2004, Lenz et al. 2015, Niedzielski and Bowman 2016).

Increasing urbanization on the landscape can result in reduced amounts of native habitat and/or higher fragmentation of native habitat patches. Depending on the species' locomotive ability, resource needs, and synanthropic associations, urbanization can alter an individual's movement patterns in a variety of ways (Ryan and Partan 2014). Certain species, particularly large carnivores, have larger ranges when living in urban habitats as fragmented habitats can require animals to move more broadly than they would in pristine habitats in order to obtain all

the resources they require (Ryan and Partan 2014, Morato et al. 2016). While some organisms are negatively affected by human modifications of landscapes, others are able to use human modifications as an ecological opportunity and become specialists in exploiting human resources. Such synanthropic populations successfully cohabit with human populations and gain some benefit from using habitats modified by humans. They range from obligate (i.e., major dependence) to casual (i.e., frequent exploitation without dependence) to tangential (i.e., occasional exploitation) relationships with humans, human-modified habitats, and human-provided resources, including food and habitat (Johnston 2001). Animal ranges in urban habitats are often smaller as an individual's movements are restricted by barriers such as roads or as they learn to exploit human-provided resources (e.g., feeding stations, garbage, shelter). Human-provided resources are often available in abundance year-round, reducing an individual's need to search for ephemeral or seasonally available resources (Lehrer and Schooley 2010, Martin et al. 2012, Corcoran et al. 2013, Ryan and Partan 2014, Gilbert et al. 2016, Weaving et al. 2016, Belton et al. 2016).

The American White Ibis (*Eudocimus albus*), hereafter ibis, is a common medium-sized wading bird found throughout wetland habitats of the Americas, where its natural history and annual cycles are dependent on the hydrologic regime in wetland habitats (Frederick et al. 1996, Heath et al. 2009). Considered nomadic, ibis frequently change foraging and roosting sites as they follow transient wetland conditions. Non-breeding states coincide with fall and winter, when water levels are highest as the rainy season ends and the dry season begins, resulting in wetland dry-downs (Kushlan 2008). When water levels are highest, foraging conditions, which are characterized by shallow water with dense aquatic prey populations for this species, are least abundant and patchily distributed in space (Kushlan 1979, Bancroft et al. 2002). Nomadic and

social foraging behaviors allow ibis to quickly locate and take advantage of emerging ephemeral foraging conditions in freshwater and brackish habitats as dry-downs decrease water levels and concentrate aquatic prey (e.g., small fishes, crayfish, and fiddler crabs). Ibis flocks reach peak abundance and abandon foraging sites after foraging has reduced the prey density below the productive limit of 0.5 fish/m² within approximately 10 days of a foraging site becoming available (Gawlik 2002). This pattern of locating, using, and abandoning a foraging site produces a nomadic movement pattern where an individual's daily range shifts unpredictably over time and where large seasonal ranges are created as an individual moves across the landscape.

As the dry season ends, the first big rains at the start of the rainy season signal the start of wading bird breeding. The timing and location of reproductive behaviors reflect resource selection preferences and correlate with the most optimal foraging conditions for raising young (Kushlan 1979, Herring et al. 2010, Cook et al. 2014). Ibis transition into breeding states as they identify suitable rookeries and prepare to reproduce. Rookeries are tree islands that are close to foraging habitat and offer protection from predators to serve as colonial nesting grounds. While caring for young, adult ibis must restrict their foraging to freshwater habitats, as nestlings are not able to regulate salt balance as well as adults (Bildstein 1993a, Boyle et al. 2014). Excessive salt present in the diet can impair the development of young (Bildstein 1993a). During reproduction, adult ibis movements are the most restricted, as use of freshwater foraging sites near rookery increases; adults must return to the nest periodically to feed nestlings.

The Greater Everglades region of south Florida historically hosted abundant foraging conditions throughout the year, and as such, the largest breeding populations of ibis in the southeast United States (Ogden et al. 2005, Frederick et al. 2008). The implementation of water management strategies, agricultural development, and urbanization throughout the 1900s

contributed to over 50% loss of wetland habitats in south Florida (Kranzer 2002, Dahl 2005). The remaining wetlands are fragmented, and the altered flow of water on the landscape disrupts the hydrologic cycles to which ibis are adapted. In the decades following extreme wetland degradation in the 1900s, the breeding population of ibis in South Florida declined by 90% (Frederick et al. 1996). Ibis living in South Florida year-round have increasingly used urban habitats and taken advantage of anthropogenic resources, including hand-feeding from people (Frederick et al. 2008, Hernandez et al. 2016, Welch 2016, Murray et al. 2018). Studies on ibis in urban habitats found that ibis spending time in urban parks, zoos, and landfills regularly visit urban areas throughout the non-breeding seasons, often at the same site they were originally captured. Additionally, the diets of these individuals include human-associated foods (e.g., bread) (Welch 2016, Murray et al. 2018). Although urbanized ibis may spend the majority of their time in urban habitats, these areas do not typically have the requisite resources for establishing breeding colonies and rearing young (e.g., large breeding colonies, protected tree islands, freshwater foraging). Band-resighting studies have found that some individuals living in urban habitats reduce their visits to urban habitats during the breeding season; these individuals may potentially breed elsewhere or increase movements to include wetland areas (Welch 2016).

The objectives of this study were to test if ibis that use more urban areas during their non-breeding season 1) have smaller ranges and higher site fidelity and 2) exhibit greater seasonal changes in habitat use compared to birds using more wildland areas during the non-breeding season. We used GPS transmitters to track ibis captured across an urbanization gradient in South Florida to characterize space use patterns of seasonal range size and site fidelity relative to their level of non-breeding urban habitat use, which is a time of unconstrained resource use and estimate of synanthropic association. We then examined the proportions of different habitat types

present within seasonal ranges of each individual to compare changes in habitat use between seasons.

Much of the land in our study area has been converted from native habitats to urban land uses and water management structures. Urban areas in our study area are associated with resource provisioning, including food and roost sites, while many native habitats have been modified and degraded by water management structures, reducing the quality of remaining native resources. We hypothesize, therefore, that birds that spend the majority of their non-breeding season in urban habitat types, potentially relying on human-provided resources, will exhibit smaller non-breeding season ranges and greater site fidelity than birds that spend less time in urban habitats during the non-breeding season, which will have both larger ranges and lower site fidelity. Here we define high site fidelity as repeated use of a limited number of sites within an individual's seasonal range and low site fidelity as the use of many sites within an individual's seasonal range). However, because breeding and rearing young requires more specific resource needs in terms of nest site selection and feeding requirements for young, we expect breeding season space use to change to accommodate these changed needs. Our second hypothesis is that, during an individual's breeding season, urban individuals' space use will expand as individuals reduce their site fidelity to urban areas to use more appropriate foraging and nest site opportunities, while wildland birds will restrict their space use as they are constrained to a nest location. Lastly, we hypothesized that their fine-scale habitat use will differ between non-breeding and breeding seasons and between birds with different levels of non-breeding season synanthropy such that: a) more synanthropic individual's urban habitat use in the non-breeding season will include heavily altered habitats such as high and medium intensity urban areas while urban habitat use in breeding seasons will include urban areas that mimic

wetland features such as golf courses and zoos; b) all individuals will increase overall use of freshwater wetland habitats in breeding seasons as compared to non-breeding seasons; and c) less synanthropic individuals will exhibit less pronounced changes habitat selection between seasons.

Methods

Ibis Captures

Ibis were captured at 15 sites in Palm Beach County, Florida including urban parks, a zoo, a landfill, and wetland habitats that represent a variety of habitat types across the urbanization gradient and that report regular sightings of ibises foraging during the day or roosting at night (Figure 2.1). To outfit ibis with GPS transmitters, they were captured using fishing line leg lassos, manual flip-traps, and mist nets. Once captured, ibises were aged by plumage, weighed, and fitted with Ecotone GPS-GSM transmitters using a backpack harness (Bildstein 1993b, Herring and Gawlik 2011, Humphrey and Avery 2014). Transmitters were only applied to ibis when the transmitter, harness, and identification band were less than 3% of the bird's mass (Casper 2009). All animal handling procedures were reviewed by the University of Georgia's Institutional Animal Care and Use Committee (IACUC #A2016 11-019-Y2-A0). GPS units received up to 12 locations per day at a maximum of 2-hour intervals, primarily during daylight hours. GPS units were allocated among capture sites such that there were 2-4 deployed units per capture site.

Capture occasions during which ibis were fitted with transmitters were October - November 2015 (n=15), February - March 2016 (n=17), June - July 2016 (n=5), October - November 2016 (n = 4), and February - March 2017 (n=7). Ibis GPS transmissions were monitored until 8 November 2017, or until we ceased to receive locations from the transmitter.

As ibis got older through the duration of their deployment, we added one to the ibis's estimated age at capture each summer in the deployment history. For example, an ibis captured in winter 2015 that was aged as a 2-year-old was considered a 3-year-old in summer 2016 seasons. Conversely, an adult ibis with all white plumage cannot be reliably aged to a specific year beyond a 3 year old. As such, we recorded all adult ibis as their youngest possible age and similarly added 1 to their age each to each summer (e.g., an adult ibis captured in winter 2015 that was considered 3, and then aged to 4 in the summer 2016 season).

Behavioral Seasons

GPS tracking produces a series of consecutive points, known as a trajectory or track, which form the basis of understanding of how and where an animal is moving. Location data are samples of a true movement path representing the actual movement and characteristics of an individual, such as speed and time spent at a particular site. Individual tracks were split into non-breeding and breeding states to calculate seasonal space use. Using the methods detailed in Chapter 2, non-breeding and breeding behavioral seasons were extracted from tracks using behavioral change point analysis and hierarchical clustering to determine the temporal points in which an individual shifts their behavior from one behavior to another.

Urban Habitat Use

Ibis daytime locations during non-breeding states were used to represent the level of synanthropic association (i.e., referring to their use of human-modified habitats) for each individual. This subset of locations was chosen to represent an individual's least constrained habitat use (i.e., can use freshwater wetlands, brackish wetlands, or urban habitats) as opposed to nighttime or breeding locations in which an individual's choices are constrained by specific resource needs (e.g., wetland foraging for young, tree island roosts). Non-breeding urban habitat

use was summarized using the 2016 Cooperative Land Cover (CLC version 3.2) map for the state of Florida (FWC and FNAI 2016) and the C-CAP coastal land cover dataset (NOAA 2010) for coastal regions of southeastern states outside of Florida. The CLC map is a 10-meter-resolution raster geospatial layer with 234 land cover classes, while the C-CAP map is a 30-m-resolution layer with 24 land cover classes. For this study, we were primarily interested in differentiating urban versus other habitat use, so we collapsed land cover classes into 6 classes: urban, wetland, agriculture, coastal, open water, and all other terrestrial land cover types (see (Murray et al. 2018)). We classified urban habitat use within a 650-meter radius determined by first passage time analysis as the scale of localized movements for ibis to account for uncertainty in ibis locations within the 2-hour window of locations, use of edge habitats, and GPS error. Thus, urban habitat use was defined as the mean proportion of urban land cover within a 650-meter radius of daytime non-breeding locations (see (Murray et al. 2018)).

