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Ecological Outcomes of Movement Behavior in Brown Pelicans from the South Atlantic Bight

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ECOLOGICAL OUTCOMES OF MOVEMENT BEHAVIOR IN BROWN PELICANS FROM THE SOUTH ATLANTIC BIGHT

A Dissertation
Presented to
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In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Wildlife and Fisheries Biology

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by
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Accepted by:
Patrick Jodice, Committee Chair
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ABSTRACT

Vagile organisms are expected to display movement behaviors that respond to a wide variety of both intrinsic and extrinsic factors. Identifying drivers of movement is fundamental to understanding the ecology of species, as well as implementing effective conservation measures. Technological advancements have allowed for the collection of fine-scale positional data at rapid temporal scales, which can be a powerful tool for assessing the movement behavior of tracked species and for understanding the potential fitness implications resulting from variations in animal space use. The goal of this dissertation was to identify important drivers of movement behavior and to describe the ecological outcomes of movement decisions in Eastern brown pelicans (*Pelecanus occidentalis carolinensis*) from the South Atlantic Bight. A total of 86 individual pelicans were outfitted with solar-powered GPS satellite transmitters in coastal South Carolina and Georgia, USA, from 2017 – 2020. Two cohorts of pelicans tracked during the passage of three tropical cyclones demonstrated a reduction in movement correlated with anomalies in barometric pressure and wind speed relative to ambient conditions, indicating a shelter-and-wait strategy for increasing survival during these extreme weather events. By measuring the concentrations of an environmental contaminant, poly- and perfluoroalkyl substances, in the eggs of pelicans from three colonies located near Charleston, South Carolina, I demonstrated that eggs contained relatively elevated concentrations of chemicals regardless of proximity to likely point sources. GPS tracking of adults from the same colonies further suggested that variations in urban habitat use for foraging adults during the breeding season were also not reflected in egg contaminant concentrations. In contrast, the relative risk to foraging adult pelicans of encountering surface oil from a ship-based spill near Charleston Harbor was significantly influenced by location, as demonstrated through the use of an oil spill modeling toolkit combined with pelican telemetry data. Finally, the partial migration strategy of brown pelicans in the South Atlantic Bight is likely maintained by the ontogenetic migration of their primary prey, Atlantic menhaden (*Brevoortia tyrannus*), and aligns with the fasting endurance hypothesis of partial migration. Understanding the causes and consequences of movement in brown pelicans in the South Atlantic Bight has important implications for the ecology and conservation of this species throughout their range.

DEDICATION

To Marie Wilkinson

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Chapters 2–5 of this manuscript represent stand-alone publications either intended for submission to or already published in peer-reviewed journals, and multiple collaborators participated as co-authors on the manuscripts. Patrick Jodice co-authored all four data chapters. Juliet Lamb and Yvan Satgé co-authored Chapter 2. Anna Robuck, Rainer Lohmann, and Heidi Pickard co-authored Chapter 3. Their contributions included project design and management (PJ), data collection (JL, YS), lab analyses and interpretation (AR, RL, HP), and manuscript preparation (PJ, AR, RL). Additional collaborators are included in the acknowledgement sections of individual chapters.

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CHAPTER ONE

INTRODUCTION

The advancement of ecological understanding is inherently a spatial endeavor (Cagnacci *et al.* 2010). Ecological processes are variable in space and time, creating heterogeneous environments which directly alter organism fitness (Morales *et al*. 2005). For vagile organisms, movement represents a common thread linking individual behavior with environmental variation (Cagnacci *et al.* 2010, Morales *et al*. 2005). For example, seasonal changes in resource abundance may drive migrations spanning entire hemispheres (Shaffer *et al*. 2006) or prompt elevation-related movements covering only a few linear kilometers (Guillaumet *et al.* 2017). The boundaries of home ranges may be modulated by variations in environmental features (Ford 1983). Predation risk can be described as a function of space use (Laundré *et al*. 2001). Understanding both the mechanisms and consequences of animal movement is therefore foundational to understanding the ecology of species.

Movement-based decisions by vagile organisms are expected to be influenced by a wide variety of both extrinsic and intrinsic drivers. Multiple drivers of animal movement often operate concomitantly across overlapping temporal and spatial scales, forming a nested hierarchy of stimuli that can also produce a nested hierarchy of responses (Fauchald 2009, Wakefield *et al*. 2009, Weimerskirch 2007). Movement decisions can also be influenced by different drivers both within and between each scale (Grünbaum & Veit 2003, Lesage *et al*. 2017). For example, an individual may respond to one driver at the microscale (e.g., to initiate a foraging bout) while at the same time responding to a different driver at the macroscale (e.g., to migrate across ecosystems). Drivers of movement may include but not be limited to aspects of optimal foraging theory, predator avoidance, or phenology, yet underlying these proximate drivers are the physiological requirements of the organism.

Physiology may act as a driver of movement decisions (e.g., requirements for energy precipitating certain foraging strategies or migratory behaviors) but conversely movement decisions may also act upon the physiology of the organism. For example, exposure to chemical contaminants or anthropogenic food subsidies may be a function of movement behavior (Furness *et al*. 2006, Leat *et al*. 2013). In this way, the movement behaviors of vagile organisms represent the integration of environmental information with the internal state of the individual, which subsequently influences the fitness of the organism ultimately leading again to changes in movement behavior. Movement behavior has therefore become its own subdiscipline within ecology, with particularly relevant applications towards the conservation of wildlife.

The advanced development of animal-borne devices capable of recording, in detail, the movement behavior of individual organisms has significantly increased our understanding of ecological processes from the microscale to the macroscale (Hays *et al*. 2016). This technological revolution has been particularly valuable for the study of highly mobile species or species inherently difficult for humans to observe directly (Rutz & Hays 2009). One taxa for which the application of tracking technology has been particularly successful is the seabirds (Burger & Shaffer 2008). Seabirds, as upper trophic level species, are generally regarded as good indicators of conditions within the marine environment, and as a result the analysis of their movement behavior has been particularly valuable for advancing ecological knowledge of marine systems (Piatt *et al*. 2007).

Nearshore and coastal systems are some of the most dynamic, yet threatened, habitats globally (Gray 1997). Indeed, despite being biologically rich, coastal systems occupy a proportionally small area relative to other ecosystems and are therefore of particular conservation concern (Lotze *et al*. 2006). Similarly, organisms that inhabit coastal and marine systems are declining at a more rapid pace than in terrestrial systems (McCauley *et al*. 2015). Occupying the interface of terrestrial and marine processes, seabirds that inhabit these systems likely react to and integrate information from a wide variety of extrinsic factors in addition to individual intrinsic variation. Analyzing the movement behavior of nearshore seabirds may therefore relate a wide variety of ecological information about the systems they inhabit, just as analysis of the ecology of the system may relate information about the species.

Eastern brown pelicans (*Pelecanus occidentalis carolinensis*) possess many characteristics lending themselves to the study of the ecology of nearshore systems through the analysis of movement behavior. They are large, mobile seabirds capable of exploiting habitats ranging from the estuarine to the fully marine, occupy a broad geographic distribution, and are upper trophic level predators (Shields 2020). Due largely to toxins such as dichlorodiphenyltrichloroethane (DDT), brown pelicans were historically considered an endangered species, being formally listed in the United States from 1970 - 2009 (Vander Pol *et al*. 2012). Current conservation concerns include but are not limited to toxicological exposure, habitat loss, climate change, human disturbance, energy development, and resource competition (Jodice *et al*. 2019, Velarde *et al*. 2013, Walter 2012). As well as being a high-profile and iconic species, brown pelicans accurately reflect environmental change and act as reliable samplers of the coastal environment, evidenced in part by previous declines (Anderson *et al*. 1982). Large data gaps still exist for this species, however, especially in terms of annual movement, behavior, and reproduction (Jodice *et al*. 2013, Jodice *et al*. 2019).

Compounding these data gaps, much of the previous research on brown pelicans has been localized and unrepeated despite regional-specific differences in threats, habitats, and natural history across the range of the species (Vander Pol *et al*. 2012). For example, much early research for this subspecies was conducted along the Florida Gulf coast (Schreiber & Risebrough 1972, Schreiber 1980), a relatively unique ecosystem within the range of the species while more recent work has focused on the northern Gulf of Mexico (Geary 2018, Lamb 2016, Streker 2019, Walter 2012). In contrast, comparatively less is known about the species in the South Atlantic Bight, an area ranging from the Cape Fear River Basin, North Carolina, to Cape Canaveral, Florida (Jodice *et al*. 2007, Jodice *et al*. 2013). The coastal areas of this region are characterized by a highly dynamic system of estuaries, salt marshes, and barrier islands, with a comparatively high number of riverine input features into the local oceanography. Despite the importance of the South Atlantic Bight as a unique and valuable nearshore system, many questions concerning the ecology of the seabirds which rely upon it remain unanswered (Jodice *et al*. 2007, Jodice *et al*. 2013).

Summary of dissertation content

The goal of this dissertation is to assess the influence of both extrinsic and intrinsic factors on the movement behavior of brown pelicans in the South Atlantic Bight, and in turn to use a spatial analytic framework to investigate how movement decisions may contribute to the ecology and conservation of pelicans in the region. Here I review the content of each chapter and how each contributes to this theme.

Chapter 2 examines the influence of tropical cyclones on the behavior of brown pelicans as assessed via short-term changes in movement patterns. Coastal organisms regularly exposed to tropical cyclones are hypothesized to display one of two behaviors; seeking shelter and staying in place, or fleeing from the storm and moving rapidly away. Despite these hypotheses, comparatively few examples exist in the literature recording the behavior of animals during cyclones, especially seabirds, likely due to both logistical and safety constraints. I used GPS tracking data to examine the amount of active behavior in comparison to sedentary behavior displayed by two cohorts of pelicans during the passage of three tropical cyclones, and related activity levels to the environmental variables of barometric pressure and wind speed.

Chapter 3 assesses the concentrations of a chemical contaminant in the eggs of brown pelicans as a function of urban habitat use during the breeding season. Estuarine habitats surrounding Charleston, South Carolina, have previously been reported to contain elevated concentrations of perfluoroalkyl substances (PFAS) compared to other urban centers in the country. However, it is unclear if there is a relationship between

PFAS exposure and urban habitat use for relatively mobile coastal organisms. I reported concentrations of PFAS in the eggs of brown pelicans from three colonies near the urban center of Charleston, and linked population-level assessments of urban habitat use as recorded via tracking data to possible variation in PFAS concentrations. Understanding the spatial footprint of chemical contamination is critical to implementing relevant mitigation measures for affected species.

Chapter 4 discriminates the factors most relevant to oil spill risk exposure for urban colonies of brown pelicans near Charleston Harbor, South Carolina. Predicting the spatial extent and risk to wildlife of oil spills is challenging, especially in dynamic coastal systems. I leveraged a predictive tool constructed by the National Oceanic and Atmospheric Administration (NOAA) for generating realistic oil spill simulations in Charleston Harbor to craft a variety of spill scenarios based upon a matrix of relevant environmental variables. I then assessed the degree of overlap between spilled oil from these scenarios with movement data collected from pelicans tracked from two nearby colonies. Describing the factors most important in determining the relative extent of wildlife contamination to spilled oil is critical for informing sound policy and generating appropriate response guidelines in the event of future oil releases. I also demonstrated the applicability of the NOAA tool for use in other urban areas and with other nearshore wildlife taxa.

Chapter 5 investigates the extrinsic and intrinsic factors underlying the maintenance of partial migration in brown pelicans. Partial migration, whereby some individuals within a population migrate while others do not, is characteristic of pelicans in both the South Atlantic Bight and northern Gulf of Mexico. Evidence for a density-dependent relationship exists for the Gulf of Mexico, but hypotheses remained untested in the South Atlantic Bight, a region driven to a much greater extent by latitudinal movements. I used time-to-event models to discriminate the most important variables triggering migration out of the South Atlantic Bight, and connected the resultant model to competing theories concerning the evolution and maintenance of partial migration. As partial migration is often characterized as a precursor state to full migration, understanding the mechanisms behind partial migration serve to advance ecological knowledge of the development of migration at large.

