

MOVEMENT ECOLOGY OF WOOD STORKS IN THE SOUTHEASTERN U.S.

By

SIMONA PICARDI

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2019

© 2019 Simona Picardi

To my teachers and mentors

ACKNOWLEDGMENTS

I was fortunate to receive guidance from five outstanding committee members during the past four and a half years. Each of them contributed differently to my growth according to their areas of expertise and personalities, but the common thread was that I could tell they all sincerely cared about helping me succeed. I have appreciated their kindness and humanity on top of their professional qualities. The following paragraphs acknowledge each of their unique contributions.

I am thankful to my advisor, Dr. Mathieu Basille, for making sure that my PhD experience would not only result in this dissertation, but also maximize my all-around professional development. He generously provided me with any resource on his hands to make sure I never lacked the means to work at the best of my capacity, he trusted me with the freedom to manage my own time, he encouraged me to seize valuable career-building opportunities on the side of my main duties, and he made sure that I maintained a healthy work/life balance all the while.

I am grateful to my co-advisor, Dr. Peter Frederick, first, for teaching me the importance of knowing my study system like the back of my hand; he is a living testimony of how sound science must be built on the foundation of detailed ecological understanding. I am grateful that he shot down unrealistic research ideas before they became a waste of my time and for steering my curiosity towards attainable and rewarding goals; he did all of this with unmatched grace and respect. Beyond the guidance on my research, I am grateful to have been able to count on his experience and wisdom for questions related to any aspect of my professional growth.

I sincerely thank my committee members, Drs. Robert Fletcher, José Miguel Ponciano, and Francesca Cagnacci, for their guidance and support throughout my PhD.

In particular, I thank Rob for his constructive criticism, which has been instrumental in shaping this dissertation from the very beginning, and for his thoughtful and long-sighted career advice, which has guided some important decisions and taught me how to plan successfully for my long-term goals. I thank José for his endless patience, his generosity in always making more time than he possibly had to meet with me, and for never showing any sign of doubt that I could master even the concepts that intimidate me the most. Last but not least, Francesca has been a constant point of reference in my career since long before my PhD, and her influence on my style of thinking and doing science is a trademark that I carry with me as I move on. I am thankful that she took the time to accompany me in yet another step of my professional growth.

The wood stork tracking project had started long before I set foot at the University of Florida. I want to acknowledge the people who have been involved with it from the beginning for their hard work obtaining funding and collecting the data. In particular, I thank Dr. Rena Borkhataria, Dr. Albert L. Bryan, and Donna Bear for sharing their data and discussing ideas with me and once more Dr. Peter Frederick for overseeing the project. Financial support for the project came from the U.S. Fish and Wildlife Service, the Army Corps of Engineers, the National Park Service, the Environmental Protection Agency, the USDA National Institute of Food and Agriculture, and the Everglades Foundation.

An important part of this dissertation was made possible by a collaboration with Dr. Jacopo Cecere from the Italian Institute for Environmental Protection and Research and Dr. Diego Rubolini from the University of Milan. I am very proud of the result of that collaboration and happy that it gave me an excellent excuse to cultivate professional

ties to my home country. I thank Jacopo and Diego for their support and friendship, and I hope we will work together again in the future.

My PhD experience has been greatly enriched by interactions with members of the MabLab at FLREC: David Bucklin, Alexis Bruant, Melissa Moreno, Caitlin Jarvis, Rocío Joo, Valeria Guerrero, Matt Boone, and Jenicca Poongavanan. David and Matt deserve special mentions for their assistance with data and programming tasks that were beyond my level of expertise. In addition, I especially thank Matt for his friendship and tireless emotional support, which never failed to brighten even the most stressful work days.

The MabLab is lucky to share an office space with Dr. Laura Brandt, from the U.S. Fish and Wildlife Service. Over time, Laura has become an important mentor to me. I sincerely thank her for the time and attention she devoted to answering my many questions and for the wise advice she has given me over the years. I have learned much from her about how to make good decisions, how to manage interactions with people on the workplace, and how science can be reconciled with real-world applications.

During my time at the Fort Lauderdale Research and Education Center, Jan and Jack Falk kindly donated an endowment in memory of their son, Jack A. Falk III, to support graduate students conducting research in the Everglades. I was a recipient of the first Jack A. Falk III Scholarship for Everglades Conservation, Restoration, and Sustainability that was granted thanks to their generosity, and I want to thank them for their continued support, friendship, and interest in my work.

Even though my time in Gainesville was short, it was long enough for me to establish connections with people who left an important mark on my PhD experience both as colleagues and as friends. I am especially grateful to have met Caroline Poli, Jessica Hightower, Sergio Marconi, Pauline Dufour, Noah Burrell, and Kwanmok Kim.

The most formative extra-curricular experiences I have had during my PhD came from my involvement with the UF Carpentries Club. While serving on the Club's Board I learned about leadership, community building, and teamwork, and instructing numerous Carpentries workshops has made me a better teacher. I am grateful that I have had the opportunity to build these important skills in such a positive, friendly environment. I thank all the colleagues I have shared this experience with, and in particular, Dr. Hao Ye and Matthew Collins, who – knowingly or not – have been important role models that I have looked up to many times.

This dissertation would not look the way it does, and I would not be the scientist I am today, if it was not for my partner, Brian Smith. His influence on my work has been pervasive: exchanging ideas with him has stimulated my critical thinking, looking at his example has inspired me on practical ways to build a successful career, and he has directly taught me many critical concepts and skills. Being around him has felt like having a 24-hour/7-day personal trainer for my career. I am extremely thankful to be able to discuss ideas, exchange advice, and share knowledge and enthusiasm about my work with the person who is also my partner in life.

Finally, I thank my parents and siblings for their support: pursuing a PhD on the other side of the world entails some challenging life decisions, and I am thankful that my family was supportive of the ones I made. I am also grateful for the value my parents

have always placed on education and culture and for nurturing an appreciation of nature in me since I was a child. Thanks to their lifelong hard work, I found myself well-equipped to pursue this PhD.

TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS.....	4
LIST OF TABLES.....	11
LIST OF FIGURES.....	12
LIST OF ABBREVIATIONS.....	14
ABSTRACT.....	15
CHAPTER	
1 GENERAL INTRODUCTION.....	17
2 PARTIAL MIGRATION IN A SUBTROPICAL WADING BIRD IN THE SOUTHEASTERN U.S.	24
Introduction.....	24
Methods.....	28
Study Area and Species.....	28
Wood Stork Captures and Data Collection.....	29
Operational Definitions.....	30
Classification of Migratory Behavior.....	30
Data Preparation.....	31
A-priori Model Constraints.....	32
Stepwise Specification of Starting Parameter Values.....	33
Post-hoc Model Evaluation.....	33
Seasonal Distributions, Range Fidelity, and Migratory Consistency.....	34
Results.....	35
Migratory Choices and Strategies.....	35
Migration Routes and Timing.....	36
Seasonal Ranges and Population Distribution.....	37
Discussion.....	37
3 NEST-SITE DETECTION AND ESTIMATION OF AVIAN REPRODUCTIVE OUTCOME FROM GPS-TRACKING DATA.....	53
Introduction.....	53
Methods.....	55
Method Description.....	55
Nest-site detection.....	55
Reproductive outcome estimation.....	57
Software Description.....	59
Study Cases.....	60

Results	62
Discussion	63
Nest-Site Detection	63
Reproductive Outcome Estimation	66
Synthesis and Significance.....	67
Conclusions.....	68
4 MECHANISMS FOR HUMAN-DRIVEN CHANGES OF MIGRATION PATTERNS: A CASE-STUDY WITH A PARTIALLY MIGRATORY WADING BIRD	76
Introduction	76
Methods	82
Data Collection	82
Breeding Attempts.....	82
Migratory Behavior	83
Urban Areas	83
Resource-Selection Analysis.....	83
Nest-Survival Analysis.....	84
Results	86
Discussion	86
Conclusions.....	90
5 GENERAL CONCLUSIONS	97
APPENDIX	
A SENSITIVITY ANALYSIS OF CONSTRAINT VALUES FOR NET SQUARED DISPLACEMENT MODELS.....	103
B STARTING VALUES FOR NET SQUARED DISPLACEMENT MODEL PARAMETERS	108
C INDIVIDUAL-YEARS DISCARDED FROM ANALYSES OF MIGRATION PATTERNS.....	110
D SUPPORTING INFORMATION FOR THE ANALYSES OF THE EFFECT OF URBAN AREAS ON WOOD STORK FORAGING-SITE SELECTION AND NEST SURVIVAL	112
LIST OF REFERENCES	119
BIOGRAPHICAL SKETCH.....	139

LIST OF TABLES

<u>Table</u>		<u>page</u>
2-1	Number of individuals tagged at each capture site	45
3-1	Differences among GPS-tracking datasets for wood storks, lesser kestrels, and Mediterranean gulls.	70
3-2	Performance metrics of the nest identification.	71
4-1	Results of Resource Selection Function for foraging sites used by wood storks during breeding as a function of distance to urban areas and migratory behavior.	92
A-1	Results of the classification of wood stork individual-years deriving from the use of different values as a spatial threshold for migratory movements.	106
A-2	Results of the classification of wood stork individual-years deriving from the use of different values as a temporal threshold for migratory movements.	107
B-1	Starting parameter values used in our analysis to progressively improve model convergence until full convergence.	109

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1 Map of the study area, located within the breeding range of the southeastern U.S. wood stork population.....	46
2-2 Conceptual illustration of non-linear models of Net Squared Displacement used to classify wood stork migratory behavior at the year scale	47
2-3 Maximum likelihood estimates of individual migration probabilities with 95% confidence intervals.....	48
2-4 Wood stork migration routes and timing	49
2-5 Heat maps of wood stork population distribution.	50
2-6 Heat map of year-round distribution of resident wood storks.....	51
2-7 Model predictions for seasonal range size of wood storks.	52
3-1 Workflow of the analysis to identify nest sites and estimate reproductive outcome from telemetry data.....	72
3-2 Output of CART to discriminate nest and non-nest sites.....	73
3-3 Probability of visit detection and survival through time estimated at the population level.....	74
3-4 Estimates of survival probabilities for breeding attempts.....	75
4-1 Conceptual framework illustrating mechanisms of human-induced migratory shifts	93
4-2 Maps of wood stork foraging locations, nesting locations, and Florida urban areas	94
4-3 Model predictions of Resource Selection Function for foraging sites used by wood storks during breeding attempts as a function of distance to urban areas and migratory behavior.....	95
4-4 Model predictions of daily nest survival as a function of distance to urban areas	96
C-1 Annual time-series of Net Squared Displacement for the 12 discarded individual-years.....	111
D-1 Density plot of distance of nests to urban areas in wood storks.	112

D-2	Generation of available foraging locations based on the empirical distribution of foraging trip distances	113
D-3	Density plots of distance of foraging sites to urban areas	114
D-4	Density plots of distance of foraging sites to urban areas for each individual breeding attempt.....	115
D-5	Diagnostic autocorrelation plots for daily nest survival model	116
D-6	Diagnostic traceplots for daily nest survival model.	117
D-7	Diagnostic density plots for daily nest survival model.....	118

LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
CART	Classification And Regression Trees
GLM	Generalized Linear Model
GPS	Global Positioning System
JAGS	Just Another Gibbs Sampler
MCMC	Markov-Chain Monte Carlo
NSD	Net Squared Displacement
SD	Standard Deviation
USFWS	U.S. Fish and Wildlife Service

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

MOVEMENT ECOLOGY OF WOOD STORKS IN THE SOUTHEASTERN U.S.

By

Simona Picardi

December 2019

Chair: Mathieu Basille
Cochair: Peter Frederick
Major: Wildlife Ecology and Conservation

Organisms move to colonize new environments, reproduce, and find resources. Migration is a specialized type of movement that allows animals to track resources that are heterogeneous in space and time. Migration can take different forms according to the temporal periodicity and predictability of resource variation; partial migration, where a population includes both migrant and resident individuals, emerges in environments where seasonality is paired with year-to-year unpredictability of resources. While most of the research on partial migration to date has focused on how it is controlled at the individual level, our understanding of its ecological implications and adaptive value is still limited. This dissertation contributes to furthering our understanding of partial migration by focusing on a population of wood storks (*Mycteria americana*) in the southeastern U.S. as a study model. The overall objective of my work was to investigate the adaptive value of behavioral heterogeneity within the wood stork population in terms of migratory behavior; if different individual migratory strategies are associated with different fitness advantages, behavioral heterogeneity might help wood storks persist in the face of resource unpredictability and environmental change. I addressed the following specific objectives:

1. Provide a quantitative description of individual migration patterns in the wood stork population;
2. Develop an analytical method to estimate reproductive outcome from movement data, to be used as a proxy for fitness;
3. Assess whether individuals that differ in their migratory behavior also differ in terms of resource selection and fitness.

My findings show that the wood stork population includes ~60% migrant and ~40% resident individuals, thus establishing its status as partially migratory. Residents and migrants differ in their foraging-site selection during breeding, with residents foraging closer to urban areas than migrants do; foraging sites located closer to urban areas are also associated with higher reproductive outcome, estimated from individual movement data using the method I developed. Overall, these results suggest that partial migration may be an adaptive strategy in the wood stork population because, when migrants fail to reproduce because of unpredictably bad foraging conditions, the contribution of residents to recruitment may provide a smaller but more reliable demographic reservoir.

CHAPTER 1 GENERAL INTRODUCTION

Movement is a fundamental component of the life history of virtually any living organism, and it plays a fundamental role in shaping ecological communities and enabling evolution; organisms move to spread and colonize new environments, to reproduce, and to track resources (Nathan et al. 2008). Movement ecology is the study of movement in living organisms and how it affects ecological dynamics (Nathan et al. 2008). The work presented in this dissertation focuses on animal movement ecology (hereafter, simply “movement ecology”). While all studies in animal movement ecology have in common a focus on movement processes, they usually accomplish one of three main goals: pattern description, inference on underlying processes, or evaluation of the role of movement in ecological and evolutionary dynamics. First, in its most basic form, movement ecology is concerned with describing patterns of animal movement. While it may seem trivial, mapping movements of individuals or populations and describing their repeatability across space, time, and individuals establishes important baseline knowledge for both ecology and conservation (Hebblewhite and Haydon 2010). Second, much effort in movement ecology today is directed towards uncovering processes underlying movement. Individual movement patterns arise from behavior; therefore, the signature of underlying behavioral processes is locked away in the patterns of movement that we observe. By deciphering these patterns, researchers can unlock those behavioral signatures and transition from answering the question, “where do animals go?” to “what are animals doing?” This quest has propelled the field of movement ecology forward in recent years, with the development of several analytical techniques to segment individual trajectories into homogeneous behavioral units

(Gurarie et al. 2016, Edelhoff et al. 2016). Third, and ultimately, the goal of movement ecology is to evaluate the role of movement in driving and influencing both ecological and evolutionary processes. Movement couples spatio-temporal resource dynamics with animal distributions at several hierarchical levels, and thus plays a central role in population, community, and ecosystem dynamics. Understanding how individual movement decisions scale up to higher hierarchical levels is a major ongoing challenge that movement ecologists are currently undertaking (Jeltsch et al. 2013). This dissertation includes three chapters that exemplify the three ways of doing movement ecology described so far: pattern description (Chapter 2), inference on underlying processes (Chapter 3), and evaluation of the role of movement in ecological and evolutionary processes (Chapter 4).

Specifically, the work presented in this dissertation focuses on partial migration. Migration is traditionally viewed as a periodical movement between separate areas that enable survival and reproduction at different times of the year (Dingle 1996); it has the function of allowing species to track resources that are heterogeneous in space and time (Dingle and Drake 2007). Partial migration is the condition where a population includes both migrant and resident individuals (Chapman et al. 2011). Migrants usually commute between separate seasonal ranges, while residents remain in a single range year-round. To date, much of the empirical research on partial migration has been focused on disentangling how it is controlled at the individual level, both through experimental (Biebach 1983, Berthold 1984) and observational studies (Ogonowski and Conway 2009, Hegemann et al. 2015). Other (mostly theoretical) studies have addressed the evolutionary underpinnings of partial migration, proposing hypotheses on

how it might arise and what advantages it may bring to populations (Lundberg 1988, Vélez-Espino et al. 2013). While the evidence for evolutionary mechanisms is still mixed (Pulido 2011), the fact that partial migration is an advantageous strategy in environments that are both seasonally variable and unpredictable is generally accepted (Dingle and Drake 2007, Newton 2012). Further, some have proposed that partial migration can be maintained over evolutionary time scales because it works as an evolutionarily stable strategy (Lundberg 1987, Kaitala et al. 1993), while others have suggested that it might be an intermediate form of migration for populations transitioning from complete migration to residency, or vice-versa (Bell 2000, Berthold 2001). Overall, very little empirical work has been conducted regarding the ecological implications of partial migration, which nonetheless constitute the inner workings of evolution. In particular, significant gaps remain regarding the relative advantages of different migratory behaviors within partially migratory populations, and therefore the adaptive significance of partial migration itself.

Another limitation of our current understanding of partial migration is that most empirical research so far has been carried out on temperate species. Little is known about partial migration in tropical and sub-tropical species. Since seasonality of resources in non-temperate areas is often driven by rainfall rather than temperature, focusing on non-temperate species can help disentangle the role of seasonality in shaping migration strategies regardless of the specific environmental driver. This is an important piece of the puzzle to understand the adaptive significance of partial migration (Sekercioglu 2010).

Finally, the adaptive value of partial migration needs to be evaluated in relation to anthropogenic environmental change. Nowadays, virtually all natural environments on the planet are being altered by human activities. When addressing the adaptive significance of partial migration or any other movement phenomenon, scientists must now consider the newly emerging selective pressures that humans are imposing on wildlife populations (Fahrig 2007, Tucker et al. 2018). Accounting for these new selective pressures is as much of a necessity to make accurate predictions on future ecological responses as it is an opportunity to watch evolution happen in real time.

This dissertation addresses partial migration using wood stork (*Mycteria americana*) as a study species. Wood storks are the only stork species breeding in North America (Coulter et al. 1999). Their species range includes wetlands of Latin America as well as the southeastern U.S., which is inhabited by a distinct population segment (USFWS 2014). Wood storks are an ideal study model to further our understanding of partial migration for several reasons: first, their range in the southeastern U.S. is at the ecotone of temperate and sub-tropical latitudes, with the bulk of the breeding grounds located at the southern extreme of the distribution (towards the sub-tropical end of the gradient; Coulter et al. 1999); second, wood storks rely on food sources whose seasonal fluctuations are driven by hydrological dynamics, rainfall especially (Kahl 1964); finally, wood storks inhabit one of the most heavily human-impacted states of the U.S. and are subject to emerging pressures from habitat degradation, loss, and introduction of novel resources.

To address the ecological and adaptive implications of partial migration in wood storks, I leveraged an existing GPS-tracking dataset including 133 individuals and

spanning 14 years between 2004 and 2018. The strengths of this dataset lie in its size (in terms of number of individuals tracked) and temporal extent, as well as the fact that several individuals were tracked for multiple years in a row, which provided an opportunity to quantify year-to-year behavioral plasticity.

The overall objective of my dissertation was to understand the adaptive significance of wood stork partial migration in the context of anthropogenic environmental change. Specific objectives were: 1) Describing migration patterns of wood storks, focusing on individual differences in migratory behaviors within the population (Chapter 2); 2) Developing a method to infer components of individual fitness from movement data (Chapter 3); 3) Evaluating fitness consequences of individual migratory behavior in a human-impacted landscape (Chapter 4). Therefore, Chapters 2 and 3 provide the baseline information necessary for Chapter 4.

Chapter 2 provides the first quantitative description of migration patterns in wood storks, formally establishing their status as partially migratory. Wood storks were previously known to undertake large-scale seasonal movements across their range, but they were labeled as “not true migrants” (Coulter et al. 1999), likely because of failure to identify seemingly irregular population movement patterns as due to individual variation in migration behavior. Using a state-of-the-art modeling approach, I classified individual migratory choices in each year as either migration or residency and evaluated the repeatability of migratory choices across years for each individual. Results of this chapter show that both migrant and resident individuals coexist within the wood stork population and that individuals are generally consistent in their migratory behavior across years, with a small reservoir of behavioral plasticity.

Chapter 3 introduces a method to estimate reproductive outcome from movement data. This was necessary to later quantify the fitness consequences of different migratory behaviors. Reproductive outcome is only one component of individual fitness; I used it as a proxy based on the known importance of reproduction for wood stork population dynamics (Frederick and Ogden 1997, Frederick et al. 2009). However, Chapter 3 does more than just serving the purpose of my specific case-study, by providing a tool to link movement and the reproductive component of fitness in any avian species that can be GPS-tracked and cares for their young. To demonstrate its broad applicability, in addition to wood storks I illustrated the use of the method to two more model species, the lesser kestrel (*Falco naumanni*) and the Mediterranean gull (*Ichthyaetus melanocephalus*), which all differ from one another in their breeding ecology.

Finally, Chapter 4 combines results of the previous two, linking individual migratory behavior to its fitness consequences, mediated by habitat selection. Specifically, I examined the effect of foraging-site selection in relation to proximity to urban development on the reproductive component of fitness, quantified using nest survival as a proxy. By quantifying differences in habitat selection of migrants and residents and evaluating how this selection translates in terms of individual fitness, this chapter addresses the two necessary components for evolutionary responses to novel resources and circles back to the overall goal of this dissertation: evaluating the adaptive significance of wood stork partial migration in a human-altered environment.

An important aspect of this dissertation is its focus on behavioral heterogeneity within the wood stork population, specifically in terms of migratory behavior, which had

not been described before and whose potential role in ecological and evolutionary processes had not been addressed. The focus on individual variation is an important perspective: ecologists today are directing growing attention to deviations rather than averages, recognizing that mean responses alone are rarely sufficient to explain the complexity of ecological feedbacks (Bolnick et al. 2011). For example, an increased attention to animal personalities (i.e., behavioral qualities of individuals that are consistent across situations and through time, Carere and Eens 2005) in recent years has yielded promising insight into a variety of ecological issues including population stability and resilience (Schindler et al. 2010), colonization and invasion dynamics (Chapple et al. 2012), disease transmission (Lloyd-Smith et al. 2005), and human-wildlife conflicts (Found and St. Clair 2016). The challenge of disentangling the great complexity of individual variation is potentially paid off by a leap forward in terms of realism and forecasting ability. The profusion of individual-level data that current ecological studies produce, especially tracking studies, is making more and more room for this focal shift; movement ecology has the potential of leading the way towards it. This is an exciting time to uncover the role of behavioral variability as an evolutionary reservoir that might allow wild populations to persist in a rapidly changing environment.

CHAPTER 2
PARTIAL MIGRATION IN A SUBTROPICAL WADING BIRD IN THE SOUTHEASTERN
U.S.

Introduction

Migration is a widespread phenomenon across taxa, including birds, and it has the function of allowing individuals to track resources whose distribution is heterogeneous in space and time (Dingle and Drake 2007). Different forms of migration arise in response to different patterns of resource variation (Dingle 1996, Van Moorter et al. 2013). In temperate areas, where seasonality is generally repeatable, migrations take the familiar form of back-and-forth movements between ranges that are resource-rich at different times of the year (Cox 1985). However, even seemingly nomadic or irregular movements can be considered migrations if their function is to allow the exploitation of resources that do not follow seasonal fluctuations (Dingle 1996, Roshier et al. 2008, Van Moorter et al. 2013). For example, ephemeral resource outbreaks with no periodicity often lead to erratic migration (Kingsford et al. 2010). Some bird populations exhibit facultative migration when a key environmental factor that drives the availability of resources exceeds a critical threshold (Streich et al. 2006). Partial migration, when a population includes both migratory and resident individuals, often emerges when variability in the distribution of resources is paired with ecological trade-offs – such as density-dependence, the energetic cost of migration, or predator avoidance (Chapman et al. 2011). Partial and facultative migration can also be combined, when a population includes both individuals that consistently migrate and individuals that only migrate in some years (Berthold 2001, Newton 2012). Individual variability in migratory behavior is associated to demographic consequences which allow different forms of partial migration to be maintained over evolutionary time scales

in spatially structured and seasonally variable environments (Reid et al. 2018).

Altogether, migration is a complex phenomenon encompassing a wide spectrum of behaviors which manifest as adaptations to different patterns of resource heterogeneity in space and time (Dingle and Drake 2007).

Generally, less conventional forms of migration are thought to be associated with unpredictable environments, of which wetlands are a prime example (Fletcher and Koford 2004, Niemuth et al. 2006, Sergio et al. 2011). Variation in resource distribution can happen quickly and over broad scales in wetland ecosystems (Kushlan 1986, Weller 1999). Besides within-year variability, many wetland systems are characterized by unpredictability of local conditions between years (Niemuth and Solberg 2003, Sergio et al. 2011). Accordingly, wetland-dwelling birds evolved high mobility as an adaptation to resources that pulsate unpredictably across the landscape (Haig et al. 1998, Poiani 2006). Many wading bird species (where by “wading birds” we collectively refer to Pelecaniformes, Ciconiiformes, Gruiformes, and Phoenicopteriformes; Hegemann et al. 2019) undertake large-scale movements to exploit temporary resource breakouts across the landscape (Kushlan 1981), and such movements can take many different forms and often present intra-specific differences as well (Frederick and Ogden 1997, Melvin et al. 1999, Beerens 2008).

Because they inhabit environments where resource unpredictability is brought to an extreme, wading birds seem to be a natural choice as model species to learn about the adaptive relations between migratory patterns and resource distribution. This is especially true for species inhabiting tropical and sub-tropical wetlands, where seasonality is fundamentally driven by rainfall rather than by temperature (Junk 1993).

Recent literature has advocated for an increased focus on non-temperate species to deepen our understanding of migration as an adaptation to resource fluctuations in different contexts (Sekercioglu 2010). Nonetheless, few studies have explicitly quantified migration patterns of wading bird species (but see Mckilligan et al. 1993 for an example on cattle egrets, *Bubulcus ibis*) and, to our knowledge, none in non-temperate areas. In this paper, we provide a quantitative description of migratory patterns of a subtropical wading bird in the southeastern U.S., the wood stork (*Mycteria americana*).

Wood storks are distributed in the southeastern U.S. (hereafter, the Southeast), east of Mississippi and as far north as North Carolina (Coulter et al. 1999). Wood storks can travel remarkably long distances over short time frames and with low energy expenditure by soaring (Kahl 1964, Ogden et al. 1978). This is an adaptation to high heterogeneity and unpredictability of food resources, which are an important driver of wood stork population responses (Frederick and Ogden 2001, Gawlik 2002, Herring 2008). Wood storks are tactile foragers that feed almost exclusively on fish (Kahl 1964, Ogden et al. 1976, Kushlan 1986). For them to forage efficiently, prey need to be highly concentrated (Kahl 1964, Kushlan 1986, Gawlik 2002). As a result of local differences in hydrological dynamics, high fish concentrations occur at different times and in different locations within wetland systems in the wood stork range, and they are generally ephemeral (Loftus and Eklund 1994, Frederick et al. 2009, Botson et al. 2016). For example, in the Florida Everglades, where historically most wood stork nesting activities occurred in the U.S. (Frederick and Ogden 1997), high water levels promote the growth of fish populations during the rainy season (DeAngelis et al. 2010, Botson et al. 2016).

Then, as the water recedes in the dry season, retention of pockets of water in shallow depressions across the landscape concentrates fish, making them available for birds (Kahl 1964, Kushlan 1986, Frederick et al. 2009). The result is a spatio-temporally heterogeneous mosaic of foraging habitat, where food availability changes rapidly through time and space due to the interaction of hydrology and topography (Chick et al. 2004, Ruetz et al. 2005, DeAngelis et al. 2005). Other wetland systems in the Southeast may present different phenologies and mechanisms of food concentration, but their hydrological dynamics are also largely influenced by rainfall patterns, affecting the distribution of resources (Snodgrass et al. 1996, Baber et al. 2002).