Range Analysis

Seasonal ranges were calculated using auto-correlated kernel density estimation (AKDE) in the R version 3.4.3 *ctmm* package (Fleming et al. 2015, Calabrese et al. 2016, Fleming and Calabrese 2016, 2017a, R Core Team 2016). AKDE is a utilization distribution based area estimation method that accounts for temporal and spatial autocorrelation in fine-scale (i.e., hourly) GPS tracking data, as opposed to other area estimation methods (i.e., MCP, KDE) that assume that data are independent and identically distributed. We followed the recommended protocol in the *ctmm* package vignettes for each individual to fit a movement model and to calculate range size (Fleming and Calabrese 2017b, 2017c). Variograms were plotted for each individual to record the level of autocorrelation at short time lags where the temporal autocorrelation is highest to longer time lags where the variogram reaches an asymptote called

the *sill*, which is the minimum spatial autocorrelation or the approximate size of the animal's home range. The *range* is time lag where temporal autocorrelation reaches the minimum corresponding to the time it takes an individual to cross its home range. These three values (the lag at which initial curvature ends, the range, and the sill) reflect the type of movement model to use (e.g., a Brownian motion model if there is a linear increase at short time lags and no observed asymptote versus an Ornstein-Uhlenbeck with foraging model if there is curvature at short time lags and an asymptote, see (Fleming et al. 2015)). The values derived from the variogram were used as starting values to calculate parameters and fit a continuous time movement model (ctmm) using maximum likelihood with the `ctmm.fit` function. The ctmm model is then used to calculate a utilization distribution using the `akde` function. The outputs of `akde` are the rasterized utilization distribution and a maximum likelihood area estimate with confidence intervals. Ibis range sizes were calculated as the 95% maximum likelihood AKDE contour and scaled by the number of days in the season. These range estimates reflect the area that the individual would use if it continued its pattern of movement reflected in the model indefinitely; in other words, it calculates the area available to the individual within the sampling time period (Fleming et al. 2015)

Site Fidelity Analysis

Site fidelity is the degree to which an animal repeatedly uses a specific site (Martin et al. 2012). The term is typically used in reference to yearly return to breeding or other seasonal grounds. However, here we use this term to refer to repeated use of areas within a particular season, rather than the return to seasonal ranges between years. We calculated repeated use of areas within the seasonal range as the 50% maximum likelihood AKDE contour using only daytime locations, which we refer to as the core area(s) of an individual's range. We exclude

nighttime locations to ensure that the core area estimate would reflect the locations where ibis actively choose to spend time (e.g., foraging, loafing), rather than including areas where ibis sleep. Site fidelity was then calculated as the ratio of the core area to the total seasonal range area (95% AKDE contour). If the 50% maximum likelihood contour was larger than the total seasonal range area, we used the 50% lower confidence interval estimate to represent the core area. This anomaly can occur when an individual has an aggregation of locations outside of their main activity center. The overall range size may interpret these sites as outliers, occurring outside the 95% contour; however, when only looking at daytime locations, and because of the calculation methods in AKDE, this outlier aggregation could be deemed important and included in the 95% contour of the core area. Site fidelity can be “high”, with intensive, repeated use of one or a few areas or “low” with many areas receiving low to moderate use with limited repeated use.

Statistical Modeling

We used linear mixed models to explore how range size or site fidelity was related to season, non-breeding urban habitat use, sex, age, and mass. Our response variable range was log₁₀ transformed, and site fidelity, which was a proportion of the range size, was logit transformed. We included ibis identification code as a random effect. We included season to test if space use changes between non-breeding and breeding states; non-breeding urban habitat use as a measure of synanthropic associations; sex to test if space use differs between males and females; age to test if space use changes as ibis gain experience; mass and scaled mass index (lower values indicate poorer body condition where the individual’s body mass is lower than expected from its body size, (see (Murray et al. 2018)) to test if space use is different based on the ibis’s body condition. We also included quadratic effects of urban habitat use to account for non-linear trends based on urban habitat use and two-way interactions between urban habitat use

and season, quadratic urban habitat use and season, urban habitat use and age, urban habitat use and sex, urban habitat use and scaled mass index, season and sex, and season and scaled mass index. We generated models for all possible combinations of these covariates and two-way interactions using all-subsets modeling (Barton 2018). Model average estimates and covariate importance were calculated from competitive models that were less than 2 AICc from the top models using the *MuMIn* package in R version 3.4.3 (R Core Team 2017, Barton 2018).

Habitat Use

As a preliminary examination of the seasonal habitat use and selection of ibis, we extracted the proportion of habitat types as defined by the Florida's Community Land Cover map (CLC version 3.2) (FWC and FNAI 2016) within each individual's seasonal ranges derived in the space use analysis above. We compared proportions of used habitat for each individual to the proportion of available habitat within the state of Florida to determine a basic measure of habitat selection. For individuals with multiple range estimates for a season, we averaged habitat use to get the average amount of each habitat class used for non-breeding and breeding seasons across years.

We considered the entire state of Florida to represent available habitat because ibis nomadic behaviors give them the ability to easily travel between regions and their social behaviors may allow them to communicate habitat suitability across broad landscapes. This nomadic and social behavior has been previously described in several reviews of ibis behavior (Bildstein 1993c, Frederick et al. 1996, Heath et al. 2009) and we saw evidence of this high mobility as several of our GPS tracked ibis moved considerable distances from their capture locations in Palm Beach County, FL to Tampa, FL, Georgia, North Carolina, and Louisiana. Habitats were considered selected for, as opposed to randomly used, if the proportion within the

seasonal range was at least 1% greater than the proportion available in the state. We used this liberal definition of selection due to the large number of mapped classes (n= 234); future analyses of resource selection will be done with fewer, collapsed classes based on a more detailed analysis of selection patterns.

Results

Ibis Captures

Space-use analyses were based on data from 29 ibises (20 males and 9 females) captured across the urbanization gradient from areas with 0-91% urban land cover within a 650-meter radius around the capture site (Figure 2.1). We only included individuals that had at least one non-breeding and breeding season detected. This set of ibis is the same as the set used in Chapter 2, minus one bird which lacked a breeding season for comparison. The duration of deployment from release date until we ceased to receive locations due to some unknown cause (e.g., transmitter failure, individual death) or 8 November 2017 ranged from 10 days to 757 days (mean: 327 days). Of the transmitter failures, 13 occurred between 30 December 2016 and 2 January 2017 corresponding to the deactivation of some 2G GSM cellular network towers, which were the method of remote data transmission between the transmitters and the data server. The mass of individuals ranged from 800 to 1240 grams (mean: 962). The mean transmitter to body weight percentage was 2.67% [2.05 – 3.29%] and thus, assuming that transmitter weight (vs shape or attachment method) is the predictor for influencing movement, any influence of the transmitter should be minimal (Casper 2009). Due to this mass requirement, most individuals selected for transmitter deployment were adult males (80% age 3 or older at capture; 36 males, 12 females). Estimated ibis age over the sampling duration ranged from 2 to 6 or more years. The amount of urban habitats used ranged from 1.27% to 95.55% of the area within 650-meter of

daytime non-breeding locations to reflect ibis synanthropic associations. Urban habitat use was negatively correlated with wetland habitat use, meaning individuals using low amounts of urban habitat were also using high amounts of wetland habitat.

Range Size Analysis

Ibis non-breeding range sizes were highly variable ranging from 0.11 km² to 226,351 km² (median = 12.72 km²; mean = 11,573 km²). Scaled by the number of days spent in the non-breeding state, range sizes range from 0.001 km² per day to 8,108 km² per day (median = 0.13 km² per day; mean = 345 km² per day). Breeding ranges were similar in size ranging from 0.48 km² to 97,969 km² (median = 111 km²; mean = 8,963 km²), or 0.01 km² per day to 1,737 km² per day (median = 1.40 km² per day; mean = 130 km² per day).

Eight models predicting range size were within two delta-AIC of the top ranked model and, therefore, considered competitive (Table 3.2). All of the top models contained season, non-breeding urban habitat use, a quadratic effect of urban habitat use, and an interaction between season and the quadratic effect on urban habitat use. Seven of the eight top models contained an additional interaction between season and urban habitat use. Three included sex or age, and two of the three also included their interaction with urban habitat use. Two models contained the scaled mass index, and one model used centered mass.

Range size varied strongly by season and by a quadratic effect of non-breeding urban habitat use (Figure 3.1). In the non-breeding season, range size decreased with increasing use of urban habitats; however, the strength of the trend declined as urban habitat use increased. While breeding, range size decreased for the individuals who used the least amount of urban habitat during the non-breeding season and increased for the individuals using the most urban habitat during the non-breeding season. During the breeding season range size is lowest at intermediate

levels of urban habitat use and is more similar to non-breeding range sizes than the trends seen for individuals on the extreme ends of the urbanization scale.

Site Fidelity

Average ibis site fidelity was lower in breeding states than in non-breeding states. Breeding site fidelity ranged from 0.11 to 0.69 (mean = 0.21, SE = 0.01) whereas non-breeding site fidelity ranged from 0.06 to 0.38 (mean = 0.17, SE = 0.02).

Three models were within two delta-AIC of the top ranked model and therefore considered competitive. All of the top models contained season, non-breeding urban habitat use, and a quadratic effect of urban habitat use during the non-breeding season. Two of the top models contained an interaction between season and the quadratic effect of urban habitat use during the non-breeding season, and one also included an interaction between season and non-breeding urban habitat use. Sex, age, scaled mass index, mass, or interactions including those covariates were not included in any of the top models.

Higher ratios indicate lower site fidelity as an individual's activity center is distributed throughout the seasonal range, as opposed to concentrated in a portion of the seasonal range. Birds with more non-breeding urban habitat use had higher site fidelity increases (Figure 3.2). The quadratic effect indicates that the effect of non-breeding habitat use is nonlinearly related to site fidelity. Site fidelity reached a minimum at intermediate levels of non-breeding urban habitat use that was maintained through increasing non-breeding urban habitat use. However, an interaction with season indicates that the strength of the quadratic trend changes between non-breeding and breeding seasons. Site fidelity was lower in the breeding season across all ibis with the most pronounced differences observed for the most urban ibis (Figure 3.2); however, the effect is weak and confidence intervals of the model average coefficient include 0 (Table 3.1).

Habitat Use

In our preliminary habitat use and selection analysis, the proportion of different habitat types within ibis' ranges varied by season and daytime non-breeding season urban habitat use. Similar to our designation of wild-urban ibis in previous sections, in the non-breeding season, the ranges of ibis with high non-breeding urban habitat use based on the area around GPS locations (hereafter, "high urban-use" ibis) had higher proportions of a variety of urban land use classes compared to ibis with low non-breeding urban habitat use (hereafter "low urban-use" ibis). Low urban-use ibis ranges instead included higher proportions of freshwater wetlands and agricultural land cover classes (Figure 3.3A). In breeding seasons, high urban-use ibis changed their habitat use to include urban habitats to a lesser degree, while the habitat use of low urban-use ibis was similar to that of the non-breeding season (Figure 3.3B).

In comparing habitat use between non-breeding and breeding seasons, the types of land cover used shifted between seasons (Figure 3.3C). Although high urban-use ibis continued to use several residential and utility urban classes year-round, the use of other urban classes changed between seasons, such as the use of parks, zoos, and golf courses which was higher in non-breeding seasons than in breeding seasons. In the breeding season, these high urban-using ibis increased their use of freshwater wetland, agricultural, and estuarine habitats. Low urban-use ibis showed little change in their habitat use in breeding season compared to non-breeding seasons; they mostly shifted their use from wetland to agricultural classes between seasons.