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CHAPTER TWO

TROPICAL CYCLONES ALTER SHORT-TERM ACTIVITY PATTERNS OF A COASTAL SEABIRD[1]

Abstract

Mobile organisms in marine environments are expected to modify their behavior in response to external stressors. Among environmental drivers of animal movement are long-term climatic indices influencing organism distribution and short-term meteorological events anticipated to alter acute movement behavior. However, few studies exist documenting the response of vagile species to meteorological anomalies in coastal and marine systems. Here we examined the movements of Eastern brown pelicans (*Pelecanus occidentalis carolinensis*) in the South Atlantic Bight in response to the passage of three separate hurricane events in two years. Pelicans (*n* = 32) were tracked with GPS satellite transmitters from four colonies in coastal South Carolina, USA, for the entirety of at least one storm event. An Expectation Maximization binary Clustering algorithm was used to discretize pelican behavioral states, which were pooled into 'active' versus 'inactive' states. Multinomial logistic regression was used to assess behavioral state probabilities in relation to changes in barometric pressure and wind velocity. Individual pelicans were more likely to remain inactive during tropical cyclone passage compared to baseline conditions generally, although responses varied by hurricane. When inactive, pelicans tended to seek shelter using local geomorphological features along the coastline such as barrier islands and estuarine systems. Our telemetry data showed that large subtropical seabirds such as pelicans may mitigate risk associated

with spatially-extensive meteorological events by decreasing daily movements. Sheltering may be related to changes in barometric pressure and wind velocity, and represents a strategy common to several other classes of marine vertebrate predators for increasing survival probabilities.

[1] Wilkinson, B.P., Satgé, Y. G., Lamb, J. S., & Jodice, P. G. R. (2019). Tropical cyclones alter short-term activity patterns of a coastal seabird. Movement Ecology, 7(1), 1-11.

Background

Mobile organisms display common movement syndromes across vertebrate taxa, with movements based on both intrinsic (e.g. body condition) and extrinsic factors (e.g. resource availability; Abrahms *et al*. 2017). While intrinsic variation operates on the level of the individual, extrinsic factors acting concurrently on groups of individuals have a role in determining the movement behavior of populations (Nathan *et al*. 2008). Among these extrinsic factors in marine and coastal systems are climatic variations that affect distributions on monthly, yearly, or decadal timescales. Long-term drivers include extensive and cyclic events such as seasonality (Bocher *et al*. 2000, O'Toole *et al*. 2015, Xavier *et al*. 2013), oscillation events (e.g. El Niño Southern Oscillation; Crocker *et al*. 2006, Thorne *et al*. 2016), and oceanographic-atmospheric regime coupling (Bond *et al*. 2011, Louzao *et al*. 2013, Weimerskirch *et al*. 2012, Weise *et al*. 2006). Extrinsic drivers of animal movement also occur at more local scales, where acute meteorological events such as storms can influence animal movement from hours to weeks (Spruzen & Woehler

2002, Weimerskirch *et al*. 2000). These short-term events are expected to fluctuate stochastically compared to longer-term climatic drivers, and therefore the extent of and mechanisms by which each affect movement may be variable. While the spatial impacts of macroscale events are relatively well-studied, effects of shorter-term acute drivers (e.g. local storms) are less known (Weimerskirch & Prudor 2019).

While organisms may respond to seasonally-typical meteorological conditions in repeatable and often predictable ways, anomalous conditions offer an opportunity to examine behavioral responses to environmental stressors that occur stochastically (Senner *et al*. 2015, Wilson 2004, Zhou *et al*. 2013). Among the most disruptive meteorological events in coastal and marine systems are hurricanes and tropical storms (also called cyclones or typhoons). These spatially-extensive, temporally-focused natural perturbations can affect coastal geomorphology, alter local oceanography, and induce widespread mortality among wildlife populations (Huang *et al*. 2017, Marsh & Wilkinson 1991, Nicoll *et al*. 2017). Typically categorized by relative severity, they are regularly-occurring yet unpredictable phenomena (Weinkle *et al*. 2012). Hurricanes introduce extreme wind velocities, elevated tidal surges, intense rainfall, widespread flooding, and chaotic sea surface conditions to the local system, and therefore have the potential to reduce organism fitness directly (e.g. mortality events) and indirectly (e.g. reduced foraging opportunities; Dewald & Pike 2014).

Species that occupy ecosystems regularly subjected to hurricanes demonstrate behavioral modifications for increasing survival during cyclonic activity, although direct studies appear limited (Weimerskirch & Prudor 2019). For example, marine species commonly display one of two contrasting strategies for mitigating negative effects from intense but short-duration weather events; relocation and sheltering in place. Studies of elasmobranchs (e.g. juvenile blacktip sharks (*Carcharhinus limbatus*)) have demonstrated increased movement rates upon the approach of a cyclone indicating relocation from shallow nursery areas to deeper, offshore water that is less prone to disturbance (Heupel *et al*. 2003, Udyawer *et al*. 2013). Conversely, Florida manatees (*Trichechus manatus latirostris*) remain in the same discrete patch during passage of a cyclonic event, with daily movements contained within areas utilized prior to cyclonic exposure (Langtimm *et al*. 2006). Littoral abundance of sea kraits (*Laticauda* spp.) in Taiwan appears to be influenced by cyclonic events, with individuals likely seeking shelter among coastal geologic features such as sea caves (Liu *et al*. 2010). Results from loggerhead and hawksbill sea turtles (*Caretta caretta* and *Eretmochelys imbricate*, respectively) indicate marked changes in swimming and diving behavior during storm interaction, although with variable and sometimes contrasting responses depending on breeding stage (Sakamoto *et al*. 1990, Storch *et al*. 2006, Wilson *et al*. 2017).

Of particular utility for examining differential responses to cyclonic events, seabirds present a group of taxonomically and morphologically diverse organisms often impacted by marine storms. For example, smaller-bodied pelagic seabirds may attempt to avoid or circumnavigate an approaching hurricane (Hass *et al*. 2012, Weimerskirch Prudor 2019). Individuals unable to do so may be displaced far from their preferred habitat (often inland), leading to the observed wrecks of these species following major events (e.g., Bugoni *et al*. 2007). Conversely, larger-bodied coastal-dwelling species may reduce daily activities and attempt to shelter during storm passage, but this remains unexamined. Variation in hurricane response may also differ by life stage in addition to morphology (Weimerskirch & Prudor 2019). Understanding how various seabird species respond to large-scale environmental irregularities may therefore clarify apparent discrepancies in displacement susceptibility (Hass *et al*. 2012). However, due to the stochastic and unpredictable nature of hurricane events, as well as the difficulties and dangers of collecting data on animal movement during these times, published literature is lacking on this topic particularly for larger-bodied coastal-dwelling species.

As part of ongoing research examining movement patterns of Eastern brown pelicans (*Pelecanus occidentalis carolinensis*) in the South Atlantic Bight, we report the behavioral strategies utilized by two cohorts of satellite-tracked individuals in coastal South Carolina and Georgia during the passage of three hurricane events. The Eastern brown pelican is a large-bodied coastal seabird with breeding colonies distributed along barrier and estuarine islands ranging from tropical to temperate waters of the western North Atlantic. As a facultative migrant, the brown pelican displays a range of individual post-breeding movement strategies (Lamb *et al*. 2017a), which when combined with timing of departure and location of breeding colony, annually exposes many individuals to potential cyclonic events throughout their range. During peak hurricane activity in the South Atlantic Bight (late August to September), adult pelicans may variably disperse from the breeding colony but are generally not yet engaged in migratory behavior (B.W. pers. obs.). We hypothesized that the movement behavior of individual pelicans would correlate with meteorological condition during passage of a hurricane by either (a) increasing movement activity and fleeing the storm or (b) decreasing movement activity and sheltering in place.

Methods

Study area

We conducted our study in the South Atlantic Bight, USA, which extends from the Cape Fear River Basin to approximately Cape Canaveral (Fig. 2.1). The coast here is characterized by a complex geomorphology of barrier islands, estuaries, and salt marshes. The area supports ca. 15 brown pelican colonies annually (active breeding from April – September) and many of the beaches and islands are used as migratory stopover, staging, or wintering grounds for this species and others (Jodice *et al*. 2013).

Satellite transmitter deployments

Nesting pelicans were outfitted with GPS satellite transmitters (GeoTrak Inc., North Carolina, USA) at four colonies in coastal South Carolina (Bird Key Stono, 32° 38’ N, 79° 58’ W, n = 21; Castle Pinckney, 32° 46’ N, 79° 54’ W, n = 12; Marsh Island, 32° 59’ N, 79° 33’ W, n = 7; Deveaux Bank, 32° 32’ N, 80° 10’ W, n = 5). Colony size ranged from ca. 50 – 2000 pairs. Deployments commenced during the chick-rearing stage (May-July) of the 2017 and 2018 breeding seasons. Transmitters weighed ~65 g (10 x 3.5 x 3 cm) and constituted ≤ 3% body mass of instrumented individuals (range = 2475 – 4350 g), the recommended threshold for large seabirds (Phillips *et al*. 2003). Briefly, nest-attending adults were captured via either neck or leg noose and equipped with a solar

GPS Platform Terminal Transmitter dorsally using a backpack-style harness system. For a description of specific attachment procedures, see Lamb *et al*. (2017b). During the post-breeding stage of deployment (September – November), units were programmed to record 10 locations per day at 90 min intervals between the hours of 01:00 – 23:30 GMT and were duty-cycled on an 8 hr on to 36 hr off activity schedule. Unit error was assumed to be similar to that of Lamb *et al*. (2017a), i.e. 4.03 ± 2.79 m.

Hurricane events

Our opportunistic analysis of pelican movement in relation to hurricane activity includes three storm events. On 10 September 2017, Hurricane Irma made landfall in southwestern Florida, USA, as a Category 4 tropical cyclone. Over the subsequent 1.5 days, Irma proceeded north along the coast of western Florida before weakening and degenerating near the central Georgia-Alabama border. Although the storm was centered mainly along the Gulf coast of Florida, much of the southeastern Atlantic seaboard was affected by the outer cyclonic bands (Fig. 2.1).

Hurricane Florence made landfall on 14 September 2018 in southern North Carolina, USA, as a reduced Category 1 tropical cyclone, having been a Category 4 cyclone four days prior. Florence tracked inland in a southeasterly direction as it weakened, degenerating over West Virginia, USA, three days after landfall, affecting predominantly the coastal Carolinas (Fig. 2.1).

Less than one month later, Hurricane Michael made landfall in the panhandle of Florida on 10 October 2018 as a Category 4 tropical cyclone. Michael followed a northeasterly trajectory after landfall, weakening incrementally over the southeastern United States before restructuring as an extratropical cyclone two days later off the Mid-Atlantic coast (Fig. 2.1). Similar to Irma, Michael impacted much of the Atlantic seaboard due to the trajectory, strength, and spatial extent of the storm.

Meteorological data

A kernel density analysis was used to identify the core spatial area utilized by instrumented pelicans during each hurricane event. Subsequent utilization distributions (UDs) were used to determine a representative location for assessing pelican response to meteorological indices. This approach allowed for the acquisition of meteorological data that would represent shared conditions for the greatest number of individuals throughout the tracking period. We used only locations recorded during the calendar month of the respective hurricane event, which corresponded with peak cyclonic activity but limited seasonal changes in weather. Distributions therefore reflected core use areas during the entire passage of the cyclone as well as the remainder of the month in which the cyclone occurred. Erroneous locations were identified and removed through a combination of visual inspection (e.g. consecutive locations separated by unrealistic distances) and a speed filter of ≥ 65 km per hour (Schnell & Hellack 1978). Kernel bandwidth was determined using R statistical software (v 3.4.2.) through a plug-in bandwidth selector in package *ks* (Duong 2017). Locations within the 25% UD (i.e. core range) identified in the kernel density output during the month of each respective hurricane (grid = 400, extent = 0.4°) were then used to assess movement patterns in relation to storm events. Roughly, the area of highest use by pelicans during these time periods paralleled the coastline from central South Carolina to north-central Georgia (Fig. 2.1). Individual pelicans located outside of the prior 25% UD at the time of hurricane passage (e.g. in Chesapeake Bay) were manually excluded from further analysis, as well as individuals for whom movement data was not complete for the entire time period.

Meteorological data were obtained via the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information from the Hunter U.S. Army Airfield, Savannah, Georgia (station 74780413824), to represent conditions experienced during Hurricane Irma, and from the Marine Corps Air Station Beaufort, Beaufort, South Carolina (station 72208593831), to represent conditions during Hurricanes Florence and Michael (https://www.ncdc.noaa.gov/). These sites were within the 25% UD in the kernel density analysis. Although spatially similar, multiple weather locations were required as neither station had complete data for all three hurricane events in totality. Meteorological data were collected hourly and spanned the entire month of each cyclonic event. Data were requested 04 November 2017, 28 November 2018, and 12 December 2018, respectively.