Wood stork movements reflect patterns of resource availability at fine spatio-temporal scales. For example, during the breeding season, wood storks move long distances from breeding colonies to foraging grounds to accommodate shifting resource availability patterns (Kahl 1964, Ogden 1986, Bryan and Coulter 1987). At a broad spatio-temporal scale, the annual range of wood storks includes wetlands located in different states that are subject to different, sometimes asynchronous, and usually unpredictable rainfall patterns (Frederick et al. 2009). For example, southern Florida is a winter dry, summer wet monsoonal system, while much of the rest of the southeast gets most of its rainfall in winter and dries during summer months. Because their range includes wetland systems subject to different climatic regimes, local conditions within seasonal ranges used by wood storks are characterized by high year-to-year unpredictability as well (Gawlik 2002, Frederick et al. 2009). Landscape-scale movements of wood storks might respond to heterogeneity in food resources at this

scale similarly to how fine scale movements reflect heterogeneity in food availability patterns within seasonal ranges.

Landscape-scale movements of wood storks remain poorly understood. Previous literature reported large scale movements of wood storks between different parts of their U.S. range in different seasons, but defined the species as “not a true migrant” (Coulter et al. 1999). Indication that movements between different areas within the range are repeated year after year, thus presenting typical migration features, was provided by a study on juveniles (Hylton 2004). Other tracking studies have described fine-scale movements (Borkhataria et al. 2013) or dispersal (Bryan et al. 2008, Picardi et al. 2018), but not migration. Overall, we lack a formal understanding of the migratory status of the wood stork population.

The objective of this study was to address the outlined knowledge gaps by providing an individual-based, quantitative description of wood stork migratory patterns in the Southeast. By leveraging a large, long-term GPS-tracking database, we quantified migratory behavior of a large number of individuals over 14 years and evaluated behavioral consistency across years at the individual level. We determined correlations between migratory behavior and life-history traits including age and sex. We mapped seasonal distribution patterns of wood storks as a result of migration patterns and quantified individual site-fidelity. Our results provide the first individual-based documentation of migration patterns in a subtropical wading bird.

Methods

Study Area and Species

The wood stork population range in the Southeast encompasses both temperate and sub-tropical latitudes, with marked differences in climate between the northern and

southern portions. In the southernmost part of the range (southern Florida), seasonality of rainfall is the most distinctive climatic feature; annual precipitation is concentrated between the months of May and October, and seasonal fluctuations in temperature are not pronounced (Kahl 1964). At higher latitudes, the climate is more typically temperate, with cool winters, hot summers, and less marked seasonality of precipitation. Within this geographical area, wood storks are found in a diversity of wetland habitats, ranging from freshwater marshes and swamps (Kahl 1964), to coastal and estuarine creeks (Gaines et al. 1998), to natural and artificial ponds (Coulter and Bryan 1993). Wood stork are the only stork species breeding in North America (Coulter et al. 1999). They are large, long-legged wading birds between 85 and 115 cm tall (Coulter et al. 1999). Sexual dimorphism is not pronounced (Coulter et al. 1999). Neck and head are covered in feathers in subadults and are gradually lost with age; sexual maturity is reached at 3 years of age (Coulter et al. 1999).

Wood Stork Captures and Data Collection

We used GPS telemetry to track wood stork individual movements throughout the population range (centroid 28.8967°N, 81.3310°E) between 2004 and 2017. Wood storks were captured at 11 sites throughout the population range (Figure 2-1; Table 2-1) either by hand (in the case of juveniles) or using rocket nets. Juveniles were hand-captured at the nest before fledging, whereas adults were captured either in the advanced stages of breeding or while non-breeding. Whenever reasonable, we extracted <0.5 ml of blood from the brachial vein for sexing. Captured storks were hooded to reduce stress during handling and equipped with solar-powered ARGOS-PTT GPS transmitters (Microwave Telemetry, Columbia, MD), which are not limited by battery life. The transmitters were programmed to record a location every hour. Each

individual was tracked until death or failure of the GPS transmitter, between 1 and 10 consecutive years.

Operational Definitions

We operationally defined migration as a round-trip between ranges that were spatially separated and used at different times during the year – thus implying return to the initial range. We defined migratory choice as a binary variable at the year level, namely whether an individual migrated or not in a given year. We then combined migratory choices for an individual in different years to assess multi-year migratory strategies. Thus, we defined migratory strategy as the history of yearly migratory choices of an individual. For example, an individual whose migratory choice is migration every year adopts a pure migrant strategy, or an individual whose migratory choice is different in different years shows a facultative migrant strategy.

Classification of Migratory Behavior

We used GPS tracking data to investigate individual migratory choices based on net squared displacement (NSD), i.e. the squared linear distance between any point along a movement trajectory and an arbitrarily chosen starting point (Kareiva and Shigesada 1983, Calenge et al. 2009). This metric provides an intuitive measure of how far an individual is from a reference point in space at any time (Kareiva and Shigesada 1983, Calenge et al. 2009). To classify wood stork migratory behavior at the yearly scale, we used a modeling approach adapted from a method first introduced by Bunnefeld et al. (2011) and later improved by Spitz et al. (2017). The approach consists of fitting a set of non-linear models to yearly individual NSD time series and selecting the one that best fits the data using AIC. For the purpose of our study, following our binary definition of migratory choice, we took two possible models into consideration: a

migrant model and a resident model (Figure 2-2; see Spitz et al. 2017 for details on model specification). In the migrant model, the yearly time series of NSD follows a double sigmoid curve, indicating initial residency in one range (initial low NSD phase), displacement to a second (high NSD phase), and subsequent return to the initial range (final low NSD phase; Figure 2-2). The departure range is whichever range an individual was located in at the arbitrarily chosen reference time that marks the start of the trajectory. The resident model is represented by a horizontal asymptotic curve, indicating permanence in a single range after an initial phase of increase of NSD until settlement around a constant value (Figure 2-2). We applied model selection based on Akaike's Information Criterion (AIC) differences on these two competing models to classify wood stork annual trajectories and determine migratory choice. The analysis was performed in R (R Core Team 2018) using functions implemented in the `migrateR` package (Spitz et al. 2017).

Data Preparation

After visual exploration of the trajectories, we divided the tracking data into yearly individual trajectories starting on January 15th, to minimize the probability of the starting point falling within a migration (following recommendations in Spitz et al. 2017). We used the R packages `adehabitatLT` (Calenge 2006) and `rpostgisLT` (Dukai et al. 2016) for data processing and exploration, respectively. We screened the resulting yearly individual trajectories to assess whether they included sufficient data for model fitting. In order to ensure detection of migrations, we set the minimum data requirements for an individual-year to at least 15 locations every 4 months (Jan-Apr, May-Aug, Sep-Dec). The resulting dataset consisted of 212 individual-years from 66 storks, of which 20 had

a single individual-year and 46 had multiple individual-years (range = 2-10, mean = 3.96 \pm 1.73 SD).

A-priori Model Constraints

Following recommendations in Spitz et al. (2017), we enforced a-priori constraints in the model parameters to satisfy the following quantitative characterization of migration: for an individual to be considered a migrant on a given year, it has to spend at least 60 days in a range at least 260 km away from the departure range. The chosen spatial threshold corresponds to double the maximum distance documented for wood stork trips from the colony to foraging grounds (130 km; Kahl 1964, Ogden et al. 1978), which is presumably a distance that storks are able to cover within their everyday movements. Thus, this value seems appropriate to discriminate between the scale of within- versus between-ranges movements. Temporal fluctuations of resource availability usually occur with seasonal (i.e. multiple months) periodicity at a broad spatial scale in the wood stork population range, which is expected to reflect in the emergence of migration as a seasonal phenomenon. The function of repeatedly tracking resource availability over broad spatial and temporal scales is what distinguishes migration from other types of movements which were not the focus of this study. Thus, the chosen temporal threshold of approximately 2 months has the purpose of preventing brief but spatially broad excursion movements, which are functionally different from migration, from being misclassified as migrations. We performed a sensitivity analysis on the use of different constraint values (see Appendix A) and found both the chosen spatial and temporal thresholds to be conservative, since classification results were robust to the use of a broad range of values around the chosen one, within a range of biologically meaningful values.

Stepwise Specification of Starting Parameter Values

In addition to specifying constraints for two of the model parameters as described above, we ensured model convergence on all trajectories by progressively specifying different starting values for model parameters, following recommendations in Spitz et al. (2017). These include, for the migrant model, the midpoint of the departing migratory movement, the duration of the migratory movement, the permanence time in the arrival range, and the distance between seasonal ranges (Spitz et al. 2017). For the resident model, parameters include the average NSD of the resident range and the rate of the initial NSD increase (Spitz et al. 2017). Stepwise manual specification of starting parameter values facilitates parameter optimization, helping to overcome commonly encountered convergence issues due to the use of a single set of starting values for all trajectories in a sample (Spitz et al. 2017). All models converged after 21 iterations with a different set of starting parameters (see Appendix B).

Post-hoc Model Evaluation

Following recommendations in Spitz et al. (2017), we visually inspected results of model fitting as a *post hoc* evaluation. While the minimum data requirements we chose were adequate in most cases (200 individual-years), for 12 individual-years the placement of the 15+ locations within the first or third quadrimester did not allow for an unequivocal classification (see Appendix C). The most common issue was failure to classify seemingly migratory individual-years as migrants because of insufficient temporal cover of the data ($n = 8$): while the first range shift was identified, the return movement from the second range and the subsequent residency back in the first range were not captured in the data, resulting in a poor fit of both the migrant and the resident model. Conversely, 4 individual-years that did not seem to exhibit migratory behavior,

and were thus classified as residents, had similar limitations in terms of temporal cover of data that did not allow for reliable classification: we cannot exclude that migrations were not observed because they simply happened outside of the tracking period. Therefore, we discarded these 12 individual-years from further analyses. Out of the remaining 200 individual-years, 2 consecutive years for one migrant individual were erroneously classified as residents because the individual migrated over the start of the new tracking year, resulting in the migratory movement being split into two. For this individual only, we repeated model fitting and selection after splitting the yearly trajectories on December 1st instead of January 15th. Finally, by visual comparison between model output and mapped trajectories, we identified 2 individual-years that were classified as migrations as controversial cases. These individuals continuously performed movements at a broader spatial scale than other resident individuals in the sample, but without a clear pattern of seasonal periodicity or spatial separation. Because these movements did not fit the chosen definition of migration, we manually assigned these individual-years to the resident category.

Seasonal Distributions, Range Fidelity, and Migratory Consistency

The output of the NSD models provided estimates for key migratory parameters, including the time of migration start and end where applicable. Based on these, we subsetted individual tracking datasets into residency and migration phases. For migrant individuals, we computed seasonal home ranges (winter and summer) using locations during residency phases only (i.e., excluding locations during migration trips). For resident individuals, we computed both year-round home ranges, and seasonal home ranges using locations included between the mean spring and fall migration dates observed in the population. All home ranges were computed using the kernel density

estimation method, extracting the 90% density isopleth of the utilization distribution, as recommended by Börger et al. (2006), using the R package `adehabitatHR` (Calenge 2006). We used linear mixed models to assess differences in home range size between migrants and residents in each season while taking individual variation into account. We log-transformed home range size before fitting the model. We fit an interaction between season and migratory behavior and added the individual identity as a random effect. We evaluated model predictions at the fixed effects level to assess differences between migrants and residents in different seasons. We evaluated model fit using the pseudo- R^2 method of Nakagawa and Schielzeth (2013). For individuals that were tracked for multiple years ($n = 46$), we investigated seasonal range fidelity using home range overlap, with 1 representing perfect overlap and 0 representing disjunct ranges. For summer and winter separately, we computed the percent area of overlap between all pairwise combinations of ranges of each individual, and averaged them in a synthetic value of individual site fidelity. Finally, we quantified migration strategies at the individual level by modeling migratory choices of an individual in different years as a binomial process. Using the binomial likelihood, we computed maximum likelihood estimates of individual migration probability along with 95% confidence intervals. Values reported in the Results are means \pm SD.

Results

Migratory Choices and Strategies

The final classification of wood stork migratory choices consisted of 200 individual-years from 64 individuals (15 captured as juveniles of unknown sex, 25 adult females, and 24 adult males), of which 121 were migrations (~60%) and 79 (~40%) residencies. The maximum likelihood estimates of migration probability, which describe

individual migratory strategies, were 1 for 36 individuals (of which 27 tracked for multiple years), 0 for 22 (of which 13 tracked for multiple years), and between 0 and 1 for 6 (all tracked for multiple years; Figure 2-3). Confidence intervals around the estimates of migration probability were large due to the limited number of tracking years (range 1-10). Among the individuals tracked for multiple years, 40 showed consistent migratory choices across years, thus adopting a pure migrant (~59%) or pure resident strategy (~28%), while 6 (~13%) showed variable migratory choices across years. Among pure migrants, 15 were male and 16 female (5 were of unknown sex); among pure residents, 6 were male and 7 female (8 were of unknown sex); among individuals with variable migratory choices, 3 were male and 2 female (2 were of unknown sex). Among the 15 storks that were captured as juveniles, 8 were tracked into subsequent years as subadults ($n = 8$) or adults ($n = 2$). Of these, 6 exhibited consistent behavior across years (3 pure migrants and 3 pure residents), while 2 showed variable migratory choices in different years. Overall, we found no correlation between individual migratory choices and age or sex.

Migration Routes and Timing

The mean departure dates were May 7th and October 2nd for spring ($n = 121$) and fall migrations ($n = 121$), respectively. The distribution of migration departure dates was bimodal in spring, with a peak in late March and one in June (Figure 2-4 A), while departure dates in fall showed an early surge followed by a single peak in mid-October (Figure 2-4 A). Storks followed two general migration routes along the east and west coastline of Florida, with the east one used more in spring and the west in fall (Figure 2-4 B).

Seasonal Ranges and Population Distribution

The overall population distribution was highly dispersed throughout the Southeast in summer, while highly concentrated in south Florida in winter (Figure 2-5). However, the year-round ranges of resident individuals were concentrated in a few hotspots in southeast Florida and in the Jacksonville area (Figure 2-6). Therefore, migrant individuals are responsible for most of the spread across the Southeast pictured in the left panel of Figure 2-5. The interaction between season and migratory behavior significantly affected home range size ($p < 0.05$). The marginal R^2 was 0.07 and the conditional R^2 was 0.44, suggesting that individual variability explained most of the variance rather than the fixed effects. Migrants, but not residents, showed larger seasonal ranges in winter than in summer (Figure 2-7). Migrant winter ranges were larger than both summer and winter ranges of residents (Figure 2-7). Wood storks exhibited moderate range fidelity (migrants = 0.51 ± 0.37 and residents = 0.62 ± 0.38 in winter, migrants = 0.51 ± 0.43 and residents = 0.61 ± 0.41 in summer).

Discussion

We provided an individual-based quantitative description of migratory patterns in a subtropical wading bird, the wood stork, in the southeastern U.S. Our findings revealed that the population is partially migratory, with a group of individuals that seasonally commute between spatially distinct ranges and others that remain resident in the same area year-round. Migration and residency appeared to be alternative choices adopted by different individuals, but less frequently by the same individuals in different years. Thus, the population exhibits a combination of partial and facultative migration. Between-year consistency of migratory choices was high for most storks, but flexible behavior of a few individuals provided an indication of the potential for plastic

responses. The coexistence of different migratory strategies in wood storks may be an adaptation to high spatio-temporal heterogeneity and unpredictability of resource availability within their range. Partial migration has been increasingly recognized as a widespread form of migration across taxa, if not the most common (Chapman et al. 2011). Our findings provide the first individual-based description of migration patterns in a subtropical wading bird.

Our analysis of migratory strategies at the individual level revealed three strategies in the wood stork population: consistent migration, consistent residency, and an intermediate, flexible behavior of facultative migration (Figure 2-3). Individuals adopting different migratory strategies also differed in their collective seasonal distribution. The distribution of migrants was widely dispersed across the Southeast in the summer and densely concentrated in south Florida in the winter (see overall distribution in Figure 2-5). This is consistent with previous literature on wood stork seasonal movements (Kahl 1964, Coulter et al. 1999). Migrants likely relocate to south Florida to exploit the winter pulse of food availability in the Everglades as rains cease, pools are isolated and reduced in extent and depth, and fishes are more concentrated and available, and then move north when the rains start, dispersing prey (Kahl 1964, Kushlan 1986). Migration to southern Florida in the winter may also be driven by reduced prey availability in the northern part of the range because of cold temperatures (Frederick and Loftus 1993).

It is unclear whether all migrant storks that spend the winter in south Florida also attempt to nest there. The bimodal distribution we observed for departure dates in the spring (Figure 2-4 A) might result from the fact that some of the migrants leave the

winter grounds in south Florida early to go breed elsewhere. An alternative explanation is that among migrant wood storks that attempt to nest in south Florida, those that fail go back to their summer ranges before those that are successful and stay longer to care for their offspring. The existence of different migratory strategies within the population, and particularly of facultative migrants, also suggests that wood storks may behave as “comparison shoppers” when selecting general areas for nesting on any given year. Variable migratory patterns may be associated with variable choices of nesting locations as well, based on a relative comparison of conditions in different parts of the population range. The routes followed by migrant storks varied between seasons, possibly as a response to seasonal variation of thermal air currents which may determine least-cost migratory paths for soaring birds (Kahl 1964, Bohrer et al. 2012, Vansteelant et al. 2017; Figure 2-4 B).

The degree of seasonal range fidelity we observed for migrants suggested that storks tended to repeatedly use the same areas across years, both in winter and summer. For comparison, values of home range overlap corresponding to highest year-to-year breeding site fidelity for wild turkeys (*Meleagris gallopavo*; Badyaev and Faust 1996), on one hand, and capercaillie (*Tetrao urogallus*; Storch 1997) and Egyptian vultures (*Neophron percnopterus*; López-López et al. 2014), on the other, are smaller or comparable, respectively, to those we found for wood stork ranges in both seasons. We found that home range size can vary widely for the same individual in different years, possibly according to the degree of dispersion of food resources (Ford 1983, Zabel et al. 1995, Schradin et al. 2010). Consequently, overlap between ranges in different years was rarely exact, but storks tended to return to the same general area equally in

summer and winter. Range fidelity may be a critical adaptation to achieve reliable access to resources (Switzer 1993, Vergara et al. 2006), but it might entail susceptibility to changes in habitat quality, which may lead birds into an ecological trap if they remain faithful to areas that were formerly suitable but deteriorated (Schlaepfer et al. 2002, Weldon and Haddad 2005, Lok et al. 2011).

We observed the highest density of year-round residents in southeast Florida – near the northern Everglades and urban coastal areas – and in Jacksonville (Figure 2-6). Neither of these areas appeared to be intensively used by migrants. The hotspot of resident distribution we observed in the northern Everglades overlaps with the Everglades Agricultural Area (EAA) and Loxahatchee National Wildlife Refuge (i.e. Water Conservation Area (WCA) 1; Figure 2-6). Water levels are artificially managed throughout the EAA and WCAs through a system of levees and canals according to agricultural schedules and water supply or flood protection needs (Bancroft et al. 2002, Pearlstine et al. 2005). The EAA covers former marsh habitat which was converted to agricultural use starting in the mid-1900s (Pearlstine et al. 2005). In the EAA, whole fields are periodically flooded as part of their crop rotation strategy, often in coincidence with the beginning of the rainy season and rapidly rising water levels in the Everglades (Schueneman et al. 2001, Sizemore 2009, Sizemore and Main 2012). Canals and ditches are periodically drawn down in response to crop needs, and this may provide patches of concentrated fish for foraging wading birds (Pearlstine et al. 2005). The WCAs were impounded in the 1960s with the double purpose of providing water for agricultural and municipal use and flood protection (Light et al. 1989, Light and Dineen 1994). Loxahatchee National Wildlife Refuge is composed of different vegetation

communities and characterized by greater micro-topographic relief than other parts of the Everglades, which may provide suitable foraging habitat for storks over a wider temporal range than in situations of uniform topography (Hoffman et al. 1994, Bancroft et al. 2002). The high density of year-round residents we observed in Loxahatchee and the EAA may be ascribed to these features of topography and artificial flooding-and-drying schedules which may result in foraging chances even out of season and out of sync with natural water-level regimes.

We hypothesize that the high concentration of residents near urban areas might be partly linked to the exploitation of supplemental food sources provided deliberately or unintendedly by humans. Resident wood storks in the Jacksonville area were captured at the Jacksonville Zoo. These storks are wild and free-roaming, but regularly receive food supplementation (Bear D., Jacksonville Zoo, personal communication). The high density of storks we observed in Jacksonville might be an artifact of the unequal number of tracked storks at different capture sites, but remarkably most storks captured at the Jacksonville Zoo were consistently resident (7 out of 9). We do not have any direct evidence of food supplementation for storks in southeast Florida, but this is one of the most densely populated urban areas in the Southeast and likely presents several supplementation opportunities. Landfills are a possible source of supplemental food, and there is growing evidence that their use by bird populations, including bald eagles (*Haliaeetus leucocephalus*, Turrin et al. 2015), yellow-legged gulls (*Larus michahellis*, Egunez et al. 2017), and white storks (*Ciconia ciconia*, Gilbert et al. 2016), is increasing in different parts of the world. White ibises (*Eudocimus albus*) have been increasingly observed in the same urban areas of south Florida where we observed the highest

concentration of resident storks (Hernandez et al. 2016), and a recent study showed that they heavily rely on artificial food provisioning in urban parks and landfills (Murray et al. 2018). We have anecdotal evidence of wood storks regularly being hand-fed and eating trash in urban environments (Picardi S., personal observation), and ongoing studies on the diet of chicks in urban colonies in southeast Florida have revealed consumption of a diversity of human-derived food that may come from landfills and other sources of trash (Evans B., personal communication). Together, these clues lead us to hypothesize that the availability of supplemental food sources of an artificial nature might be playing a role in determining the distribution of resident storks.

The wood stork population is facing environmental change pressures in many regards, from alterations of the natural hydrological dynamics in the Everglades (Kushlan 1987, Sklar et al. 2001, 2005) to increasing urbanization (Hefner and Brown 1984, Reynolds 2001, Terando et al. 2014), to which the population might respond in the long run by altering migratory patterns. This is an increasingly documented phenomenon in bird populations in response to various drivers, including climate change, changes in resource phenology, and supplemental feeding (Cotton 2003, Visser et al. 2009, Satterfield et al. 2018). Changes in migratory patterns might be expected both through adaptation and behavioral plasticity (Pulido 2007, Ghalambor et al. 2007, Charmantier and Gienapp 2013). Our analysis on consistency of individual migration choices across years highlighted that most of the population (87% of individuals among those monitored over several years) showed highly consistent yearly migratory choices (Figure 2-3). Notably, the inference we can draw from our data in this sense is limited by the fact that individuals were tracked for only a few years each, if

more than one. However, a small proportion of individuals (13% of those monitored over several years) showed some degree of plasticity, making different migratory choices in different years and behaving as facultative migrants (Figure 2-3). Thus, storks seem to be able to adjust their migratory strategies within the course of a lifetime, implying some potential for plastic changes of migratory behavior at the population level.

Understanding the adaptive significance of partial migration requires a comprehensive assessment of how species inhabiting different ecosystems differ in their migration patterns. By looking at which populations exhibit partial migration or not, researchers can comparatively assess which characteristics of environmental variability lead to its emergence. Studies on multiple species across avian orders have highlighted that partial migration is associated with environments where resource distribution is unstable and highly variable between years (Chan 2001, Jahn et al. 2012). For this reason, most comparative studies of ecological drivers of avian partial migration have focused on the Australian continent, whose trademark is high climatic variability and unpredictability (Chan 2001). Wetlands worldwide are another prime example of heterogeneous and unpredictable environments. Thus, wading birds are good model species to evaluate predictions on partial migration in relation to unpredictable resources, and yet their migration patterns are understudied. To our knowledge, among wading bird species and before the present study, partial migration patterns have only been described at the individual level in a population of cattle egrets in the temperate zone of eastern Australia (Mckilligan et al. 1993). While we did not directly analyze resources in this paper, seasonality of resource availability within the wood stork range has been described in detail by previous studies, which have established broad-scale

annual patterns of resource dynamics in the Southeast (Kahl 1964, Kushlan 1986, Frederick and Ogden 1997). In agreement with previous literature, our findings exemplify that in a highly heterogeneous and unpredictable environment, where the availability of key resources varies substantially between years according to variations in rainfall patterns, a combination of partial and facultative migration may be advantageous. Partial migration may buffer between-year stochasticity in survival or reproduction, if the conditions that promote fitness of migrants are different than those of residents. Concurrently, the behavioral flexibility of facultative migrants may work as a reservoir of plasticity, improving population responses to year-to-year variation and allowing rapid change of migratory patterns in response to environmental change. Future research should focus on explicitly testing this hypothesis.

Table 2-1. Number of individuals tagged at each capture site. Adults = age >3 years;
 Subadults = age between 1 and 3 years; Juveniles = age <1 year.

Capture site	N. captures	N. adults	N. subadults	N. juveniles
Chew Mill	2	-	1	1
Corkscrew Swamp Sanctuary	4	4	-	-
Everglades National Park	9	9	-	-
Harris Neck NWR	10	8	1	1
Jacksonville Zoo	9	9	-	-
Kings Bay Naval Base	1	-	-	1
Noxubee NWR	2	2	-	-
Palm Beach SWA	14	6	4	4
St Mary's	1	1	-	-
Washo Preserve	9	9	-	-
Welaka Fish Hatchery	3	3	-	-

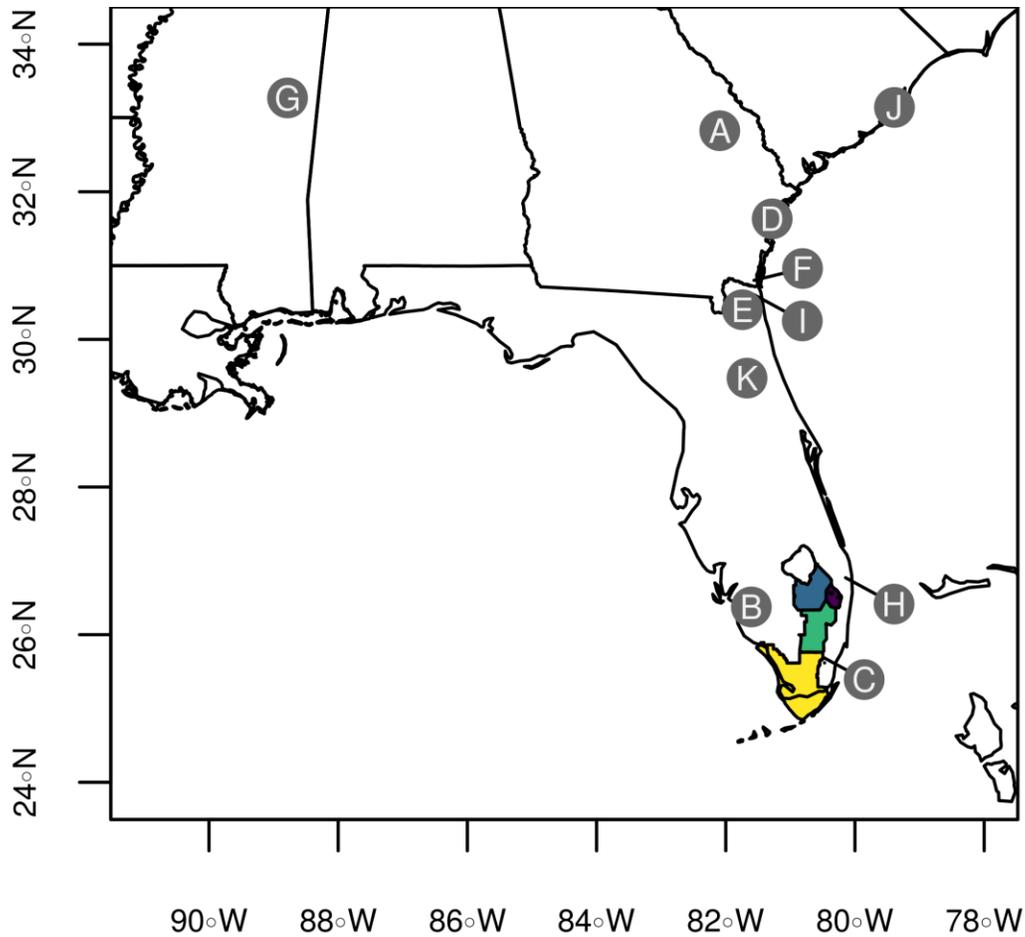


Figure 2-1. Map of the study area, located within the breeding range of the southeastern U.S. wood stork population. The letters indicate capture sites. A = Chew Mill Pond, B = Corkscrew Swamp Sanctuary, C = Everglades National Park, D = Harris Neck National Wildlife Refuge, E = Jacksonville Zoo, F = Kings Bay Naval Base, G = Noxubee National Wildlife Refuge, H = Palm Beach Solid Waste Authority, I = St. Mary's, J = Washo Preserve, K = Welaka Fish Hatchery. The colored polygons depict the boundaries of relevant management units within the Everglades watershed. Blue polygon = Everglades Agricultural Area, Purple polygon = Loxahatchee National Wildlife Refuge, Green polygon = Water Conservation Areas 2 and 3, Yellow polygon = Everglades National Park.