For most individuals, the proportion of habitats within their ranges differed from the proportion of habitat types available throughout the state of Florida, clearly indicating that ibis are selecting for some habitats over others (Figure 3.4). In both non-breeding and breeding seasons, high urban-use ibis selected urban areas, though the degree of selection for urban parks,

zoos, and golf courses was lower in breeding seasons. Low urban-use ibis selected agricultural and freshwater wetlands.

Discussion

Defining ibis space use and habitat use patterns from GPS tracking data provided new insights into ibis movement ecology, especially for those individuals exhibiting synanthropic behaviors. We assessed changes in movement behaviors and habitat use of ibis with variable degrees of synanthropic behaviors across non-breeding and breeding seasons. We found four clear patterns relative to our predictions. First, high urban-use ibis had smaller ranges and higher site fidelity during the non-breeding season compared to low urban-use ibis. Second, high urban-use ibis range sizes increased and low urban-use ibis range sizes decreased in breeding seasons compared to non-breeding seasons. Additionally, intermediate urban-use ibis had the smallest ranges and highest site fidelity in breeding seasons with values similar to those in the non-breeding season. Third, non-breeding ranges of high urban-use ibis included a high proportion of a variety of urban habitat types, including urban parks, zoos, and golf courses. However, contrary to our prediction, some ibis maintained use of some urban classes, such as residential and utility classes, within their breeding ranges but reduced their inclusion of urban parks, zoos, and golf courses. Fourth, breeding ranges for all ibis included more freshwater wetland habitats, estuarine habitats, and agricultural habitats compared to non-breeding ranges suggesting that these habitat types contain higher quality resources for breeding.

Shifts from Non-Breeding to Breeding Ranges

Non-migratory populations often exhibit seasonal space use patterns through behavioral shifts from nomadic movements in non-breeding states, to restricted movements in breeding states (Ferguson and Elkie 2004, Lenz et al. 2015). Low urban-use ibis (i.e., low synanthropic

associations) have large ranges and low site fidelity; this is likely a reflection of moving between ephemeral wetland foraging sites in a nomadic fashion. Ibis-appropriate foraging sites become ephemerally available stochastically through wetland dry-downs after the rainy season, requiring nomadic behaviors to find enough food throughout the non-breeding season (Bancroft et al. 2002). Since their movements are not restricted to nest sites, and their foraging site selection is not restricted by the types of foods young can consume, ibis are likely to move between available freshwater and brackish foraging sites based on site availability. Other nomadic or non-urban foragers are found to shift their daily ranges in pursuit of ephemeral or fragmented resources, sometimes across several habitat types (e.g., marshes, impoundments, agricultural lands), or by travelling long distances between habitat patches (Martin et al. 2012, Varner et al. 2014, Lenz et al. 2015).

As the seasons change to signal appropriate time for rearing young, nomadic or wide-ranging populations reduce their range to high quality habitat (e.g., productive marshes, forest interiors) where the resources required for successful breeding are available (Varner et al. 2014, Lenz et al. 2015). Likely restricted to nest sites and freshwater foraging opportunities as they care for young, low urban-use ibis have smaller ranges while breeding, versus during non-breeding seasons. Interestingly, ibis with both low and high levels of urban habitat use in non-breeding seasons have similar range sizes and site fidelity while breeding. However, the relationship between non-breeding and breeding space use is different for the two groups. While low urban-use ibis had large non-breeding ranges that were reduced in breeding states, high urban-use ibis have much smaller non-breeding ranges as they are likely using abundant, locally available urban resources with high site fidelity to specific foraging and roosting locations.

Other studies comparing space use of animals living in urban versus non-urban habitats find that individuals in urban habitats often have much smaller range size compared to their non-urban counterparts (Lehrer and Schooley 2010, Ryan and Partan 2014, Varner et al. 2014, Belton et al. 2016). In similar studies, Lehrer and Schooley (2010) found urban ranges were 10% the size of non-urban ranges, while Varner *et al.* (2014) found urban ranges to be as small as 1% the size of non-urban ranges. Individuals living in urban habitats are often able to find and exploit abundant resources that are available year round. These resources can provide opportunities that promote synanthropic behaviors where highly mobile nomadic or migratory species give up their movement behaviors to exhibit high site fidelity to urban areas (Martin et al. 2012, Gilbert et al. 2016).

However, as urban ibis transition into reproductive states and their resource needs change, their non-breeding ranges may no longer provide all the resources they need; this requires them to expand or relocate their ranges to acquire the resources required to care for young. Exhibiting similar space use patterns to low urban-use ibis, high urban-use ibis reduce their site fidelity and increase their range size. As the reproductive needs of ibis are not present in urban habitats, it is possible that high urban-use ibis relocate or expand their ranges to include habitats more suitable for raising young, shifting their habitat use to be more similar to low urban-use ibis.

Intermediate urban-use ibis had, overall, the smallest range sizes and highest site fidelity, with the least pronounced change across seasons compared to ibis with low and high non-breeding season urban habitat use. Some species that live in mixed habitats (e.g., on the edge of urban habitats) are able to have small ranges as they optimize the cost-benefit tradeoffs of several habitat types. They can simultaneously take advantage of resources that exist in different

habitats rather than being restricted to one set of resources, such as shelter in forests or human-modified habitats, or foraging opportunities in native or urban habitats (e.g., open areas with higher prey densities, landfills, agricultural lands) (Prange et al. 2004, Rutz 2006, Boyce et al. 2010, Brearly et al. 2011, Ofstad et al. 2016). South Florida has several areas that provide these opportunities. For example, the Arthur R. Marshall Loxahatchee Wildlife Refuge is a large protected wetland that is surrounded by agricultural and urban habitat in Palm Beach County, FL (USFWS 2015) and contains several rookeries and large year-round roosts. By balancing the availability of both urban and non-urban resources, ibis using intermediate urban habitats may be able to occupy the same space year round with smaller ranges, since they have all the resources they require for themselves and rearing young within a small area.

Seasonal Habitat Use

The trends in our exploratory assessment of ibis fine-scale habitat use warrant further investigation. As expected, high urban-use ibis reduced their use of urban habitats while increasing their selection of freshwater wetland, estuarine, and agricultural habitat types in the breeding season. Due to the foraging restrictions of young, we expected that breeding ibis would increase their use of freshwater wetlands while foraging to best support the growth of their nestlings. However, we also see increased selection of estuarine habitats. Impaired development can result if young are fed food with high salt content, such as fiddler crabs. Studies on breeding ibis found that they forage in freshwater wetlands for food for their young, while foraging in brackish and estuarine habitats for themselves (Bildstein 1993a). Although GPS data can provide fine-scale information about animal movement and habitat use, without direct observations of individuals in their habitats, it is impossible to determine the actual behavior of the individuals

using GPS data alone. Therefore, we can only hypothesize on the behaviors and resource needs behind the observed habitat use.

High urban-use ibis did not completely abandon their use of urban habitats in the breeding season, but instead switched their use from one type of urban habitat to another. Other wetland-dependent species that have adapted to breed in urban areas, such as the Australian White Ibis and Hadedda Ibis, use urban areas with wetland-like features as refuge habitats in human-modified landscapes (Martin et al. 2012, Duckworth and Altwegg 2014). However, during breeding seasons we saw that most individuals actually reduced their use of classes including urban parks, zoos, and golf courses, which are likely to host some wetland-like features that ibis require for breeding such as constructed tree islands. The urban habitats most frequently used in breeding seasons included residential and utilities classes, which includes landfills. Several bird species have been recognized taking up residence at or near landfills and foraging on human refuse (Gilbert et al. 2016, Welch 2016). The Solid Waste Authority (SWA) landfill in Palm Beach County, FL is known to host a large flock of foraging ibis on the landfill and a large rookery in the wetland habitats adjacent to the property (Welch 2016). It is possible that some of our ibis with highest urban-use are moving from their non-breeding ranges in Palm Beach County parks to breeding ranges centered around the SWA landfill. The short distance travelled between Palm Beach County parks and SWA would support findings in Chapter 2 that high urban-use ibis have shorter, or a lack of dispersal periods between non-breeding and breeding seasons since they are moving directly to and from a known, stable breeding site to a known, stable human-provisioned food resource.

Future Directions

To continue increasing our understanding of how ibis are adapting to urban landscapes, we should investigate in more detail ibis space use and habitat use over time. In this study we found the size of seasonal ranges and site fidelity within those seasonal ranges varied by an individual's reproductive state and their synanthropic associations during the non-breeding season. In Chapter 2, we found that age was related to shorter search-and-dispersal seasons and longer breeding seasons, potentially related to increased breeding success. Further investigation could find that younger ibis use less suitable habitats for rearing young, such as estuarine or urban habitats, which may be a cause for their shorter breeding seasons as they experience reduced nesting success. As ibis age and experience the landscape, we could see trends where ibis switch between urban and wetland habitat uses as they learn to exploit new resources, as they experience variability in native foraging quality, and as they learn which resources contribute to reproductive success.

Additionally, we could explore changes in habitat use between foraging, roosting, and nesting sites. In the breeding season, ibis habitat use is the most constrained requiring them to select habitats that will support the growth of young. Therefore, we could expect to see nest site, or rookery, selection in wetland areas surrounded by native foraging options, which may be in contrast to foraging and roost site selection in non-breeding seasons, when ibis habitat use is the least constrained, as ibis vary in the selection of wetland and urban foraging sites, and can use lower quality roosts, such as constructed tree islands in golf courses or urban parks. Investigating multiple scales of habitat selection is important to identify the different resources and habitats needed to support ibis throughout the annual cycles. The intensity of use of these different resources could also be a mechanism of changes in ibis space use across the urbanization

gradient. Future investigations could examine finer scale selection by comparing the intensity of use of certain habitat types using the utilization distribution output of the range analysis or the proportion of habitats associated with point locations to the proportion of available habitat within an individual's range.

The results from this analysis produced additional hypotheses that: a) individuals that are using non-urban habitats in non-breeding states cannot sustain their large ranges while breeding and, therefore, reduce their space use to a particular location within their non-breeding range for breeding; b) ibis using intermediate levels of urban habitat during non-breeding seasons maintain their ranges and habitat year round or select ranges that include a variety of habitat types and resources as they balance their synanthropic behaviors and resource needs to reproduce; c) ibis habitat use will change as ibis gain experience learning which locales provide the best resources for survival and reproduction; and d) ibis habitat selection differs based on their resource needs for foraging, roosting, or nesting. To investigate these hypotheses, we should 1) investigate inter-seasonal site fidelity to compare the spatial locations of non-breeding and breeding ranges and 2) explore more thoroughly how habitat use varies across habitat types, seasons, behaviors, and ibis experience.

Figure 3.1. Model averaged standardized range size according to non-breeding urban habitat use (horizontal axis) and season (non-breeding blue, breeding red). Model averaged estimates for range size were calculated based on models within delta-AIC 2 of the top model. Each of the top models included season, non-breeding urban habitat use, a nonlinear effect of urban habitat use, and an interaction between season and the nonlinear effect on urban habitat use. Thicker lines indicate the average range estimate while thin lines show the minimum and maximum range estimate when accounting for variation in sex, age, and scaled mass index. Points show estimates for each individual and each season.