Behavioral clustering

We used an Expectation Maximization binary Clustering (EMbC) algorithm to derive biologically-relevant behavioral states for individual brown pelicans (Garriga *et al*. 2016). EMbC uses unsupervised relationships between successive locations incorporating path distance and tortuosity (i.e. velocity and turning angle) to infer underlying behavioral processes. EMbC is particularly appropriate for remotely-sensed location data as it accounts for spatial and temporal correlations and uncertainties in the input features and is robust to spatial data collected at relatively long intervals (Bennison *et al*. 2018). Critically, EMbC is capable of producing biologically-relevant classifications for locational data recorded at timescales relevant to the current study (e.g., Afán *et al*. 2019). Each point within individual tracks was clustered into one of four categories: low velocity/ low turning angle (LL), low velocity/ high turning angle (LH), high velocity/ low turning angle (HL), and high velocity/ high turning angle (HH) (Fig. 2.2). These four behavioral nodes were biologically interpreted as corresponding to inactive, localized search, commuting, and dispersive search behaviors, respectively. Following Garriga *et al*. (2016), a post-processing smoothing procedure was applied based on consecutive behavioral correlations to manage temporally-irregular data. This smoothing procedure searches for clusters of the same behavioral assignment that contain a single point of a different classification, and adds additional likelihood weight to that single point belonging to the larger cluster, a feature explicitly implemented in state-space models. In this way, the smoothing procedure favors homogenized bouts of behavior instead of single-point behavioral switches during clusters of equal assignment. We also calculated mean step length (distance between successive points) and net displacement (maximum distance from the first location in the series) for descriptive purposes. Each point was finally matched temporally to the closest hourly meteorological variable for statistical analysis.

Statistical analyses

We assessed the effects of meteorological drivers on pelican behavioral state with multinomial logistic regression following de Grissac *et al*. (2017). To simplify model interpretation and to examine activity patterns more accurately matched to the temporal resolution of the data, models were conducted on a reduced set of two behavioral nodes classified as either active (including localized search, commuting, and dispersive search; LH, HL, and HH, respectively) or inactive (LL). Environmental variables of interest (barometric pressure and wind velocity) were chosen *a priori* based on data completeness, relevance to cyclonic activity, and probability of being sensed by individual pelicans (Weimerskirch & Prudor 2019).

Both tracking and meteorological data were further subset to exclude other potentially confounding anomalous conditions. We defined an anomalous event as a barometric pressure reading ≥ 1 SD from the monthly mean. Only data collected from the end of the last pressure anomaly pre-cyclone to the first pressure anomaly post-cyclone were therefore included in our regression analysis, thus creating a temporal segment of activity that was exclusively characterized by 'baseline' conditions with the exception of the cyclonic event. Significant differences of barometric pressure and wind velocity between study periods were assessed via Kruskal-Wallis chi-squared tests, with Wilcoxon rank sum tests used when significant differences were found.

Four multinomial logistic regression models were fit to the data using R package *mlogit* (Croissant 2013), including a null model, single-effect wind velocity model, single-effect barometric pressure model, and global model including both wind velocity and barometric pressure. Model selection was performed within each set using Akaike's Information Criterion (AIC), with the best-performing model indicated by the lowest AIC value. Given low AIC similarity between models, we did not model average. Environmental variables were interpreted as having a significant effect on individual behavioral states at $p < 0.05$. We further assessed transition probabilities using the top-performing model, with the null state (i.e., reference level) defined as inactive (i.e., the probabilities are reflective of transitioning from inactivity to activity).

Results

After removal of individuals with incomplete tracks and those located outside of the 25% UD, 32 instrumented Eastern brown pelicans remained in the sample population for Hurricanes Irma (n = 18), Florence (n = 16), and Michael (n = 12). Due to the multi-year duration of tag deployment as well as the temporal spacing of cyclonic events, some individuals were tracked for more than one event (2 events, n = 8; 3 events, n = 3).

Hourly barometric pressure and wind velocity were relatively consistent throughout each defined study period with the exception of hurricane passage (Fig. 2.3). Local minima of barometric pressure and local maxima of wind velocity were both greater than one standard deviation away from the monthly mean during the day that the center of the storm passed through the study area (Table 2.1), indicating anomalous conditions.

Barometric pressures were significantly different during each period of study (Kruskal-Wallis $\chi^2 = 442.27$, $p < 0.001$), with lower values during Hurricane Irma than

Hurricanes Florence (Wilcoxon rank sum test $Z = -5.26$, $p < 0.001$) and Michael ($Z = -18.66$, $p < 0.001$), and significantly lower values during Hurricane Florence than Hurricane Michael ($Z = -16.19$, $p < 0.001$). Significant differences likewise existed between measured wind velocities (Kruskal-Wallis $\chi^2 = 15.89$, $p < 0.001$), but not between every event. Wind velocities were higher during Hurricane Irma than Hurricanes Florence (Wilcoxon rank sum test $Z = -3.39$, $p < 0.001$) and Michael ($Z = -2.39$, $p = 0.017$), but wind velocities between Hurricane Florence and Hurricane Michael were not significantly different ($Z = -1.66$, $p = 0.096$).

Pelicans tended to make relatively short daily movements during each period of analysis, and these movements were typically ≤ 5 km seaward from the immediate coastline ($\underline{x}$ step length = 3.8 ± 7.1 km, range = 0 – 94.9 km). Individual pelicans displayed both sedentary and dispersive behavior at the regional level, consistent with individual variation in post-breeding dispersal ($\underline{x}$ net displacement = 51.7 ± 69.0 km, range = 0 – 267.4 km). Behavioral assignments discretized by the EMbC algorithm were more likely to be in active state (66.1 ± 17.9%) than in inactive state (33.4 ± 17.8%). Multinomial logistic regression and AIC-driven model selection indicated global models (i.e., barometric pressure + wind speed) as best candidates for explaining pelican behavioral state probabilities during both Hurricanes Irma and Florence ($\Delta AIC_c = 11.52$ and 9.38, respectively). Both the global model and a model including only wind speed were selected as best candidates during Hurricane Michael ($\Delta AIC_c = 1.51$).

During Hurricane Irma, individuals were significantly more likely to transition from an inactive state to an active state when barometric pressure increased, but were significantly more likely to remain in an inactive state when wind velocity increased (Table 2.2). The odds of an individual transitioning from an inactive state to an active state decreased by 0.91 for every unit decrease in barometric pressure while the odds of an individual transitioning from an inactive state to an active state decreased by 0.84 for every unit increase in wind velocity. During Hurricane Florence, individuals were significantly more likely to transition from an inactive state to an active state given an increase in barometric pressure as well as an increase in wind velocity (Table 2.2). The odds of an individual transitioning from an inactive state to an active state decreased by 0.77 for every unit decrease in barometric pressure and increased by 1.20 for every unit increase in wind velocity. According to the global model, during Hurricane Michael individuals were significantly more likely to remain in an inactive state given an increase in wind velocity (Table 2.2). There was no significant relationship between barometric pressure and activity. The intercept was the only significant coefficient in the model that included only wind speed, and is therefore not reported. The odds of an individual transitioning from an inactive state to an active decreased by 0.90 for every unit increase in wind velocity.

Discussion

Based on results from EMbC analysis and multinomial logistic regression, we demonstrate that Eastern brown pelicans in the South Atlantic Bight respond to the passage of spatially-extensive cyclonic events by increasing time of inactivity, regardless of initial landfall proximity. We also found that barometric pressure and wind velocity were significant predictors of behavioral state, indicating that individuals may adjust their behavior in response to meteorological changes associated with storm conditions.

Among several classes of marine taxa, perturbations in barometric pressure appear to be a consistent predictor of behavioral change during storm events (Heupel *et al*. 2003, Liu *et al*. 2010, Udyawer *et al*. 2013, Udyawer *et al*. 2015). Evidence from terrestrial ecosystems also indicate that some bird species adjust their behavior in response to sudden decreases in atmospheric pressure. For example, Breuner *et al*. (2013) demonstrated that declining barometric pressure instigated an increase in food intake for captive white-crowned sparrows (*Zonotrichia leucophrys*). Similar results were obtained by Metcalfe *et al*. (2013) in white-throated sparrows (*Zonotrichia albicollis*). Our data suggest that pelicans likewise modify their behavior given sudden decreases in barometric pressure. Although fine scale fluctuations in absolute pressure may not be meaningful, or possibly even detectable, precipitous declines like those experienced during cyclonic events could indicate environmental conditions detrimental to individual condition.

Our results also show a strong predictive relationship between wind velocity and behavioral state in brown pelicans. Although wind velocity is infrequently considered as a driver of behavioral changes in strictly aquatic species compared to barometric pressure, it is reasonable to conclude that avian species requiring flight to forage or relocate would be especially sensitive to anomalous wind conditions. Observations of the movements of red-footed boobies (*Sula sula)* and great frigatebirds (*Fregata minor*) during cyclonic activity in the Southern Hemisphere suggest that individuals of these species are able to detect approaching gale-force winds as an indicator of an impending cyclone and utilize them for avoidance behavior, although this relationship was not explored quantitatively (Weimerskirch & Prudor 2019). In contrast to more pelagic species, pelican locomotion may be hampered by severely elevated wind velocities (Hainsworth 1988, Spear & Ainley 1997a), precluding avoidance behavior. Intrinsic differences in wing morphology (i.e. aspect ratio) and flight characteristics support this differential response in flight to increasing wind conditions (Spear & Ainley 1997b), although life stage and breeding status may be relevant as well (Weimerskirch & Prudor 2019).

Model results suggest that behavioral responses to storm activity may also vary with the magnitude of the storm itself. Of the three cyclonic events we assessed, meteorological conditions during Hurricane Irma included the highest and lowest absolute values for wind velocity and barometric pressure, respectively, and were significantly different from both Florence and Michael. These anomalous conditions were also maintained over a longer duration of time compared to other events. Our models for pelican behavior during Hurricane Irma indicated that both low barometric pressure and high wind velocity were highly significant predictors of inactivity; however, this trend differed among cyclonic events (Table 2.2). For example, pelicans experienced significantly lower wind velocities during Hurricane Florence and for a shorter duration. As such, our models showed a positive relationship between wind speed and activity, but this may be an artefact of the overall lower magnitude of wind velocity change from baseline during the event period. Similarly, Hurricane Michael was characterized by a moderate but relatively sudden decrease in barometric pressure, and models indicated an unexpected negative relationship with pelican activity (Fig. 2.3). It should be noted, however, that this term was non-significant in the top model and that a model including only wind velocity was also highly supported. We posit that cyclone characteristics contribute significantly to the degree of behavioral modification among individuals, and that events with a higher magnitude of change from 'baseline' over a longer period of time, such as experienced during Hurricane Irma, result in a greater reduction of activity than comparably weaker events. Events of greater magnitude may be more easily sensed by pelicans and with greater certainty of producing inclement conditions, eliciting a more detectable behavioral response.

Alternative sources of variation in model coefficients include sample size discrepancies, manifested as 'pelican-hours' (i.e., the number of tracked pelicans multiplied with the number of hours of each study period). For example, fewer individual pelicans were tracked during Hurricane Florence (n = 15) in comparison to Hurricane Irma (n = 18), exacerbated by a ten-day study period compared to a nineteen-day study period, respectively. This resulted in over twice as many 'pelican-hours' and subsequent behavioral classification points for Hurricane Irma than Florence, potentially adding greater resolution to behavioral contrasts between hurricane and non-hurricane time series. Models may also be sensitive to the magnitude of behavioral change displayed during different events, with comparatively weak reductions in activity being undetected. Additional data would therefore be required to determine if spatial sampling rate during data collection or storm characteristics (e.g. duration and intensity) would have greater influence on the magnitude of behavioral change detectable during future cyclonic events.

Timing of cyclones with respect to date and stage of the breeding cycle may also affect the overall activity rates. While Hurricanes Irma and Florence both occurred in early-to-mid September (soon after the end of chick-rearing), Hurricane Michael made landfall in early October, nearly a full month later in the annual cycle. Pelicans may endogenously be less active during later months as temperatures drop and energy maintenance becomes more prominent, but this requires further study, as does the extent of post-fledging care in this species.