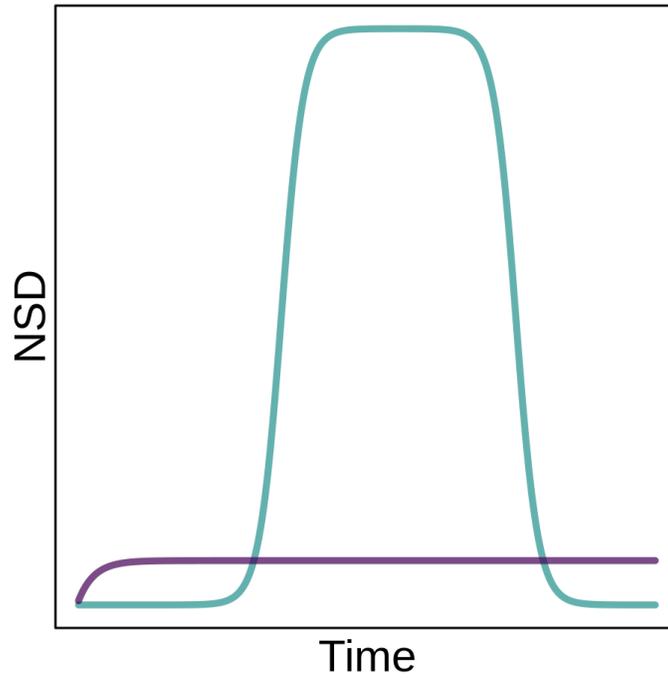


Figure 2-2. Conceptual illustration of non-linear models of Net Squared Displacement used to classify wood stork migratory behavior at the year scale. Resident model in purple, migrant model in blue. Figure adapted from Bunnefeld et al. (2011) and Spitz et al. (2017).

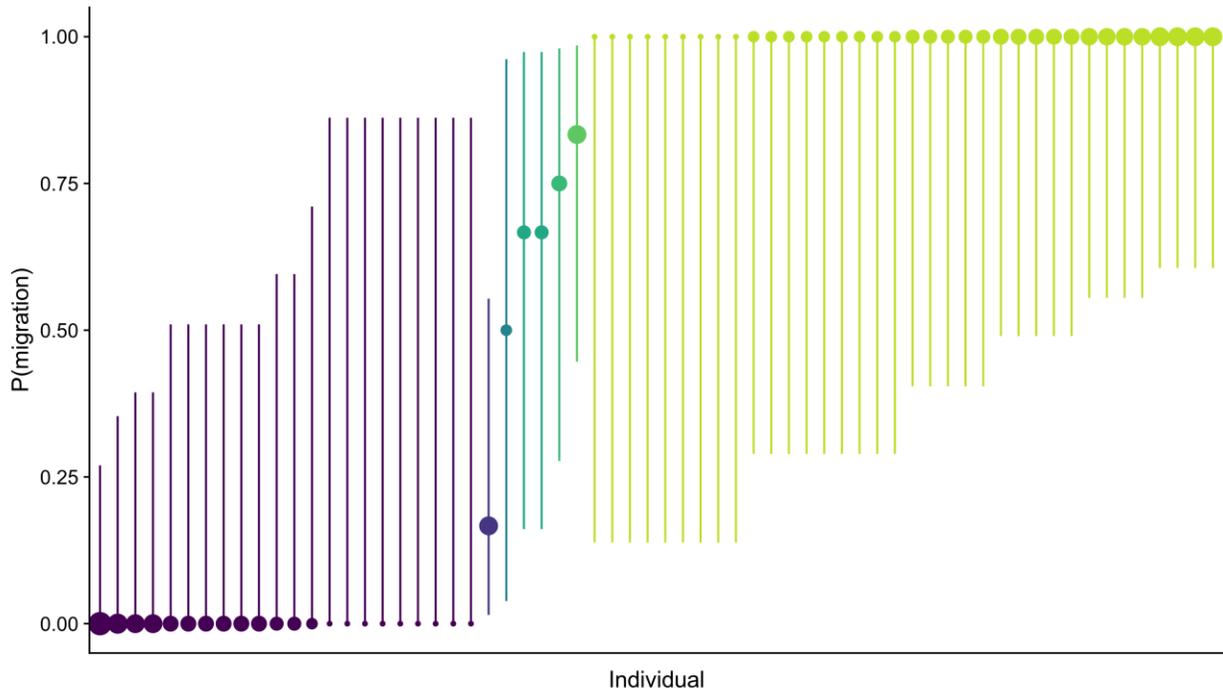


Figure 2-3. Maximum likelihood estimates of individual migration probabilities with 95% confidence intervals. Colors vary on a gradient according to the values of migration probability. The size of the points is proportional to the number of tracking years for each individual.

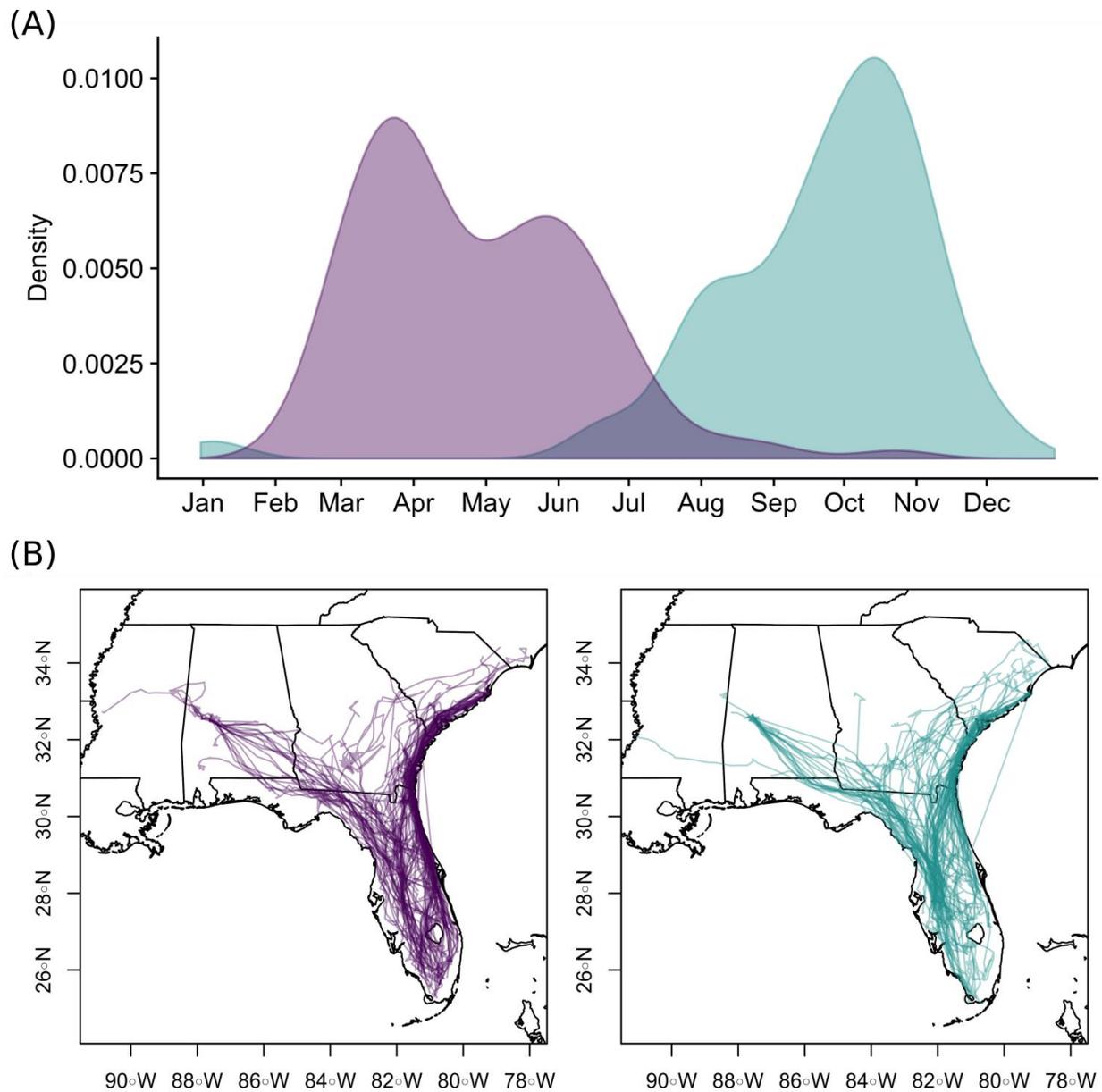


Figure 2-4. Wood stork migration routes and timing. **(A)** Frequency distribution of departure times for spring (purple) and fall (blue) migration. **(B)** Routes of migration for spring (purple, left panel) and fall (blue, right panel).

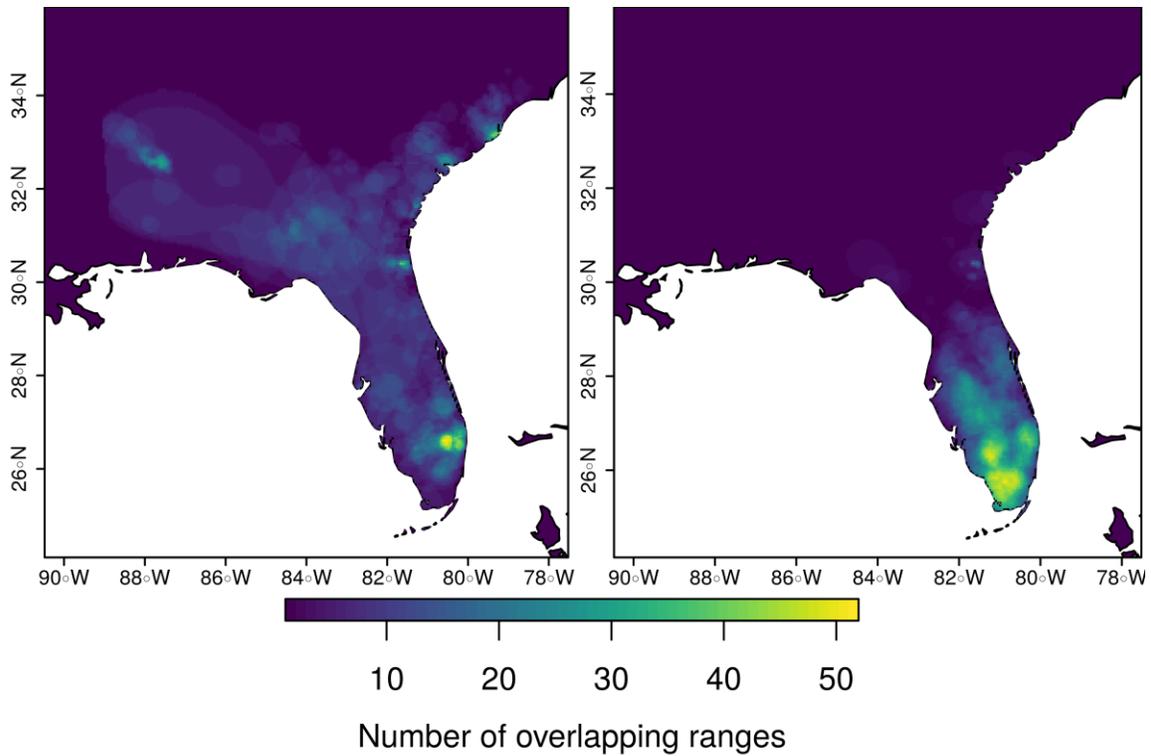


Figure 2-5. Heat maps of wood stork population distribution. Summer = left panel, winter = right panel. Seasonal ranges of both migrant and resident individuals are included. Home ranges used in different years are overlaid. Most of the seasonal difference in distribution is due to migrant individuals because residents spend the whole year in a single range (Figure 2-6).

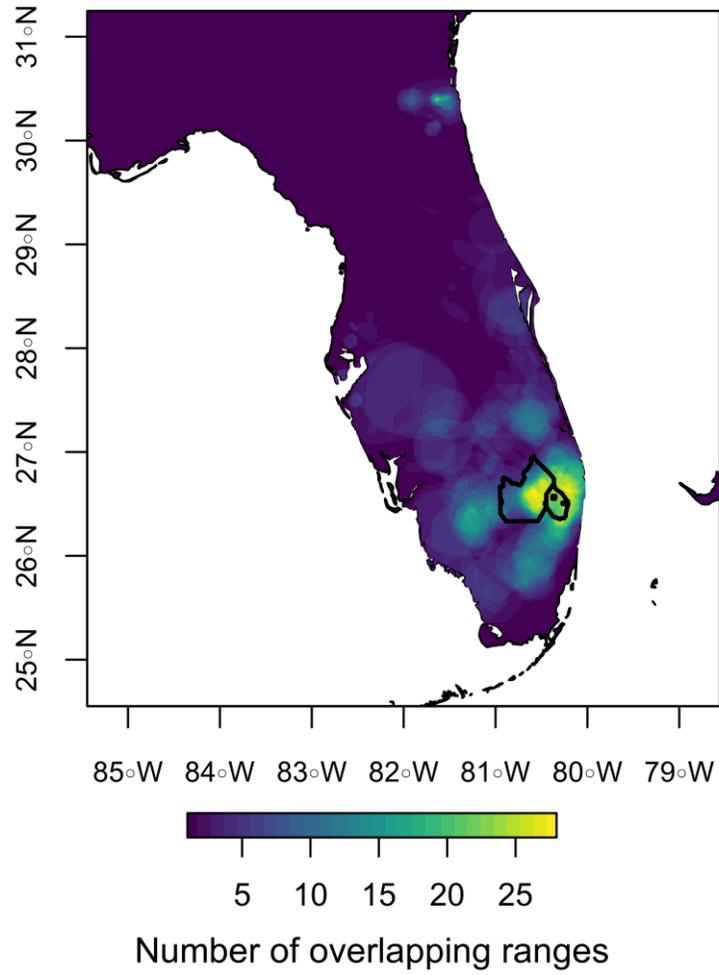


Figure 2-6. Heat map of year-round distribution of resident wood storks. Yearly ranges used by resident individuals in different years are overlaid. The black outlines depict the boundaries of Everglades Agricultural Area (left polygon) and Loxahatchee National Wildlife Refuge (right polygon).

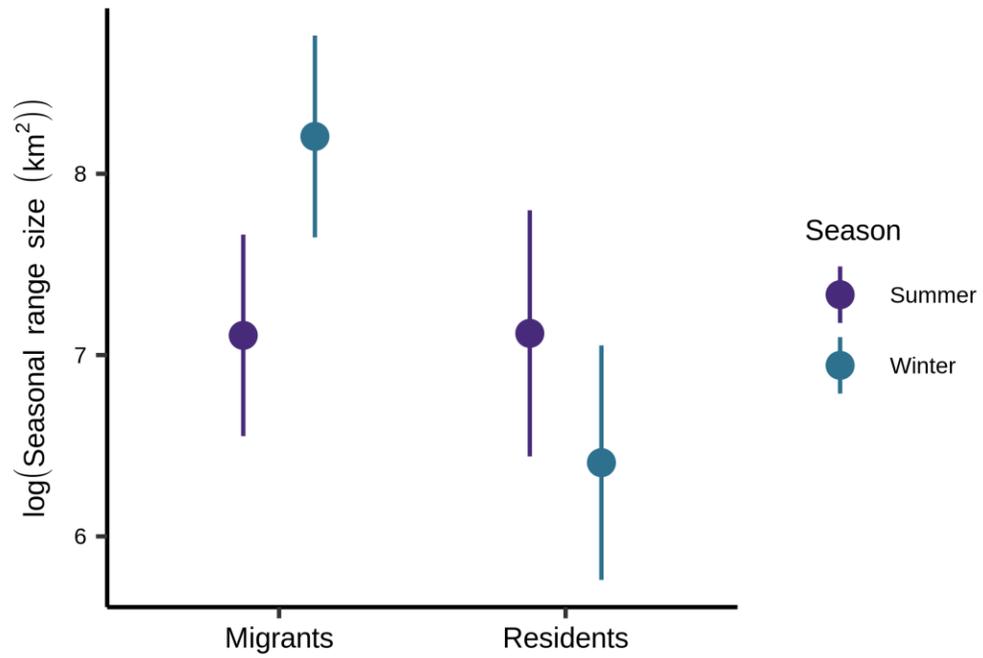


Figure 2-7. Model predictions for seasonal range size of wood storks. Migrants = left, residents = right; summer = purple, winter = blue.

CHAPTER 3 NEST-SITE DETECTION AND ESTIMATION OF AVIAN REPRODUCTIVE OUTCOME FROM GPS-TRACKING DATA

Introduction

A major goal of movement ecology is to uncover behaviors underlying, and thus shaping, movement trajectories (Schick et al. 2008, Nathan et al. 2008, Wilmers et al. 2015). New methodologies are increasingly allowing scientists to uncover latent processes underlying movement and space-use patterns, such as migratory responses to seasonality (Spitz et al. 2017), spatio-temporal repeatability of behaviors (Bracis et al. 2018), and demography (Royle et al. 2018). Knowing what animals are doing when moving a certain way can improve our understanding of the links between movement and resource dynamics, species interactions, distribution, and individual fitness (Mueller and Fagan 2008, Schick et al. 2008, Morales et al. 2010). Given the central role of fitness in ecological and evolutionary processes, estimating it from movement patterns is a long-sought goal (Morales et al. 2010, Singh and Ericsson 2014). Specifically, connecting movement to reproduction, an important component of fitness, is a promising emerging application. For example, recent studies used changes in movement patterns to detect parturition events along ungulate GPS (Global Positioning System) tracks, particularly moose (*Alces alces*; Severud et al. 2015, Nicholson et al. 2019) and caribou (*Rangifer tarandus*; DeMars et al. 2013, Bonar et al. 2018). However, to our knowledge, no study has attempted to infer avian reproductive fitness from movement data.

Recursive movement patterns can reveal when and where birds are breeding, and whether they are successful. Recursive movements are repeated returns to a same location, and they are indicative of places of ecological relevance for many taxa, such

as dens, nests, and foraging patches (Berger-Tal and Bar-David 2015, Bracis et al. 2018). Recursive movement patterns can also provide insight into life-history: some animals are tied to specific locations in specific phases of their life cycle and exhibit recursive movements to and from those locations (Bracis et al. 2018). These include altricial birds. While breeding, altricial bird species act as central place foragers (*sensu* Orians and Pearson 1979), recursively departing from their nest site to embark on foraging trips and returning to incubate eggs or provide food for nestlings (Andersson 1981, Alonso et al. 1994, Burke and Montevicchi 2009). Back-and-forth trips can therefore be observed in movement data and potentially used to identify when and where a bird is nesting. Once the location of a nest has been identified, patterns of nest-site re-visitation may reveal information about the fate of a breeding attempt and may be used to infer reproductive outcome.

Estimating avian reproductive outcome from tracking data can be valuable whenever gathering data on reproductive outcome through direct observation in the field is logistically difficult or causes excessive disturbance (Etterson et al. 2011, Wilmers et al. 2015, Nicholson et al. 2019). Moreover, linking reproductive outcome to foraging conditions can be challenging when nests are monitored in the field and researchers do not have information on locations visited by birds away from the nest. Inferring reproductive outcome from movement would allow researchers to directly relate components of individual fitness to environmental conditions experienced by birds not only at the nest but also at other locations used during breeding, by coupling tracking data with remote sensing (Cagnacci et al. 2010, Pettorelli et al. 2014). This would open

important research avenues regarding links between movement strategies, habitat use, and reproductive fitness.

Here, we introduce a data-driven method to locate breeding attempts along movement trajectories of altricial bird species and estimate their outcome based on patterns of nest re-visitation. We demonstrate the broad applicability of our approach by illustrating its use on GPS-tracking data for three species differing in their breeding habitat and ecology: wood storks (*Mycteria americana*), lesser kestrels (*Falco naumanni*), and Mediterranean gulls (*Ichthyaetus melanocephalus*).

Methods

Method Description

Nest-site detection

Our workflow is composed of two parts: first, the detection of nest sites, and second, the estimation of reproductive outcome (Figure 3-1). Nest sites are identified as repeatedly visited locations along individual trajectories (Figure 3-1). Returns to a location are defined as returns to a circular area of a user-defined radius buffering each point of the trajectory. Using buffers accounts for the spatial scattering of GPS points around a location due to both behavior and GPS error (Frair et al. 2010). The buffer size sets the spatial scale at which re-visitation patterns are calculated and is chosen according to the expected scale of movements, which should be small in the case of a nest (compared, for example, to returns to a same foraging area but not exact location). Re-visitation patterns are described by the following set of parameters: the maximum number of consecutive days a location is visited; the percentage of days it is visited between the first and last visit; and the percent fixes at a location on the day with maximum attendance. Each re-visited location is a potential nest site. Parameter values

are then used as diagnostic features to filter actual nest sites among re-visited locations, based on the rationale that re-visitation patterns differ between nest and non-nest sites. Nest sites are often visited for longer stretches of consecutive days, on more days, and more frequently or for longer within a day than other types of re-visited locations. The parameters we use to describe re-visitation patterns are meant to capture these diagnostic behaviors and identify nest sites among re-visited locations. Combined, an appropriate buffer size and the thresholds imposed for re-visitation parameters should isolate breeding behavior from other types of repetitive movements such as foray search (Conradt et al. 2003) and territoriality (Brown et al. 2000). The method can be tailored to different case studies by restricting the analysis within the breeding season for a given species and accounting for data sampling rate and fix failure rate.

Unless prior knowledge is available about re-visitation patterns to nest sites, researchers will need ways to inform their choice of parameter values used for identifying nest sites among re-visited locations (Figure 3-1). If the true location of nests is known for a subset of the data, researchers can compare re-visitation patterns at known nest sites to those of non-nest sites and find one or more sets of parameter values to discriminate between them. If on-ground data are not directly available, an alternative is to visually explore the data and identify trusted nest sites, where possible. For example, likely nest sites may be recognized in some species based on habitat features or proximity to known breeding colonies. Once known or trusted nest sites are identified, non-nest sites can be selected based on a criterion of temporal overlap; locations re-visited simultaneously with a breeding attempt can be considered non-nest

sites, assuming birds cannot breed in two places at the same time (which may not be true in all study systems).

Several approaches are possible to identify sets of parameter values to distinguish nest from non-nest sites. We propose one based on Classification And Regression Trees (CART; De'ath and Fabricius 2000). We apply CART to a dataset of known nest and non-nest sites, and prune the tree to the optimal number of nodes based on a minimum relative error criterion (De'ath and Fabricius 2000). More sophisticated classification tools, such as random forests (Breiman 2001), may also be appropriate for this task, but CART has the advantage of providing outputs that are easy to interpret biologically. CART identifies one or more sets of parameter values that best discriminate between nest and non-nest sites, which is then applied to the complete set of re-visited locations to identify nest sites among them (Figure 3-1). In case of temporal overlap between breeding attempts that satisfy the criteria, and again assuming birds cannot breed in two places at the same time, the recommended option is to pick the most visited candidate and discard the rest. For each nest site, we compile a history of nest re-visitation, in the form of a presence/absence time series (0/1 for each GPS point), which is then used to estimate the outcome of each breeding attempt.

Reproductive outcome estimation

The outcome of each identified breeding attempt is estimated using a Bayesian hierarchical modeling approach (Figure 3-1). We define success as survival of at least one nestling until fledging and failure to none. A breeding attempt is considered successful if the nest site was visited until the end of a complete breeding cycle for the focal species, which includes nest-building, egg-laying, incubation, and chick-rearing until the nestlings reach autonomy and no longer receive parental care. Nest survival is

estimated based on patterns of nest-site re-visitation, taking into account imperfect detection of nest visits and missing fixes. The MCMC (Markov Chain Monte Carlo) algorithm is implemented in JAGS (Plummer 2003) via the R package ‘rjags’ (Plummer 2018).

The model specification includes two processes: the survival process, which is not directly observable, and the observation process, which is the re-visitation history. Much like a Bayesian implementation of a Cormack-Jolly-Seber capture-mark-recapture model (Lebreton et al. 1992, Schaub and Royle 2014), the latent nest survival variable, z , is modeled as a Bernoulli variable at the daily scale as a function of survival status and daily survival probability, ϕ , at the previous time-step:

$$z_t \sim \text{Bern}(z_{t-1} \times \phi_{t-1})$$

Observed visits on a given day are modeled as a binomial variable as a function of current nest survival status, probability of visit detection, p , and number of GPS fixes available, N , on day t :

$$Y_t \sim \text{Bin}(N_t, z_t \times p_t)$$

Where the probability of detection is conditional to N and to the nest being alive on that day:

$$p_t = \text{Pr}(\text{visitdetected} | z_t = 1, N_t)$$

Reproductive outcome is defined as the probability P that the nest was still surviving on the last day of the theoretical duration of a complete breeding attempt, T :

$$P = \text{Pr}(z_T = 1)$$

Both survival and detection probability are modeled using a binomial Generalized Linear Model (GLM) as a function of the day of the attempt:

$$\text{logit}(\phi_t) = \beta_{\phi_0} + \beta_{\phi_1} \times t$$

$$\text{logit}(p_t) = \beta_{p_0} + \beta_{p_1} \times t$$

The model is fully specified by using uninformative priors on the β parameters, in this case a normal distribution with a mean of 0 and precision of 1e-5. In the current implementation, daily survival and detection are assumed to be the same for all nests in the population. The model outputs daily estimates of survival and detection probability at the population level, as well as daily survival estimates for each breeding attempt along with credible intervals.

Assumptions underlying this model include: birds are tracked for the entire duration T of a complete nesting attempt (if birds were tagged part-way through an attempt, T needs to be adjusted by subtracting the age of the nest (in days) at tagging); the GPS tag does not permanently fail before the end of the attempt; parents visit the nest until fledging, or nestling mortality is negligible between the time when parental care is interrupted and fledging; parents stop visiting a nest after failing.

Software Description

Our method is implemented in the R package 'nestR' (<https://github.com/picardis/nestR>; Picardi et al. 2019b). The package includes functions to implement each step of the described workflow (Figure 3-1). The function 'find_nests()' is used to identify re-visited locations and nest sites among them. An interactive visualization tool for dynamic exploration of re-visited locations is available in the form of a Shiny application launched by the function 'explore_nests()'. Exploratory data on nest and non-nest sites is compiled using the function 'get_explodata()' and used to identify parameter values for the detection of nests using the function

'discriminate_nests()'. Once nests are identified, re-visitation histories are formatted using the function 'format_attempts()' for input in 'estimate_outcomes()', the function for estimating the outcome of breeding attempts. The package also includes several functions for plotting and summarizing results ('summarize_outcomes()', 'plot_nest_surv()', 'plot_survival()', 'plot_detection()'; Figure 3-1). For a thorough description of package structure and features, we direct the reader to the 'nestR' package vignette.