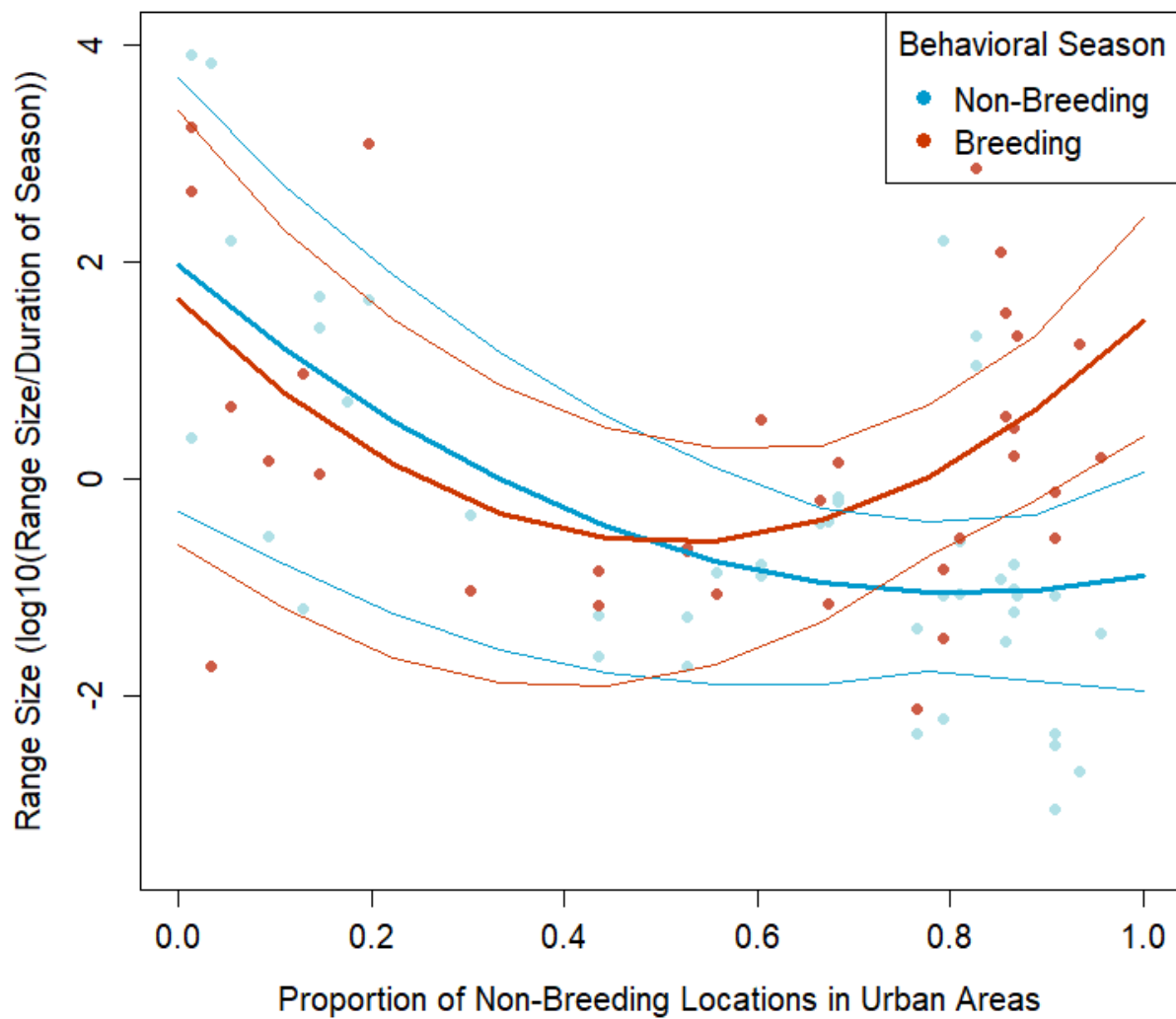


Figure 3.2. Model averaged site fidelity according to non-breeding urban habitat use and season. Site fidelity is estimated as the ratio of the size of the seasonal range to the size of the core range, such that low values indicate higher site fidelity as an individual intensely uses a small portion of its seasonal range compared to high values. Model averaged estimates for site fidelity were calculated based on models within delta-AIC 2 of the top model. Each of the top models contained season, non-breeding urban habitat use, and a quadratic effect of urban habitat use during the non-breeding season. Points show estimates for each individual and each season.

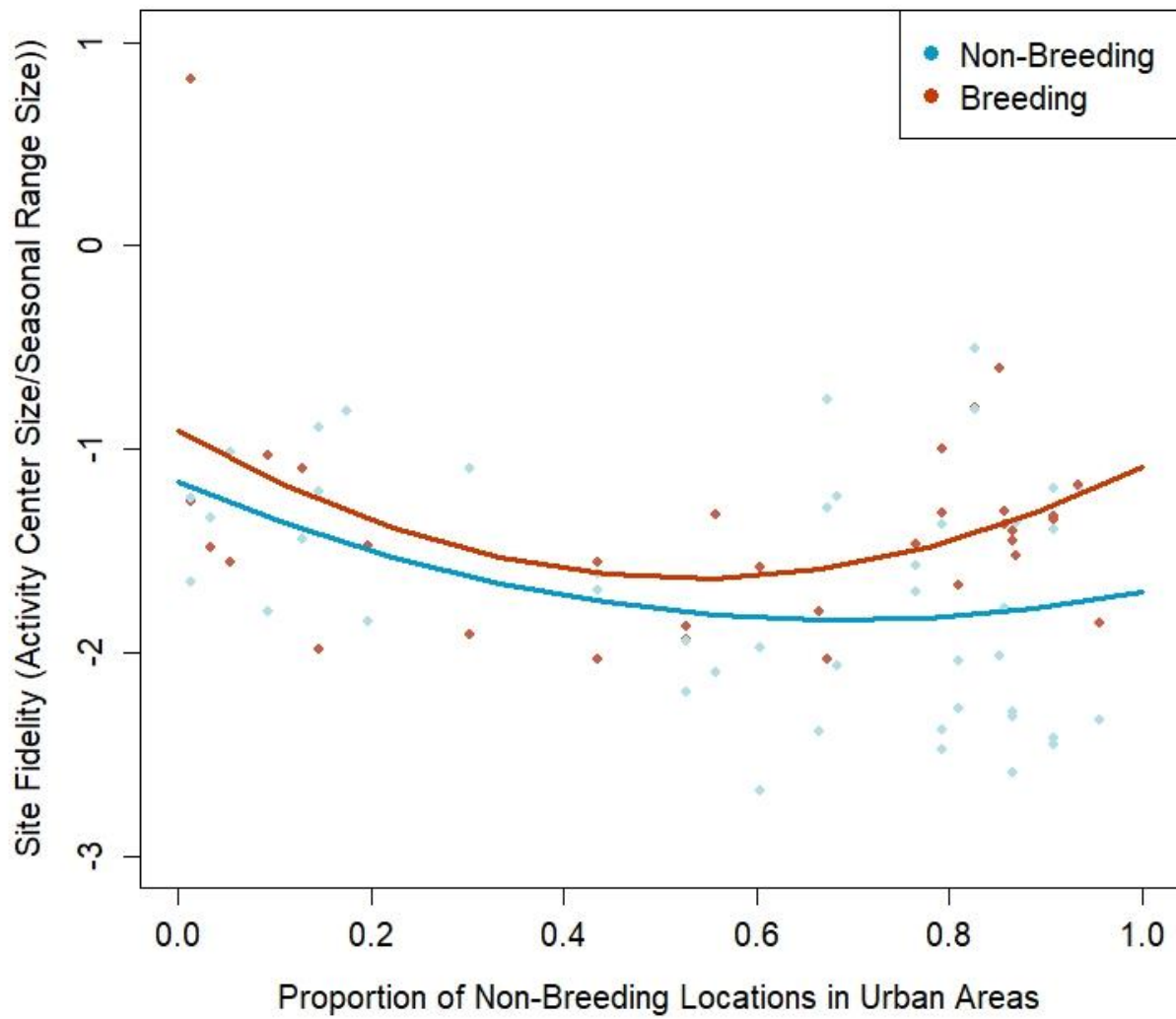


Figure 3.3. Proportion of each habitat used within non-breeding and breeding ranges. The CLC land use classes are arranged in a hierarchical structure to organize similar land use classes. The 234 land use layers are colored according to the second or third classification level to indicate terrestrial (green), urban (red), urban parks, zoos, and golf courses (dark pink), agricultural (yellow), freshwater wetland (light blue), deep freshwater (dark blue), riverine (purple), estuarine habitats (light pink), marine (tan), and other (grey). Individuals are organized in order from the least to most urban based the amount of urban habitat within 650-meters of daytime, non-breeding locations, representing the ibis's least constrained habitat use and reflection of their synanthropic association. The stacked bar plots depict the proportions of habitat types within (A) non-breeding and (B) breeding ranges. Missing bars indicate individuals without breeding season data, or ranges that went outside of Florida. Additionally, panel (C) shows the difference in habitat use between non-breeding and breeding ranges, such that habitats used more often in non-breeding ranges are positive and habitats used more often in breeding ranges are negative.