Access to readily-available refugia in the form of barrier islands and estuarine systems may also positively act upon coastal seabirds to remain stationary during extreme meteorological conditions (Fig. 2.4). As strictly pelagic seabird species typically remain offshore for resource acquisition, access to shelter during the passage of a hurricane is functionally negligible. It is unclear whether pelagic species would attempt resting on the surface of the water as a sheltering strategy, given the likely turbulent conditions, probable reduction in foraging opportunity, and ability to maintain efficient flight even during severe wind conditions. Indeed, some tropical species appear to make use of terrestrial structures when cyclones approach breeding colonies and access to refugia is available, yet display avoidance behavior when encountering a cyclone at sea (Weimerskirch & Prudor 2019). Visual inspection of pelican tracks indicate a frequent use of protected estuarine habitats during severe storms, although further analysis of habitat associations is needed to determine the magnitude and significance of these relationships.

Lastly, the behavioral changes described in the present study occurred during cyclonic events that only indirectly impacted core-use areas. This indicates that the effects of hurricanes on coastal and marine taxa may extend well beyond those habitats centered on the eye of the storm. If changing global climate precipitates hurricanes of greater spatial extent (Knutson *et al*. 2015), impacts to wildlife may be more widespread than previously reported.

Conclusion

Hurricanes are acute meteorological disturbances that can act as significant environmental stressors to coastal and marine organisms. Despite the potential fitness consequences that they incur, species have adapted to the presence of episodic cyclonic events through behavioral modification and risk mitigation strategies. For Eastern brown pelicans in the South Atlantic Bight, this mitigation appears to be achieved through a decrease in movement and a prolonged maintenance of inactive behavior. These periods of rest occur in natural coastal structures such as barrier islands and estuarine systems, which provide shelter from many of the direct effects of hurricane exposure. While this strategy may be prevalent for large, coastal-dwelling seabirds, it is likely vastly different from strategies employed by other seabird guilds and by other marine vertebrate taxa, particularly those frequenting pelagic systems. Increased examination of animal movement responses to cyclonic events would greatly advance our understanding of how mobile organisms utilize behavioral modification to manage spatially-extensive environmental stressors, particularly in the face of climate change and the potential consequences for increased disruption therein.

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Table 2.1. Summary of meteorological data for each cyclonic event in the South Atlantic Bight from 2017 – 2018 with the number of pelican locations recorded during each study period (temporal range of ‘baseline’ conditions, defined in-text). BP = barometric pressure, WV = wind velocity. Letters within each column indicate significant differences between study periods based on Wilcoxon rank sum test.

Cyclone	BP Monthly Mean (kPa)	BP Minimum (kPa)	WV Monthly Mean (km/h)	WV Maximum (km/h)	Study Period	Locations (*n*)
Irma	101.25 ± 0.43^{a}	99.59^{a}	10.4 ± 10.9^{a}	61.2^{a}	6 – 24 Sept. 2017	2901
Florence	101.56 ± 0.49^{b}	100.17^{b}	10.2 ± 7.2^{b}	33.8^{b}	9 – 18 Sept. 2018	1323
Michael	101.63 ± 0.58^{c}	99.80^{c}	11.3 ± 8.4^{b}	49.9^{b}	1 – 20 Oct. 2018	2124

Table 2.2. Results of pooled behavioral state modeling using multinomial logistic regression in relation to environmental variables representing passage of Hurricanes Irma (I), Florence (F), and Michael (M). Asterisks represent *p*-values for significant terms ($p < 0.05$ = *, $p < 0.001$ = **).

Variable	Coefficient	Standard Error	t-value
Intercept (I)**	0.9991	0.0424	23.5649
Barometric Pressure (I)*	0.0978	0.0462	2.1166
Wind Speed (I)**	-0.1744	0.0474	-3.6760
Intercept (F)**	0.6370	0.0584	10.9010
Barometric Pressure (F)**	0.2600	0.0776	3.3498
Wind Speed (F)*	0.1822	0.0780	2.3360
Intercept (M)**	0.3678	0.0443	8.2979
Barometric Pressure (M)	-0.0872	0.0466	-1.8701
Wind Speed (M)*	-0.1088	0.0467	-2.3314

Figure 2.1. Path and windswath extent of Hurricanes Irma (A), Florence (B), and Michael (C) in the South Atlantic Bight with (D) 25% utilization distribution obtained from kernel density analysis of tracked pelicans during the month corresponding to the passage of each hurricane. White stars represent locations of meteorological data collection, with NOAA station identification numbers. Red dots represent Savannah, Georgia, USA. Hurricane data obtained from the NOAA National Hurricane Center and Central Pacific Hurricane Center (https://www.nhc.noaa.gov/gis/).

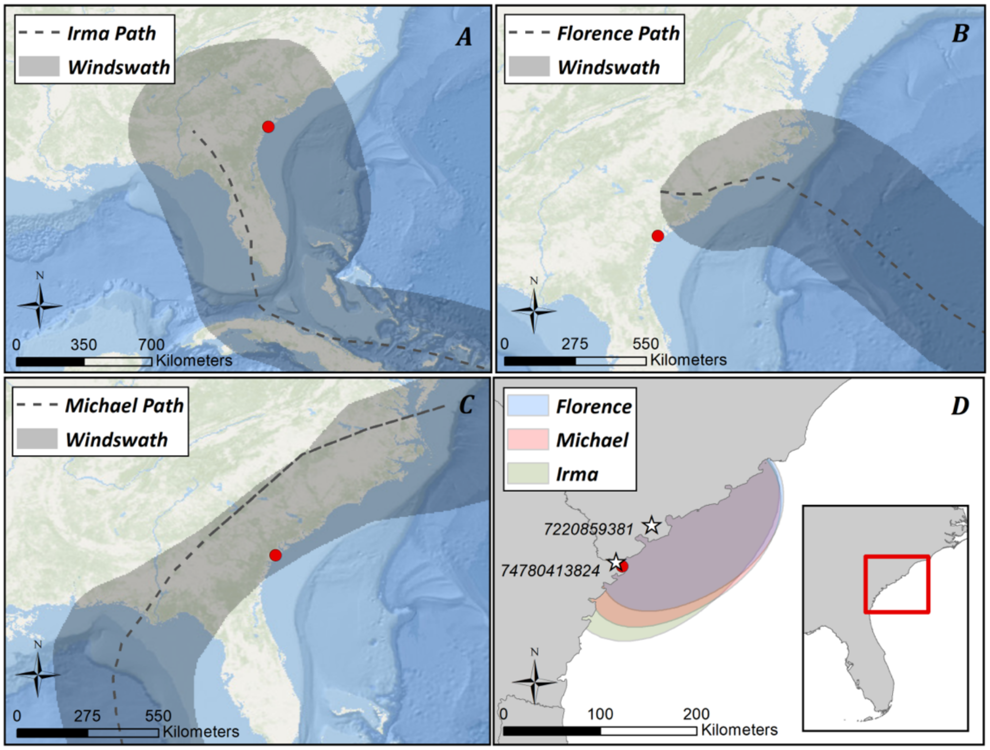

Figure 2.2. Example scatterplot of Expectation Maximization binary Clustering (EMbC) discretization for one individual Eastern brown pelican in the South Atlantic Bight from 6 – 24 September 2017. Gray lines represent delimiters for categorizing the four possible behavioral states. Note that delimiters do not determine a perfect partition of the variable space, and therefore do not converge perfectly on a graphical plane. Additionally, some points are within the delimiters of separate behavioral states; this is a result of the applied smoothing parameter. See [38] for additional details. All points labeled LH, HL, and HH represent active states; LL represents an inactive state.

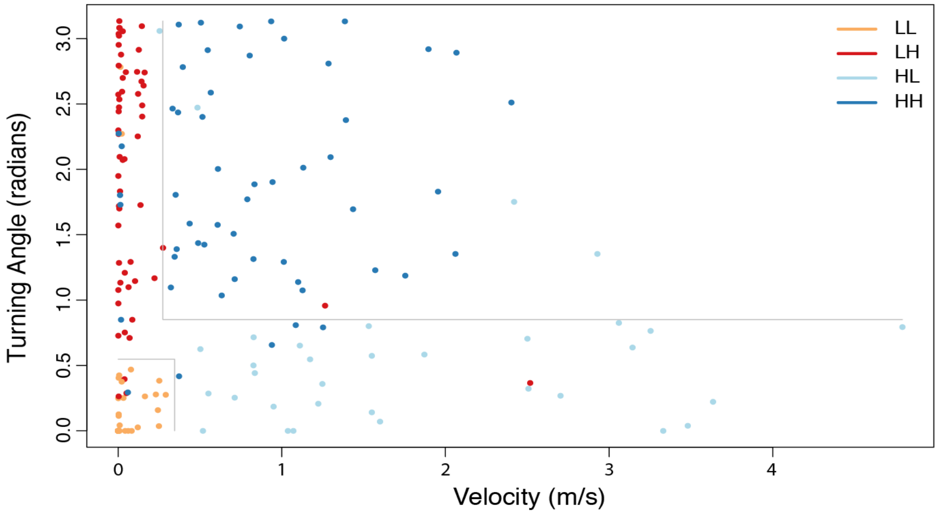

Figure 2.3. Hourly barometric pressure and wind velocity recorded during the study period of Hurricanes Irma, Florence, and Michael. Solid or light grey lines represent Irma, dotted or black lines represent Florence, and dashed or medium grey lines represent Michael, respectively.

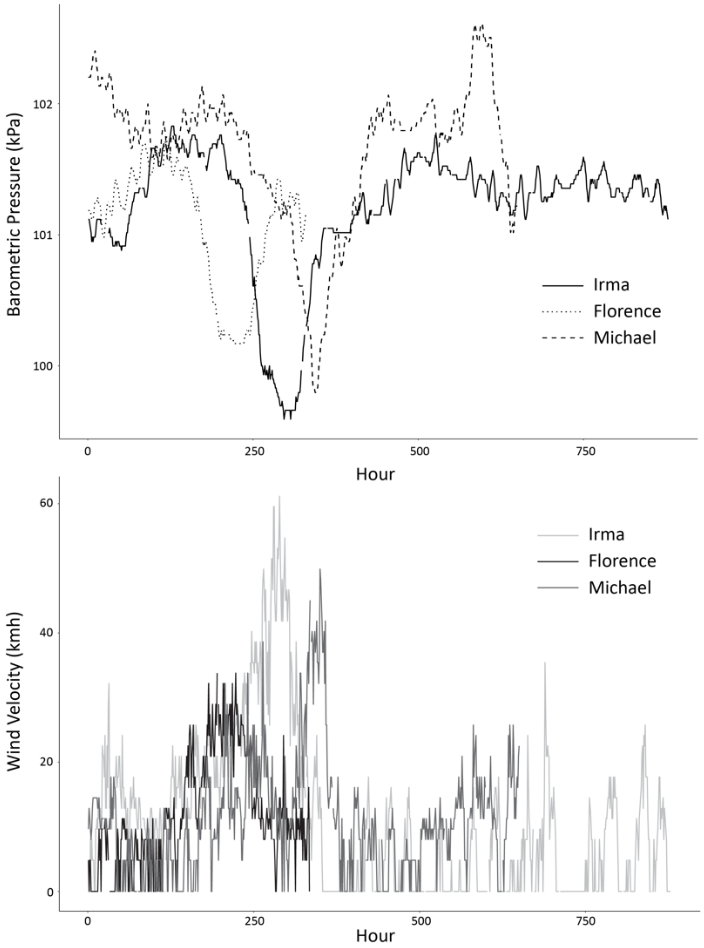

Figure 2.4. Example habitats used by Eastern brown pelicans during the passage of Hurricane Irma through the South Atlantic Bight on 11 September 2017. A) Individual pelican moving progressively inland up a coastal river, settling on both a barrier island and in an estuary. B) Individual pelican sheltering on a small barrier island for the duration of the cyclone, with C) inset of the island.