Study Cases

We applied our method to GPS-tracking data for 148 individual-years for wood storks (henceforth storks), 56 for lesser kestrels (henceforth kestrels) and 29 for Mediterranean gulls (henceforth gulls; Table 3-1). All tags were solar-powered and recorded fixes primarily during daytime. Details about devices, settings, harnesses, and study areas regarding storks and kestrels can be found in Borkhataria et al. (2008) and Cecere et al. (2018), respectively. To find nest sites, we restricted the analysis to the breeding season only for each species (Table 3-1). While both kestrels and gulls have a well-defined breeding season between April and August in our study areas (Snow et al. 1997), storks in the southeastern U.S. can breed at slightly different times of the year depending on latitude (Coulter et al. 1999; Table 3-1). In this case, we used a conservative approach and only excluded the period where no breeding activities were expected to occur anywhere in the range.

Given the spatial resolution of the GPS data (Table 3-1) and the expected scale of movements around the nest site for all three species, we used a buffer of 40 m around each GPS position. We initially screened trajectories for any re-visited locations using non-constraining values for parameters describing re-visitation patterns (thus not

applying any filtering). We then used on-ground data on known nest locations to select true nests and non-nest sites from the re-visited locations. Kestrels and gulls were captured at the nest site (Table 3-1), so the location of the nest was known. For storks, on-ground data on nest locations was available for 10 individual-years (Bear D., unpublished data). We explored the remaining stork trajectories and identified those for which the top visited location was at a known breeding colony (data from U.S. Fish and Wildlife Service 2018). We marked these as trusted and treated them as known nest sites for the rest of the analysis.

We used CART to compare re-visitation patterns between nest and non-nest sites, and used the resulting sets of parameter values to filter nest sites among re-visited locations in the trajectories of breeding individuals. We only retained individual-years where data exceeded the minimum number of consecutive days visited indicated by CART (Table 3-1). Even when CART did not suggest that the number of consecutive days visited was an important predictor of true nest sites, we chose a reasonable value to use as a threshold for this parameter, as we did not expect to have enough power to discern nest from non-nest sites for attempts that failed in the first handful of days. We only retained the candidate with the most visits among any sets of breeding attempts that were temporally overlapping. We used non-breeder trajectories (sub-adults in the case of storks, non-breeding season data in the case of kestrels and gulls) to validate our results against false positives. We calculated positive predictive value of our algorithm as the percentage of nest sites that were known among those we found for each species; sensitivity as the percentage of known nest sites that were identified; false negative rate as the percentage of known nest sites that we failed to identify; and

false positive rate as the percentage of non-breeding individual-years for which we erroneously identified a nest site.

We fit the nest survival model described above to estimate the outcome of identified breeding attempts, using only individual-years for which the tag was active throughout the attempt to meet model assumptions (Table 3-1). Since kestrels and gulls were captured after they had already started breeding (immediately after hatching and in late incubation, respectively, although the exact age of the nest at tagging was unknown), the initial part of every breeding attempt was missing from the data. To account for this, we subtracted the theoretical number of days until hatching (for kestrels, 25 days) and late incubation (for gulls, 20 days) from the value of T (Table 3-1). We evaluated performance of the method by comparing survival estimates to known outcomes.

Results

The initial screening with no filtering identified 9871 re-visited locations (i.e., potential nest sites) for storks, 511 for kestrels, and 1379 for gulls. Results from CART showed that the optimal set of parameter values to discriminate nest from non-nest sites was 14 minimum consecutive days visited and 79% minimum nest attendance on the top day for storks, 7 minimum consecutive days visited for kestrels, and 26% minimum attendance on the top day for gulls (Figure 3-2). Because CART did not indicate a minimum number of consecutive days visited for gulls, we added a reasonable constraint for this value by exploring the data and determining which value would allow us to rule out most non-nest sites while retaining most nest sites (8 days). By filtering re-visited locations using these parameter values, we identified 109 nest sites for storks, 45 for kestrels, and 30 for gulls, which closely matched the number of nest sites we

were expecting to find (Table 3-1). As a consequence, the positive predictive value of the algorithm ranged between 73-100%, the sensitivity between 87-92%, and the false negative rate between 8-12% for the three species (Table 3-2). The false positive rate was 7% for storks and 0% for gulls but reached 44% for kestrels (Table 3-2). The probability of detecting nest visits decreased throughout the breeding attempt for all three species, while survival remained constant (Figure 3-3). We correctly estimated the outcome of 100% of breeding attempts for gulls and 86% for kestrels (1 failure and 2 successes incorrectly estimated; Figure 3-4). No data on true outcomes were available for storks, therefore we were unable to verify survival estimates for this species.

Discussion

We presented a data-driven method to identify nest-site locations of altricial avian species and estimate the outcome of breeding attempts based on GPS-tracking data. This is among the first attempts to infer the reproductive component of fitness from telemetry data (DeMars et al. 2013), and to our knowledge, the first applied to birds. We demonstrated the broad applicability of our method by illustrating its use on GPS-tracking data from three species which differ in their breeding behavior and ecology, including a subtropical wading bird, a small steppe raptor, and a seabird.

Nest-Site Detection

Our nest-site detection method performed well for all three species, allowing us to correctly identify most or all known nest sites from movement trajectories of breeding individuals. As a cautionary note for interpreting nest detection results, we reiterate that most nest locations we treated as known for storks were trusted nest sites for which we did not have on-ground confirmation but that were located in known colonies (97 out of 107). We achieved high positive predictive value (73-100%) and sensitivity (87-92%) for

all species. Importantly, the positive predictive value quantifies how many of the nest sites we found were known, which does not necessarily imply that the remaining were non-nest sites: it is possible that those we were unable to confirm for storks and gulls included second attempts (true but unknown nest sites) in addition to non-nest sites, as both species may attempt to breed again at a different location if their first clutch fails early in the season. In support of this possibility, all unknown nest sites we found for gulls were from birds whose known attempt failed early on, and they were thus plausible second attempts. The same might be true for storks, although we did not have on-ground data to confirm it. False negative rates were low for all species (8-12%) and mostly associated with early failures: 2 out of 2 nest sites that we failed to identify for gulls and 2 out of 5 for kestrels corresponded to attempts that failed before the enforced limit of consecutive days visited (as early as the day after tagging in the case of gulls). This may be true for storks as well, where the breeding attempts we were unable to identify might have failed before the 14-day mark. Not identifying breeding attempts whose duration does not exceed the minimum constraint applied is a logical implication of the approach rather than a failure of the algorithm. The remaining 3 nest sites that we were unable to identify for kestrels did not fail within the first week, but were never visited for 7 consecutive days. False positives were none or negligible for gulls and storks (0% and 7% respectively), but reached 44% for kestrels. This is likely explained by species-specific behavior: non-breeding kestrels spend long stretches of time and consecutive days on a perch while scanning for prey or resting. Distinguishing these patterns of attendance and re-visitation from those of a nest might be challenging

without applying restrictions based on seasonality and geographical area (e.g., breeding versus wintering range).

Error rates for nest-site identification vary in importance depending on the study objectives. If the objective is to estimate reproductive outcome, ensuring that attempts are not missed should receive priority over avoiding the selection of non-nest sites. Any re-visited location that gets erroneously identified as a nest site would likely be classified as a failed attempt eventually anyway. In this case, we suggest that researchers may want to focus on minimizing false negatives. Conversely, if the objective of a study is, for instance, to analyze factors associated with nest-site selection, minimizing false positives should be the priority.

Once on-ground data on nest locations are used to identify parameter values to distinguish nests among re-visited locations, these parameter values can then be applied to new individuals of the same species for which on-ground information is not available, assuming other data characteristics are the same. If CART is the tool of choice to inform the choice of parameter values, we recommend that classification thresholds in output should be used with caution, and considered more as range indications than as clear-cut rules. We also recommend that parameter values suggested by CART should be critically evaluated for their biological significance before use, and that adjustments should be made as needed based on knowledge of the species biology. Future efforts to improve our method for the identification of nest locations will include incorporating uncertainty in our estimates of nest sites, allowing us to interpret classification results in a probabilistic framework.

Reproductive Outcome Estimation

We correctly estimated reproductive outcome of 100% of breeding attempts for gulls and 86% for kestrels, with probability of success estimated as $P > 0.97$ for true successes and as $P = 0$ for true failures. The remaining attempts were two successes that we estimated as failures ($P \leq 0.3$) and one failure that we estimated as a success ($P = 0.98$). The two attempts that we erroneously estimated as failures corresponded to one male and one female kestrel whose original clutch included four eggs and was partially lost, leading to two and one fledglings, respectively. When the brood is reduced, remaining nestlings may grow more rapidly and lead to a faster completion of the breeding cycle, which may have compromised our ability to detect these attempts as successful as they did not reach the benchmark $T = 60$. Specifically, one of the two attempts was completed within 27 days of tagging, which corresponds to $T = 52$. However, the other attempt was completed within 33 days of tagging, corresponding to $T = 58$, which is a similar duration to other successful attempts that we estimated correctly. In this case, our inability to recognize the attempt as successful might have depended on behavioral differences between parents, whereby the male we were tracking might have interrupted parental care before the female did. This result highlights the importance of taking into account sex differences in breeding behavior, where that applies. For example, in species exhibiting uniparental care, inference should only be based on the sex that carries out parental care. The failed attempt that we erroneously estimated as successful corresponded to a male that occasionally visited the nest site after failing, thus violating one of the assumptions of our model. Unfortunately, this was the only failed attempt for kestrels in our dataset, which makes it difficult to generalize our ability to estimate nest failures for this species. Overall, the

three instances of incorrect estimation might suggest that model assumptions, such as interruption of nest visits after failure, might not always hold across species; or that the duration of a complete breeding cycle may be too variable to lend itself to generalizations in some species; or that not knowing the exact age of the nest at tagging might have reduced our power to distinguish late failures from successful attempts that were completed in less-than-average time.

We did not have on-ground data to validate our estimation of reproductive outcome for storks; however, most attempts were estimated as either $P = 1$ or $P = 0$, while intermediate values (between 0.25 and 0.75) were relatively rare (14 out of 109). This is an important result given that data for storks were at lower temporal resolution compared to kestrels and gulls (Table 3-1). Low temporal resolution of data in combination with decreasing frequency of nest visits can, in principle, increase the uncertainty of outcome estimation by reducing probability of visit detection especially towards the end of a breeding attempt (Figure 3-3). Thus, the higher proportion of intermediate values for estimates of breeding success probabilities we observed in storks compared to kestrels and gulls was to be expected, but results were still rather polarized, suggesting that the method is largely able to distinguish between successes and failures at this temporal resolution, given the frequency of nest visits in storks.

Synthesis and Significance

The most important implication of our work is the ability to use telemetry data to obtain estimates of bird reproductive outcome. Reproductive outcome is an important component of fitness, and estimating it from tracking data will help establish the long-sought bridge between movement and fitness at the individual level (Nathan et al. 2008, Morales et al. 2010). Our method allows researchers to obtain critical information on

reproductive outcome for birds that nest in remote or inaccessible locations where it is difficult or risky to collect on-ground data (Götmark 1992, Mayer-Gross et al. 1997, Etterson et al. 2011, Wilmers et al. 2015). Information on reproductive outcome obtained from tracking data can also be combined with environmental conditions experienced by individual birds, not only at the nest but in other important locations visited during breeding attempts, such as foraging grounds (Cagnacci et al. 2010, Pettorelli et al. 2014). This opens new research avenues regarding links between components of individual fitness, movement strategies, and habitat. Important exceptions to the applicability of our method are precocial species and nest parasites, where parental care is limited or absent. Another limitation of our approach is that it does not provide estimation of reproductive success in terms of number of offspring, but only in terms of overall success or failure. Under this aspect, our method does not compare to the level of detail obtainable with conventional field methods.

Besides estimating reproductive outcome, our method is useful as a tool to identify nest-site locations. Identifying nest sites is valuable in and of itself: for example, it may allow researchers to find previously unknown nesting sites in species for which breeding locations are partly or entirely unknown.

Conclusions

Our method for nest-site detection and estimation of avian reproductive outcome from GPS-tracking data can appeal to researchers with different objectives. First, it may be useful to researchers that want to investigate reproductive outcome in relation to movement and environmental factors away from the nest. Second, it may serve researchers that want to obtain data on reproductive outcome for species that are not easy to monitor on the ground. Third, it may be of use to researchers that want to

identify the location of nest sites for analyses of breeding site fidelity, nest-site selection, or discovery of new breeding sites. Our method can be applied both in situations of opportunistic use of historical tracking data or in cases where the study is explicitly designed with these objectives in mind. Conservation and management applications may both benefit from the availability of our method and its implementation in an open-access, user-friendly R package, 'nestR'. Knowledge of the biology and ecology of the target species and careful consideration of data characteristics and limitations are critical for successful use of the tools we presented. As technology improves and tracking devices are miniaturized, our method will allow researchers to identify nest sites and estimate reproductive outcome of an increasingly broad variety of avian species.

Table 3-1. Differences among GPS-tracking datasets for wood storks, lesser kestrels, and Mediterranean gulls. The datasets differ in terms of sample sizes, data characteristics, and species seasonality and ecology.

		Wood stork	Lesser kestrel	Mediterranean gull
Spatial resolution (m)		18	<10	<10
Temporal resolution (min)		60	15 (summer)/30 (winter)	15
Fix failure rate		High	Low	Low
Tagged at		Fledging/non-breeding	Early nestling-rearing	Incubation
Number of tracks (individual-years)	Total	148	56	29
	Known nest location	107	50	24
	Known outcome	0	21	12
	Non-breeders	41 (subadults)	16 (winter)	16 (winter)
Breeding season		Nov-Aug (varies with latitude)	Apr-Jul	Apr-Jul
Breeding cycle (days)		110	60	60

Table 3-2. Performance metrics of the nest identification. Definitions are reported in Methods.

	Wood stork	Lesser kestrel	Mediterranean gull
Positive predictive value	86.24%	100.00%	73.33%
Sensitivity	87.85%	90.00%	91.67%
False negative rate	12.15%	10.00%	8.33%
False positive rate	7.32%	43.75%	0.00%

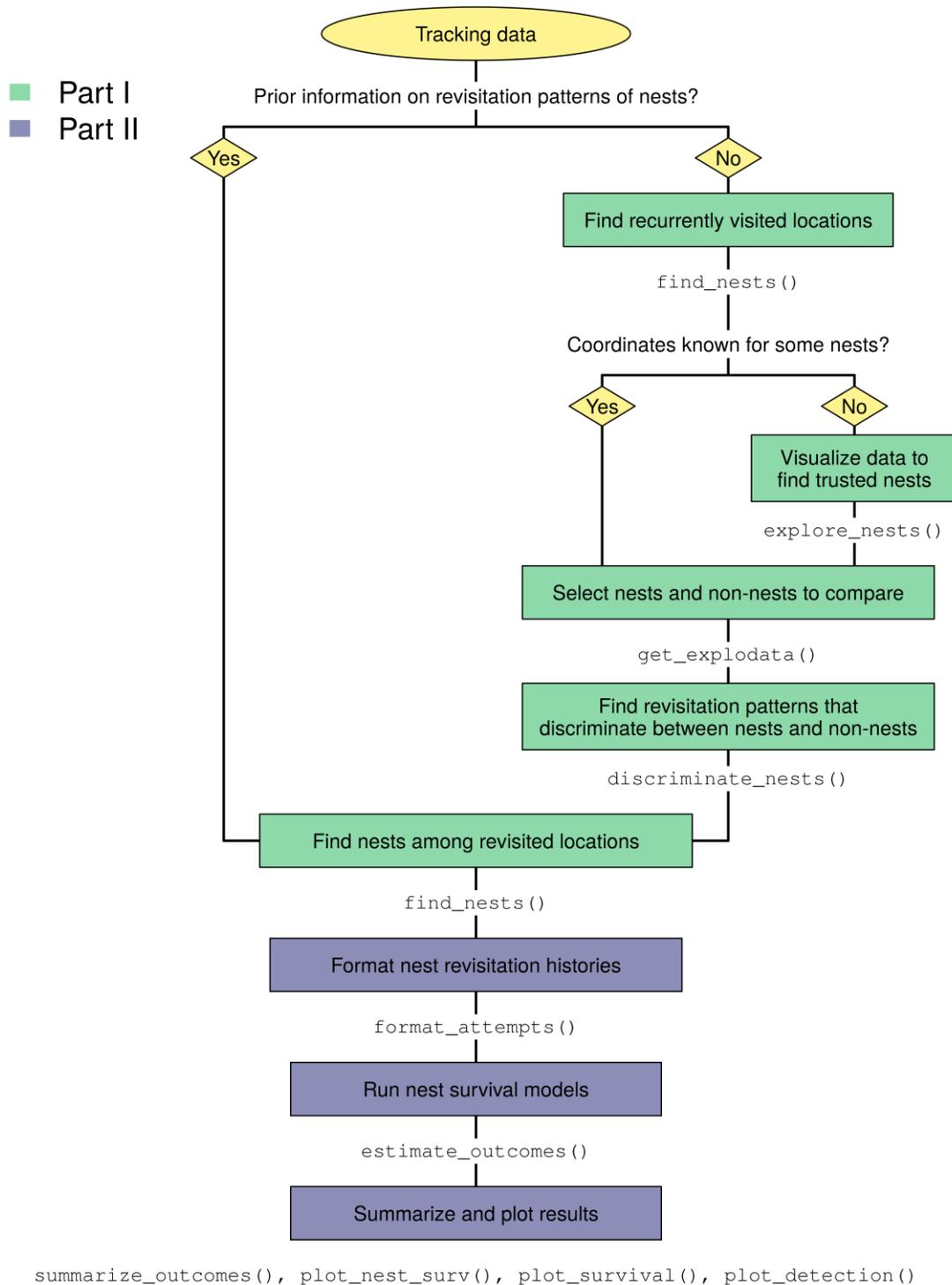


Figure 3-1. Workflow of the analysis to identify nest sites and estimate reproductive outcome from telemetry data. Part I = nest-site detection, Part II = reproductive-outcome estimation. The R package ‘nestR’ includes functions to tackle each of the steps depicted in the boxes.

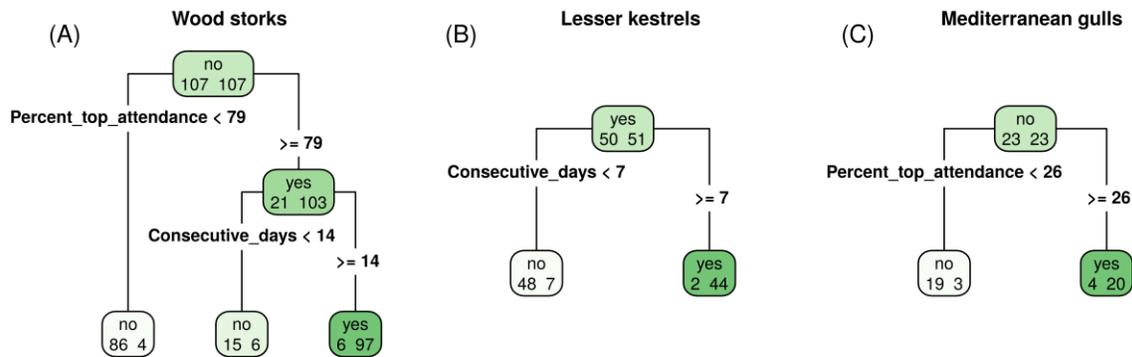


Figure 3-2. Output of CART to discriminate nest and non-nest sites. A) Wood stork, B) lesser kestrel, C) Mediterranean gull. Within each node (box), the number of known non-nest and nest sites are reported on the left and right, respectively. The root node (top) is recursively split into two until the terminal nodes (bottom). The criterion used to split each node is shown on the corresponding stems (bold font). The label on each node represents the class that was assigned to the content of that node (nest site for “yes” boxes, non-nest site for “no” boxes). Thus, the number on the right in “yes” terminal nodes and the number on the left in “no” terminal nodes correspond to correct classifications, while the number on the left in “yes” terminal nodes and on the right in “no” terminal nodes correspond to incorrect classifications.

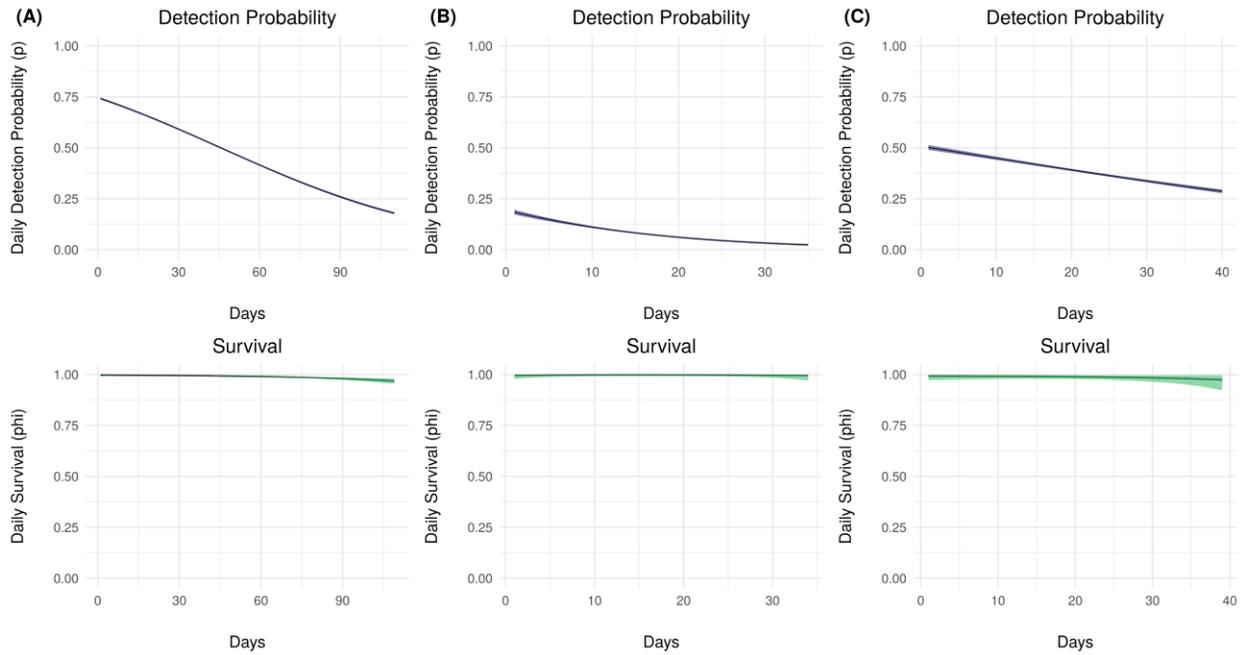


Figure 3-3. Probability of visit detection and survival through time estimated at the population level. Top row = detection, bottom row = survival. A) Wood stork, B) lesser kestrel, C) Mediterranean gull. 95% credible intervals are shaded.

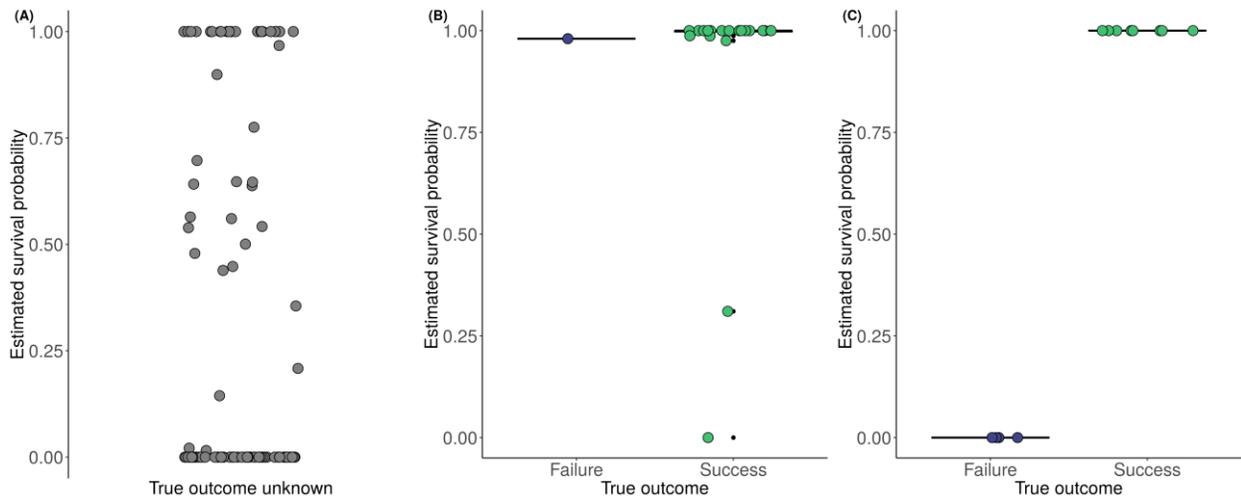


Figure 3-4. Estimates of survival probabilities for breeding attempts. A) Wood stork, B) lesser kestrel, C) Mediterranean gull. For kestrels and gulls, estimates are plotted in relation to their true outcome. True outcome was unknown for storks. Raw data points are shown as dots (purple for failures, green for successes, gray when true outcome is unknown) overlaid to boxplots (black).

CHAPTER 4 MECHANISMS FOR HUMAN-DRIVEN CHANGES OF MIGRATION PATTERNS: A CASE-STUDY WITH A PARTIALLY MIGRATORY WADING BIRD

Introduction

Animal migration as a whole is a declining phenomenon, and many of the reasons for this decline are linked to human activities (Wilcove and Wikelski 2008). By changing the environment, humans are changing the selective pressures insisting on migratory populations, and changes of migratory patterns are to be expected as a consequence (Shaw 2016). Changes of migratory patterns are being observed almost ubiquitously across taxa, including changes of migration timing (Butler 2003, Charmantier and Gienapp 2013), distance (Jones et al. 2014), and destination (Plummer et al. 2015); but the most generalized response to human-driven environmental change seems to be the decline of migration behavior in favor of residency (Van Leeuwen et al. 2016, Found and St. Clair 2016, Greig et al. 2017, Satterfield et al. 2018). Humans are causing these shifts by posing physical impediments, such as barriers that hamper movement (Van Leeuwen et al. 2016) and increase mortality (Palacín et al. 2017); or by altering resource patterns through climate change (Pulido 2007, Németh 2017) and food supplementation (Hebblewhite et al. 2006, Peterson and Messmer 2007, Greig et al. 2017). Movement strategies, including migration, are shaped by spatio-temporal dynamics of resource availability (Van Moorter et al. 2013, Bastille-Rousseau et al. 2017), so it is logical that changes of resource patterns will result in changes of migratory patterns. In this paper, we formalize a conceptual framework for disentangling mechanisms for human-driven changes of migratory patterns, and we apply it to a partially migratory wading bird population as a case-study, focusing on food supplementation as a possible anthropogenic driver.

Human activities have increasingly provided free-ranging animals with novel food sources, whether intentionally or not. Feeding stations are often used as a tool for game management (Peterson and Messmer 2007, Jones et al. 2014, Found and St. Clair 2016), recreational feeding associated with tourism or backyard wildlife-watching has become popular (Maljković and Côté 2011, Clergeau and Vergnes 2011), exotic ornamental species are introduced alongside their native counterparts (Satterfield et al. 2018), and trash increasingly appears on the menu of many species that forage in urban parks or landfills (Ramos et al. 2009, Sha and Hanya 2013, Turrin et al. 2015). Urban areas are hotspots of availability of anthropogenic food sources (Rodewald and Gehrt 2014).

Recent research has provided compelling and widespread evidence that anthropogenic food supplementation in urban areas often leads to shifts from complete or partial migration to residency (reviewed by Satterfield et al. 2018). However, the mechanisms by which these shifts happen are not well understood. First, it is unclear whether migratory populations become resident in response to food supplementation through plastic behavioral changes or evolutionary adaptation. Second, if changes of migratory patterns are adaptive rather than plastic, little is known about the exact mechanisms. For adaptive changes to happen, there needs to be, first, a difference in resource use whereby some use more anthropogenic resources than others; and second, a fitness advantage for the individuals who forego migration by relying on anthropogenic food. The fitness advantage could be increased survival of one or more age classes, increased reproductive performance, or both. Plasticity and adaptation may also act in concert, possibly with more plastic individuals being selectively favored

(Nussey et al. 2005). All in all, there is a need to shift the focus from pattern description to an understanding of the mechanisms by which food supplementation is affecting migration, so that we can predict consequences of human activities and intervene effectively.