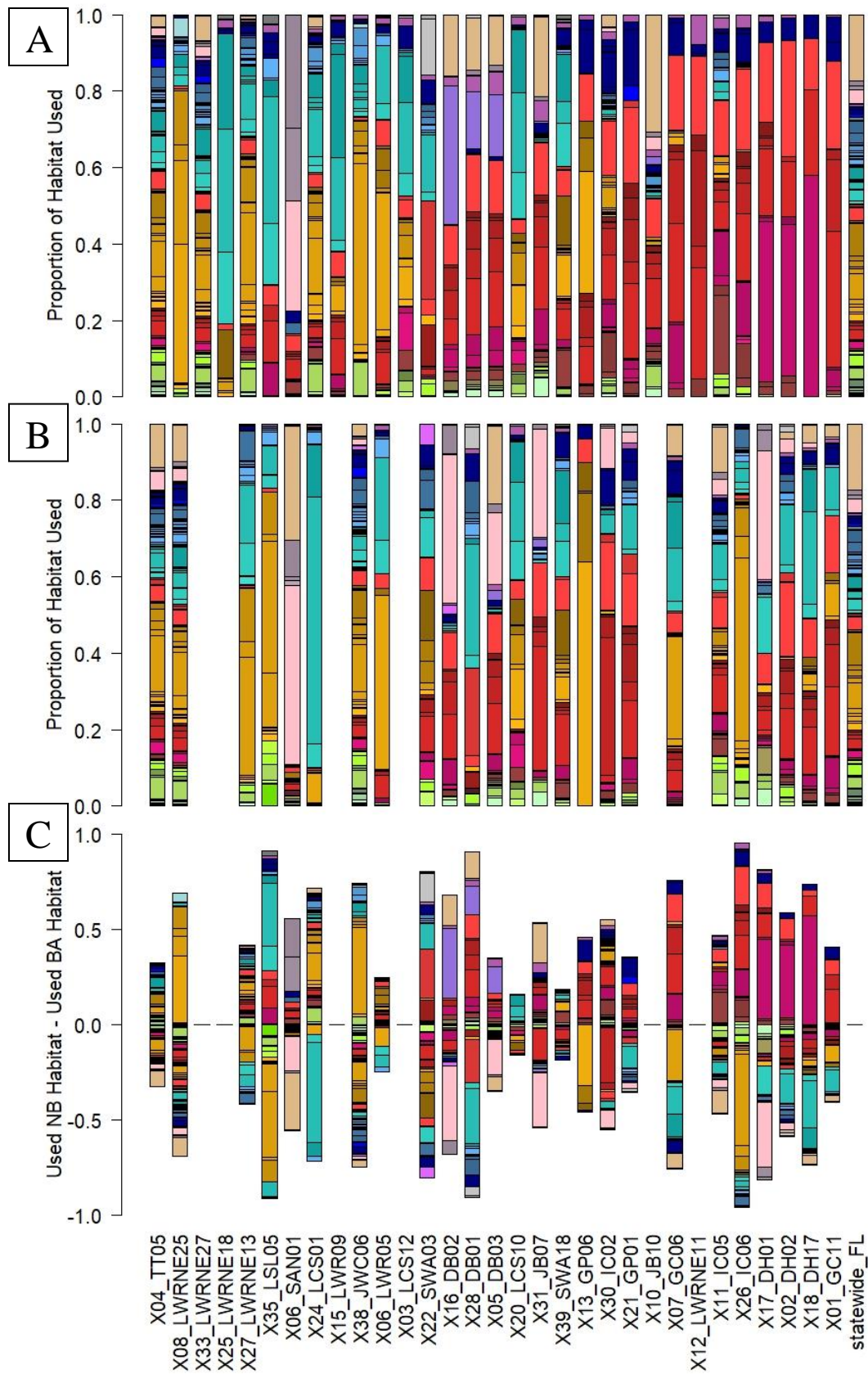


Figure 3.4. Selection of habitats within seasonal ranges compared to habitat availability in the state of Florida. Stacked bar charts show the selection of habitats in non-breeding (top graph) and breeding (bottom graph) seasons, calculated as the proportion of habitat types within individual ranges minus the proportion of habitat types available throughout the state of Florida. Individuals are ordered from least to most use of urban habitats during the non-breeding season.

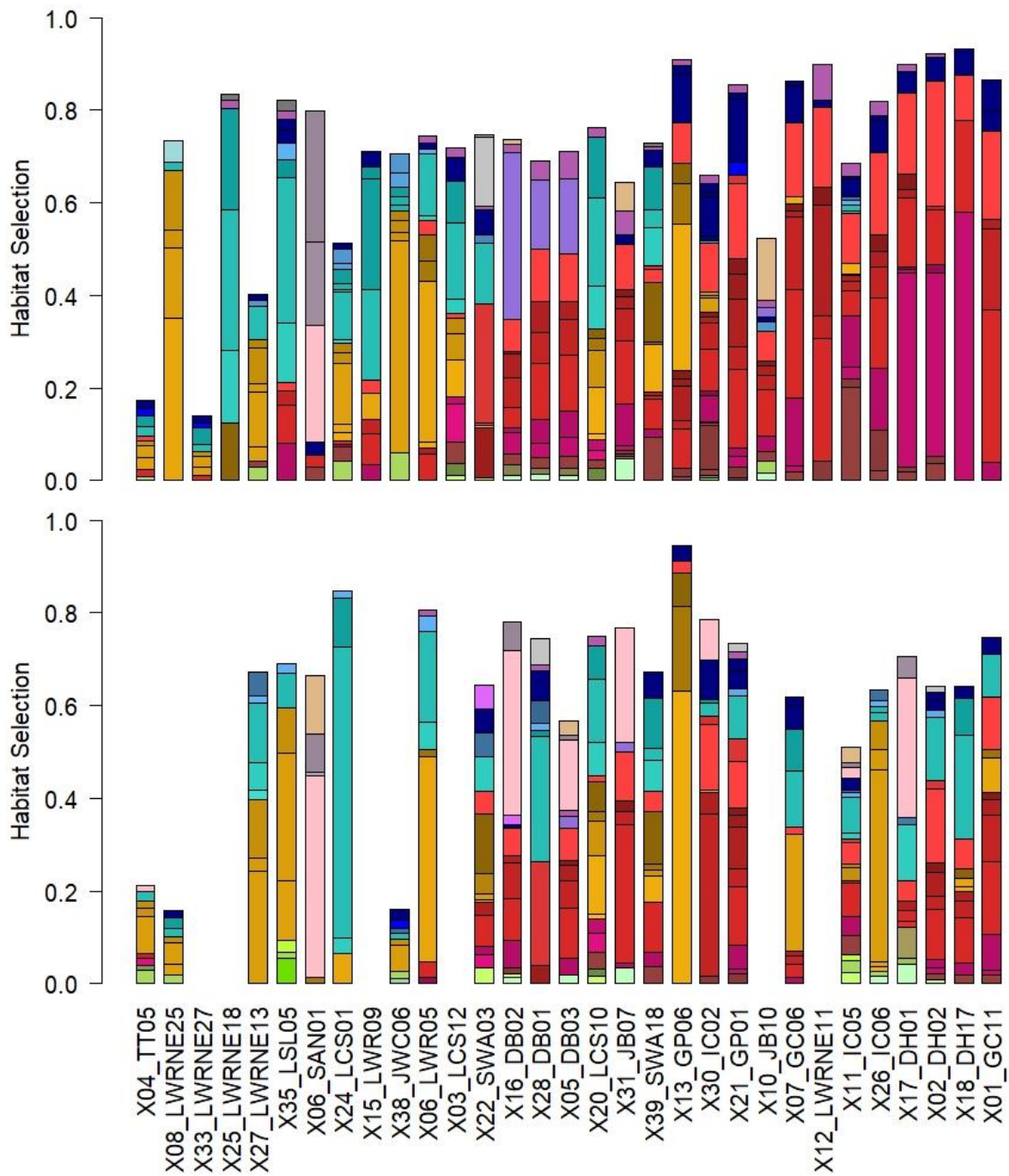


Table 3.1. Model average parameter estimates and importance. Model-averaged parameter estimates are estimated from the top model set (less than 2 delta-AIC) for linear mixed models with range size or site fidelity as response variables and individual as a random effect.

Importance refers to the sum of all model Akaike weights. Confidence intervals may include 0 for parameters that were included in few models. NB = non-breeding season.

Response Variable	Covariate	Beta Estimate	CI low, 2.5%	CI high, 97.5%	Importance
log10 scaled range size	Intercept	1.769	-0.066	3.604	
	Non-breeding urban use	-7.810	-13.099	-2.522	1.000
	Non-breeding urban use^2	6.580	2.026	11.133	1.000
	Season (Breeding)	-0.218	-1.102	0.666	1.000
	Season (Breeding) x NB Urban Use ^2	2.816	-1.225	6.858	1.000
	Season (Breeding) x NB Urban Use	-1.072	-5.355	3.210	0.870
	Sex (male)	0.146	-1.494	1.786	0.470
	Sex (male) x NB Urban Use	-1.666	-3.987	0.655	0.350
	age (3)	-6.605	-13.314	0.104	0.300
	age (4)	-1.611	-7.244	4.023	0.300
	age (5)	-3.514	-6.818	-0.209	0.300
	age (6)	-0.126	-1.605	1.353	0.300
	age (3) x NB Urban Use	8.105	-0.441	16.652	0.300
	age (4) x NB Urban Use	1.317	-5.859	8.493	0.300
	age (5) x NB Urban Use	4.463	0.241	8.686	0.300
	age (6) x NB Urban Use	-0.036	-2.050	1.978	0.300
	Scaled Mass Index	-0.107	-0.167	-0.047	0.230
	Mass	-0.010	-0.013	-0.006	0.110

Response Variable	Covariate	Beta Estimate	CI low, 2.5%	CI high, 97.5%	Importance
logit site fidelity	Intercept	-1.037	-1.353	-0.720	
	Non-breeding urban use	-2.337	-4.033	-0.641	1.000
	Non-breeding urban use ²	1.980	0.250	3.710	1.000
	Season (Breeding)	0.181	-0.105	0.467	1.000
	Season (Breeding) x NB Urban Use ²	1.215	-3.055	0.415	0.660
	Season (Breeding) x NB Urban Use	-1.320	-0.534	2.964	0.410

Table 3.2. Models used in model averaging. Weights are recalculated such that the cumulative sum of all model weights from the top model set is 1.

Response Variable	Model Terms	K	Log Likelihood	AIC	Delta AIC	Weight
log10 scaled range size	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), (Season x NB Urban Use), Sex, (Sex x NB Urban Use)	10	-116.072	255.477	0.000	0.227
	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), (Season x NB Urban Use), Scaled Mass Index	9	-117.949	256.585	1.108	0.130
	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), Sex, (Sex x NB Urban Use)	9	-117.990	256.667	1.191	0.125
	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), (Season x NB Urban Use), Sex	9	-118.031	256.748	1.272	0.120
	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), (Season x NB Urban Use), Age, (Age x NB Urban Use), Animal Mass	17	-106.259	256.890	1.414	0.112
	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), (Season x NB Urban Use), Age, (Age x NB Urban Use), Scaled Mass Index	17	-106.356	257.086	1.609	0.102
	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), (Season x NB Urban Use)	8	-119.536	257.191	1.714	0.096
	NB Urban Use, NB Urban Use ² , Season, (Season x NB Urban Use ²), (Season x NB Urban Use), Age, (Age x NB Urban Use)	16	-108.158	257.382	1.905	0.088
	logit site fidelity	NB Urban Use, Season, NB Urban Use ² , (Season x NB Urban Use ²), (Season x NB Urban Use)	8	-56.505	131.129	0.000
NB Urban Use, Season, NB Urban Use ²		6	-59.145	131.489	0.360	0.343
NB Urban Use, Season, NB Urban Use ² , (Season x NB Urban Use ²)		7	-58.268	132.158	1.030	0.246

CHAPTER 4

CONCLUSIONS

Introduction

Human coastal communities experience faster growth in population and housing and a larger increase in population density compared to inland areas of the United States (NOAA 2013). Urbanization simultaneously removes native habitats for wildlife. In particular, the human population in Florida is expected to increase to 35 million by the year 2060, resulting in a predicted loss of an additional 2.7 million acres of native habitats (Zwick and Carr 2006). Studying changes in wildlife ecology in human-dominated landscapes is therefore vital for understanding how wildlife populations may adapt to urbanized landscapes, and how best to manage human-wildlife interactions given closer and more frequent contact of wildlife with people (Johnston 2001).

Human-wildlife interactions also can have benefits for wildlife and humans. Patches of natural habitat, restored habitats, or human-created wild-like habitats within an urban matrix can serve as refuge habitats in highly degraded landscapes, allowing adaptable species to persist despite the loss of their native habitats (Martin et al. 2010, Duckworth and Altwegg 2014). As wildlife populations move into urban landscapes, opportunities arise for people to experience nature, with benefits for their wellbeing (Marzluff and DeLap 2014), and opportunities to learn how to be better stewards of wildlife populations and the environment (Warren and Lepczyk 2012). Efforts to connect with urban wildlife include: watching wildlife in parks, attempting to

interact with wildlife directly through activities such as feeding, or seeking out educational opportunities to learn about wildlife and their relationships to their environment.