CHAPTER THREE

URBAN PROXIMITY WHILE BREEDING IS NOT A PREDICTOR OF PERFLUOROALKYL SUBSTANCE CONTAMINATION IN THE EGGS OF BROWN PELICANS[2]

Abstract

Identifying sources of exposure to chemical stressors is difficult when both target organisms and stressors are highly mobile. While previous studies have demonstrated that populations of some organisms proximal to urban centers may display increased burdens of human-created chemicals compared to more distal populations, this relationship may not be universal when applied to organisms and stressors capable of transboundary movements. We examined eggs of brown pelicans (*Pelecanus occidentalis*), a nearshore seabird with daily movements ranging from local to 50 km and annual migrations ranging from year-round residency to 1500 km. Thirty-six eggs from three breeding colonies located at increasing distances to a major urban center (Charleston, South Carolina, USA) were analyzed for concentrations of per- and polyfluoroalkyl substances (PFAS). Areas of high use for each colony during the breeding season were also assessed via the tracking of adult pelicans from each colony using GPS-PTT satellite transmitters and overlapped with measures of relative urbanization via land cover data. We report potentially significant ∑PFAS concentrations in the eggs of pelicans (175.4 ± 120.1 ng/g w wt. SD), driven largely by linear perfluorooctane sulfonate (n-PFOS) (48 – 546 ng/g w wt.). Residues of the precursor compound perfluorooctane sulfonamide (FOSA) were also present in pelican eggs, suggesting continued exposure of local wildlife beyond implemented phaseouts of some PFAS. For most analytes, egg concentrations did not

exhibit a significant spatial structure despite some differentiation in high-use areas unlike similar data for another regional apex predator, the bottlenose dolphin (*Tursiops truncatus*). We suggest that the partially migratory nature of brown pelicans during the non-breeding season, combined with daily ranges that may extend to 50 km from local point sources, may have homogenized exposure across individuals. Charleston likely remains a major source for PFAS in the overall region, however, given the high concentrations observed as well as known releases of PFAS in the nearshore environment.

[2] Wilkinson, B. P., Robuck, A. R., Lohmann, R., Pickard, H. M., & Jodice, P. G. R. (2022). Urban proximity while breeding is not a predictor of perfluoroalkyl substance contamination in the eggs of brown pelicans. Science of the Total Environment, 803, 150110.

Introduction

Ranging behaviors of highly mobile organisms can expose these species to lethal and sublethal stressors not experienced by more sedentary organisms (Jodice & Suryan 2010, Mello *et al*. 2016, Odsjö 1975). The risks to vagile organisms are amplified when the stressors themselves are also mobile in nature, capable of affecting organisms across relatively broad spatial or temporal scales (Cabrera-Cruz *et al*. 2018, Henkel *et al*. 2012). The opportunity for individuals far from local sources of exposure to encounter the stressor should be greater when both organism and stressor are capable of frequently moving among systems, compared to organisms which occupy a distinct spatiotemporal distribution removed from the stressor or for which the stressor is relatively concentrated in a given area. Proximity to sources of environmental stressors may therefore only be a good predictor of exposure for relatively sedentary populations or those with distinct, consistent, or local ranges, and may not be as relevant for highly mobile species interacting with a highly mobile environmental stressor (Adams *et al*. 2008, Power *et al*. 2020).

Anthropogenic chemicals, including compounds of emergent interest such as per- and polyfluoroalkyl substances (PFAS), can act as mobile stressors because they are capable of long-range dispersal from point sources (Lohmann *et al*. 2007). PFAS are widespread chemicals that are persistent in both marine and terrestrial environments worldwide (Houde *et al*. 2006a). Manufactured for their stability and ability to repel both oily and aqueous substances, PFAS have been used for coating paper and packaging products, non-stick cookware, stain-resistant carpet and clothing, as industrial surfactants, and in fire-fighting foams (Sunderland *et al*. 2019). In production since the 1940s, PFAS contamination in the environment has occurred globally via both direct release and remote transport (Armitage *et al*. 2009). Perfluorooctane sulfonate (PFOS) and perfluorooctanoate (PFOA), two of the most commonly-detected PFAS, have been observed to be pervasive in the blood of both wildlife and human populations, and are associated with harmful and diverse biological effects across taxa (Fenton *et al*. 2020, Houde *et al*. 2006a, Houde *et al*. 2011, Sunderland *et al*. 2019).

Exposure to PFAS can vary by physicochemical properties of the compound, toxicokinetic and ecological qualities of the organism at risk, or characteristics of the ecosystem within which the organism resides. For example, PFAS bioaccumulate and biomagnify in apex predators via direct consumption of contaminated prey, making them particularly harmful to species that occupy upper trophic levels (Houde *et al*. 2006b). Individual exposure can also be affected by intrinsic properties of the ecosystem in which the species forages as well as the behavior of the organism itself. For example, large-scale boundary habitats (i.e., coastal systems) which integrate pollution inputs from both marine and terrestrial domains may present a higher risk to individuals that forage there as opposed to individuals that forage in systems that tend to function as isolated units or have less input from adjacent systems (i.e., pelagic habitats or upland systems) (Crain *et al*. 2009). Furthermore, exposure potential may not be spatially predictable within an ecosystem, and different aspects of the abiotic environment may serve to collect or distribute risk. For example, although areas with high levels of urban development can concentrate anthropogenic stressors such as toxic pollutants (Adams *et al*. 2014, Gewurtz *et al*. 2016), the transport capabilities of many ecological toxicants can result in high levels of exposure even to organisms relatively far from source inputs (Robuck *et al*. 2020). The long-range broadcasting of risk may thus create a heterogenous exposure landscape that is not defined simply by the location of the source.

Our goal was to assess PFAS concentrations in the eggs of a highly mobile apex predator breeding near an urbanized landscape. Charleston, South Carolina, USA is a rapidly developing city located within a complex coastal morphology of rivers, estuaries, and nearshore marine environments. Prior research suggests that habitats in the Charleston region have significantly elevated levels of PFAS relative to other regions (Keller *et al*. 2005, Houde *et al*. 2006b, Vander Pol *et al*. 2012, Bangma *et al*. 2017). For example, White *et al*. (2015) reported sediment PFAS concentrations from estuarine habitats in and around Charleston Harbor in excess of any other previously examined U.S. city, with approximately half of tested sites within the study area above the global median concentration for PFOS (0.54 ng/g d wt.). Bottlenose dolphins (*Tursiops truncatus*) resident within the harbor possess plasma PFAS levels comparable to occupationally exposed humans and are some of the highest recorded in marine mammals globally (Houde *et al*. 2005, Houde *et al*. 2006b, Fair *et al*. 2013, Fair & Houde 2018). Several fish species frequently consumed by both humans and wildlife in the Charleston area also were commonly above recommended levels for safe consumption by mammals, posing a potentially significant health risk (Fair *et al*. 2019).

Here we assess concentrations of 24 PFAS in 36 eggs of a locally abundant seabird, the Eastern brown pelican (*Pelecanus occidentalis carolinensis*). Pelicans nest colonially on only 2-3 islands within the vicinity of Charleston in any given year, and these islands and the colonies on them vary in both distance from the urban center (~ 2 – 35 km) as well as in the number of breeding adults (~ 250 – 3000 pairs). We hypothesized there would be an inverse relationship between distance to Charleston Harbor and ΣPFAS, with birds breeding closer to the urban center and therefore also closer to likely point sources acquiring greater toxicity burdens. Therefore, we sought to (i) assess the presence of PFAS in pelican eggs from the Charleston Harbor region relative to published values for other seabird eggs collected from other locales and (ii) investigate the influence of urban habitat use on concentrations of PFAS in pelican eggs using movement data from an additional subset of GPS-tracked adult pelicans from each colony.

Methods

Sample collection and processing

Eggs for contaminant analysis were collected from three breeding colonies of Eastern brown pelicans located at progressively greater distances from urban Charleston (Fig. 3.1 & 3.2). Castle Pinckney (32° 46’ 26’’ N, 79° 54’ 40’’ W) is an urban seabird colony centrally located on a small shell island within the harbor and has hosted approximately 250 breeding pairs of brown pelicans near-annually since individuals first started nesting in 1999 (Jodice *et al*. 2007). Bird Key Stono (32° 38’ 00’’ N, 79° 58’ 04’’ W) is a larger sand island located at the mouth of the Stono River approximately 17 km to the southwest of Charleston Harbor. This island is a regionally important nesting site for brown pelicans, with approximately 3000 nesting pairs annually since recolonization in 2014 (Jodice *et al*. 2007, F. Sanders 2021). Deveaux Bank (32° 32’ 46’’ N, 80° 11’ 30’’ W) has hosted annual breeding pairs of brown pelicans since 1989, with an average count of 1300 nests per year (Jodice *et al*. 2007). Deveaux Bank is located approximately 37 km southwest of Charleston Harbor at the outflow of the North Edisto River.

Thirty-six eggs were collected in total, with efforts split evenly among colonies (*n* = 12 per breeding site). All eggs were collected between 10 May 2019 and 15 May 2019, with procedures approximating those of Vander Pol *et al*. (2012). Briefly, eggs were floated to estimate approximate age, with an effort made to collect eggs in as early a stage of incubation as possible. Brown pelicans typically lay a clutch of three eggs, and we aimed to collect first-laid eggs as these tend to have higher concentrations of maternally transferred chemical compounds than second- and third-laid eggs (Parolini *et al*. 2021, Vicente *et al*. 2015). The laying order of eggs was based on visual inspection of shell cleanness. Only eggs which sank in water were collected for analysis, with resting angles ranging from approximately 0°- 60° relative to the bottom of the floating vessel (Rush *et al*. 2007). Only one egg was collected per nest, and an attempt was made to distribute the collection throughout the spatial footprint of the colony (~ 0.01 km^2). Eggs were transported from the colony to an off-site refrigerator (4°C) until homogenization. Egg contents were separated from the shell and homogenized using a bag mixer (BagMixer 400 W, Interscience Laboratories, Inc.) in non-filter 400 mL polyolefin blender bags (BagLight PolySilk, Interscience Laboratories, Inc.). Aliquots of homogenized sample (15 mL) were then transferred to polypropylene vials via individual transfer pipettes and stored at -80°C until sample extraction and analysis (March 2020).

Sample preparation and analysis

Sample preparation and analysis followed a modified protocol based on Chu & Letcher (2008). Sample aliquots were thawed at room temperature, and 0.5 g of homogenate were weighed into polypropylene centrifuge tubes and spiked with 20 µL of isotopically labeled internal standard (0.5 ng/µL). Samples were extracted with 4 mL 10 mM potassium hydroxide (KOH) in methanol (MeOH) and vortexed. Following sonication (20 min) and centrifugation (2 min x 4000 rpm), the resulting supernatant was transferred to 15 mL polypropylene tubes. Remaining pellets received a secondary wash of 4 mL 10 mM KOH in MeOH, sonication, and centrifugation (10 min x 4000 rpm), with supernatant decanted and added to the prior fraction.

Supernatant samples were diluted with 80 mL of Milli-Q (MQ) water prior to solid phase extraction (SPE). Waters Oasis WAX cartridges (Waters Corp.) were preconditioned with 4 mL 0.1% ammonium hydroxide (NH_4OH) in MeOH, 4 mL MeOH, and 4 mL MQ water. Samples were then loaded onto cartridges at an approximate flow rate of 1 drop/sec. Cartridges were then allowed to dry under vacuum for 5 min and eluted with 4 mL MeOH and 4 mL 0.1% NH_4OH in MeOH. Eluent was collected in 15 mL polypropylene tubes containing 200 mg ENVI Carb sorbent. Following vortexing and centrifugation (10 min x 4,000 rpm), the resulting supernatant was transferred to 50 mL polypropylene tubes. The ENVI Carb sorbent was rinsed with MeOH, centrifuged, and the resulting supernatant was decanted and combined with the prior sample fraction. Samples were evaporated to dryness, and reconstituted using 50:50 water:MeOH with 2 mL ammonium acetate. Solutions were microcentrifuged at 15,000 rpm for 15 min and transferred to autosampler vials for analysis.

Sample extracts were analyzed for 24 PFAS using an Agilent (Santa Clara, CA, U.S.A.) 6460 triple quadrupole liquid chromatograph tandem mass spectrometer (LC-MS/MS) equipped with an Agilent 1290 Infinity Flex Cube online SPE, following previously published methods with slight modifications (Weber *et al*. 2017). A 100 µL aliquot of each sample extract was injected and loaded onto an Agilent Zorbax SB-Aq (4.6 x 12.5 mm; 5 µm) online SPE cartridge with 0.85 mL of 0.1% formic acid at a flow rate of 1 mL min^{-1}. Following sample loading, analytes were eluted from the SPE cartridge and loaded onto an Agilent Poroshell 120 EC-C18 (3.0 x 50 mm; 2.7 µm) reversed-phase HPLC column using ammonium acetate (2 mM) in MQ water (A) and ammonium acetate (2mM) in MeOH (B) at a flow rate of 0.5 mL min^{-1} and a column temperature of 50°C. Initial gradient conditions were 97% A and 3% B. From 0.85 to 3.5 min the gradient was linearly increased to 54% B and from 3.5 to 15 mins, linearly increased to 85% B, before increasing to 100% B and maintaining at 100% B from 15.5 to 16.5 mins. Sample analytes were introduced to the tandem mass spectrometer after being ionized with an electrospray ionization source operated in negative ion mode at a temperature of 300°C, gas flow rate of 13 L min^{-1}, and nebulizer pressure of 45 psi.