A few studies have addressed human-driven shifts of migration patterns from a mechanistic perspective. For example, Teitelbaum et al. (2016) showed that changes of migratory patterns in whooping cranes (*Grus americana*) are due to behavioral shifts in older individuals, which highlights the importance of plasticity. Partecke and Gwinner (2007) showed that changes of migratory propensity in European blackbirds (*Turdus merula*) in urban areas are genetically determined, but did not address the ecological mechanism by which selection happens. Handrigan et al. (2016) showed that a shift towards residency in trumpeter swans (*Cygnus buccinator*) is inherited and possibly linked to increased survival due to food subsidies. A suite of different studies on white storks (*Ciconia ciconia*) showed that a population in Spain is becoming resident due to the use of landfills (Gilbert et al. 2016), which is enhancing their reproduction (Tortosa et al. 2002) and juvenile survival (Rotics et al. 2017). Isolated pieces of evidence are available and suggest that both plastic and adaptive responses are possible; however, an explicit consideration of the mechanisms driving the disappearance of migration in favor of residency, which accounts for both individual differences in resource use and consequent fitness advantages in a cohesive framework, is so far lacking.

In this paper, we provide a framework for addressing the mechanisms driving human-induced migratory shifts (Figure 3-1), and we apply it to a partially migratory bird population as a study model. We focused on the southeastern U.S. population of the

American wood stork (*Mycteria americana*), a large wetland-dwelling bird distributed east of Mississippi and south of North Carolina (Coulter et al. 1999). Migrant individuals spend the winter in south Florida and relocate north to other southeastern states during the summer, while residents stay in Florida year-round (Picardi et al. 2019a). Florida is one of the most populous states of the U.S., and its natural landscapes have been impacted by humans in many different ways, of which urbanization is only one (Marshall et al. 2004, Grunwald 2006, Foti et al. 2013). Humans have also strongly altered the dynamics of natural ecosystems, including the hydrological dynamics of the Florida Everglades. Historically, the Everglades constituted the breeding grounds for the bulk of the wood stork population (Frederick and Ogden 1997). Starting in the 1940s, humans began constructing a widespread network of canals across south Florida, and the Everglades were partly drained to make room for urban settlements (Sklar et al. 2005). South Florida was transformed into a mosaic of urban development and artificially controlled water bodies, including reservoirs for public water, retention ponds, and seasonally flooded agricultural fields, with the Everglades relegated to only 50% of their original extent (Sklar et al. 2005).

The natural dynamics of water in the Everglades provided a mechanism for production and concentration of wood stork prey. During the wet season, heavy rainfall increased water levels enhancing productivity of fish populations (DeAngelis et al. 2010, Botson et al. 2016), and in the dry season, water levels dropped and concentrated fish (Kahl 1964, Kushlan 1986, Frederick et al. 2009). The Everglades are highly oligotrophic and have relatively low standing stocks of aquatic fauna (Trexler and Goss 2009), making concentration of prey necessary to make food available to birds. Wood

storks are tactile foragers and almost exclusively piscivorous, and their breeding activities were adaptively synchronized with the pulse of fish availability in the dry season (Kahl 1964, Ogden et al. 1976, Kushlan 1986). Outside of the dry season, the Everglades provide few opportunities for foraging because the water is too deep and fish are too hard to catch by tactile foraging (Kahl 1964, Kushlan 1986, Gawlik 2002). The landscape modifications implemented in the 20th century altered natural hydrology dynamics so that both fish production and availability were affected, resulting in massive colony failures, a drastic drop in wood stork population size, and a shift of nesting to northern states (USFWS 1984, Frederick and Ogden 1997). This highlights how important breeding success is for population viability, and how critical the availability of abundant food is for wood storks to reproduce successfully (Frederick et al. 2009). After the crash, the population has been recovering since the 1980s thanks to both restoration efforts and expansion of the breeding range beyond south Florida (Brooks and Dean 2008, USFWS 2014).

It is unclear if partial migration in wood stork pre-dated the 20th-century landscape changes or if it emerged in response to those. The only study addressing wood stork migration patterns covered the time span between 2004 and 2017 (Picardi et al. 2019a), long after humans started impacting the landscape, and migratory patterns prior to that are unknown. We cannot exclude that the population was historically fully migratory, and that residency may have recently emerged as an individual strategy thanks to the year-round availability of alternatives to natural food sources.

Scientists are collecting increasing evidence that wood storks have started to use novel resources of anthropogenic nature in recent times. Anthropogenic food sources include, but are not limited to, trash and direct hand-feeding in cities and urban parks; humans have also created new foraging habitat in the form of artificial bodies of water that are both more productive (because of nutrient discharge from cities and crops) and predictable (because of artificial flooding schedules) than natural wetlands in south Florida; in turn, the presence of larger standing stocks of prey relaxes the need for prey concentration via water recession. Wood storks intensively use urban ponds, canals, and ditches for foraging (Van Os 2008). Evans et al. (personal communication) studied the diet composition of wood stork nestlings in south Florida and frequently found human food scraps, including chicken nuggets and hot dogs; non-native fish also constituted a prominent part of the gut contents, abundant in both artificial and natural bodies of water after being released from ornamental fish tanks. The use of anthropogenic food sources seems to be generally on the rise among wading birds in the southeastern U.S.: a study by Murray et al. (2018) showed regular use of food subsidies by the sympatric white ibis (*Eudocimus albus*). To date, researchers have not evaluated whether the use of anthropogenic resources is associated with residency in these populations, nor if it carries fitness advantages that may result in evolutionary change of migration patterns.

Building on the existing pieces of evidence, our objectives were to determine whether the use of urban foraging sites by wood storks differed between individuals with different migratory behavior, and if it was associated with differences in reproductive performance. Our approach addressed the two necessary components for a shift of

migratory patterns: first, differential resource selection between individuals (a source of variation) and second, a fitness advantage connected to the use of certain resources (a mechanism for selection; Figure 3-1). We assessed the first component by evaluating selection of foraging sites used during breeding in relation to proximity to urban areas. We assessed the second component by evaluating the effect of proximity to urban areas on reproductive performance, quantified in terms of daily nest-survival probability. If the use of anthropogenic food sources promotes a shift from partial migration to residency, we expected residents to use these resources more than migrants and to gain a fitness benefit in the form of higher reproductive performance.

Methods

Data Collection

Wood storks were captured between 2004 and 2012 at 11 sites spread across their population range and equipped with solar-powered GPS tags programmed to collect one location per hour (Picardi et al. 2019a). Details on capture colonies, and age and sex composition of the sample are reported in Picardi et al. (2019a).

Breeding Attempts

We focused on the breeding season because of its critical importance for wood stork population dynamics. We identified nesting attempts within yearly individual tracks based on the analysis of recursive movement patterns, following a procedure described in Picardi et al. (2019c) and using the R package 'nestR' (Picardi et al. 2019b). Nests were identified among repeatedly visited locations based on distinctive temporal patterns of re-visitation, using known nesting attempts as a reference (Picardi et al. 2019c). The algorithm returned information on the location of the nest, the temporal limits of the breeding attempt, and a history of nest re-visitation whereby locations within

an individual track are classified as either on the nest or away from it. Locations were classified as on the nest if they fell within the 40m buffer used to spatially define re-visitation (Picardi et al. 2019c). We considered any location away from the nest during a breeding attempt as a foraging location (Figure 4-2 A).

Migratory Behavior

We classified individual migratory behavior in each year as either migration or residency using non-linear models of net squared displacement, using the R package 'migrateR' (Spitz et al. 2017, Picardi et al. 2019a). We retained for further analyses any individual breeding attempt for which migratory behavior in the season prior to breeding was known. The resulting dataset consisted of 100 breeding attempts, of which 52 associated with migration and 48 with residency prior to breeding, from 35 different individuals between 2006 and 2016 (Figure 4-2 B).

Urban Areas

Proximity to urban areas is a good proxy for the use of anthropogenic food sources of various nature, including landfills, artificial water bodies, and urban parks. We obtained information on the location of urban areas across Florida from the Florida Cooperative Land Cover Map, version 3.2 (Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory, 2016). We defined urban land use by pooling together the categories labeled “high intensity urban” and “low intensity urban” (Figure 4-2 C), and computed distance of each foraging location from the closest urban patch.

Resource-Selection Analysis

We evaluated the effect of proximity to urban areas on selection of foraging sites during breeding attempts using resource selection functions (Boyce and McDonald

1999) implemented with generalized linear mixed models (Bolker et al. 2009). We evaluated resource selection by comparing used with available foraging locations. For each individual breeding attempt, we defined available locations by randomly placing points around the location of the nest (ten times as many available points as used). To account for constraints to availability imposed by the movement process, we simulated points with decreasing density as the distance from the nest increases (Forester et al. 2009). We fitted an exponential function to the empirical distribution of foraging trip distances observed across all individuals to define the decay in the density of available points as a function of distance from nest (Appendix D). We used logistic regression with use versus availability as a response variable. We included distance to urban areas both as a linear and quadratic term, in interaction with migratory behavior, as fixed effects. We included the individual identity as a random effect to account for individual differences (Gillies et al. 2006). We evaluated model predictions at the fixed effects level and used bootstrapping to compute 95% confidence intervals around model estimates.

Nest-Survival Analysis

We evaluated the effect of proximity to urban areas on reproductive performance of wood storks using a daily nest survival model based on the history of nest re-visitation obtained from the GPS-tracking data, specified in a Bayesian hierarchical modeling framework. We used daily nest survival probability as a measure of reproductive performance. Nests were considered alive so long as they were visited, and dead once visits were interrupted, while accounting for imperfect detection of nest visits and missing GPS fixes. We built upon the model specification described in Picardi et al. (2019c), where survival is modeled as a latent, unobserved process which is

inferred through the observed history of nest re-visitation. For each attempt, i , we modeled daily nest survival status, z , as a Bernoulli random variable that was a function of survival probability, ϕ , and status on the previous day:

$$z_{i,t} \sim \text{Bern}(z_{i,t-1} \times \phi_{i,t-1})$$

Differently from the version described in Picardi et al. (2019c), we included the mean distance of foraging sites to urban areas, d , as a covariate by modeling probability of survival as a function of it using a binomial generalized linear model:

$$\text{logit}(\phi_{i,t}) = \beta_{\phi_0} + \beta_{\phi_1} \times d_i$$

We modeled observed nest visits on each day, Y , as a binomial random variable, with probability of success as a function of current nest survival status, probability of visit detection, p , and number of GPS fixes available, N :

$$Y_{i,t} \sim \text{Bin}(N_{i,t}, z_{i,t} \times p_t)$$

Where the probability of detection is conditional on N_t and the nest being alive on that day:

$$p_t = \text{Pr}(\text{visitdetected} | z_t = 1, N_t)$$

Note that, while the probability of survival is estimated at the individual-attempt level, the probability of visit detection is estimated at the population level. We allowed detection probability to vary through time by modeling it as a function of the day of the attempt using a binomial generalized linear model:

$$\text{logit}(p_t) = \beta_{p_0} + \beta_{p_1} \times t$$

We used uninformative priors on the beta parameters, specified as normal distributions with a mean of 0 and precision of 1e-5.

We fit the described model using JAGS v 4.3.0 (Plummer 2003) via the R package 'rjags' (Plummer 2018). We evaluated model predictions for daily nest survival probability as a function of proximity to urban areas using 95% Bayesian credible intervals.

Results

Results of the resource selection function indicated a significant difference in foraging site selection of migrant and resident wood storks according to distance from urban areas (Figure 4-3, Table 4-1). Residents selected foraging sites at distances between ~2 and ~16.5km from urban areas and strongly avoided foraging farther from those. On the contrary, migrants avoided foraging sites closer than ~7km to urban areas and selected for sites as far as >40km from those (Figure 4-3). We found a negative association between daily nest survival rate and distance to urban areas, whereby survival was the highest ($\varphi = 0.99$) in proximity to urban areas and quadratically decreased as the distance increased ($\beta_{\varphi 0} = 4.90$, $\beta_{\varphi 1} = -5.04 \text{ e-}5$; Figure 4-4).

Discussion

We introduced a framework for evaluating mechanisms of human-driven shifts of migratory patterns and applied it to a partially migratory population of wood storks in the southeastern U.S. as a case study. We showed that resident and migrant individuals within the wood stork population differ in their foraging-site selection, with residents selecting for sites close to urban areas and avoiding ones farther than 16.5km, and migrants selecting for a broad range of distances from urban areas with the exception of the immediate vicinity (within 7km). We showed that proximity to urban areas is positively associated with reproductive performance, with daily nest survival decreasing as distance from urban areas increased. These results quantify the two mechanistic

components necessary for a human-driven shift of migratory patterns towards residency: first, a source of variability between individuals in the use of anthropogenic resources; and second, a fitness advantage related to the use of such resources, in the form of increased reproductive performance. Our results suggest that residency might have emerged as an individual strategy in the wood stork population in response to the availability of anthropogenic resources, leading to the partial migration pattern we observe today. Understanding mechanisms driving migratory shifts is important to be able to predict population responses to human activities, and to manage these according to conservation objectives.

We found that resident wood storks selected foraging sites closer to urban areas compared to migrants. Generally, resident individuals tended to also nest closer to urban areas than migrants (Figure 4-2B; Appendix D), which suggests they may be selecting urban habitat for breeding as well as foraging. The effect of colony placement is important to acknowledge because the range of foraging sites available to individual wood storks during breeding is, to a certain extent, constrained by nest-site selection: our study design took that into account by defining availability relative to the position of the nest. Our results quantify selection as higher (and avoidance as lower) use than would be expected based on chance alone given the array of foraging opportunities available. Our results suggest that, while residents might be taking advantage of anthropogenic food sources on a regular basis, migrants may be sticking to historical, non-urbanized foraging sites. While non-urbanized, these historical foraging grounds have been heavily impacted by anthropogenic interventions linked to the drainage of the Everglades that have exacerbated the already high year-to-year unpredictability of prey

availability for wood storks (Frederick and Ogden 1997, Frederick et al. 2009). Consequently, reliance on natural prey may have become less efficient than the exploitation of novel, more reliable food sources such as those available year-round and with no naturally-driven periodicity in urban areas. From this perspective, humans may be responsible for both the advantages of foraging in urban areas and the disadvantages of foraging in historical sites (Sklar et al. 2005).

We found daily nest survival of wood storks to be higher in proximity to urban areas, presumably in relation to the consumption of anthropogenic food subsidies. The role of food supplementation in enhancing reproductive output of animals, especially birds, is not new to the literature (Richner 1992, Weiser and Powell 2010, Harrison et al. 2010, Ruffino et al. 2014). Similarly, other fitness benefits, including increased adult and juvenile survival, have also been observed in several species in response to food supplementation (Robb et al. 2008). Different fitness advantages are not mutually exclusive: increased use of urban areas could result in both increased survival of one or more age classes and increased reproduction. In this study, we were only able to measure differences in wood stork daily nest survival, but additional and unmeasured fitness effects may be acting in concert. Furthermore, we estimated nest survival as a binary outcome but we had no information on brood size, and thus we were not able to account for possible differences in fecundity.

Increased individual fitness due to anthropogenic food supplementation can have important demographic consequences (Robb et al. 2008). In the case of wood storks, residents may provide a demographic reservoir for the population, which might be especially important in years where prey production in the Everglades is low and

foraging conditions in non-urbanized sites are suboptimal. In profitable years, colony productivity in natural sites can numerically dominate recruitment; however, these profitable years are relatively infrequent. Anthropogenic food sources might buffer the stochasticity of natural environments and substantially support the population in otherwise bad years. At the same time, increased consumption of anthropogenic food sources by wildlife is associated with many risks. Ingestion of plastic (Katlam et al. 2018), increased pathogen transmission (Hernandez et al. 2016, Murray et al. 2016, Brown and Hall 2018), exacerbated human-wildlife conflicts (Dubois and Fraser 2013, Newsome and Van Eeden 2017), and biotic homogenization (McKinney 2006) are all documented consequences of food supplementation in urban areas.

Altogether, our findings provide a mechanism for changes of migratory patterns linked to the use of anthropogenic food sources. Resident wood storks may have an advantage over migrants by exploiting supplemental food in urban areas, and they might achieve better reproductive performance because of that. If migratory behavior is genetically controlled, residents may become more prevalent in the population as a result of higher fitness. We were not able to confirm that genetics is responsible of migratory behavior in wood storks, but individual migratory choices are for the most part consistent across years (Picardi et al. 2019a), which supports the hypothesis of intrinsic qualities being at play. Even if some degree of plasticity is involved, more plastic individuals may be more prone to experimenting with novel resources and to stick to innovative behavior if it proves successful (Lowry et al. 2013). Our findings support the idea that wood storks may have become partially migratory in response to human-driven environmental change. While we are not able to directly demonstrate that, we

provide evidence that a mechanism for a switch of migratory patterns is already in place. Ultimately, the interplay between individual fitness, relative proportions of migrants and residents, and the carrying capacity of non-urban foraging sites in favorable years is going to determine whether partial migration is maintained or will transition towards complete residency in the future. A chicken-or-egg question remains about whether resident wood storks are resident because they forage in urban areas, or if they forage in urban areas because they are residents; however, our results provide a potential mechanism for the former but not the latter, making it a plausible conclusion. Our findings are compatible with the hypothesis that partial migration can be an intermediate evolutionary stage for populations that are transitioning from complete migration to residency, or vice-versa (Berthold 2001, Pulido 2011). Recent literature has shown that such changes can happen relatively quickly in response to rapid, human-driven environmental change (Sutherland 1998, Fiedler 2003, Pulido and Berthold 2010).

Conclusions

Future research should strive to move beyond the description of patterns and gain a deeper understanding of mechanisms driving changes of animal migratory strategies. Knowing the population-specific mechanisms underlying human-induced migratory shifts is important because it gives us the ability to make accurate predictions and intervene when needed. A mechanistic understanding is necessary to predict the effects of anthropogenic pressure on migratory populations and manage human activities according to conservation objectives. The unintended consequences of the decline of migration can be far-reaching: losing migration entails the loss of the many ecosystem services that come with it (Wilcove and Wikelski 2008, Bauer and Hoyer

2014). Migratory populations are responsible for transport of nutrients, energy, pathogens, parasites, and seeds across the globe, and they establish key trophic interactions in the communities they encounter along their routes (Bauer and Hoye 2014). Many have argued that, rather than conserving populations only, scientists and managers should be concerned with conserving ecological processes (Ricklefs et al. 1984, Pickett et al. 1992, Smith et al. 1996); an improved understanding of the mechanisms driving the current decline of migration will be essential to preserve the functionality of many ecosystems.

Table 4-1. Results of Resource Selection Function for foraging sites used by wood storks during breeding as a function of distance to urban areas and migratory behavior. The model is implemented using mixed-effects logistic regression. Marginal pseudo-R² = 0.014; conditional pseudo-R² = 0.015.

Variable	β	SE	<i>p</i> -value
(Intercept)	-2.36	0.02	<0.001
Distance to urban	0.21	0.02	<0.001
Resident	0.27	0.03	<0.001
Distance to urban ²	-0.04	0.00	<0.001
Distance to urban * Resident	0.20	0.02	<0.001
Distance to urban ² * Resident	-0.32	0.02	<0.001

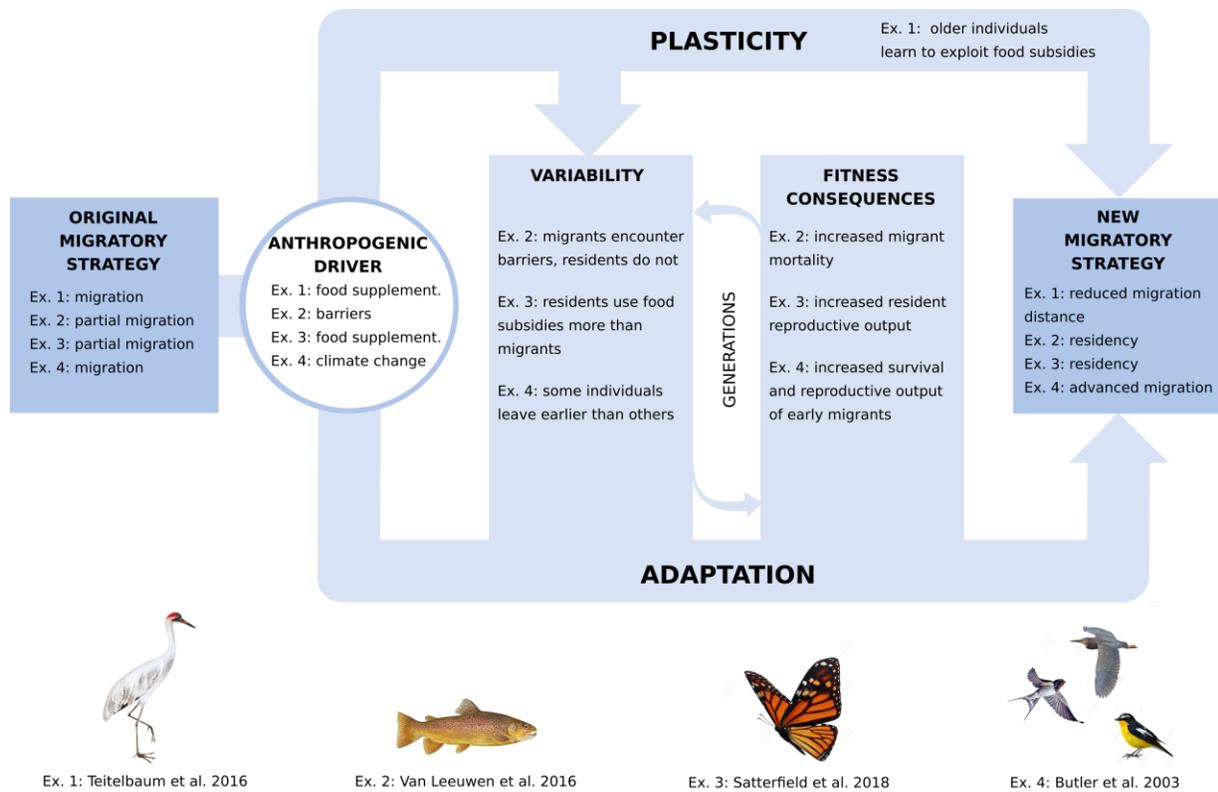


Figure 4-1. Conceptual framework illustrating mechanisms of human-induced migratory shifts. The introduction of an anthropogenic driver can result in changes of migratory patterns through two main pathways: plasticity or adaptation. Plasticity entails behavioral changes within the course of a lifetime, while adaptation implies inheritance of behavioral traits. The two necessary components for adaptation to occur are a source of behavioral variability between individuals and fitness consequences associated with different behaviors. Mechanisms are illustrated with four simplified examples from the literature on human-induced migratory shifts.

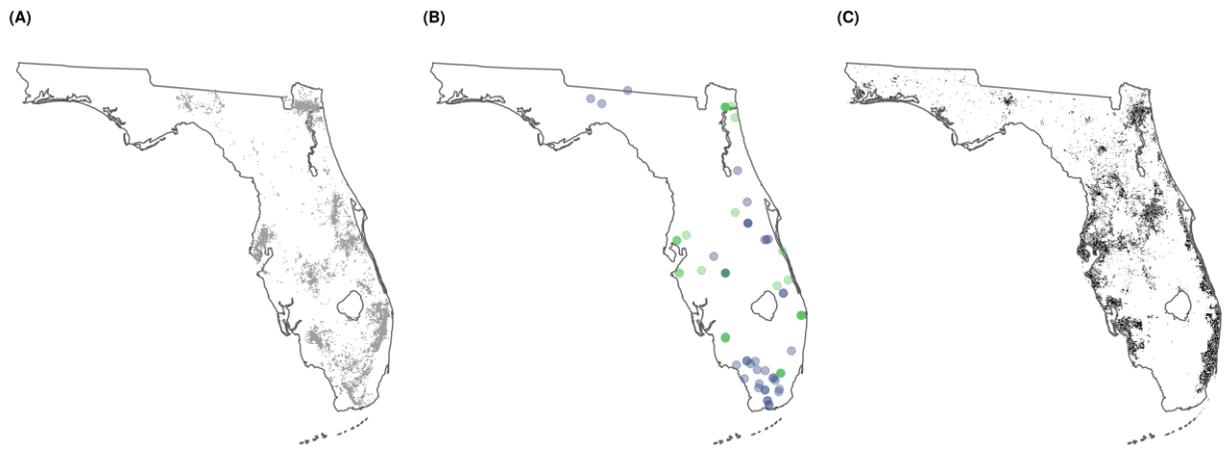


Figure 4-2. Maps of wood stork foraging locations, nesting locations, and Florida urban areas. A) Foraging locations used by wood storks during breeding attempts; B) Nesting locations for migrant (n = 52, blue) and resident (n = 48, green) wood storks; C) Urban areas across the state of Florida.

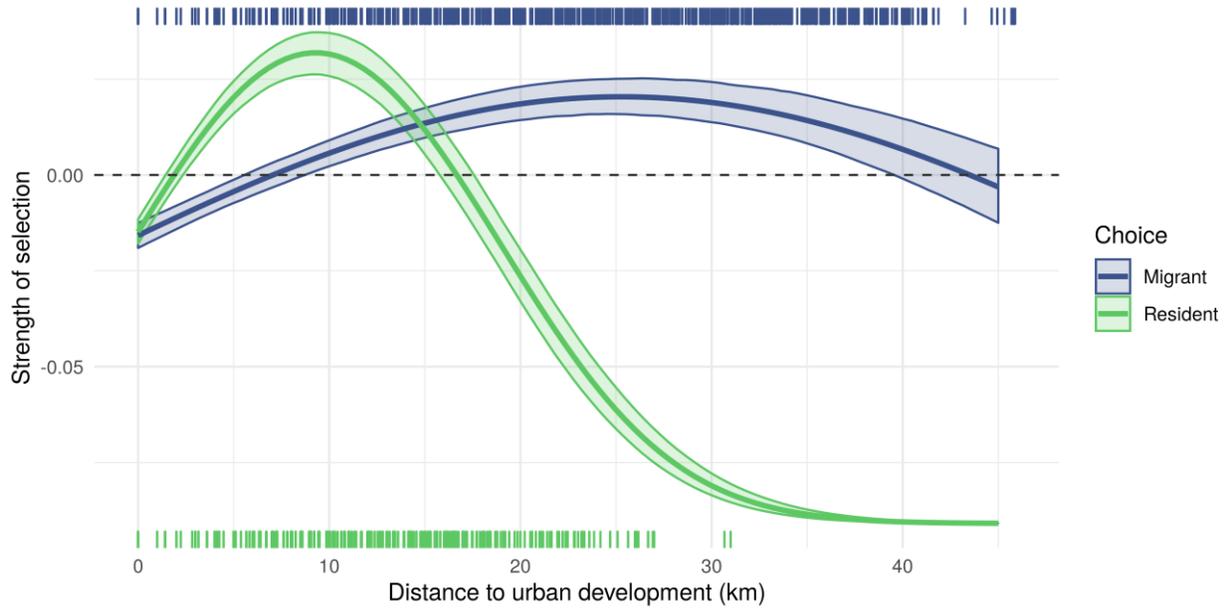


Figure 4-3. Model predictions of Resource Selection Function for foraging sites used by wood storks during breeding attempts as a function of distance to urban areas and migratory behavior. The model is implemented using mixed-effects logistic regression. Migrants in blue, residents in green. Solid line indicates mean predictions, ribbon indicates 95% confidence intervals. Rug plot at the top and bottom indicates distribution of data points (residents in green, migrants in blue).