While some people may initiate interactions with wildlife with the best intentions, others intentionally exploit or harass wildlife. Both situations can result in many potential negative consequences for wildlife and public health. These consequences can include increased stress, alterations to animal behavior that lower their fitness (e.g. reduced anti-predator vigilance or foraging efficiency in natural environments), altered health status through ingestion of low quality food, or exposure to pathogens and contaminants, and development of negative human-wildlife interactions such as nuisance behaviors and aggression.

Recent studies on the American White Ibis have investigated the consequences of urban foraging on ibis ecology with a focus on dietary shifts and the prevalence of zoonotic disease in urban habitats (Hernandez et al. 2016, Murray et al. 2018). In this thesis, I sought to characterize another aspect of ibis' life history that could be altered by urbanization: how annual cycles and space use are influenced by the degree of use of urban habitats. I quantified changes in season length, space use, and resource use for ibis across a range of synanthropic urban habitat use for ibis across a South Florida urbanization gradient. Overall, I found evidence for changes in ibis movement ecology that roughly fell at three levels of individual urban habitat use: low, intermediate, and high.

The Wild

Ibis with very little use of urban habitats exhibited behaviors more similar to what we would expect for a wild ibis. Ibis on the lower end of our synanthropic association scale, rarely used urban habitats. The urban habitat they did use included zoos and golf courses, which have been documented as alternative habitat for other wetland-dependent species living in degraded

ecosystems (Martin et al. 2010, Duckworth and Altwegg 2014). Despite their low use of urban habitats, these wild ibis primarily used and selected agricultural and freshwater habitats throughout the year, or showed less habitat selectivity by using habitats in the same relative proportions that are found in throughout the state of Florida. These habitat use trends support other studies that find that ibis captured at sites surrounded by less urban habitat have diets with less anthropogenic foods, corresponding to increased use of protein-rich foods associated with wetland foraging (Murray et al. 2018).

Wetland habitats do not continually provide ibis-appropriate foraging opportunities due to changing water depths; this causes nomadic movements as they opportunistically search for ephemeral foraging conditions. Agricultural areas, though more reliable, are similar in their function to wetlands as foraging on agricultural lands typically coincides with the timing in which property owners flood their fields. As ibis who use wetland and agriculture habitats move to take advantage of ephemeral resources, their ranges are large and their site fidelity is low, reflecting a nomadic lifestyle. In the breeding season, their ranges are restricted to rookery locations while they continue to use wetland and agricultural habitats.

The Urban

Higher use of urban habitats is related to altered seasonal movement behaviors showing evidence of season-related tradeoffs between movements and habitat use. In non-breeding seasons, urban ibis had very small ranges, high site fidelity, and spent most of their time in urban habitat types. Urban habitats often provide an abundance of year-round available resources in the form of human-provided foods, landfills, and artificial shelter (e.g., created tree islands in golf courses). Studies of urban habitat use for other species show that individuals living in urban habitats often have smaller ranges and high site fidelity compared to non-urban individuals

(Varner et al. 2014, Belton et al. 2016). My findings of reduced space use and increased site fidelity by synanthropic ibis, combined with findings that ibis captured in highly urban habitats have diets with higher levels of anthropogenic foods (Murray et al. 2018) indicates that White Ibis in Florida are learning to exploit resources found in urban habitats.

During breeding seasons however, urban ibis range sizes increase, while site fidelity decreases signaling a change in ibis behavior. In the breeding season, ibis switch their habitat selection from predominantly urban habitat types to more freshwater wetlands, and agricultural areas, exhibiting behaviors that are more similar to that of wild ibis, with the exception of birds using a large rookery located proximate to a landfill. These seasonal changes in movement behaviors indicate that urban ibis may still require some wetland habitat features that are not available in their non-breeding ranges. However, their shortened pre-breeding dispersal periods and breeding seasons, lack of post-breeding movements, and longer non-breeding seasons in comparison to our wild individuals, could indicate that urban ibis move to breeding ranges that are close to their non-breeding ranges and spend as little time outside of their non-breeding ranges as possible, make directed movements back to stable food resources, or that they fail in their nesting attempts and return to their non-breeding ranges early. To investigate further the relationships between non-breeding and breeding seasons, we should investigate the distance moved between non-breeding and breeding ranges, and compare differences in habitat selection by more specific behaviors, such as roosting, nesting, and daytime foraging.

The Intermediate

Some ibis exhibited an intermediate amount of urban habitat use compared to urban and wild individuals. These individuals had around 50% urban habitat use in non-breeding seasons, but consistently used a variety of habitat types throughout both non-breeding and breeding

seasons. These ibis consistently had small ranges and low site fidelity throughout the year, which may have indicated sufficient resources to maintain range residency. While space use was similar between seasons for these intermediate ibis, the proportions of habitat types used switched from riverine and marine habitat classes in the non-breeding season to estuarine, freshwater wetland, and agricultural habitats in the breeding season, clearly indicating a shift in resources required between seasons. These findings together leave open the question: why do these intermediate urban users consistently have small ranges, despite changing locations? One could investigate this question by attempting to ascertain if these individuals preferentially establish ranges in areas with a high variety of habitat types to take advantage of a variety of resource types within a small area.

Continuing Research

In our study of ibis movement ecology, we found relationships between seasonal space use, site fidelity, fine-scale habitat use, and three levels of synanthropic associations. In these investigations, we highlighted important areas that warrant further development for future studies of the American White Ibis movement ecology to develop a more complete picture of their response to landscape urbanization.

The biggest missing link in our understanding of ibis space use and habitat selection between non-breeding and breeding seasons is a quantification of the interseasonal site fidelity, or the distance moved between non-breeding and breeding season ranges. The observed differences in seasonal habitat selection and seasonal duration could suggest that ibis are changing the distance they are willing to disperse between seasonal ranges based on their synanthropic associations. Some ibis move long distances between breeding and non-breeding ranges, while others select breeding ranges within their larger non-breeding ranges or expand the

boundaries of their small non-breeding ranges to include the habitats necessary for breeding. Our proposed hypothesis is that urban ibis, which use more urban habitats in both non-breeding and breeding seasons, can have shorter, more direct dispersals between non-breeding and breeding habitat or will expand their non-breeding ranges to incorporate habitats needed for successful breeding attempts compared to wild individuals if suitable breeding locations are known prior to nest initiation.

Since we only performed a preliminary exploration of ibis habitat use, continued investigation of changes in habitat use are necessary to develop a better understanding of how ibis are using urban versus other habitat types. We can use the results in this study to define groupings of habitat classes that better reflect an ibis's consideration of the landscape. Future investigations into the habitat selection of ibis should consider selection for behaviors that require different resources, such as foraging, roosting, and nesting, as well as examining habitat selection at different spatial scales.

The conclusions presented in this thesis and future studies inspired by our findings can be used to develop future management and conservation plans for these and other urban wildlife populations. In the face of continued human-modification of native habitats, individuals may continue to move into and learn to exploit the resources found in urban habitats. Urban populations may continue to increase as individuals are attracted to wetland-like features and join existing urban flocks. These individuals may become dependent on human provided habitats and food resources reducing seasonal variation in habitat use and increasing site fidelity to urban areas (Martin et al. 2011, Varner et al. 2014, Gilbert et al. 2016). By understanding the changes in ibis movement behaviors and the habitats they require throughout their lifetime, future

management plans can incorporate this information to better support the conservation of the species and to reduce the risk of future negative human—wildlife interactions.

REFERENCES

- American Forests. 2007. Urban Ecosystem Analysis Palm Beach County, Florida: Calculating the Value of Nature. Palm Beach County.
- Bancroft, G. T., D. E. Gawlik, and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths. *Waterbirds: The International Journal of Waterbird Biology* 25:265–277.
- Barton, K. 2018. MuMIn: Multi-Model Inference.
- Belton, L. E., E. Z. Cameron, and F. Dalerum. 2016. Spotted hyaena space use in relation to human infrastructure inside a protected area. *PeerJ* 4:e2596.
- Bennetts, R. E., and W. M. Kitchens. 2000. Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? *Oikos* 91:459–467.
- Bildstein, K. L. 1993a. Salt stress and prey choice. Pages 149–165 *White Ibis: Wetland Wanderer*. Smithsonian Institution Press, Blue Ridge Summit, PA.
- Bildstein, K. L. 1993b. On Becoming an Adult. Pages 69–93 *White Ibis: Wetland Wanderer*. Smithsonian Institution Press, Blue Ridge Summit, PA.
- Bildstein, K. L. 1993c. *White ibis : Wetland Wanderer*. Smithsonian Institution Press Washington.
- Birkett, P. J., A. T. Vanak, V. M. R. Muggeo, S. M. Ferreira, and R. Slotow. 2012. Animal perception of seasonal thresholds: Changes in elephant movement in relation to rainfall patterns. *PLoS ONE* 7.

- Börger, L., B. D. Dalziel, and J. M. Fryxell. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters* 11:637–650.
- Borkhataria, R. R., A. L. Bryan Jr., and P. C. Frederick. 2013. Movements and habitat use by fledgling Wood Storks (*Mycteria americana*) prior to dispersal from the natal colony. *Waterbirds* 36:409–417.
- Boyce, M. S., J. Pitt, J. M. Northrup, A. T. Morehouse, K. H. Knopff, B. Cristescu, and G. B. Stenhouse. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2213–2219.
- Boyle, R., N. Dorn, and M. Cook. 2014. Importance of crayfish prey to nesting white ibis (*Eudocimus albus*). *Waterbirds* 37:19–29.
- Brearley, G., J. Rhodes, A. Bradley, G. Baxter, L. Seabrook, D. Lunney, Y. Liu, and C. McAlpine. 2013. Wildlife disease prevalence in human-modified landscapes. *Biological Reviews* 88:427–442.
- Brearly, G., C. McAlpine, S. Bell, and A. Bradley. 2011. Squirrel glider home ranges near urban edges in eastern Australia. *Journal of Zoology* 285:256–265.
- Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos Trans R Soc London Ser B - Biol Sci* 365:2157–62.
- Calabrese, J. M., C. H. Fleming, and E. Gurarie. 2016. ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution* 7:1124–1132.
- Casper, R. M. 2009. Guidelines for the instrumentation of wild birds and mammals. *Animal*

- Behaviour 78:1477–1483.
- Clucas, B., and J. M. Marzluff. 2012. Attitudes and actions toward birds in urban areas: Human cultural differences influence bird behavior. *The Auk* 129:8–16.
- Cook, M. I., E. M. Call, R. Mac Kobza, S. D. Hill, and C. J. Saunders. 2014. Seasonal movements of crayfish in a fluctuating wetland: Implications for restoring wading bird populations. *Freshwater Biology* 59:1608–1621.
- Corcoran, M. J., B. M. Wetherbee, M. S. Shivji, M. D. Potenski, D. D. Chapman, and G. M. Harvey. 2013. Supplemental Feeding for Ecotourism Reverses Diel Activity and Alters Movement Patterns and Spatial Distribution of the Southern Stingray, *Dasyatis americana*. *PLoS ONE* 8.
- Dahl, T. E. 2005. Florida's wetlands: An update on Status and Trends 1985 to 1996. Washington, D.C.
- DeAngelis, D. L., J. C. Trexler, and W. F. Loftus. 2005. Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland. *Canadian Journal of Fisheries and Aquatic Sciences* 62:781–790.
- Dorn, N. J., M. I. Cook, G. Herring, R. A. Boyle, J. Nelson, and D. E. Gawlik. 2011. Aquatic prey switching and urban foraging by the White Ibis *Eudocimus albus* are determined by wetland hydrological conditions. *Ibis* 153:323–335.
- Duckworth, G. D., and R. Altwegg. 2014. Environmental Drivers of an Urban Hadedda Ibis Population. *Ardea* 102:21–29.
- Duckworth, G. D., R. Altwegg, and D. Guo. 2010. Soil moisture limits foraging: A possible mechanism for the range dynamics of the hadeda ibis in southern Africa. *Diversity and Distributions* 16:765–772.