Quality assurance and quality control

Matrix spikes and procedural blanks were included with the sample set to monitor matrix effects, process recovery, and background contamination. Matrix effects were addressed using a 7-point matrix-matched curve, made up of chicken egg homogenate extracted in an identical fashion to egg samples, and spiked with native and isotope-labelled standards directly prior to analysis. The chicken egg matrix used for the curve contained trace levels of n-PFOS and was corrected for background n-PFOS using the average of triplicate chicken egg samples taken through the extraction. Recoveries for detected compounds ranged from 27 - 150% for FOSA, perfluorotridecanoate (PFTrDA), and perfluorotetradecanoate (PFTeDA) having the lowest recoveries due to predictable loss of these analytes during sample preparation (Taniyasu *et al*. 2005). Excluding these outliers, average analyte recovery ranged from 63 - 150%, with an average recovery of 78%. Data reported in this study were not blank corrected, due to low levels of process contamination identified in procedural blanks. Method detection limits (MDLs) were defined as procedural blank levels of a given analyte plus 3 times the standard deviation. In the absence of quantifiable blank concentrations, the lowest curve point (0.25 ng/mL) was deemed the method detection limit. Values below MDLs were considered zero for summation purposes. Summary statistics and group comparisons were derived using uncensored data analyzed using the *cenfit* function in the R package *NADA* version 1.6 - 1.1 (Lee 2020) to account for artifacts of left-censored data (Helsel 2011). Significant differences in contaminant concentrations among colonies were assessed using both uncensored and censored log-transformed data. The *cendiff* function in the R package *NADA*, which uses Kaplan-Meier (KM) model estimates, was used to evaluate group differences via Peto & Peto modification of the Gehan-Wilcoxon test. Left-censored data was also assessed for significant differences by habitat and compound using Kruskal-Wallis tests followed by post-hoc application of Dunn's test for multiple comparisons.

GPS tracking and spatial analysis

Movements of representative adult brown pelicans were ascertained via GPS satellite tracking during the nesting period. GPS-equipped pelicans were not the same individuals from which eggs were collected; therefore comparisons between contaminant exposure and movement are population-based (i.e., at the level of the colony) and not individual-based. For the purposes of contaminant exposure, we also assume that habitat use before and after egg laying is approximately equivalent. Adult pelicans typically spend 2-3 weeks at the colony engaged in courtship activities (e.g. nest site selections, mate advertisement, nest construction) prior to egg laying (Schreiber 1977) and during incubation and chick-rearing forage within the vicinity of the colony while mates trade-off incubation, nest attendance, and provisioning duties. A total of 68 solar-powered GPS-PTT units (GeoTrak Inc., North Carolina, USA) were deployed annually in spring/summer from 2017-2020 on adult pelicans during incubation or early (i.e., 2-4 weeks post-hatch) chick-rearing (Castle Pinckney, $n = 20$; Bird Key Stono, $n = 25$; Deveaux Bank, $n = 23$). Transmitters weighed ~65 g (10 x 3.3 x 3 cm) and were ≤3% body mass of instrumented pelicans (range = 2475 – 4350 g). Adult pelicans were captured at the nest with either a leg or neck lasso and equipped in the field. Transmitters were attached dorsally via a backpack-style harness system as described in Lamb *et al*. (2017a), and were programmed to record 12 GPS positional fixes per day at 90 min intervals between the hours of 10:00 – 02:30 GMT (fixes limited by power availability). Unit error was assumed to be approximate to that of Lamb *et al*. (2017b), i.e. 4.03 ± 2.79 m. Equipped pelicans were typically released within 20 mins of capture and 50 m of the nest site.

We used a recursive detection algorithm in the R package *recurse* (Bracis *et al*. 2018) to identify nest-site attendance of instrumented pelicans for delimiting breeding locations. Exact nest coordinates were extracted from release locations, with a 250 m radius buffer established around each nest. Regular nest attendance was defined as the presence of locational fixes within the 250 m radius buffer separated by $\leq$168 hrs. This relatively conservative time cutoff was chosen to balance the infrequency of locational fixes compared to the amount of time an adult may spend at the nest, which decreases as chicks age (Sachs & Jodice 2009), with the observation that pelican chicks may be able to survive without provisioning for at least 2 – 3 wks (Shields 2020). All GPS points were then extracted from initial deployment to the last date of nest attendance for each individual. For pelicans that remained near the nest site beyond the breeding season (i.e. non-migratory individuals), a 90-day cutoff was imposed for adults that were initially instrumented with chicks and a 120-day cutoff for adults initially instrumented with eggs, corresponding to the maximum recorded time to successfully raise offspring (Lamb *et al*. 2017b, Shields 2020). We included telemetry data from both incubation and chick-rearing stages in spatial analyses, as the majority of locations were collected during chick-rearing. It should be noted that home ranges tend to decrease in size as chicks age, so estimates of overlap in high-use areas by colony may be somewhat biased towards increased segregation (Geary *et al*. 2019). However, home range size reduction is driven by increased foraging site fidelity, so that habitats used during chick-rearing are derived from those used during incubation (Geary *et al*. 2019).

Breeding movements included n = 22,274 locational fixes and ranged from 12 May – 21 October within each year (mean duration = 34.4 ± 27.8 days). To identify high-use areas for each colony, we utilized a grid-cell based approach based on the number of GPS fixes per cell. To reduce spatial bias introduced by time spent at the nest, all points within 250 m of the relevant breeding colony were removed. A 2.25 km^2 grid was then imposed over the study area, and the number of locations in each cell was calculated using ArcMap version 10.1 (ESRI, Redlands, California, USA). For each colony, the upper quartile (25%) of grid cells containing the most points was defined as the area of high use and subsequently mapped. The upper quartile was chosen in part because the majority of cells above this threshold contained multiple relocations, indicating high use; additional grid cells beyond this level were populated almost exclusively by single relocations which is likely not reflective of frequent use at the population level.

We used the boundaries of 8-digit watersheds along the coastline of South Carolina to describe potential differences in urban habitat use by pelicans from each colony. We chose to use watershed boundaries not only because they are ecologically meaningful for coastal birds, but also because each watershed likely has a varying contaminant profile based on differences in source inputs. Hydrologic unit levels are defined by the U.S. Geological Survey and represent the standard units of measurement for describing watersheds. These definitions correspond to regional, subregional, accounting, and cataloging levels (nested from largest to smallest in size, respectively). 8-digit watersheds correspond to the cataloging level, and are therefore of relatively high resolution. Watershed boundaries were obtained from the S.C. Watershed Atlas (SCDHEC 2020a). Within ArcMap, we calculated the relative percentages of dominant land cover types by watershed following the Anderson Level I Land Use classification system (Anderson 1976) using data from the 2016 USGS National Land Cover Database (Jin *et al*. 2019). We also calculated the number of facilities with a National Pollutant

Discharge Elimination Discharge (NPDES) permit registered in each watershed (SCDHEC 2020b). Finally, the percentage of high-use grid cells for each pelican colony that occurred in each watershed was calculated as a measure of overlap with urbanized habitats, for the purpose of making qualitative comparisons in urban habitat use between colonies. In this way, we expected that eggs from pelican colonies linked to highly urbanized habitat use (i.e., a large percentage of high-use grid cells occurring in watersheds dominated by urban land cover) would contain greater concentrations of PFAS than eggs from pelican colonies linked to lower urban habitat use if urban exposure was indeed a reliable predictor of PFAS contamination (e.g., Adams *et al*. 2008).

Results and Discussion

Of the 24 PFAS analytes assessed, 15 were measured above detection limits in ≥ 50% of pelican eggs sampled across colonies (Table 3.1). Perfluorohexanesulfonic acid (PFHxS), PFOS, PFOA, perfluorononanoic acid (PFNA), perfluorodecanoic acid (PFDA), perfluoroundecanoic acid (PFUnDA), perfluorododecanoic acid (PFDoA), and PFTeDA were found in 100% of tested samples. When averaged by colony location, eggs from Deveaux Bank contained the highest mean ∑PFAS concentration (202 ± 148 ng/g w wt, $n = 12$), followed by Castle Pinckney (192 ± 137 ng/g w wt, $n = 12$), and Bird Key Stono (132 ± 46 ng/g w wt, $n = 12$), although these differences were not statistically significant likely due to the high variability among samples within colonies (Fig. 3.3). The most abundant compound across all samples was n-PFOS (mean = 127.5 ± 17.5; range = 48 – 546 ng/g w wt, $n = 36$). After n-PFOS, the following most abundant compounds included PFDA (12.7 ± 0.8; 3 – 25 ng/g w wt), PFUnDA (7.5 ± 0.5; 2 – 14 ng/g w wt), PFTrDA (6.2 ± 0.5; 0 – 15 ng/g w wt), and PFNA (4.1 ± 0.2; 1 – 7 ng/g w wt). Of these, only PFNA exhibited significant differences in concentrations among colonies, being higher at Deveaux Bank compared to Castle Pinckney (Fig. 3.4). Other analytes found to significantly differ in concentration among colonies were FOSA, perfluoropentanoic acid (PFPeA), and PFOA although the pattern of differences among colonies differed among analytes (Fig. 3.4). Concentrations of all remaining analytes examined did not differ significantly among colonies. Although few statistical differences were found, we should note some caution may be warranted given the relatively small number of sampled eggs and potential limitations of statistical power.

Five watersheds contained at least 10% of high-use grid cells for any of the three pelican colonies, including the Edisto River, St. Helena Island, Cooper River, Bulls Bay, and Stono River watersheds. Of these, the most highly urbanized watershed was the Cooper River (17.3% developed land), which also contained nearly 4 times the number of NPDES-registered facilities (68) as the next nearest watershed (Table 3.2). All remaining watersheds contained < 10% developed land cover, and < 20 NPDES facilities. Pelicans from Castle Pinckney used the Cooper River watershed the most frequently (58.8% overlap), while use by individuals from Bird Key Stono was infrequent (8.9%) and use by individuals from Deveaux Bank was absent(Table 3.2). Individuals from Bird Key Stono instead used all five watersheds at relatively similar levels (range = 8.9 – 28.3%), while over half of the high-use grid cells for individuals from Deveaux Bank occurred within the Edisto River watershed.

Potential sub-lethal effects

Brown pelican eggs from the Charleston region displayed relatively elevated levels of ∑PFAS (175.4 ± 120.1 ng/g w wt) compared to published values of ∑PFAS from eggs of other seabirds. These high concentrations were driven in large part by PFOS loads in individual eggs. Exposure to PFAS may precipitate reproductive impacts for seabirds, including pelicans. Critically, it remains unclear exactly which PFAS analytes or mixtures of analytes may induce reproductive impairment and at what concentrations these effects begin to manifest (Custer 2021). Research examining reproductive impacts to wild populations in field setting is especially limited (Custer 2021). Tree swallows (*Tachycineta bicolor*) at a contaminated location experienced a detectable reduction in hatching success when PFOS levels in eggs were as low as 148 ng/g w wt, and a 50% reduction in hatching success compared to the average rate throughout the USA with PFOS levels of 494 ng/g w wt (Custer *et al*. 2014). In the current study, 5 of 36 pelican eggs were above the 148 ng/g value and 2 of 36 were above the 494 ng/g value. Tartu *et al*. (2014) reported a correlation between plasma PFDoA concentrations and reduced hatching success in black-legged kittiwakes (*Rissa tridactyla*) from the Arctic. Additional research on tree swallows as well as great tits (*Parus major*) has suggested a possible association between reduced hatching success and elevated levels of PFDA at concentrations similar to those found in pelican eggs from this study (Groffen *et al*. 2019, Custer 2021). Taken together, these results suggest that further study of hatchability in relation to concentrations of PFAS may be warranted at pelican colonies in the region.