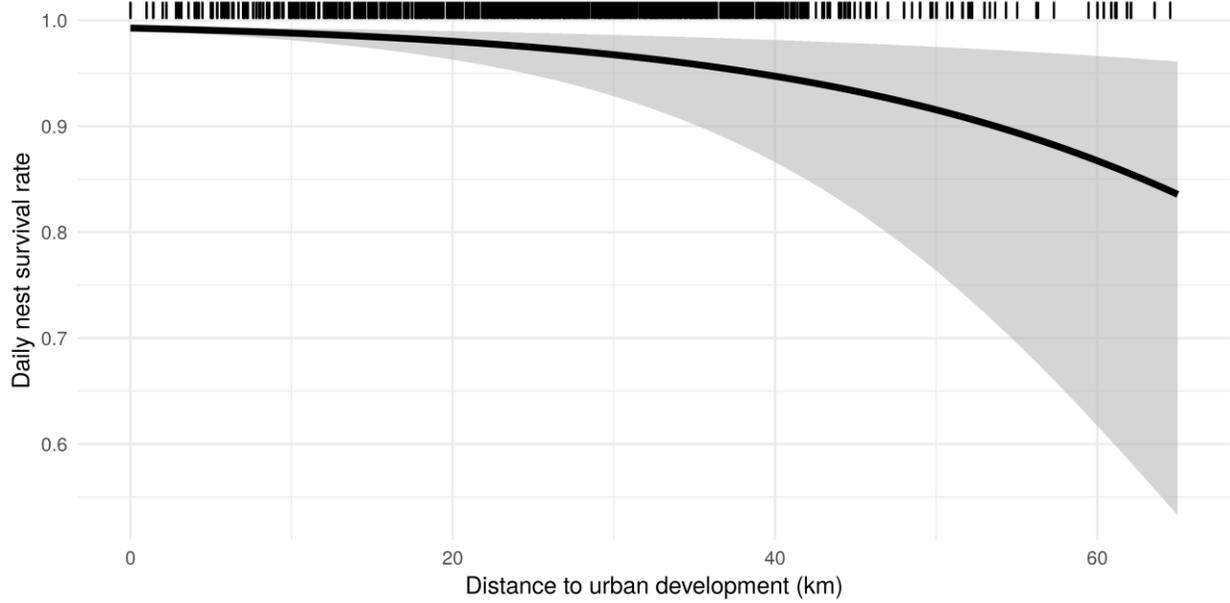


Figure 4-4. Model predictions of daily nest survival as a function of distance to urban areas. The model is implemented in a Bayesian hierarchical modeling framework. Solid line indicates mean predictions, ribbon indicates 95% credible intervals. Rug plot at the top indicates density of data points.

CHAPTER 5 GENERAL CONCLUSIONS

This dissertation addressed the adaptive significance of partial migration in a subtropical wading bird, the wood stork, in a human-impacted landscape. First, I established the status of the population as partially migratory by quantifying differences in migratory behavior between individuals (Chapter 2). Then, by applying a method I developed to estimate avian reproductive outcome from movement data (Chapter 3), I established a link between wood stork migratory behavior and reproductive fitness, mediated by habitat selection (Chapter 4).

When evaluating habitat selection in Chapter 4, I focused on differences in selection of foraging sites during the breeding season as a function of their distance to urban areas. The choice to focus on this aspect of habitat selection stemmed from the observation of the different annual distribution patterns of migrants and residents across the landscape; results of Chapter 2 showed that, while migrants spend winter in the Everglades and summer in the northern portion of the population range (Georgia, South and North Carolina, and the Gulf Coast), residents are concentrated in the proximity of urban areas in Florida year-round. I wanted to evaluate whether this difference in distribution was also matched by a difference in the selection of foraging sites, with residents foraging in more urbanized areas than migrants do. The final results confirmed that individuals with different migratory behavior also differ in their propensity to forage in sites that are close to urbanization, which in turn are associated with better reproductive performance.

Contributions of this work are three-fold: first, my results improve our understanding of wood stork ecology. To date, large-scale movement patterns of wood

storks had not been quantified, and the population had not been recognized as partially migratory. There had been no evidence that different individuals in the population differ in their propensity to forage in urban areas, nor that foraging in urban areas during the breeding season can bring fitness advantages. These new pieces of information have implications for wood stork conservation and management. Mainly, these results suggest that a suite of actions (including but not limited to restoring the functionality of historical breeding grounds in the Everglades, which remains the main goal) can be taken in concert to help conserve the wood stork population. Wood stork conservation in the current human-impacted Southeast is probably best achieved by a combination of actions geared towards both the restoration of historical breeding grounds and the maintenance or creation of opportunities for nesting and foraging in newly exploited areas, including urbanized ones. Scientists and conservation practitioners working on conserving the wood stork population have long recognized the importance of preserving wetlands in the northern part of the range, where breeding activities did not use to occur in historical times but that today support a substantial portion of the breeding population (Ogden et al. 1987). Similarly, explicitly including management of urban areas for wood stork breeding and foraging may be beneficial to the population. While acknowledging and even promoting the reliance of part of the wood stork population on anthropogenic structures and resources may seem unnatural, we probably have to come to terms with the fact that a fully non-urbanized wood stork population will not be a reality in the next decades. Rather, there are ways to make the most of human-induced modifications of wood stork ecology: if the reproductive contribution of urban-adjusted individuals buffers the population against environmental

stochasticity in natural foraging sites, the use of urban areas for breeding by some individuals may turn out to be an overall advantage for the population. However, realistic predictions of the possible contribution of urban areas in supporting the population will require filling some critical knowledge gaps that remain. These include the effect of foraging-site location on food quality in urban versus non-urban colonies, which in turn may affect post-fledging survival; the effect of increased opportunities for the spread of parasites and pathogens on survival of urban fledglings compared to non-urban ones; finally, an accurate estimation of the relative proportion of individuals breeding in urban versus non-urban colonies is lacking, but it is necessary to assess how individual differences in fitness might scale up to the population level in terms of net demographic effects.

Second, this dissertation brings a contribution to our ability to link animal movement with fitness. Bridging the gap between movement and fitness is one of the major challenges that movement ecologists today are trying to address (Morales et al. 2010). The method presented in Chapter 3 contributes to this effort, by providing a way to estimate individual reproductive outcome from the analysis of movement trajectories and allowing researchers to relate movement strategies, space use, and habitat selection to their fitness consequences using a single set of data. The wealth of avian tracking data made available by scientists worldwide is constantly growing and providing unprecedented insight on the movement ecology of birds, including cryptic species or those inhabiting remote and inaccessible areas. Being able to use these existing (as well as newly-collected) tracking data not only for movement *per se*, but also to estimate reproduction and survival would be invaluable. While the application of

movement data to estimating individual survival is not new (Heisey and Fuller 1985, Bennetts et al. 1999, Powell et al. 2000), few have attempted to estimate reproductive parameters (but see DeMars et al. 2013), hence the novelty of my contribution. From the individual level, extrapolation to the population level is also possible. Some issues remain with possible sources of bias, for example those due to the probability of missing early failures when detecting nesting attempts, which is akin to a long-known problem in field data-based estimations of nest survival (Mayfield 1975, Johnson 1979, Hensler and Nichols 1981). Accounting for biases may be possible with careful design and statistical improvements, and if accomplished, tools like the one presented in Chapter 3 can be used to estimate population-level demographic parameters from individual-level fitness measures obtained from tracking data.

Third, this dissertation brings a contribution to our understanding of animal migratory strategies, specifically partial migration. We knew that partial migration is adaptive in variable and unpredictable environments, where the availability of resources is seasonal but also not guaranteed from one year to the next (Newton 2012). One hypothesis is that partial migration may work as a bet-hedging strategy at the population level; the coexistence of migrants and residents might help counterbalance demographic losses (low survival or reproduction) when conditions are sub-optimal for a portion of the population. On the long run, partially migratory populations might persist thanks to the fact that, when migrants fail to survive or reproduce because of unpredictably bad conditions, residents may provide a demographic reservoir, and vice-versa. The findings I presented in Chapter 4 are compatible with this idea. In the wood stork population, residents seem to constitute a smaller but reliable source of

recruitment, while the success of migrants in bringing new individuals to the population might be more unpredictable – but potentially numerically overwhelming when conditions are favorable. The evidence I presented in this dissertation supports the idea that partial migration may be adaptive, even in the face of emerging selective pressures, because it combines high-reward/high-uncertainty behavioral strategies with lower-reward/low-uncertainty ones.

Gaps that remain open in our understanding of wood stork partial migration provide exciting possibilities for future research directions. One fundamental missing piece has to do with the heritability of individual behavioral characteristics, including migratory behavior. This question could not be answered in the context of this dissertation because I did not have genetics data and did not track related individuals. Consequently, I could not draw any definitive conclusions as to whether migratory behavior is genetically determined, and therefore, whether it is evolvable or not. While results of Chapter 4 are sufficient to demonstrate that migratory behavior is under natural selection, only demonstrating heritability can confirm that it also undergoes evolution.

Another knowledge gap and possible future research direction is related to behavioral syndromes (Sih et al. 2004). My results show that individual variation is adaptive in wood storks; however, I only looked at two behavioral traits: migratory behavior and habitat selection for urban foraging sites. These two behavioral traits are correlated at the individual level in wood storks, but we do not know whether they are part of a broader behavioral syndrome that could include other aspects of individual personality. For example, other behavioral traits that could be investigated are: the

propensity for novelty (for instance, measured as the tendency to explore new foraging or breeding locations); the degree of optimality in foraging behavior (for instance, measured as individual-specific giving-up density); or aggressiveness (for instance, measured as the individual tendency to build a nest ex-novo versus taking over an occupied one, a behavior frequently documented by other studies in wood storks; e.g., Bryan and Coulter 1991, Bruant et al. 2019). An improved understanding of what behavioral traits correlate with one another will bring important insight into the evolutionary value of individual heterogeneity in wild populations.

Finally, while the temporal extent of the current tracking dataset is not sufficient to assess whether changes of migratory patterns have already occurred or are occurring, it would be interesting to keep monitoring the wood stork population and see if a shift towards increased residency will truly happen in the next decades, as my findings suggest is possible. This highlights the importance of long-term monitoring to move from indication to evidence, which is true not only in this study case but almost universally in ecology (Franklin 1989, Magnuson 1990, Clutton-Brock and Sheldon 2010). Long-term monitoring is of paramount importance to provide compelling evidence of ongoing effects of human activities and environmental change on wildlife populations (Turner et al. 2003, Lindenmayer et al. 2012), which is fundamental to leverage attention and funding for conservation.

APPENDIX A SENSITIVITY ANALYSIS OF CONSTRAINT VALUES FOR NET SQUARED DISPLACEMENT MODELS

For the analyses described in Chapter 2, we enforced a spatial and a temporal constraint in the migrant model of Net Squared Displacement by specifying the minimum value of two model parameters, the distance between migratory ranges and the time spent on the second range. The spatial constraint is the minimum distance an individual had to move to be considered a migrant. In our models, we used a value of 260 km. The temporal constraint is the minimum time an individual had to spend in the second range to be considered a migrant. In our models, we used a value of 60 days. Spatial and temporal constraints were applied simultaneously in our models. To ensure that the classification was not affected by the chosen values, we performed a sensitivity analysis on parameter values. We identified a biologically relevant range of values for each constraining parameter. We compared classifications of individual-years resulting from using different values within this range for each of the two parameters, while keeping the other fixed (at 260 km or 60 days). For the spatial constraint, we considered values between 140 km and 500 km, by increments of 30 km. We placed the lower bound of the range at 140 km because wood storks have been observed to travel as far as 130 km from their breeding colony to foraging grounds on a daily scale. Therefore, any value lower than 140 km did not make sense for targeting migratory movements. We chose 500 km as an upper bound because that was approximately the average migration distance we identified during visual inspection of the data. For the temporal constraint, we considered values between 30 and 90 days, by increments of 10 days. We chose 30 days as a lower bound because we found that excursions lasting as long as several weeks were not uncommon during visual inspection of the data. Unlike

migrations, excursions lack repeatability and are often at a shorter spatial scale than migrations. We chose 90 days as an upper bound because that was approximately the average time we observed wood storks to spend in the summer range during visual inspection of the data (while they would generally spend longer in the winter range).

Results of the classification corresponding to the use of each possible value of spatial and temporal threshold are reported in Table A-1 and Table A-2, respectively. For the purpose of this analysis and for simplicity, we only compared the classifications of individual-years for which all models converged at the first iteration (127 and 129 individual-years out of 200 in the case of the spatial and temporal constraint, respectively). Out of 127 individual-years, 108 were consistently classified across the entire range of values considered for the spatial parameter. Out of the 19 that were classified inconsistently, 6 were migrants that failed to be recognized as such for values above 410 km, because the spatial scale of their migration was lower than the threshold (but larger than 380 km); 8 were residents that failed to be recognized as such for values below 230 km, because their daily movements sometimes exceeded that spatial scale (but not 260 km). The remaining 5 individuals were correctly classified as migrants for low threshold values (between 260 and 290 km) and erroneously classified as residents for large values (between 320 and 350 km). Therefore, the classification resulted generally robust between values of 230 and 410 km, with only ~4% of individual-years classified inconsistently within this range. Within this robust range, the classification of the inconsistent ~4% individual-years was correct for values lower than 290 km. This supports the use of 260 km as the optimal spatial threshold value to use in the models of migratory behavior. Out of 129 individual-years, 127 were consistently

classified across the entire range of values considered for the temporal parameter. Out of the remaining 2, one was a migrant that failed to be recognized as such for values greater than 80 days. The last individual-year was one of the controversial cases that continuously performed non-migratory large scale movements and that we manually assigned to the resident category (see Chapter 2, Methods). Thus, the classification was highly robust for the entire range of values considered, and unanimous for values between 30 and 80 days. Overall, results of the sensitivity analysis demonstrate the robustness of our approach, while highlighting variability of the spatial scale of migratory movements in wood storks. This underlines the usefulness and appropriateness of combining a spatial constraint with a temporal constraint, as the latter helps resolving distinctions between migratory and non-migratory movements that would be difficult to disentangle using a spatial criterion alone.

Table A-1. Results of the classification of wood stork individual-years deriving from the use of different values as a spatial threshold for migratory movements. We used values ranging between 140 and 500 km, by increments of 30 km. The temporal threshold was fixed at 60 days.

Spatial threshold (km)	Number of migrants	Number of residents
140	71	58
170	70	59
200	65	64
230	63	66
260	61	68
290	59	70
320	59	70
350	57	72
380	57	72
410	54	75
440	55	74
470	51	78
500	50	79

Table A-2. Results of the classification of wood stork individual-years deriving from the use of different values as a temporal threshold for migratory movements. We used values ranging between 30 and 90 days, by increments of 10 days. The spatial threshold was fixed at 260 km.

Temporal threshold (days)	Number of migrants	Number of residents
30	62	67
40	62	67
50	62	67
60	61	68
70	61	68
80	61	68
90	60	69

APPENDIX B STARTING VALUES FOR NET SQUARED DISPLACEMENT MODEL PARAMETERS

The method we used for the classification of migratory behavior relies on the estimation of model parameters, which include the the midpoint of the departing migratory movement, the duration of the migratory movement, the permanence time in the arrival range, the distance between seasonal ranges (in the case of the migratory model), and the average NSD of the resident range and the rate of the initial NSD increase (in the case of the resident model). If starting values for these parameters are not specified by the user, functions in the package `migrateR` will estimate them based on an internal optimization algorithm. Poor correspondence between starting values of model parameters and the data can impede model convergence. When the models are applied to behaviorally heterogeneous data a single set of starting values for model parameters will likely not be sufficient to ensure convergence of all models. Therefore, a new set of starting values for model parameters can be manually specified in a step-wise process, progressively increasing the number of models that converge until they all do. In our study, 120 models out of 200 converged after the first iteration, and all models converged after 21 iterations with a different set of starting values. We report the sets of starting values we used in Table B-1.

Table B-1. Starting parameter values used in our analysis to progressively improve model convergence until full convergence. Sets of values are reported in the order in which we used them.

Distance between ranges (km)	Mean NSD of starting range (km ²)	Time to complete ½ to ¾ of migratory movement (days)	Failed convergences (n)
Not specified	Not specified	Not specified	80
260	Not specified	Not specified	73
300	Not specified	Not specified	67
400	Not specified	Not specified	66
500	Not specified	Not specified	64
550	Not specified	Not specified	63
Not specified	100	Not specified	36
Not specified	400	Not specified	24
Not specified	900	Not specified	18
Not specified	1600	Not specified	15
Not specified	3600	Not specified	13
Not specified	4900	Not specified	10
Not specified	8100	Not specified	8
Not specified	10000	Not specified	7
Not specified	14400	Not specified	6
Not specified	28900	Not specified	5
Not specified	Not specified	3	4
Not specified	Not specified	12	3
Not specified	Not specified	13	2
Not specified	100000	Not specified	1
Not specified	650000	Not specified	0

APPENDIX C
INDIVIDUAL-YEARS DISCARDED FROM ANALYSES OF MIGRATION PATTERNS

We discarded 12 individual-years from subsequent analyses in Chapter 2 because the temporal extent or arrangement of their data did not allow us to unequivocally classify them (Figure C-1 A-L).

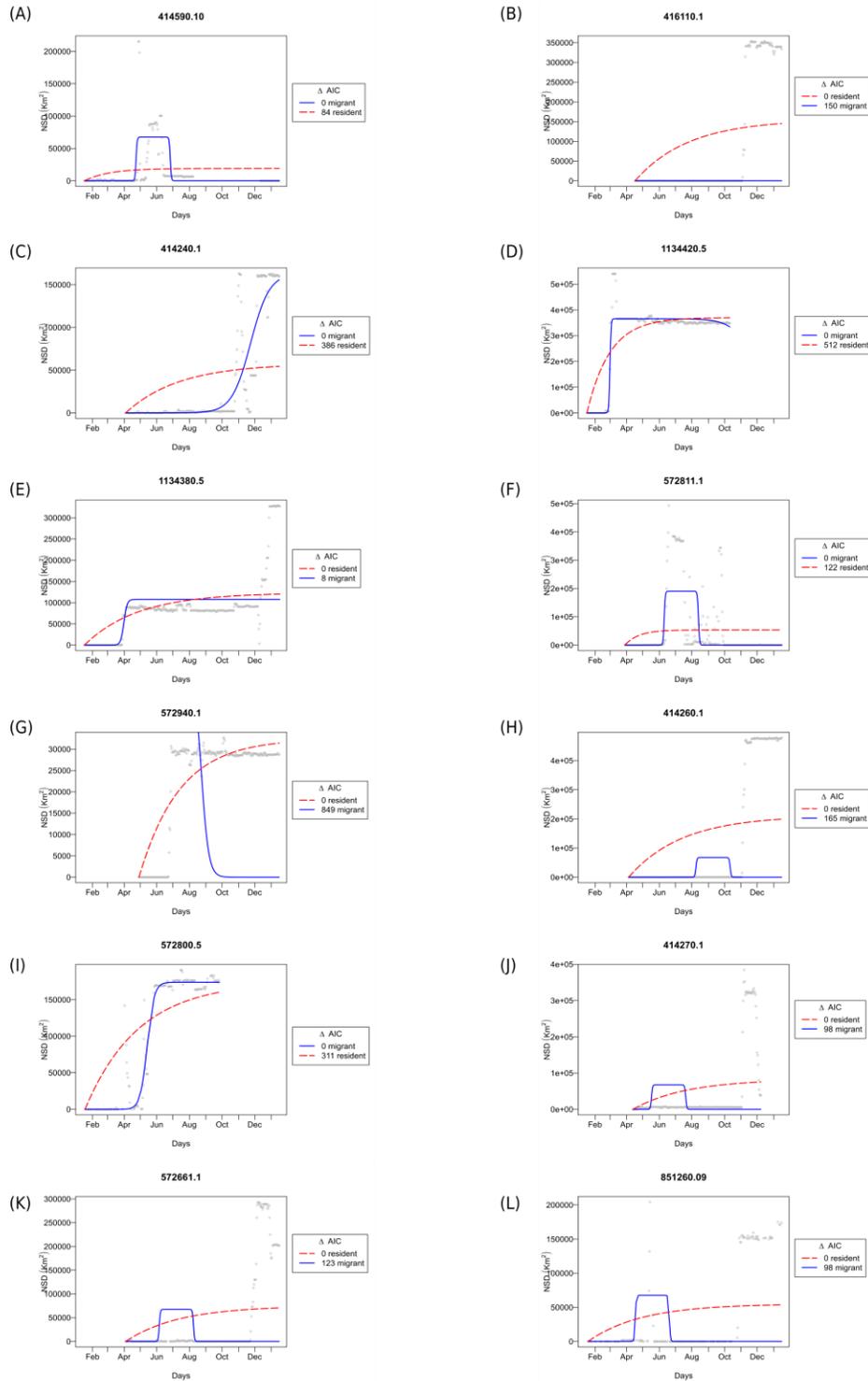


Figure C-1. Annual time-series of Net Squared Displacement for the 12 discarded individual-years. These were discarded from the final sample due to insufficient temporal cover of the data. We were unable to unequivocally classify these individual-years as either migrants or residents and we therefore excluded them from further analyses.

APPENDIX D
SUPPORTING INFORMATION FOR THE ANALYSES OF THE EFFECT OF URBAN
AREAS ON WOOD STORK FORAGING-SITE SELECTION AND NEST SURVIVAL

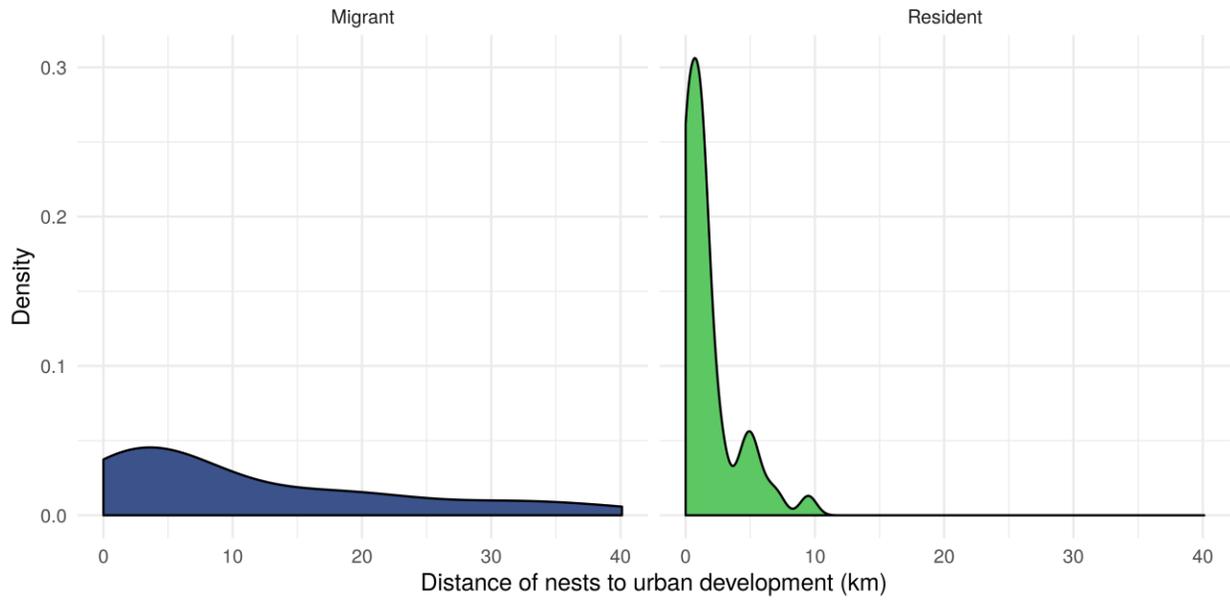


Figure D-1. Density plot of distance of nests to urban areas in wood storks. Migrant = blue, resident = green.

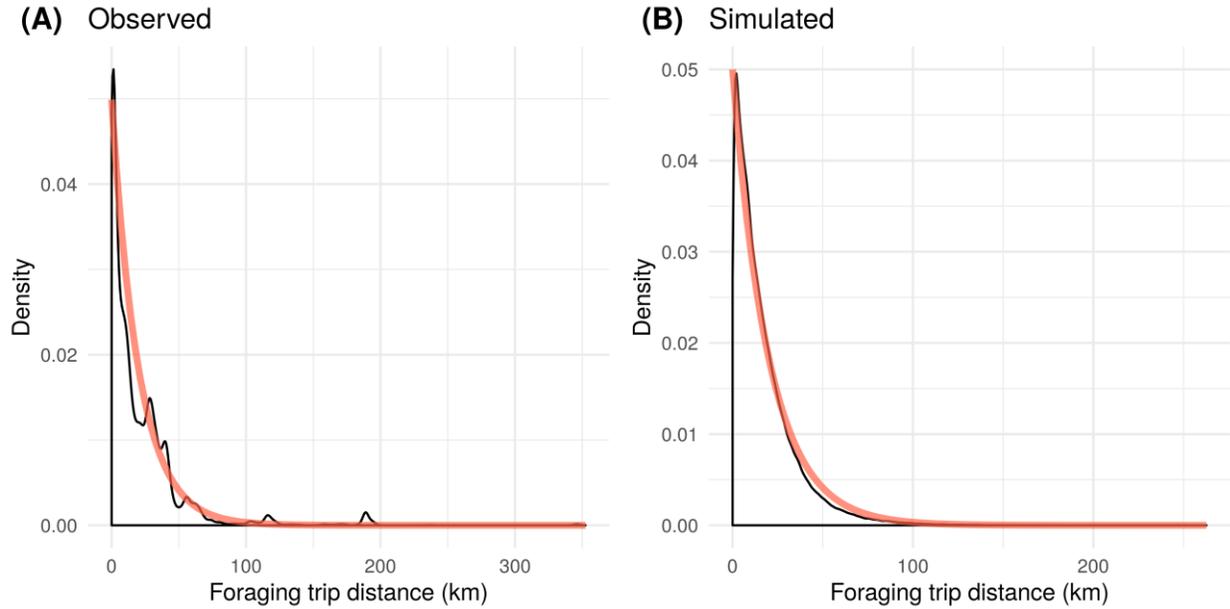
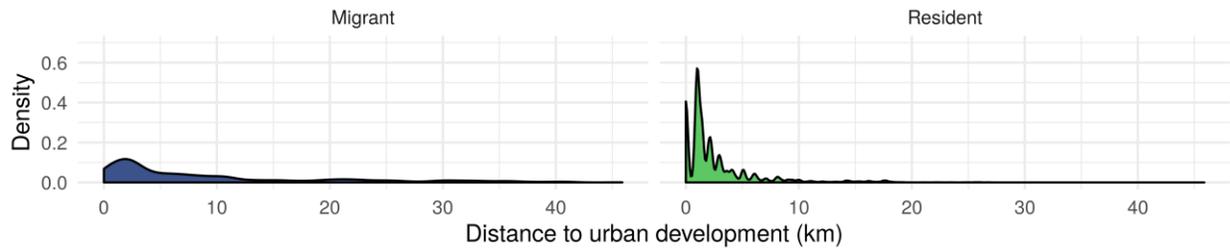


Figure D-2. Generation of available foraging locations based on the empirical distribution of foraging trip distances. A) Empirical distribution of foraging trip distances, i.e., distance of nest to used foraging sites (black density line). Fitted exponential distribution (rate = 0.048) is overlaid (red line). We used the fitted exponential distribution to define the probability to simulate available points at different distances from the nest. B) Results: distribution of distances of simulated available points from nest. Exponential distribution (rate = 0.048) fitted to empirical distribution is overlaid (red line).