- Edelhoff, H., J. Signer, and N. Balkenhol. 2016. Path segmentation for beginners: an overview of current methods for detecting changes in animal movement patterns. *Movement Ecology* 4:21.
- Ehrenfeld, J. G. 2000. Evaluating wetlands within an urban context. *Ecological Engineering* 15:253–265.
- Epstein, J. H., J. McKee, P. Shaw, V. Hicks, G. Micalizzi, P. Daszak, A. M. Kilpatrick, and G. Kaufman. 2006. The Australian white ibis (*Threskiornis molucca*) as a reservoir of zoonotic and livestock pathogens. *EcoHealth* 3:290–298.
- ESRI. 2016. ArcMap 10.4.1. Environmental Systems Research Institute, Redlands, CA.
- Fayet, A. L., R. Freeman, A. Shoji, H. L. Kirk, O. Padget, C. M. Perrins, and T. Guilford. 2016. Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology* 85:1516–1527.
- Ferguson, S. H., and P. C. Elkie. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology* 262:125–134.
- Fleming, C. H., and J. M. Calabrese. 2016. A new kernel density estimator for accurate home-range and species-range area estimation. *Methods in Ecology and Evolution*:1–9.
- Fleming, C. H., and J. M. Calabrese. 2017a. *ctmm: Continuous-Time Movement Modeling*.
- Fleming, C. H., and J. M. Calabrese. 2017b. Variograms and Model Selection Variograms:1–11.
- Fleming, C. H., and J. M. Calabrese. 2017c. Autocorrelated Kernel Density Estimation:0–2.
- Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, J. M. Calabrese, and E. G. Cooch. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96:1182–1188.
- Frederick, P. C., K. L. Bildstein, B. Fleury, and J. C. Ogden. 1996. Conservation of large,

- nomadic populations of White Ibises (*Eudocimus albus*) in the United States. *Conservation Biology* 10:203–216.
- Frederick, P. C., D. E. Gawlik, J. C. Ogden, M. I. Cook, and M. Lusk. 2008. The White Ibis and Wood Stork as indicators for restoration of the everglades ecosystem. *Ecological Indicators* 9S:S83–S95.
- Frederick, P. C., and S. M. McGehee. 1994. Wading bird use of wastewater treatment wetlands in Central Florida, USA. *Colonial Waterbirds* 17:50–59.
- Frederick, P. C., and J. C. Ogden. 1997. Philopatry and nomadism: contrasting long-term movement behavior and population dynamics of White Ibises and Wood Storks. *Colonial Waterbirds* 20:316–323.
- Frederick, P., J. A. Heath, B. Hylton, J. D. Semones, G. Babbitt, and M. G. Spalding. 2002. Factors affecting breeding status of wading birds in the Everglades:355.
- FWC, and FNAI. 2016. Florida Cooperative Land Cover Map, Version 3.2. Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory.
- Garstang, M., R. E. Davis, K. Leggett, O. W. Frauenfeld, S. Greco, E. Zipser, and M. Peterson. 2014. Response of African elephants (*Loxodonta africana*) to seasonal changes in rainfall. *PLoS One* 9.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72:329–346.
- Gilbert, N. I., R. A. Correia, J. P. Silva, C. Pacheco, I. Catry, P. W. Atkinson, J. A. Gill, and A. M. A. Franco. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. *Movement Ecology* 4:1–13.

- González, T. M., J. D. González-Trujillo, J. R. B. Palmer, J. Pino, and D. Armenteras. 2017. Movement behavior of a tropical mammal: The case of *Tapirus terrestris*. *Ecological Modelling* 360:223–229.
- Gravolin, I., M. Key, and A. Lill. 2014. Boldness of urban Australian magpies and local traffic volume. *Avian Biology Research* 7:244–250.
- Grund, M. D., J. B. McAninch, and E. P. Wiggers. 2002. Seasonal Movements and Habitat Use of Female White-Tailed Deer Associated with an Urban Park. *Journal of Wildlife Management* 66:123–130.
- Gurarie, E. 2013. Behavioral Change Point Analysis in R : The bcpa package:1–16.
- Gurarie, E. 2014. bcpa: Behavioral change point analysis of animal movement.
- Gurarie, E., R. D. Andrews, and K. L. Laidre. 2009. A novel method for identifying behavioural changes in animal movement data. *Ecology Letters* 12:395–408.
- Gurarie, E., C. Bracis, M. Delgado, T. D. Meckley, I. Kojola, and C. M. Wagner. 2016. What is the animal doing? Tools for exploring behavioural structure in animal movements. *Journal of Animal Ecology* 85:69–84.
- Hall, A. J., and E. K. Saito. 2008. Avian wildlife mortality events due to salmonellosis in the United States, 1985-2004. *Journal of wildlife diseases* 44:585–593.
- Harris, R. J., and J. M. Reed. 2002. Behavioral barriers to non-migratory movements of birds. *Ann. Zool. Fennici* 39:275–290.
- Heath, J. A., and P. C. Frederick. 2003. Trapping white ibises with rocket nets and mist nets in the Florida Everglades. *Journal of Field Ornithology* 74:187–192.
- Heath, J. A., P. C. Frederick, J. A. Kushlan, and K. L. Bildstein. 2009. White Ibis (*Eudocimus albus*). <https://birdsna.org/Species-Account/bna/species/whiibi>.

- Hernandez, S. M., C. C. Welch, V. E. Peters, E. K. Lipp, S. Curry, M. J. Yabsley, S. Sanchez, A. Prossotto, P. Gerner-Smidt, K. B. Hise, E. Hammond, W. M. Kistler, M. Madden, A. L. Conway, T. Kwan, and J. J. Maurer. 2016. Urbanized White Ibises (*Eudocimus albus*) as Carriers of *Salmonella enterica* of Significance to Public Health and Wildlife. *PLoS One* 11:e0164402.
- Herring, G., D. E. Gawlik, and J. M. Beerens. 2008. Evaluating two new methods for capturing large wetland birds. *Journal of Field Ornithology* 79:102–110.
- Herring, G., D. E. Gawlik, M. I. Cook, and J. M. Beerens. 2010. Sensitivity of Nesting Great Egrets (*Ardea alba*) and White Ibises (*Eudocimus albus*) to Reduced Prey Availability. *The Auk*.
- Herring, H. K., and D. E. Gawlik. 2011. Resource selection functions for Wood Stork foraging habitat in the southern Everglades. *Waterbirds* 34:133–142.
- Hoelzer, K., A. I. M. Switt, and M. Wiedmann. 2011. Animal contact as a source of human nontyphoidal salmonellosis. *Veterinary Research* 42:34.
- Hooten, M. B., D. S. Johnson, B. T. McClintock, and J. M. Morales. 2017a. Background on Animal Movement. Pages 1–12 *Animal Movement: Statistical Models for Telemetry Data*. CRC Press, Boca Raton, Florida.
- Hooten, M. B., D. S. Johnson, B. T. McClintock, and J. M. Morales. 2017b. Space Use. Pages 99–107 *Animal Movement: Statistical Models for Telemetry Data*. CRC Press, Boca Raton, Florida.
- Hoque, M. A., G. W. Burgess, A. R. Greenhil, R. Hedlefs, L. F. Skerratt, C. Report—, A. G. W. Burgess, A. A. R. Greenhil, and A. R. Hedlefs. 2012. Causes of Morbidity and Mortality of Wild Aquatic Birds at Billabong Sanctuary, Townsville, North Queensland, Australia.

- Source: *Avian Diseases* 56:249–256.
- Hostetler, J. A., T. S. Sillett, and P. P. Marra. 2015. Full-annual-cycle population models for migratory birds. *The Auk* 132:433–449.
- Humphrey, J. S., and M. L. Avery. 2014. Improved satellite transmitter harness attachment technique. *Journal of Raptor Research* 48:289–291.
- Johnston, R. F. 2001. Synanthropic birds of North America. Pages 49–67 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian Ecology and Conservation in an Urbanizing World*. Springer US, Boston, MA.
- Kessel, S. T., D. D. Chapman, B. R. Franks, T. Gedamke, S. H. Gruber, J. M. Newman, E. R. White, and R. G. Perkins. 2014. Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). *Marine Ecology Progress Series* 514:175–190.
- Kranzer, B. 2002. The Human Context for Everglades Restoration: The South Florida Case Study. *Publication Series: Human Population and Freshwater Resources Bulletin* 1:25–59.
- Kushlan, J. A. 1979. Feeding Ecology and Prey Selection in the White Ibis FEEDING ECOLOGY AND PREY SELECTION IN THE WHITE IBIS 81:376–389.
- Kushlan, J. A. 2008. SITE SELECTION FOR NESTING COLONIES BY THE AMERICAN WHITE IBIS *EUDOCIMUS ALBUS* IN FLORIDA. *Ibis* 118:590–593.
- Lehrer, E. W., and R. L. Schooley. 2010. Space use of woodchucks across an urbanization gradient within an agricultural landscape Space use of woodchucks across an urbanization gradient within an agricultural landscape 91:1342–1349.
- Lenz, J., K. Bohning-Gaese, W. Fiedler, and T. Mueller. 2015. Nomadism and seasonal range expansion in a large frugivorous bird. *Ecography* 38:54–62.

- Maljkovic, A., and I. M. Cote. 2011. Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. *Biological Conservation* 144:859–865.
- Martin, J., K. French, and R. Major. 2010. Population and breeding trends of an urban coloniser: The Australian white ibis. *Wildlife Research* 37:230–239.
- Martin, J., K. French, and R. Major. 2012. Behavioural Adaptation of a Bird from Transient Wetland Specialist to an Urban Resident. *PLoS ONE* 7:1–8.
- Martin, J. M., K. French, G. A. Ross, and R. E. Major. 2011. Foraging distances and habitat preferences of a recent urban coloniser: The Australian white ibis. *Landscape and Urban Planning* 102:65–72.
- Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–48 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publishers, Boston.
- Marzluff, J. M., and J. DeLap. 2014. *Welcome to Subirdia: Sharing Our Neighborhoods with Wrens, Robins, Woodpeckers, and Other Wildlife*. Yale University Press.
- McEvoy, J. F., D. A. Roshier, R. F. H. Ribot, and A. T. D. Bennett. 2015. Proximate cues to phases of movement in a highly dispersive waterfowl, *Anas superciliosa*. *Movement Ecology* 3:13–15.
- Mingozzi, T., R. Mencacci, G. Cerritelli, D. Giunchi, and P. Luschi. 2016. Living between widely separated areas: Long-term monitoring of Mediterranean loggerhead turtles sheds light on cryptic aspects of females spatial ecology. *Journal of Experimental Marine Biology and Ecology* 485:8–17.
- Møller, A. P., M. Díaz, T. Grim, A. Dvorská, E. Flensted-Jensen, J. D. Ibáñez-Álamo, J.