FOSA contamination and recent exposure

The concentrations of the semi-volatile precursor compound FOSA measured in brown pelican eggs (mean = 1.0 ± 0.1, range = 0 – 3 ng/g w wt) suggest relatively recent inputs of PFAS into the Charleston system extending beyond the phase-out period for this compound (Robuck *et al*. 2020). As avian consumers may have the capacity to biotransform FOSA *in vivo* to more stable compounds (e.g. PFOS; Gebbink *et al*. 2009), significant concentrations of precursor compounds may indicate that the metabolic capacity for transformation has been exceeded as a result of continued, elevated exposure to FOSA or other FOSA-precursors (Gebbink *et al*. 2016, Robuck *et al*. 2020). For example, over the period 1990-2010, Gebbink *et al*. (2011) were unable to detect FOSA in herring gull (*Larus argentatus*) eggs from the Great Lakes after 2006 which is consistent with industrial PFAS phase-outs during that same time period. Importantly, FOSA generally declined throughout the two decades of study, with concentrations never exceeding 1.7 ng/g w wt (Gebbink *et al*. 2011). A follow-up study also was unable to detect FOSA and other precursor compounds from eggs of herring gulls in the same area (Letcher *et al*. 2015). These patterns suggest that the occurrence of FOSA in our samples may be due to continued exposure and not to historic exposure, particularly given that we found brown pelican eggs with maximum concentrations of FOSA approaching 3 ng/g w wt (Table 3.1).

FOSA was also one of four compounds with significant differences in concentrations among colonies, and was most elevated in eggs from Castle Pinckney.

Foraging pelicans from this urban colony consistently showed frequent use of the Cooper and Ashley Rivers during the breeding season compared to pelicans from Bird Key Stono and Deveaux Bank, which both had relatively low overlap of high-use areas with the Cooper River watershed (Table 3.2). Together with the ability of FOSA to be biotransformed, and therefore the increased likelihood of relatively recent exposure, the spatial segregation of daily breeding-season movements found here suggest that differences in habitat used for foraging during reproduction may at least partially contribute to the loads of this precursor compound. Establishing interannual trends of FOSA concentrations from urban colonies such as Castle Pinckney may therefore assist efforts to determine changes in regional production or use that may drive changes in FOSA or FOSA precursor concentrations in the environment.

Other differences in analytes

While FOSA is likely influenced primarily by recent inputs of FOSA or its precursors into the local environment, observed differences in PFNA, PFPeA, and PFOA concentrations between colonies are likely influenced not only by freshwater industrial sources of these perfluorocarboxylic acids (PFCA). Most likely, the latent transport, oxidation, and accumulation of PFCA precursors will have contributed to the observed PFCA in the marine environments and biota (Ellis *et al*. 2004, Thackray *et al*. 2020). For example, Zhang *et al*. (2019) observed higher than expected bioaccumulation of PFPeA in marine plankton off the northeastern Atlantic coast of the United States, and attributed this to the *in situ* biotransformation of precursors. Several studies have implied that the consumption of marine prey is causing a PFAS profile enriched in longer-chain PFCAs, including PFNA (Dassuncao *et al*. 2017, Robuck *et al*. 2020). Indeed, longer chain PFCAs have been increasing linearly with time in seabird eggs globally (Gebbink *et al*. 2011, Miller *et al*. 2015, Pereira *et al*. 2021), perhaps as a result of an increased bioaccumulation ability of longer-chain compounds or an increase in their anthropogenic use. Pelican eggs from the current study contained high concentrations of several long-chain PFCAs (e.g. PFDA and PFUnDA) compared to shorter-chain analytes, and this may be a result of their highly marine diet.

Similarities in contamination profiles among colonies

A thorough assessment of contaminant profiles within an ecosystem is possible only when multiple species and temporal points are considered. For example, Adams *et al*. (2008) examined PFAS contamination in plasma of bottlenose dolphins from the Charleston region and suggested a positive relationship between contaminant concentrations and urban habitat use immediately following industrial PFAS phaseouts, which was consistent with our initial prediction. While the overall pattern of analyte abundance in the plasma of dolphins was similar to that found in pelican eggs during our study (PFOS > PFDA > PFUnDA > PFNA > PFOA), dolphins residing primarily in or near the harbor exhibited significantly higher concentrations of PFOS, PFDA, and PFUnDA compared to those living in a less urbanized environment (i.e., the Stono River estuary; Adams *et al*. 2008). No differences were found spatially for PFOA and PFNA (Adams *et al*. 2008). In contrast, we found no differences in levels of PFOS, PFDA, or

PFUnDA among pelican colonies based on the same land cover and watershed classifications, while reporting significant differences for PFOA and PFNA (Fig. 3.3). Of note is that pelicans from Deveaux Bank, which primarily used the Edisto River watershed, had the highest concentrations of PFOA and PFNA in sampled eggs. Two non-exclusive hypotheses explaining the spatial structuring found in Adams *et al*. (2008) compared to our results are that (i) the dolphin study reflected the direct release of PFAS from local point sources before industrial phaseouts in comparison to our study that occurred after phaseouts were implemented or that (ii) dolphins in the region may have displayed a higher degree of fidelity to specific locations compared to pelicans, especially across the annual cycle (i.e., a lack of migration in dolphins). The contrast between our results and those of Adams *et al*. (2008) highlights the need to examine multiple apex predators with different life histories and at different temporal points when investigating contaminant profiles for a given region.

Indeed, the relatively broad similarities in concentrations of the majority of PFAS analytes among the three pelican colonies in our study suggest that the frequency of using highly urbanized watersheds by foraging adults cannot reliably predict PFAS concentrations in eggs of brown pelicans. Lamb *et al*. (2020) made a similar conclusion when assessing concentrations of polycyclic aromatic hydrocarbons (PAHs) in blood samples of adult brown pelicans from the northern Gulf of Mexico. There, it was expected that PAHs would differ among regions of the Gulf based on differing background levels of oil and gas activity but the data did not consistently support that supposition. Lamb *et al*. (2020) posited that other inputs unrelated to the level of oil and gas activity and extensive ranging patterns in individuals may have contributed to the lack of consistent regional differences. Similarly, Newtoff & Emslie (2017) were unable to find differences in methylmercury concentrations in pelican eggs between two estuarine complexes with differing intensities of anthropogenic influence, contrary to expectations. While some tissues (e.g. blood) reflect relatively local contamination due to their high turnover times, and therefore tend to minimize the influence of migratory and non-breeding areas in determining source locations (Miller *et al*. 2020 but see Leat *et al*. 2013), eggs primarily reflect the contamination levels of the nutrient sources that were used to create them (Bond & Diamond 2010). Individuals may mobilize nutrients for egg production from energy reserves acquired while on migratory or non-breeding areas (*capital* strategy) or through the rapid conversion of local resources obtained at the breeding grounds (*income* strategy) (Drent & Daan 1980). Capital and income strategies are best represented, however, not as dichotomous alternatives but as two endpoints on a spectrum containing many intermediates (Meijer & Drent 1999). While the balance of endogenous versus exogenous nutrients involved in egg deposition in brown pelicans remains unclear, it is likely to be a combination of sources rather than one or the other in totality.

According to traditional life-history theory, species with large body sizes or those undertaking relatively short migrations are likely to favor a capital breeding strategy (Klaassen *et al*. 2006). Brown pelicans are one of the largest avian species in North America and exhibit a facultative partial migration that can range from completely sedentary to highly migratory (Lamb *et al*. 2017b). However, brown pelicans also lay relatively small eggs compared to other seabirds and a full clutch may comprise < 8 % body mass of an average adult (Bartholomew & Goldstein 1984). Pelicans may therefore pay a relatively low energetic cost for producing eggs, suggesting a reduced need to build energetic reserves for this purpose. The local estuarine systems inhabited by pre-breeding pelicans are also likely relatively productive, unlike more temperate or polar systems favored by capital breeders that may not be as predictably productive during pre-breeding for individuals returning from wintering areas (Schelske & Odum 1962, Hahn *et al*. 2011, Hupp *et al*. 2018). Results from Geary *et al*. (2020) indicated that adult pelicans begin the reproductive cycle foraging in suboptimal habitats relative to the surrounding environment, foraging in optimal habitats only as chicks age and energetic costs rise. This suggests that local productivity is not a limiting factor when considering resource acquisition immediately following egg laying, and that pre-breeding conditions are likely capable of providing the energy necessary for egg formation as well.

If brown pelicans are therefore capable of using local resources for egg production, their reliance on foraging habitats at the interface of actively dynamic and complex estuarine systems near Charleston may pose a significant risk for PFAS contamination, as the potential for the release, transport, and accumulation of harmful anthropogenic compounds appears high. Prior investigations into both abiotic and biotic PFAS concentrations centered on the estuarine regions of Charleston suggest that the surrounding aquatic environment, particularly the Cooper River watershed, may indeed be more heavily contaminated than other comparable urbanized estuaries (White *et al*. 2015, Fair & Houde 2018, Fair *et al*. 2019). Identifying specific source inputs of PFAS in the Charleston region, however, is difficult. Candidate sources include PFOS-contaminated groundwater associated with relatively recent releases of aqueous film-forming foams (AFFF) from Joint Charleston Air Force Base near the Ashley River (U.S. Army Corps of Engineers 2018), as well as older AFFF events from the former Charleston Navy Base on the Cooper River (operational from 1901-1996) (White *et al*. 2015). Wastewater treatment plants (WWTP) discharging effluent into Charleston Harbor have also been identified as potential sources, with tested effluent containing relatively large amounts of both PFOS and PFOA (Houde *et al*. 2006b). Other suggested point sources include commercial container ships entering the Port of Charleston as well as various anthropogenic activities along freshwater inputs, especially the Cooper River, which aggregates discharge from numerous industrial facilities indicated by NPDES permit registries (White *et al*. 2015, Leads & Weinstein 2019) (Fig. 3.1). Importantly, increasing concentrations from 2004-2012 of some compounds in estuarine sediments from the Charleston area suggest continuing inputs into the system despite widespread production bans in the early 2000s (White *et al*. 2015). Although the Cooper River watershed contained the highest levels of urban development as well as the most NPDES facilities, no watersheds examined were completely free of development or discharge facilities, indicating the widespread potential for PFAS exposure throughout the entirety of the study area.

However, if egg production is reliant instead on resources acquired during the non-breeding season or while migrating, local point sources of PFAS in urban Charleston may have a reduced impact on observed egg concentrations. Linking overwintering areas with contaminant exposure in brown pelicans is difficult and compounded by the relatively broad range occupied at the population level, driven by variation in post-breeding movements at the level of the individual (Poli 2015). For example, pelicans from colonies in the northern Gulf of Mexico did not exhibit uniform migratory strategies among individuals but instead displayed a range of behaviors from complete sedentarism to long-distance migrations (e.g., ~1500 km; Lamb *et al*. 2017b). Preliminary observations of GPS-tracked pelicans from our study colonies in South Carolina, as well as earlier tracking work by Poli (2015), suggest that high-use areas during the non-breeding season occur in coastal Georgia, Florida Bay, and Cuba, as well as along the central and southern coast of South Carolina (i.e., our study area). Each of the aforementioned regions is likely to have a discrete contaminant profile based on anthropogenic activity, local abiotic factors, and regional transport mechanisms (O'Connell *et al*. 2010, Robuck *et al*. 2020). The highly variable nature of pelican migratory destinations, both within and between individuals, may therefore have homogenized contaminant exposure between breeding colonies over relatively long temporal scales. This study highlights the need to resolve the relative importance of endogenous versus exogenous resources in eggs when examining contaminants in avian species for making assessments about where contamination may occur during the annual cycle.

A limitation of the current study was that we were unable to assess local habitat use for the same individual pelicans from which eggs were collected, due to logistical difficulties, instead relying on colony-level assessments of both movement and contaminant levels. The conclusions made are therefore applicable at the level of the colony, and may not reflect how individual-specific habitat use and movement patterns contributes to PFAS levels. Future studies may better resolve potential associations between habitat use and PFAS contamination by tracking and assaying the same individual.

Conclusion

Our results indicate that potentially impactful ∑PFAS concentrations exist in brown pelican eggs from the Charleston region. Taken together with previous studies as well as known releases of PFAS in the region (i.e. AFFF exposure from military installations), it appears that Charleston may act as a significant source for these contaminants in the nearshore environment. Impacts of this contamination remain unclear but the potential for reproductive or physiological impairment at current exposure levels appears to be possible based on previous avifaunal studies (Custer 2021). Contrary to expectations, we were unable to find a relationship between PFAS contamination and use of urbanized habitats for the majority of analytes studied. We therefore suggest that proximity to likely point sources for environmental contaminants may not always act as a reliable proxy for exposure when both stressor and organism are capable of transboundary movement, and that individuals even relatively distant from likely sources may still show elevated risk. Given that brown pelicans were previously listed under the Endangered Species Act largely as a result of interactions with anthropogenic contaminants (Wilkinson *et al*. 1994), continued monitoring of this species for PFAS contamination may be particularly valuable (Vander Pol *et al*. 2012).