(A) Used



(B) Available

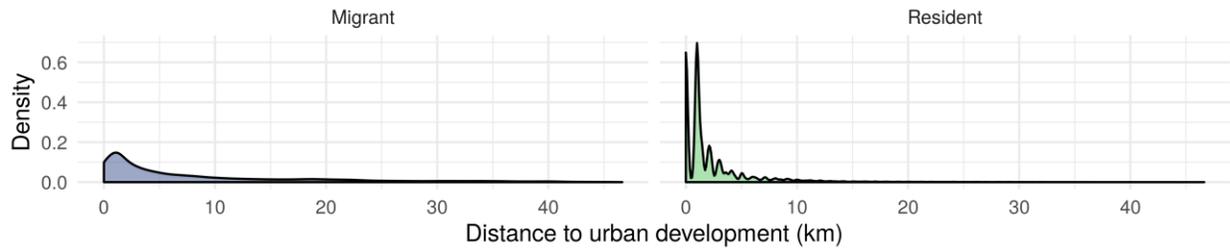


Figure D-3. Density plots of distance of foraging sites to urban areas. A) Distance of used foraging sites to urban areas for migrant (blue) and resident (green) wood storks. B) Distance of available foraging sites to urban areas for migrant (blue) and resident (green) wood storks.

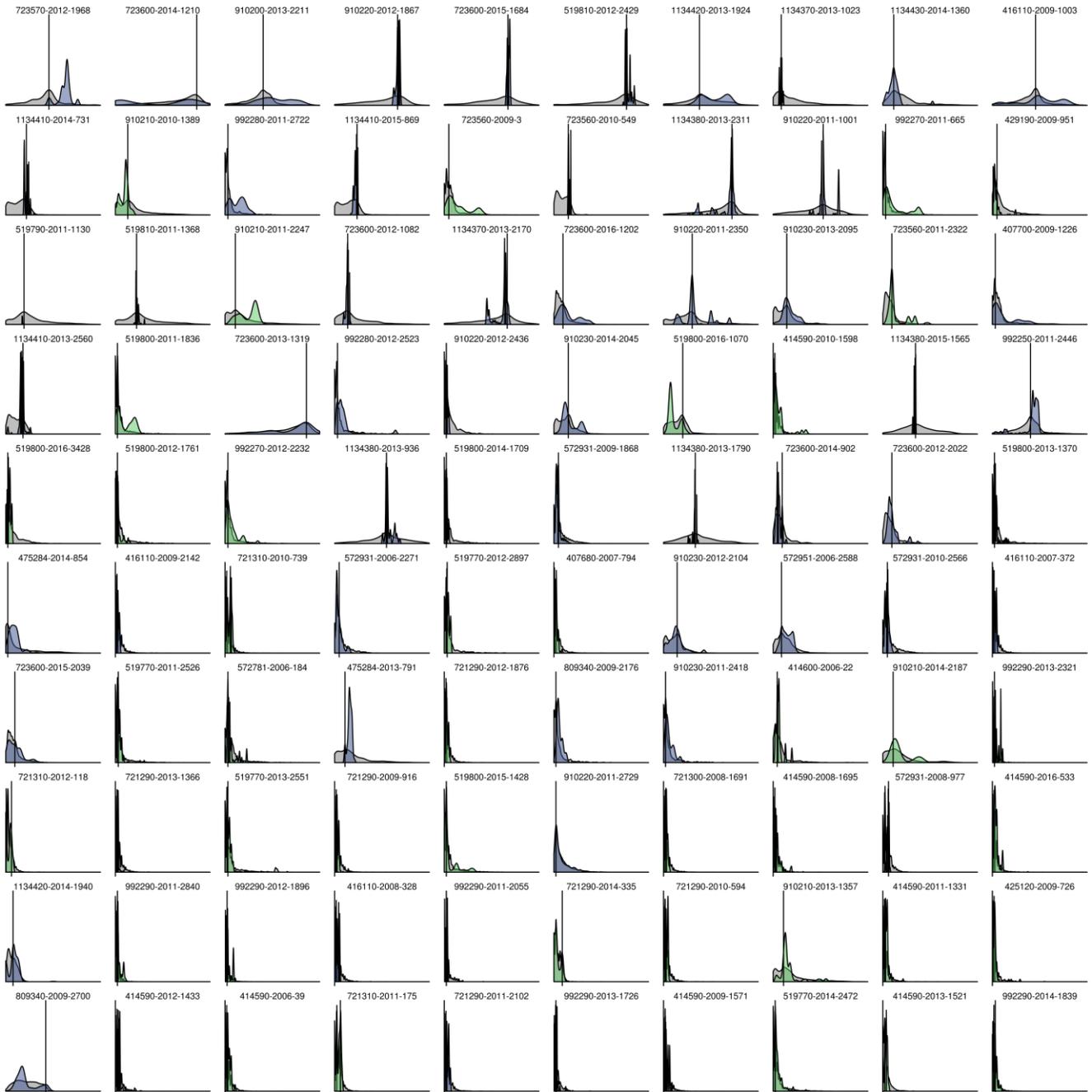


Figure D-4. Density plots of distance of foraging sites to urban areas for each individual breeding attempt. Colored density curve represents used points, gray density curve represents available points. Migrants are in blue, residents in green. The vertical line indicates the distance of the nest to urban areas.

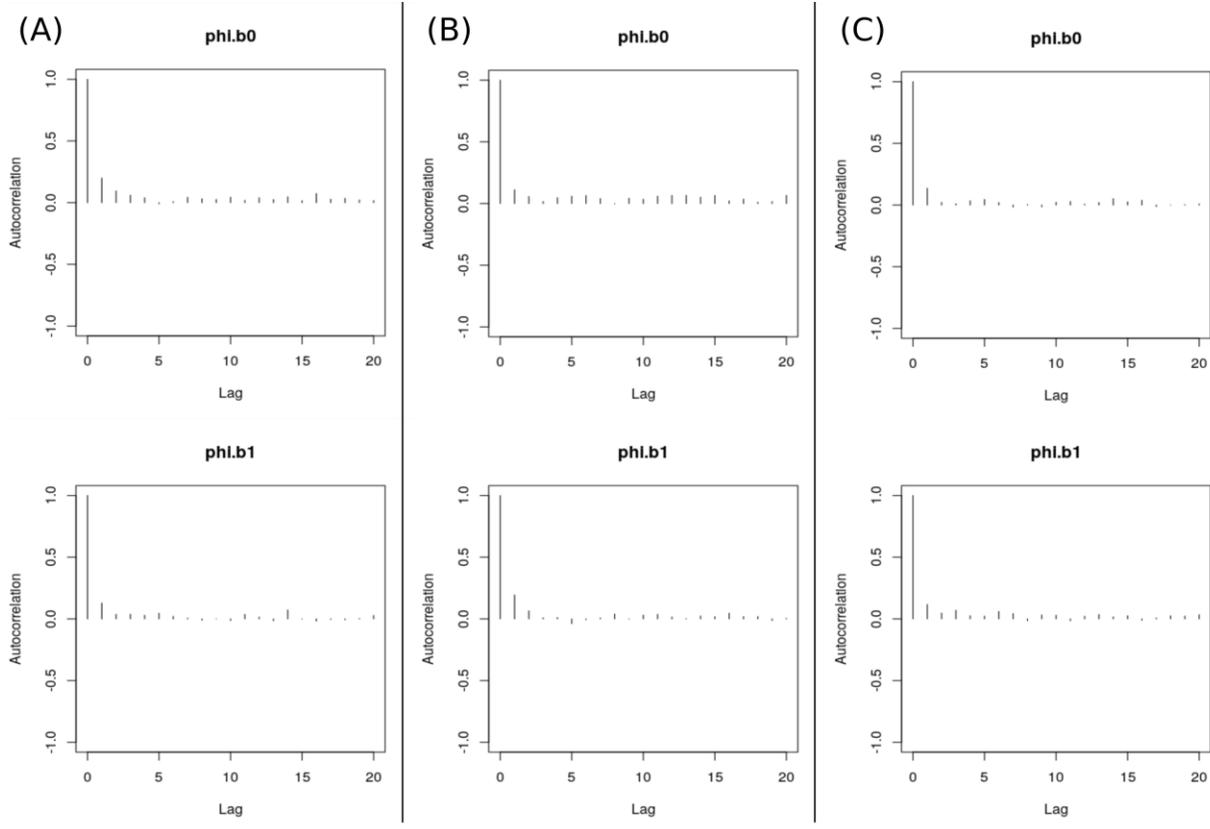


Figure D-5. Diagnostic autocorrelation plots for daily nest survival model. Top row: autocorrelation plot for $\beta_{\phi 0}$; A) MCMC chain 1, B) MCMC chain 2, C) MCMC chain 3. Bottom row: autocorrelation plot for $\beta_{\phi 1}$; A) MCMC chain 1, B) MCMC chain 2, C) MCMC chain 3.

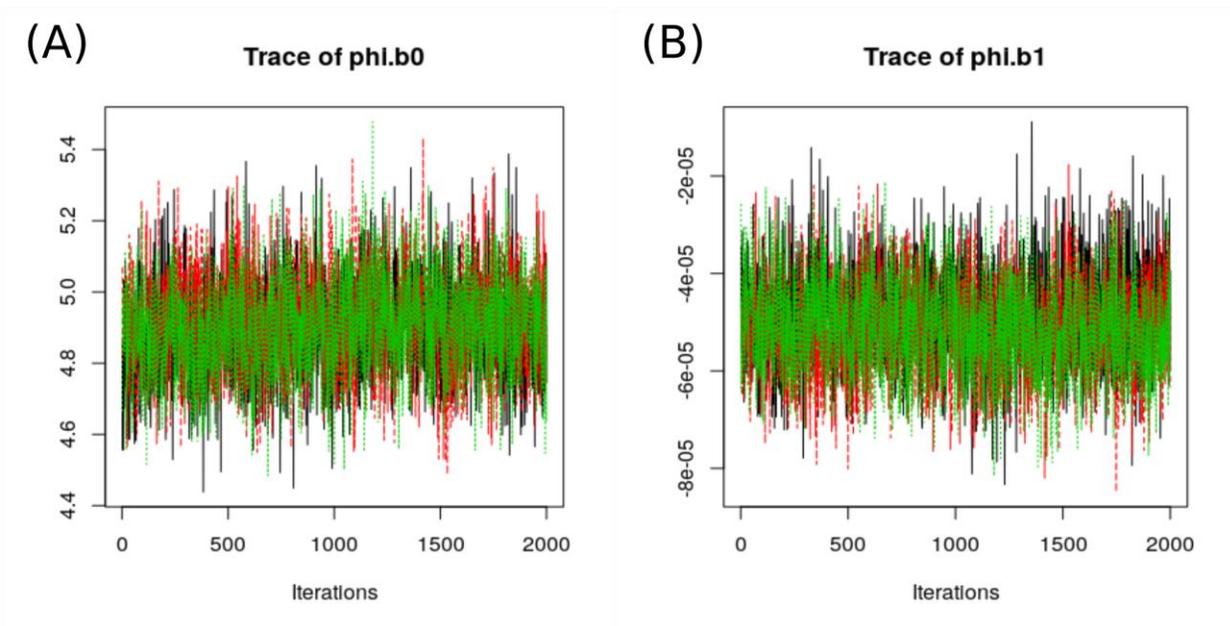


Figure D-6. Diagnostic traceplots for daily nest survival model. A) Traceplot of MCMC convergence for β_{ϕ_0} ; B) traceplot of MCMC convergence for β_{ϕ_1} .

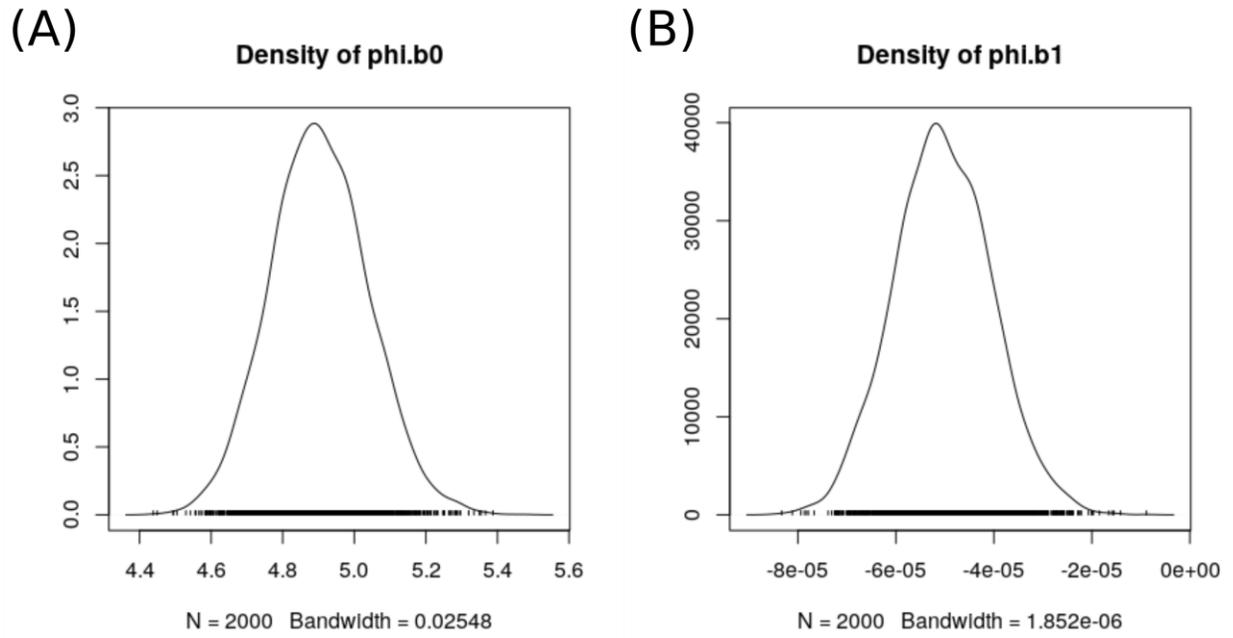


Figure D-7. Diagnostic density plots for daily nest survival model. A) Density plot of $\beta\phi_0$; B) Density plot of $\beta\phi_1$.

LIST OF REFERENCES

- Alonso, J. C., L. M. Carrascal, R. Muñoz-Pulido, and J. A. Alonso. 1994. Flock Size and Foraging Decisions in Central Place Foraging White Storks, *Ciconia Ciconia*. *Behaviour* 129:279–292.
- Andersson, M. 1981. Central Place Foraging in the Whinchat, *Saxicola Rubetra*. *Ecology* 62:538–544.
- Baber, M. J., D. L. Childers, K. J. Babbitt, and D. H. Anderson. 2002. Controls on fish distribution and abundance in temporary wetlands. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1441–1450.
- Badyaev, A. V., and J. D. Faust. 1996. Nest Site Fidelity in Female Wild Turkey: Potential Causes and Reproductive Consequences. *The Condor* 98:589–594.
- Bancroft, G. T., D. E. Gawlik, and K. Rutchey. 2002. Distribution of Wading Birds Relative to Vegetation and Water Depths in the Northern Everglades of Florida, USA. *Waterbirds* 25:265–277.
- Bastille-Rousseau, G., J. P. Gibbs, C. B. Yackulic, J. L. Frair, F. Cabrera, L.-P. Rousseau, M. Wikelski, F. Kümmeth, and S. Blake. 2017. Animal movement in the absence of predation: environmental drivers of movement strategies in a partial migration system. *Oikos* 126:1004–1019.
- Bauer, S., and B. J. Hoye. 2014. Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide. *Science* 344:1242552.
- Beerens, J. M. 2008. Hierarchical resource selection and movements of two wading bird species with divergent foraging strategies in the Everglades. M.S., Florida Atlantic University, United States – Florida.
- Beissinger, S. R. 1995. Modeling Extinction in Periodic Environments: Everglades Water Levels and Snail Kite Population Viability. *Ecological Applications* 5:618–631.
- Bell, C. P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology* 31:258–265.
- Bennetts, R. E., V. J. Dreitz, W. M. Kitchens, J. E. Hines, and J. D. Nichols. 1999. Annual Survival of Snail Kites in Florida: Radio Telemetry versus Capture-Resighting Data. *The Auk* 116:435–447.
- Berger-Tal, O., and S. Bar-David. 2015. Recursive movement patterns: review and synthesis across species. *Ecosphere* 6:1–12.

- Berthold, P. 1984. The endogenous control of bird migration: a survey of experimental evidence. *Bird Study* 31:19–27.
- Berthold, P. 2001. *Bird Migration: A General Survey*. Oxford University Press.
- Biebach, H. 1983. Genetic Determination of Partial Migration in the European Robin (*Erithacus rubecula*). *The Auk: Ornithological Advances* 100:601–606.
- Bohrer, G., D. Brandes, J. T. Mandel, K. L. Bildstein, T. A. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, and J. A. Tremblay. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters* 15:96–103.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26:183–192.
- Bonar, M., E. H. Ellington, K. P. Lewis, and E. Vander Wal. 2018. Implementing a novel movement-based approach to inferring parturition and neonate caribou calf survival. *PLOS ONE* 13:e0192204.
- Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- Borkhataria, R. R., P. C. Frederick, R. Hylton, A. L. Bryan, and J. A. Rodgers. 2008. A Preliminary Model of Wood Stork Population Dynamics in the Southeastern United States. *Waterbirds* 31:42–49.
- Borkhataria, R. R., A. Lawrence Bryan, 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.
- Botson, B. A., D. E. Gawlik, and J. C. Trexler. 2016. Mechanisms That Generate Resource Pulses in a Fluctuating Wetland. *PLOS ONE* 11:e0158864.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution* 14:268–272.
- Bracis, C., K. L. Bildstein, and T. Mueller. 2018. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography* 41:1801–1811.

- Breiman, L. 2001. Random Forests. *Machine Learning* 45:5–32.
- Brooks, W. B., and T. Dean. 2008. Measuring the Biological Status of the U.S. Breeding Population of Wood Storks. *Waterbirds* 31:50–62.
- Brown, D. R., P. C. Stouffer, and C. M. Strong. 2000. Movement And Territoriality Of Wintering Hermit Thrushes In Southeastern Louisiana. *The Wilson Journal of Ornithology* 112:347–353.
- Brown, L. M., and R. J. Hall. 2018. Consequences of resource supplementation for disease risk in a partially migratory population. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373:20170095.
- Bruant, A., S. Picardi, P. Frederick, and M. Basille. 2019. Effect of Parental Care on Reproductive Success in Wood Storks (*Mycteria Americana*). *BioRxiv*:592840.
- Bryan, A. L., W. B. Brooks, J. D. Taylor, D. M. Richardson, C. W. Jeske, and I. L. Brisbin. 2008. Satellite Tracking Large-scale Movements of Wood Storks Captured in the Gulf Coast Region. *Waterbirds* 31:35–41.
- Bryan, A. L., and M. C. Coulter. 1987. Foraging Flight Characteristics of Wood Storks in East-Central Georgia, U.S.A. *Colonial Waterbirds* 10:157–161.
- Bryan, A. L., and M. C. Coulter. 1991. Conspecific Aggression in a Wood Stork Colony in Georgia. *The Wilson Bulletin* 103:693–697.
- Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- Burke, C. M., and W. A. Montevecchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology* 278:354–361.
- Butler, C. J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis* 145:484–495.
- 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. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2157–2162.
- Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.

- Calenge, C., S. Dray, and M. Royer-Carenzi. 2009. The concept of animals' trajectories from a data analysis perspective. *Ecological Informatics* 4:34–41.
- Carere, C., and M. Eens. 2005. Unravelling Animal Personalities: How and Why Individuals Consistently Differ. *Behaviour* 142:1149–1157.
- Cecere, J. G., S. Bondì, S. Podofillini, S. Imperio, M. Griggio, E. Fulco, A. Curcio, D. Ménard, U. Mellone, N. Saino, L. Serra, M. Sarà, and D. Rubolini. 2018. Spatial segregation of home ranges between neighbouring colonies in a diurnal raptor. *Scientific Reports* 8:11762.
- Chan, K. 2001. Partial migration in Australian landbirds: a review. *Emu - Austral Ornithology* 101:281–292.
- Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011. The ecology and evolution of partial migration. *Oikos* 120:1764–1775.
- Chapple, D. G., S. M. Simmonds, and B. B. M. Wong. 2012. Can behavioral and personality traits influence the success of unintentional species introductions? *Trends in Ecology & Evolution* 27:57–64.
- Charmantier, A., and P. Gienapp. 2013. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications* 7:15–28.
- Chick, J. H., C. R. Ruetz, and J. C. Trexler. 2004. Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. *Wetlands* 24:652–664.
- Clergeau, P., and A. Vergnes. 2011. Bird feeders may sustain feral Rose-ringed parakeets *Psittacula krameri* in temperate Europe. *Wildlife Biology* 17:248–252.
- Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* 25:562–573.
- Conradt, L., P. A. Zollner, T. J. Roper, K. Frank, and C. D. Thomas. 2003. Foray Search: An Effective Systematic Dispersal Strategy in Fragmented Landscapes. *The American Naturalist* 161:905–915.
- Cotton, P. A. 2003. Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences* 100:12219–12222.

- Coulter, M. C., and A. L. Bryan. 1993. Foraging Ecology of Wood Storks (*Mycteria americana*) in East-Central Georgia I. Characteristics of Foraging Sites. *Colonial Waterbirds* 16:59–70.
- Coulter, M. C., J. A. Rodgers, J. C. Ogden, and F. C. Depkin. 1999. Wood Stork(*Mycteria americana*). *The Birds of North America*:24.
- Cox, G. W. 1985. The Evolution of Avian Migration Systems between Temperate and Tropical Regions of the New World. *The American Naturalist* 126:451–474.
- DeAngelis, D. L., J. C. Trexler, C. Cosner, A. Obaza, and F. Jopp. 2010. Fish population dynamics in a seasonally varying wetland. *Ecological Modelling* 221:1131–1137.
- 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.
- De'ath, G., and K. E. Fabricius. 2000. Classification and Regression Trees: A Powerful yet Simple Technique for Ecological Data Analysis. *Ecology* 81:3178–3192.
- DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecology and Evolution* 3:4149–4160.
- Dingle, H. 1996. *Migration: The Biology of Animals on the Move*. Oxford University Press.
- Dingle, H., and V. A. Drake. 2007. What Is Migration? *BioScience* 57:113–121.
- Dubois, S., and D. Fraser. 2013. A Framework to Evaluate Wildlife Feeding in Research, Wildlife Management, Tourism and Recreation. *Animals* 3:978–994.
- Dukai, B., M. Basille, and D. Bucklin. 2016. rpostgisLT: Managing Animal Movement Data with 'PostGIS' and R.
- 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.
- Egunez, A., N. Zorrozua, A. Aldalur, A. Herrero, and J. Arizaga. 2017. Local use of landfills by a yellow-legged gull population suggests distance-dependent resource exploitation. *Journal of Avian Biology* 49:jav-01455.
- Etterson, M. A., S. N. Ellis-Felege, D. Evers, G. Gauthier, J. A. Grzybowski, B. J. Mattsson, L. R. Nagy, B. J. Olsen, C. M. Pease, M. P. van der Burg, and A. Potvien. 2011. Modeling fecundity in birds: Conceptual overview, current models,

- and considerations for future developments. *Ecological Modelling* 222:2178–2190.
- Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. *Functional Ecology* 21:1003–1015.
- Fiedler, W. 2003. Recent Changes in Migratory Behaviour of Birds: A Compilation of Field Observations and Ringing Data. Pages 21–38 *in* P. Berthold, E. Gwinner, and E. Sonnenschein, editors. *Avian Migration*. Springer Berlin Heidelberg.
- Fletcher, Jr., Robert J., and R. R. Koford. 2004. Consequences of rainfall variation for breeding wetland blackbirds. *Canadian Journal of Zoology* 82:1316–1325.
- Ford, R. G. 1983. Home Range in a Patchy Environment: Optimal Foraging Predictions. *Integrative and Comparative Biology* 23:315–326.
- Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology* 90:3554–3565.
- Foti, R., M. del Jesus, A. Rinaldo, and I. Rodriguez-Iturbe. 2013. Signs of critical transition in the Everglades wetlands in response to climate and anthropogenic changes. *Proceedings of the National Academy of Sciences* 110:6296–6300.
- Found, R., and C. C. St. Clair. 2016. Behavioural syndromes predict loss of migration in wild elk. *Animal Behaviour* 115:35–46.
- Frair, J. L., J. Fieberg, M. Hebblewhite, F. Francesca, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2187–2200.
- Franklin, J. F. 1989. Importance and Justification of Long-Term Studies in Ecology. Pages 3–19 *in* G. E. Likens, editor. *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer New York, New York, NY.
- Frederick, P. C., and W. F. Loftus. 1993. Responses of Marsh Fishes and Breeding Wading Birds to Low Temperatures: A Possible Behavioral Link between Predator and Prey. *Estuaries* 16:216.
- 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.

- Frederick, P. C., and J. C. Ogden. 2001. Pulsed breeding of long-legged wading birds and the importance of infrequent severe drought conditions in the Florida Everglades. *Wetlands* 21:484–491.
- Frederick, P., D. E. Gawlik, J. C. Ogden, M. I. Cook, and M. Lusk. 2009. The White Ibis and Wood Stork as indicators for restoration of the everglades ecosystem. *Ecological Indicators* 9:S83–S95.
- Gaines, K. F., A. L. Bryan, P. M. Dixon, and M. J. Harris. 1998. Foraging Habitat Use by Wood Storks Nesting in the Coastal Zone of Georgia, USA. *Colonial Waterbirds* 21:43–52.
- Gawlik, D. E. 2002. The Effects of Prey Availability on the Numerical Response of Wading Birds. *Ecological Monographs* 72:329–346.
- Ghalambor, C. K., J. K. McKAY, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology* 21:394–407.
- 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* 4:7.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- Götmark, F. 1992. The Effects of Investigator Disturbance on Nesting Birds. Pages 63–104 in D. M. Power, editor. *Current Ornithology*. Springer US, Boston, MA.
- Greig, E. I., E. M. Wood, and D. N. Bontar. 2017. Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. *Proc. R. Soc. B* 284:20170256.
- Grunwald, M. 2006. *The Swamp: The Everglades, Florida, and the Politics of Paradise*. Simon and Schuster.
- 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.
- Haig, S. M., D. W. Mehlman, and L. W. Oring. 1998. Avian Movements and Wetland Connectivity in Landscape Conservation. *Conservation Biology* 12:749–758.

- Handrigan, S. A., M. L. Schummer, S. A. Petrie, and D. R. Norris. 2016. Range expansion and migration of Trumpeter Swans *Cygnus buccinator* re-introduced in southwest and central Ontario. *Wildfowl* 66:60-74-74.
- Harrison, T. J. E., J. A. Smith, G. R. Martin, D. E. Chamberlain, S. Bearhop, G. N. Robb, and S. J. Reynolds. 2010. Does food supplementation really enhance productivity of breeding birds? *Oecologia* 164:311-320.
- Hebblewhite, M., and D. T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2303-2312.
- Hebblewhite, M., E. H. Merrill, L. E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the Migratory Behavior of Montane Elk Herds in Peril? The Case of Alberta's Ya Ha Tinda Elk Herd. *Wildlife Society Bulletin* 34:1280-1294.
- Hefner, J. M., and J. D. Brown. 1984. Wetland trends in the Southeastern United States. *Wetlands* 4:1-11.
- Hegemann, A., A. M. Fudickar, and J.-Å. Nilsson. 2019. A physiological perspective on the ecology and evolution of partial migration. *Journal of Ornithology*.
- Hegemann, A., P. P. Marra, and B. I. Tieleman. 2015. Causes and Consequences of Partial Migration in a Passerine Bird. *The American Naturalist* 186:531-546.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of Survival and Cause-Specific Mortality Rates Using Telemetry Data. *The Journal of Wildlife Management* 49:668-674.
- Hensler, G. L., and J. D. Nichols. 1981. The Mayfield Method of Estimating Nesting Success: A Model, Estimators and Simulation Results. *The Wilson Bulletin* 93:42-53.
- Hernandez, S. M., C. N. Welch, V. E. Peters, E. K. Lipp, S. Curry, M. J. Yabsley, S. Sanchez, A. Presotto, 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. 2008. Constraints of landscape level prey availability on physiological condition and productivity of Great Egrets and White Ibises in the Florida Everglades. Florida Atlantic University.