- Jokimäki, R. Mänd, G. Markó, P. Szymański, and P. Tryjanowski. 2015. Effects of urbanization on bird phenology: A continental study of paired urban and rural populations. *Climate Research* 66:185–199.
- Morato, R. G., J. A. Stabach, C. H. Fleming, J. M. Calabrese, R. C. De Paula, K. M. P. M. Ferraz, D. L. Z. Kantek, S. S. Miyazaki, T. D. C. Pereira, G. R. Araujo, A. Paviolo, C. De Angelo, M. S. Di Bitetti, P. Cruz, F. Lima, L. Cullen, D. A. Sana, E. E. Ramalho, M. M. Carvalho, F. H. S. Soares, B. Zimbres, M. X. Silva, M. D. F. Moraes, A. Vogliotti, J. A. May, M. Haberfeld, L. Rampim, L. Sartorello, M. C. Ribeiro, and P. Leimgruber. 2016. Space use and movement of a neotropical top predator: The endangered jaguar. *PLoS ONE* 11:1–17.
- Murray, M., A. Kidd, S. Curry, J. Hepinstall-Cymerman, M. Yabsley, H. Adams, T. Ellison, C. Welch, and S. Hernandez. 2018. From wetland specialist to hand-fed generalist: Shifts in diet and condition with provisioning for a recently urbanized wading bird. *Philosophical Transactions of the Royal Society B* 373:In Press.
- NABCI. 2016. The State of North America's Birds 2016. Page Environment and Climate Change Canada. Ottawa, Ontario.
- Niedzielski, B., and J. Bowman. 2016. Home range and habitat selection of the female eastern wild turkey at its northern range edge. *Wildlife Biology* 22:55–63.
- NOAA. 2010. C-CAP Land Cover. National Oceanic and Atmospheric Administration.
- NOAA. 2013. National coastal population report: Population trends from 1970 to 2010. Page NOAA State of the Coast Report Series.
- Ofstad, E. G., I. Herfindal, E. J. Solberg, and B.-E. Sæther. 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proceedings of the Royal Society*

- B: Biological Sciences 283:20161234.
- Ogden, J. C., S. M. Davis, T. K. Barnes, K. J. Jacobs, and J. H. Gentile. 2005. Total system conceptual ecological model. *Wetlands* 25:955–979.
- Orams, M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management* 23:281–293.
- Palm Beach County. 2015. Palm Beach County Profile. West Palm Beach, FL.
- Parker, J. M., M. J. Folk, S. B. Baynes, and K. L. Candelora. 2008. Use of Clap Traps in Capturing Nonmigratory Whooping Cranes in Florida. *Proceedings of the Tenth North American Crane Workshop*:141–146.
- Partecke, J., and E. Gwinner. 2007. Increased Sedentariness in European Blackbirds following Urbanization : A Consequence of Local Adaptation ? *Ecology* 88:882–890.
- Poessel, S. A., S. W. Breck, and E. M. Gese. 2016. Spatial ecology of coyotes in the Denver metropolitan area: influence of the urban matrix. *Journal of Mammalogy* 97:1414–1427.
- Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of Anthropogenic Resources on Raccoon (*Procyon Lotor*) Movements and Spatial Distribution. *Journal of Mammalogy* 85:483–490.
- R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Rose, S., P. Sumasgutner, A. Koeslag, and A. Amar. 2017. Does Seasonal Decline in Breeding Performance Differ for an African Raptor across an Urbanization Gradient? *Frontiers in Ecology and Evolution* 5:1–9.

- Rutz, C. 2006. Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks *Accipiter gentilis*. *Ardea* 94:185–202.
- Ryan, A. M., and S. R. Partan. 2014. Urban Wildlife Behavior. Pages 149–173 in R. A. McCleery, C. E. Moorman, and M. N. Peterson, editors. *Urban Wildlife conservation: Theory and Practice*. Springer US, Boston, MA.
- Shephard, J. M., S. Rycken, O. Almalik, K. Struyf, and L. Van Erp van der Kooij. 2015. Migration strategies revealed by satellite tracking among descendants of a population of European white stork (*Ciconia ciconia*) reintroduced to Belgium. *Journal of Ornithology* 156:943–953.
- Singh, N. J., L. Börger, H. Dettki, N. Bunnefeld, and G. Ericsson. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications* 22:2007–2020.
- Singh, P., and C. T. Downs. 2016. Hadedas in the hood: Hadedas Ibis activity in suburban neighbourhoods of Pietermaritzburg, KwaZulu-Natal, South Africa. *Urban Ecosystems* 19:1283–1293.
- Stewart, K., T. Norton, H. Mohammed, D. Browne, K. Clements, K. Thomas, T. Yaw, and J. Horrocks. 2016. Effects of “Swim With the Turtles ” tourist attractions on green sea turtle (*Chelonia mydas*) health in Barbados , West Indies. *Journal of Wildlife Diseases* 52:S104–S117.
- U.S. Fish and Wildlife Service. 2014. Endangered and threatened wildlife and plants; reclassification of the U.S. breeding population of the Wood Stork from endangered to threatened. Final rule. *Federal Register* 79:37078–37103.
- USDA. 2012. 2012 Census of Agriculture County Profile: Palm Beach County Florida.

USFWS. 2015. Arthur R. Marshall Loxahatchee.

https://www.fws.gov/refuge/ARM_Loxahatchee/about.html.

Varner, D. M., G. R. Hepp, and R. R. Bielefeld. 2014. Movements and seasonal use of habitats by rural and urban female mottled ducks in southeast Florida. *Journal of Wildlife Management* 78:840–847.

Vander Wal, E., and A. R. Rodgers. 2009. Designating Seasonality Using Rate of Movement. *Journal of Wildlife Management* 73:1189–1196.

Walden-schreiner, C., Y.-F. Leung, T. Kuhn, and T. Newburger. 2018. Integrating direct observation and GPS tracking to monitor animal behavior for resource management. *Environmental Monitoring and Assessment*:75.

Warren, P. S., and C. A. Lepczyk. 2012. Beyond the gradient: insights from new work in the avian ecology of urbanizing lands. Pages 1–6 *in* C. A. Lepczyk and P. S. Warren, editors. *Urban Bird Ecology and Conservation*. Studies in. University of California Press, Berkely, CA.

Weaving, M. J., J. G. White, B. Isaac, A. R. Rendall, and R. Cooke. 2016. Adaptation to urban environments promotes high reproductive success in the tawny frogmouth (*Podargus strigoides*), an endemic nocturnal bird species. *Landscape and Urban Planning* 150:87–95.

Welch, C. C. 2016. Urban land use and movements of White Ibises (*Eudocimus albus*) in South Florida. University of Georgia.

Zwick, P. D., and M. H. Carr. 2006. Florida 2060. A population distribution scenario for the State of Florida. Gainesville, FL.

APPENDIX A

A TOTAL LIST OF GPS-TAGGED WHITE IBISES AND CAPTURE CHARACTERISISTICS
OCTOBER 2015 TO NOVEMBER 2017.

Ibis ID	Mass at Capture	Scaled Mass Index	Age at capture	Sex	Deployment Date	End of Track	Days Tracked	Number of Seasons
01_GC11	860	-2.474	3	F	3/19/2016	1/1/2017	288	3
02_DH02	1080	10.793	3	M	10/16/2015	1/1/2017	443	5
03_LCS12	1020	3.446	3	M	2/27/2016	4/2/2016	35	2
04_TT05	860	1.873	3	M	3/9/2016	11/4/2016	240	3
05_DB03	870	2.936	4	F	10/15/2015	1/1/2017	444	5
06_LWR05	1000	7.384	3	M	10/24/2015	8/8/2016	289	6
06_SAN01	980	7.177	4	M	11/2/2016	7/29/2017	269	3
07_GC06	800	-0.863	2	F	3/18/2016	11/08/2017	635	6
08_LWRNE25	1000	0	2	M	3/13/2016	1/1/2017	294	4
10_JB10	880	-0.118	3	F	2/26/2016	11/4/2016	252	5
11_IC05	840	8.310	4	F	10/14/2015	11/08/2017	756	9
12_LWRNE11	920	5.429	2	M	3/1/2016	12/31/2016	305	6
13_GP06	920	7.518	3	M	11/8/2015	1/1/2017	420	5
14_LWRNE12	1090	9.538	2	M	3/2/2016	12/7/2016	280	1
15_LWR09	940	7.080	3	M	10/28/2015	6/26/2016	242	2
16_DB02	950	6.236	4	M	10/15/2015	12/31/2016	443	7
17_DH01	950	8.703	4	M	10/16/2015	12/30/2016	441	5
18_DH17	1000	6.190	3	M	3/20/2016	1/1/2017	287	3
19_SWA06	1000	10.263	3	F	3/15/2016	5/20/2016	66	1
20_LCS10	860	-4.705	2	F	2/27/2016	1/2/2017	310	4
21_GP01	980	8.498	3	M	10/27/2015	1/2/2017	433	5
22_SWA03	940	2.527	3	F	10/31/2015	9/8/2017	678	8
23_TT04	1240	12.866	3	M	3/9/2016	8/11/2016	155	1
24_LCS01	900	5.688	4	F	10/17/2015	1/1/2017	442	5
25_LWRNE18	1000	13.486	3	M	3/2/2016	4/21/2016	50	1
26_IC06	910	11.297	4	M	10/14/2015	6/25/2016	255	3
27_LWRNE13	940	6.210	3	M	3/2/2016	7/17/2016	137	4
28_DB01	1000	2.889	4	M	10/15/2015	12/30/2016	442	4
30_IC02	830	3.272	4	M	10/14/2015	11/08/2017	756	9
31_JB07	830	-6.626	4	M	10/19/2015	8/19/2017	670	7

Ibis ID	Mass at Capture	Scaled Mass Index	Age at capture	Sex	Deployment Date	End of Track	Days Tracked	Number of Seasons
32_TT09	1120	9.924	3	M	3/12/2016	8/17/2016	158	1
33_LWRNE27	1100	8.236	2	M	3/13/2016	11/5/2016	237	4
34_TT02	1040	7.474	2	M	3/9/2016	3/18/2016	9	1
35_LSL05	1100	15.972	3	M	2/26/2017	11/08/2017	255	3
36_GC18	940	10.935	3	M	7/15/2016	11/08/2017	481	2
37_LKW04	880	7.053	2	M	11/10/2016	11/08/2017	363	2
38_JWC06	940	2.665	3	M	2/13/2017	10/26/2017	255	3
39_SWA18	820	-2.541	3	F	6/29/2016	11/08/2017	497	5
40_JB15	800	0.728	3	F	7/14/2016	11/08/2017	482	2
41_GP16	860	8.028	3	M	6/28/2016	11/08/2017	498	2
43_LCS19	960	64.516	4	M	11/12/2016	11/08/2017	361	2
44_LCS17	1000	47.099	4	M	10/31/2016	4/25/2017	176	2
45_GC16	900	-88.291	3	F	7/14/2016	9/10/2017	423	2
46_BWS01	1170	6.388	3	M	2/20/2017	11/08/2017	261	2
47_LSL03	1080	354.889	3	M	2/25/2017	7/29/2017	154	2
48_LSL06	1060	5.213	3	M	2/26/2017	7/1/2017	125	2
49_LSL04	1020	6.596	3	M	2/26/2017	5/4/2017	67	2
50_LSL02	1040	8.141	3	M	2/25/2017	11/08/2017	256	2