- Hoffman, W., G. T. Bancroft, and R. J. Sawicki. 1994. Foraging habitat of wading birds in the Water Conservation Areas of the Everglades. *Everglades: the ecosystem and its restoration*:585–614.
- Hylton, R. A. 2004. Survival, movement patterns, and habitat use of juvenile Wood Storks, *Mycteria americana*. University of Florida.
- Jahn, A. E., S. P. Bravo, V. R. Cueto, D. J. Levey, and M. V. Morales. 2012. Patterns of partial avian migration in northern and southern temperate latitudes of the New World. *Emu - Austral Ornithology* 112:17–22.
- Jeltsch, F., D. Bonte, G. Pe'er, B. Reineking, P. Leimgruber, N. Balkenhol, B. Schröder, C. M. Buchmann, T. Mueller, N. Blaum, D. Zurell, K. Böhning-Gaese, T. Wiegand, J. A. Eccard, H. Hofer, J. Reeg, U. Eggers, and S. Bauer. 2013. Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology* 1:6.
- Johnson, D. H. 1979. Estimating Nest Success: The Mayfield Method and an Alternative. *The Auk* 96:651–661.
- Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke, and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. *Ecological Applications* 24:1769–1779.
- Junk, W. J. 1993. Wetlands of tropical South America. Pages 679–739 *in* D. F. Whigham, D. Dykyjová, and S. Hejný, editors. *Wetlands of the world: Inventory, ecology and management Volume I: Africa, Australia, Canada and Greenland, Mediterranean, Mexico, Papua New Guinea, South Asia, Tropical South America, United States*. Springer Netherlands, Dordrecht.
- Kahl, M. P. 1964. Food Ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecological Monographs* 34:97–117.
- Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A Theory of Partial Migration. *The American Naturalist* 142:59–81.
- Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* 56:234–238.
- Katlam, G., S. Prasad, M. Aggarwal, and R. Kumar. 2018. Trash on the menu: patterns of animal visitation and foraging behaviour at garbage dumps. *CURRENT SCIENCE* 115:6.

- Kingsford, R. T., D. A. Roshier, and J. L. Porter. 2010. Australian waterbirds – time and space travellers in dynamic desert landscapes. *Marine and Freshwater Research* 61:875.
- Kushlan, J. A. 1981. Resource Use Strategies of Wading Birds. *The Wilson Bulletin* 93:145–163.
- Kushlan, J. A. 1986. Responses of Wading Birds to Seasonally Fluctuating Water Levels: Strategies and Their Limits. *Colonial Waterbirds* 9:155–162.
- Kushlan, J. A. 1987. External threats and internal management: the hydrologic regulation of the Everglades, Florida, USA. *Environmental Management* 11:109–119.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. *Ecological Monographs* 62:67–118.
- Light, S. S., and J. W. Dineen. 1994. Water control in the Everglades: a historical perspective. *Everglades: The ecosystem and its restoration* 5:47–84.
- Light, S. S., J. R. Wodraska, and S. Joe. 1989. The Southern Everglades. *National Forum*; Baton Rouge, La. 69:11–14.
- Lindenmayer, D. B., G. E. Likens, A. Andersen, D. Bowman, C. M. Bull, E. Burns, C. R. Dickman, A. A. Hoffmann, D. A. Keith, M. J. Liddell, A. J. Lowe, D. J. Metcalfe, S. R. Phinn, J. Russell-Smith, N. Thurgate, and G. M. Wardle. 2012. Value of long-term ecological studies. *Austral Ecology* 37:745–757.
- Lloyd-Smith, J. O., S. J. Schreiber, P. E. Kopp, and W. M. Getz. 2005. Superspreading and the effect of individual variation on disease emergence. *Nature* 438:355.
- Loftus, W. F., and A.-M. Eklund. 1994. Long-term Dynamics of an Everglades Small-fish Assemblage. Page Everglades: The Ecosystem and Its Restoration. CRC Press.
- Lok, T., O. Overdijk, J. M. Tinbergen, and T. Piersma. 2011. The paradox of spoonbill migration: most birds travel to where survival rates are lowest. *Animal Behaviour* 82:837–844.
- López-López, P., C. García-Ripollés, and V. Urios. 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. *Ecological Applications* 24:938–949.
- Lowry, H., A. Lill, and B. B. M. Wong. 2013. Behavioural responses of wildlife to urban environments. *Biological Reviews* 88:537–549.

- Lundberg, P. 1987. Partial bird migration and evolutionarily stable strategies. *Journal of Theoretical Biology* 125:351–360.
- Lundberg, P. 1988. The evolution of partial migration in Birds. *Trends in Ecology & Evolution* 3:172–175.
- Magnuson, J. J. 1990. Long-Term Ecological Research and the Invisible Present. *BioScience* 40:495–501.
- Maljković, A., and I. M. Côté. 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.
- Marshall, C. H., R. A. Pielke, and L. T. Steyaert. 2004. Has the Conversion of Natural Wetlands to Agricultural Land Increased the Incidence and Severity of Damaging Freezes in South Florida? *Monthly Weather Review* 132:2243–2258.
- Mayer-Gross, H., H. Q. P. Crick, and J. J. D. Greenwood. 1997. The effect of observers visiting the nests of passerines: an experimental study. *Bird Study* 44:53–65.
- Mayfield, H. F. 1975. Suggestions for Calculating Nest Success. *The Wilson Bulletin* 87:456–466.
- Mckilligan, N. G., D. S. Reimer, D. H. C. Seton, D. H. C. Davidson, and J. T. Willows. 1993. Survival and Seasonal Movements of the Cattle Egret in Eastern Australia. *Emu* 93:79–87.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247–260.
- Melvin, S. L., D. E. Gawlik, and T. Scharff. 1999. Long-Term Movement Patterns for Seven Species of Wading Birds. *Waterbirds: The International Journal of Waterbird Biology* 22:411–416.
- Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, Powell Roger A., Merrill Evelyn H., and Haydon Daniel T. 2010. Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2289–2301.
- Mueller, T., and W. F. Fagan. 2008. Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos* 117:654–664.
- Murray, M. H., D. J. Becker, R. J. Hall, and S. M. Hernandez. 2016. Wildlife health and supplemental feeding: A review and management recommendations. *Biological Conservation* 204:163–174.

- Murray, M. H., A. D. Kidd, S. E. Curry, J. Hepinstall-Cymerman, M. J. Yabsley, H. C. Adams, T. Ellison, C. N. Welch, and S. M. Hernandez. 2018. From wetland specialist to hand-fed generalist: shifts in diet and condition with provisioning for a recently urbanized wading bird. *Phil. Trans. R. Soc. B* 373:20170100.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* 105:19052–19059.
- Németh, Z. 2017. Partial migration and decreasing migration distance in the Hungarian population of the Common Blackbird (*Turdus merula* Linnaeus, 1758): Analysis of 85 years of ring recovery data. *Ornis Hungarica* 25:101–108.
- Newsome, T. M., and L. M. Van Eeden. 2017. The Effects of Food Waste on Wildlife and Humans. *Sustainability* 9:1269.
- Newton, I. 2012. Obligate and facultative migration in birds: ecological aspects. *Journal of Ornithology* 153:171–180.
- Nicholson, K. L., M. J. Warren, C. Rostan, J. Månsson, T. F. Paragi, and H. Sand. 2019. Using fine-scale movement patterns to infer ungulate parturition. *Ecological Indicators* 101:22–30.
- Niemuth, N. D., M. E. Estey, R. E. Reynolds, C. R. Loesch, and W. A. Meeks. 2006. Use of wetlands by spring-migrant shorebirds in agricultural landscapes of North Dakota's Drift Prairie. *Wetlands* 26:30–39.
- Niemuth, N. D., and J. W. Solberg. 2003. Response of Waterbirds to Number of Wetlands in the Prairie Pothole Region of North Dakota, U.S.A. *Waterbirds* 26:233–238.
- Nussey, D. H., E. Postma, P. Gienapp, and M. E. Visser. 2005. Selection on Heritable Phenotypic Plasticity in a Wild Bird Population. *Science* 310:304–306.
- Ogden, J. C. 1986. The Wood Stork. Pages 458–471 *Audubon Wildlife Report 1985*. Di Silvestro, R. L. The National Audubon Society, New York, New York, USA.
- Ogden, J. C., J. A. Kushlan, and J. T. Tilmant. 1976. Prey Selectivity by the Wood Stork. *The Condor* 78:324–330.

- Ogden, J. C., J. A. Kushlan, and J. T. Tilmant. 1978. The food habits and nesting success of Wood Storks in Everglades National Park 1974. Department of the Interior, National Park Service.
- Ogden, J. C., D. A. McCrimmon, G. T. Bancroft, and B. W. Patty. 1987. Breeding Populations of the Wood Stork in the Southeastern United States. *The Condor* 89:752–759.
- Ogonowski, M. S., and C. J. Conway. 2009. Migratory decisions in birds: extent of genetic versus environmental control. *Oecologia* 161:199–207.
- Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 154–177 *Analysis of Ecological Systems*. Ohio University Press.
- Palacín, C., J. C. Alonso, C. A. Martín, and J. A. Alonso. 2017. Changes in bird-migration patterns associated with human-induced mortality. *Conservation Biology* 31:106–115.
- Partecke, J., and E. Gwinner. 2007. Increased Sedentariness in European Blackbirds Following Urbanization: A Consequence of Local Adaptation? *Ecology* 88:882–890.
- Pearlstine, E. V., M. L. Casler, and F. J. Mazzotti. 2005. A checklist of birds of the Everglades Agricultural Area. *Florida Scientist*:84–96.
- Peterson, C., and T. A. Messmer. 2007. Effects of Winter-Feeding on Mule Deer in Northern Utah. *Journal of Wildlife Management* 71:1440–1445.
- Pettorelli, N., W. F. Laurance, T. G. O'Brien, M. Wegmann, H. Nagendra, and W. Turner. 2014. Satellite remote sensing for applied ecologists: opportunities and challenges. *Journal of Applied Ecology* 51:839–848.
- Picardi, S., R. R. Borkhataria, A. L. B. Jr, P. C. Frederick, and M. Basille. 2018. GPS Telemetry Reveals Occasional Dispersal of Wood Storks from the Southeastern US to Mexico:7.
- Picardi, S., P. C. Frederick, R. R. Borkhataria, and M. Basille. 2019a. Partial migration in a subtropical wading bird in the Southeastern U.S. *bioRxiv*.
- Picardi, S., B. J. Smith, M. E. Boone, and M. Basille. 2019b. “nestR”: locating nests and estimating reproductive outcome from avian GPS-tracking data.
- Picardi, S., B. J. Smith, M. E. Boone, P. C. Frederick, J. G. Cecere, D. Rubolini, L. Serra, S. Pirrello, R. R. Borkhataria, and M. Basille. 2019c. Nest-site detection and estimation of avian reproductive outcome from GPS-tracking data. *BioRxiv*.

- Pickett, S. T. A., V. T. Parker, and P. L. Fiedler. 1992. The New Paradigm in Ecology: Implications for Conservation Biology Above the Species Level. Pages 65–88 in P. L. Fiedler and S. K. Jain, editors. *Conservation Biology: The Theory and Practice of Nature Conservation Preservation and Management*. Springer US, Boston, MA.
- Plummer, K. E., G. M. Siriwardena, G. J. Conway, K. Risely, and M. P. Toms. 2015. Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? *Global Change Biology* 21:4353–4363.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Working Papers*:8.
- Plummer, M. 2018. “rjags”: Bayesian Graphical Models Using MCMC.
- Poiani, A. 2006. Effects of Floods on Distribution and Reproduction of Aquatic Birds. Pages 63–83 *Advances in Ecological Research*. Academic Press.
- Powell, L., M. J. Conroy, J. Hines, J. Nichols, and D. Krentz. 2000. SIMULTANEOUS USE OF MARK-RECAPTURE AND RADIOTELEMETRY TO ESTIMATE SURVIVAL, MOVEMENT, AND CAPTURE RATES. *Papers in Natural Resources*.
- Pulido, F. 2007. Phenotypic changes in spring arrival:: evolution, phenotypic plasticity, effects of weather and condition. *Climate Research* 35:5–23.
- Pulido, F. 2011. Evolutionary genetics of partial migration - the threshold model of migration revis(it)ed. *Oikos* 120:1776–1783.
- Pulido, F., and P. Berthold. 2010. Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences* 107:7341–7346.
- Ramos, R., F. Ramírez, C. Sanpera, L. Jover, and X. Ruiz. 2009. Diet of Yellow-legged Gull (*Larus michahellis*) chicks along the Spanish Western Mediterranean coast: the relevance of refuse dumps. *Journal of Ornithology* 150:265–272.
- Reid, J. M., J. M. J. Travis, F. Daunt, S. J. Burthe, S. Wanless, and C. Dytham. 2018. Population and evolutionary dynamics in spatially structured seasonally varying environments. *Biological Reviews* 93:1578–1603.
- Reynolds, J. E. 2001. Urbanization and land use change in Florida and the South. Page 28 *Current Issues Associated with Land Values and Land Use Planning Proceedings of a Regional Workshop*.

- Richner, H. 1992. The Effect of Extra Food on Fitness in Breeding Carrion Crows. *Ecology* 73:330–335.
- Ricklefs, R. E., Z. Naveh, and R. E. Turner. 1984. Conservation of ecological processes. *The Environmentalist*.
- Robb, G. N., R. A. McDonald, D. E. Chamberlain, and S. Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment* 6:476–484.
- Rodewald, A. D., and S. D. Gehrt. 2014. Wildlife Population Dynamics in Urban Landscapes. Pages 117–147 in R. A. McCleery, C. E. Moorman, and M. N. Peterson, editors. *Urban Wildlife conservation: Theory and Practice*. Springer US, Boston, MA.
- Roshier, D. A., V. A. J. Doerr, and E. D. Doerr. 2008. Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologia* 156:465–477.
- Rotics, S., S. Turjeman, M. Kaatz, Y. S. Resheff, D. Zurell, N. Sapir, U. Eggers, W. Fiedler, A. Flack, F. Jeltsch, M. Wikelski, and R. Nathan. 2017. Wintering in Europe instead of Africa enhances juvenile survival in a long-distance migrant. *Animal Behaviour* 126:79–88.
- Royle, J. A., A. K. Fuller, and C. Sutherland. 2018. Unifying population and landscape ecology with spatial capture–recapture. *Ecography* 41:444–456.
- Ruetz, C. R., J. C. Trexler, F. Jordan, W. F. Loftus, and S. A. Perry. 2005. Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance? *Journal of Animal Ecology* 74:322–332.
- Ruffino, L., P. Salo, E. Koivisto, P. B. Banks, and E. Korpimäki. 2014. Reproductive responses of birds to experimental food supplementation: a meta-analysis. *Frontiers in Zoology* 11:80.
- Satterfield, D. A., P. P. Marra, T. S. Sillett, and S. Altizer. 2018. Responses of migratory species and their pathogens to supplemental feeding. *Phil. Trans. R. Soc. B* 373:20170094.
- Schaub, M., and J. A. Royle. 2014. Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. *Methods in Ecology and Evolution* 5:1316–1326.
- Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding

- movement data and movement processes: current and emerging directions. *Ecology Letters* 11:1338–1350.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution* 17:474–480.
- Schradin, C., G. Schmohl, H. G. Rödel, I. Schoepf, S. M. Treffler, J. Brenner, M. Bleeker, M. Schubert, B. König, and N. Pillay. 2010. Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. *Animal Behaviour* 79:195–203.
- Schueneman, T. J., C. Rainbolt, and R. Gilbert. 2001. Rice in the crop rotation. University of Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, EDIS.
- Sekercioglu, C. H. 2010. Partial migration in tropical birds: the frontier of movement ecology. *Journal of Animal Ecology* 79:933–936.
- Sergio, F., J. Blas, L. López, A. Tanferna, R. Díaz-Delgado, J. A. Donázar, and F. Hiraldo. 2011. Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. *Oecologia* 166:79–90.
- Severud, W. J., G. D. Giudice, T. R. Obermoller, T. A. Enright, R. G. Wright, and J. D. Forester. 2015. Using GPS collars to determine parturition and cause-specific mortality of moose calves. *Wildlife Society Bulletin* 39:616–625.
- Sha, J. C. M., and G. Hanya. 2013. Diet, Activity, Habitat Use, and Ranging of Two Neighboring Groups of Food-Enhanced Long-Tailed Macaques (*Macaca fascicularis*). *American Journal of Primatology* 75:581–592.
- Shaw, A. K. 2016. Drivers of animal migration and implications in changing environments. *Evolutionary Ecology* 30:991–1007.
- Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* 19:372–378.
- Singh, N. J., and G. Ericsson. 2014. Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal. *Biology Letters* 10:20140379.

- Sizemore, G. 2009. Foraging quality of flooded agricultural fields within the Everglades Agricultural Area for wading birds (Ciconiiformes). PhD Thesis, University of Florida.
- Sizemore, G. C., and M. B. Main. 2012. Quality of Flooded Rice and Fallow Fields as Foraging Habitat for Little Blue Herons and Great Egrets in the Everglades Agricultural Area, USA. *Waterbirds* 35:381–393.
- Sklar, F. H., M. J. Chimney, S. Newman, P. McCormick, D. Gawlik, S. Miao, C. McVoy, W. Said, J. Newman, C. Coronado, G. Crozier, M. Korvela, and K. Rutchey. 2005. The ecological–societal underpinnings of Everglades restoration. *Frontiers in Ecology and the Environment* 3:161–169.
- Sklar, F., C. McVoy, R. VanZee, D. Gawlik, K. Tarboton, D. Rudnick, S. Miao, and T. Armentano. 2001. The Effects of Altered Hydrology on the Ecology of the Everglades. Page The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press.
- Smith, T. B., M. W. Bruford, and R. K. Wayne. 1996. The Preservation of Process: The Missing Element of Conservation Programs. Pages 71–75 *in* F. B. Samson and F. L. Knopf, editors. *Ecosystem Management: Selected Readings*. Springer New York, New York, NY.
- Snodgrass, J. W., A. L. Bryan, R. F. Lide, and G. M. Smith. 1996. Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, U.S.A. *53*:12.
- Snow, D. W., C. M. Perrins, B. Hillcoat, R. Gillmor, and C. S. Roselaar. 1997. *The birds of the Western Palearctic*. concise edition.
- Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2017. ‘MigrateR’: extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography* 40:788–799.
- Storch, I. 1997. Male territoriality, female range use, and spatial organisation of capercaillie *Tetrao urogallus* leks. *Wildlife Biology* 3:149–161.
- Streich, W. J., H. Litzbarski, B. Ludwig, and S. Ludwig. 2006. What triggers facultative winter migration of Great Bustard (*Otis tarda*) in Central Europe? *European Journal of Wildlife Research* 52:48–53.
- Sutherland, W. J. 1998. Evidence for Flexibility and Constraint in Migration Systems. *Journal of Avian Biology* 29:441–446.
- Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* 7:533–555.

- Team, R. C. 2018. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Austria, 2015. ISBN 3-900051-07-0: URL <http://www.R-project.org>.
- Teitelbaum, C. S., S. J. Converse, W. F. Fagan, K. Böhning-Gaese, R. B. O'Hara, A. E. Lacy, and T. Mueller. 2016. Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nature Communications* 7:12793.
- Terando, A. J., J. Costanza, C. Belyea, R. R. Dunn, A. McKerrow, and J. A. Collazo. 2014. The Southern Megalopolis: Using the Past to Predict the Future of Urban Sprawl in the Southeast U.S. *PLOS ONE* 9:e102261.
- Tortosa, F. S., J. M. Caballero, and J. Reyes-López. 2002. Effect of Rubbish Dumps on Breeding Success in the White Stork in Southern Spain. *Waterbirds* 25:39–43.
- Trexler, J. C., and C. W. Goss. 2009. Aquatic fauna as indicators for Everglades restoration: Applying dynamic targets in assessments. *Ecological Indicators* 9:S108–S119.
- Tucker, M. A., K. Böhning-Gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C. Alberts, A. H. Ali, A. M. Allen, N. Attias, T. Avgar, H. Bartlam-Brooks, B. Bayarbaatar, J. L. Belant, A. Bertassoni, D. Beyer, L. Bidner, F. M. van Beest, S. Blake, N. Blaum, C. Bracis, D. Brown, P. J. N. de Bruyn, F. Cagnacci, J. M. Calabrese, C. Camilo-Alves, S. Chamillé-Jammes, A. Chiaradia, S. C. Davidson, T. Dennis, S. DeStefano, D. Diefenbach, I. Douglas-Hamilton, J. Fennessy, C. Fichtel, W. Fiedler, C. Fischer, I. Fischhoff, C. H. Fleming, A. T. Ford, S. A. Fritz, B. Gehr, J. R. Goheen, E. Gurarie, M. Hebblewhite, M. Heurich, A. J. M. Hewison, C. Hof, E. Hurme, L. A. Isbell, R. Janssen, F. Jeltsch, P. Kaczensky, A. Kane, P. M. Kappeler, M. Kauffman, R. Kays, D. Kimuyu, F. Koch, B. Kranstauber, S. LaPoint, P. Leimgruber, J. D. C. Linnell, P. López-López, A. C. Markham, J. Mattisson, E. P. Medici, U. Mellone, E. Merrill, G. de Miranda Mourão, R. G. Morato, N. Morellet, T. A. Morrison, S. L. Díaz-Muñoz, A. Mysterud, D. Nandintsetseg, R. Nathan, A. Niamir, J. Odden, R. B. O'Hara, L. G. R. Oliveira-Santos, K. A. Olson, B. D. Patterson, R. Cunha de Paula, L. Pedrotti, B. Reineking, M. Rimmler, T. L. Rogers, C. M. Rolandsen, C. S. Rosenberry, D. I. Rubenstein, K. Safi, S. Saïd, N. Sapir, H. Sawyer, N. M. Schmidt, N. Selva, A. Sergiel, E. Shiilegdamba, J. P. Silva, N. Singh, E. J. Solberg, O. Spiegel, O. Strand, S. Sundaresan, W. Ullmann, U. Voigt, J. Wall, D. Wattles, M. Wikelski, C. C. Wilmers, J. W. Wilson, G. Wittemyer, F. Zięba, T. Zwijacz-Kozica, and T. Mueller. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* 359:466–469.

- Turner, M. G., S. L. Collins, A. L. Lugo, J. J. Magnuson, T. S. Rupp, and F. J. Swanson. 2003. Disturbance Dynamics and Ecological Response: The Contribution of Long-Term Ecological Research. *BioScience* 53:46–56.
- Turrin, C., B. D. Watts, and E. K. Mojica. 2015. Landfill Use by Bald Eagles in the Chesapeake Bay Region. *Journal of Raptor Research* 49:239–249.
- USFWS. 1984. Endangered and threatened wildlife and plants; US breeding population of the wood stork determined to be endangered. *Federal Register* 49:7332–7335.
- USFWS. 2014, June 30. Endangered and Threatened Wildlife and Plants; Reclassification of the U.S. Breeding Population of the Wood Stork From Endangered to Threatened. *Federal Register*.
- Van Leeuwen, C. H. A., J. Museth, O. T. Sandlund, T. Qvenild, and L. A. Vøllestad. 2016. Mismatch between fishway operation and timing of fish movements: a risk for cascading effects in partial migration systems. *Ecology and Evolution* 6:2414–2425.
- Van Moorter, B., N. Bunnefeld, M. Panzacchi, C. M. Rolandsen, E. J. Solberg, and B.-E. Sæther. 2013. Understanding scales of movement: animals ride waves and ripples of environmental change. *Journal of Animal Ecology* 82:770–780.
- Van Os, E. K. 2008. Selection of canals and ditches as foraging habitat by wood storks (*Mycteria americana*). M.S., Florida Atlantic University, United States – Florida.
- Vansteelant, W. M. G., J. Shamoun-Baranes, W. van Manen, J. van Diermen, and W. Bouten. 2017. Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic Flyway. *Journal of Animal Ecology* 86:179–191.
- Vélez-Espino, L. A., R. L. McLaughlin, and M. Robillard. 2013. Ecological advantages of partial migration as a conditional strategy. *Theoretical Population Biology* 85:1–11.
- Vergara, P., J. I. Aguirre, J. A. Fargallo, and J. A. Dávila. 2006. Nest-site fidelity and breeding success in White Stork *Ciconia ciconia*. *Ibis* 148:672–677.
- Visser, M. E., A. C. Perdeck, J. H. V. Balen, and C. Both. 2009. Climate change leads to decreasing bird migration distances. *Global Change Biology* 15:1859–1865.
- Weiser, E. L., and A. N. Powell. 2010. Does Garbage in the Diet Improve Reproductive Output of Glaucous Gulls? Inclusion de Basura en la Dieta Aumenta la Producción Reproductiva de *Larus hyperboreus*! *The Condor: Ornithological Applications* 112:530–538.

- Weldon, A. J., and N. M. Haddad. 2005. The Effects of Patch Shape on Indigo Buntings: Evidence for an Ecological Trap. *Ecology* 86:1422–1431.
- Weller, M. W. 1999. *Wetland Birds: Habitat Resources and Conservation Implications*. Cambridge University Press.
- Wilcove, D. S., and M. Wikelski. 2008. Going, Going, Gone: Is Animal Migration Disappearing. *PLoS Biology* 6:e188.
- Wilmers, C. C., B. Nickel, C. M. Bryce, J. A. Smith, R. E. Wheat, and V. Yovovich. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* 96:1741–1753.
- Zabel, C. J., K. McKelvey, and J. P. Ward Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology* 73:433–439.

BIOGRAPHICAL SKETCH

Simona Picardi was born and raised in Rome, Italy. She has been an eager learner since a very young age, and, as a kid, she manifested a spontaneous love for nature and especially the animal kingdom. While pursuing her high-school education in Rome, Simona cultivated an eclectic cultural background studying both humanities and sciences. She likes to think of her career path as a Rube Goldberg machine, where serendipitous encounters with influential people each inspired her to take a step, and these steps, taken sequentially one after the other, led her to where she is now – without the final destination being directly obvious at the beginning. The first of these influential people was her high-school biology teacher, Giacomo Puma. His lessons instilled in Simona awe for the functioning of cells and living organisms, which directed her choice to pursue a college education in biology at the University of Rome “La Sapienza”. While in college, another serendipitous encounter was with her zoology professor, Dr. Raffaele Scopelliti. His lessons blew on the fire of Simona’s innate passion for animals and made her discover the awe-striking beauty of lesser-known and -celebrated critters. It was Dr. Scopelliti who directed Simona to the person who would become her most important mentor: Dr. Luigi Boitani. Since their first meeting, Simona sought Luigi’s advice for all of her career decisions, including the one to pursue a master’s degree in ecology under his supervision at the University of Rome “La Sapienza”, after graduating with her bachelor’s *cum laude* in October 2012. From Luigi, Simona learned a wealth of knowledge about ecology and conservation, but most importantly she became savvy of what it takes to build a career in this field that is both successful and strives to be useful to the greater good. Simona internalized Luigi’s conservation-oriented mindset, which to this day fuels her motivation to do science that

has a real-world impact. During Simona's final year at the University of Rome, Luigi facilitated another important connection between Simona and Dr. Francesca Cagnacci, who would become her master's co-advisor and a pivotal figure in her career development. Simona conducted her master's thesis internship on roe deer movement ecology in Francesca's lab at the Edmund Mach Foundation, while still enrolled at the University of Rome. Working with Francesca, Simona was first exposed to a prime international research environment, which shaped her approach to science and her expectations for her own career. Francesca became an especially important role model for Simona as her first woman mentor in ecology. Under Luigi and Francesca's supervision, Simona graduated with her master's *cum laude* in March 2015. After that, Francesca triggered the next step of the chain reaction, when she learned about a PhD opportunity in Dr. Mathieu Basille's lab at the University of Florida and encouraged Simona to apply. The application was selected, and Simona started her PhD program in wildlife ecology and conservation at the University of Florida in August 2015. Four years later, in Fall 2019, Simona defended this dissertation, which is dedicated to the influential teachers and mentors who inspired her choices and shaped her career path until today.