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Table 3.1.Table of means (ng/g w wt.), standard errors, ranges, and % detection for compounds found in ≥ 50% of samples. Mean and standard error derived from NADA package to consider data below MDLs in estimation of summary stats. “n-“ and “br-“ refer to linear and branched analytes, respectively. Each colony has a sample size of (n = 12) eggs.

	Comp.	**FOSA**	**br - PFHxS**	**n - PFHxS**	**PFHpS**	**br - PFOS**	**n - PFOS**
	MDL	0.250	0.004	0.034	0.250	0.024	0.053
Castle Pinckney	**Mean**	1.135	0.041	0.504	1.425	7.615	141.17
	Std. Err.	0.1	0.002	0.1	0.4	1.4	35.5
	Range	0.4 - 3	0 - 0.1	0.2 - 1	0 - 6	0 - 16	74 - 546
	% Detect	100.0	92.3	100.0	53.8	92.3	100.0
Bird Key Stono	**Mean**	0.856	0.039	0.443	1.108	6.788	90.195
	Std. Err.	0.1	0.003	0.1	0.3	1.3	6.9
	Range	0 - 2	0 - 0.1	0.1 - 1	0 - 4	1 - 15	48 - 137
	% Detect	84.6	84.6	100.0	38.5	100.0	100.0
Deveaux Bank	**Mean**	0.986	0.041	0.503	1.479	7.678	151.22
	Std. Err.	0.2	0.002	0.1	0.4	1.8	37.6
	Range	0 - 3	0.03 - 0.1	0.2 - 1	0 - 5	0 - 28	80 - 527
	% Detect	100.0	100.0	100.0	53.8	92.3	100.0

PFTeDA	PFTrDA	PFDoA	PFUnDA	PFDA	PFNA	PFOA	PFPeA	PFDS
0.161	0.098	0.086	0.163	0.102	0.295	0.262	0.047	0.250
0.930	7.449	2.248	8.142	12.997	3.793	0.984	0.336	2.703
0.1	1.0	0.2	0.8	1.3	0.3	0.1	0.1	0.5
0.5 - 2	4 - 15	1 - 4	4 - 13	7 - 25	3 - 6	0.6 - 1	0 - 2	1 - 8
100.0	100.0	100.0	100.0	100.0	100.0	100.0	84.6	100.0
0.903	5.589	1.956	6.637	10.581	3.787	0.906	0.105	2.391
0.2	0.9	0.3	0.8	1.2	0.4	0.1	0.0	0.5
0.2 - 3	1 - 12	0.5 - 5	2 - 12	3 - 18	1 - 6	0.3 - 2	0 - 0.3	0 - 7
100.0	100.0	100.0	100.0	100.0	100.0	100.0	92.3	84.6
0.907	5.557	2.091	7.838	14.413	4.789	1.202	0.590	2.322
0.1	0.6	0.2	0.8	1.4	0.4	0.1	0.2	0.4
0.4 - 2	0 - 9	1 - 4	4 - 14	5 - 24	2 - 7	0.6 - 2	0.05 - 3	1 - 5
100.0	92.3	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 3.2. Percent land cover type, number of National Pollutant Discharge Elimination System (NPDES)-registered facilities, and percent high use grid cell occurrence by pelican colony for five watersheds in the Charleston, South Carolina region. Each watershed listed contained at least 10% of high use grid cells for at least one colony. Land cover classification follows the Anderson Level I Land Cover system.

Watershed	Edisto River	St. Helena Is.	Cooper River	Bulls Bay	Stono River
% Land Cover Type					
Developed	4.33	1.91	17.32	3.28	7.76
Forested	28.76	4.43	27.47	8.51	27.17
Agriculture	11.43	1.45	3.29	0.51	2.97
Wetland	38.93	22.74	34.40	31.54	36.67
Open Water	12.62	67.60	13.60	53.59	22.16
Barren Land	0.25	0.76	0.37	0.86	0.93
Shrub/Scrub	1.79	0.31	1.39	0.20	1.04
Grassland/Herbaceous	1.66	0.54	1.40	0.17	1.05
# of NPDES Permits					
Registered Facilities	18	5	68	11	4
% High Use Grid Cells					
Castle Pinckney	0.98	1.96	58.82	30.39	0.98
Bird Key Stono	12.78	14.44	8.89	13.89	28.33
Deveaux Bank	50.94	12.26	0.00	0.00	5.66

Figure 3.1. Map of the study area and relevant brown pelican colonies in coastal South Carolina, USA. Yellow, blue, and gray boxes indicate the locations of Castle Pinckney, Bird Key Stono, and Deveaux Bank, respectively. Red lines indicate eight-digit watershed boundaries with corresponding labels. Crosses indicate National Pollutant Discharge Elimination System (NPDES)-permitted discharge pipes, with the open circle indicating the location of Joint Base Charleston Air Force Base and the open triangle indicating the location of the former Charleston Navy Base.

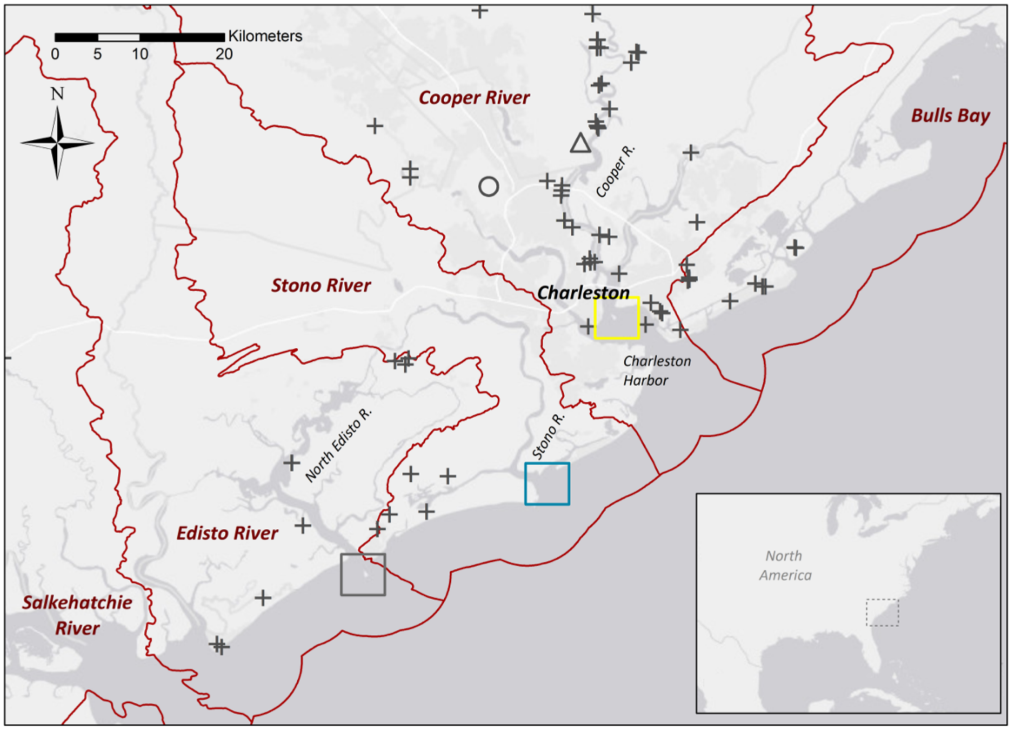


Figure 3.2. Map of the study area in coastal South Carolina, USA, with land cover types. Red lines indicate eight-digit watershed boundaries with corresponding labels. Note that specific land cover types were collated into dominant categories following the Anderson Level I Land Cover classification system for analysis.

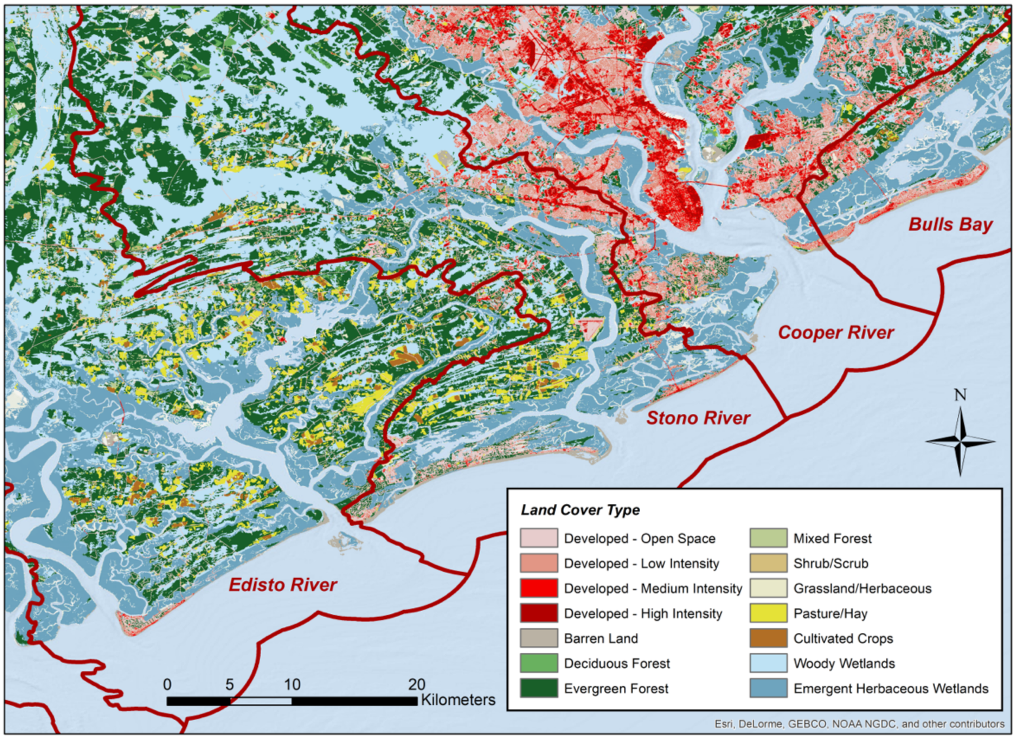


Figure 3.3. Boxplots of ∑PFAS (ng/g w wt.) representing 15 analytes found in sampled eggs from brown pelicans nesting on three colonies near Charleston, South Carolina. BK, CP, and DE signify Bird Key Stono, Castle Pinckney, and Deveaux Bank, respectively. Within the boxplots, dark lines represent the median, box limits denote the first and third quartiles, whiskers denote 1.5 times the interquartile range, and crosses denote outliers. Differences between colonies were not significant (as indicated by 'ns' notations).

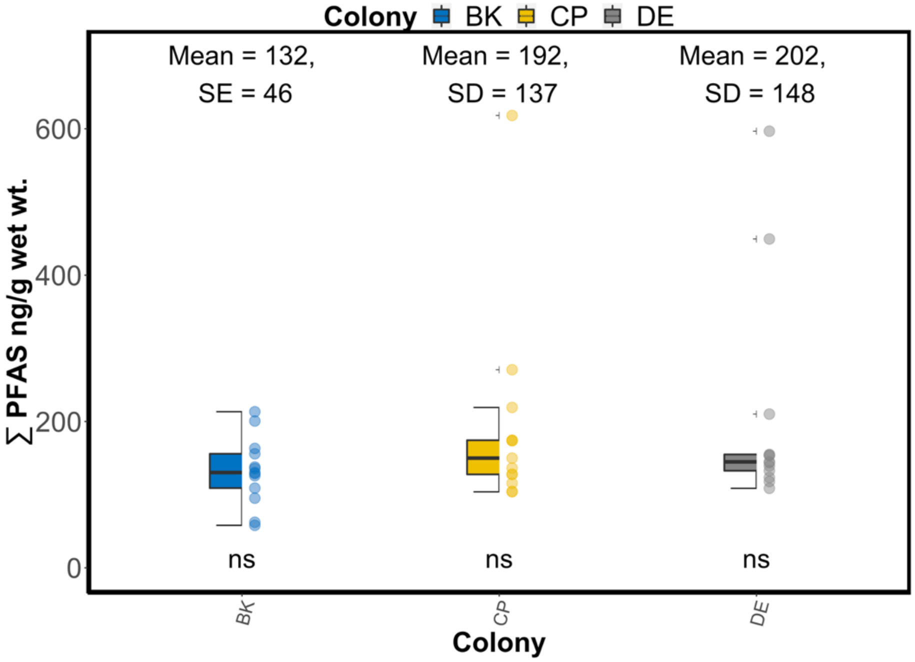
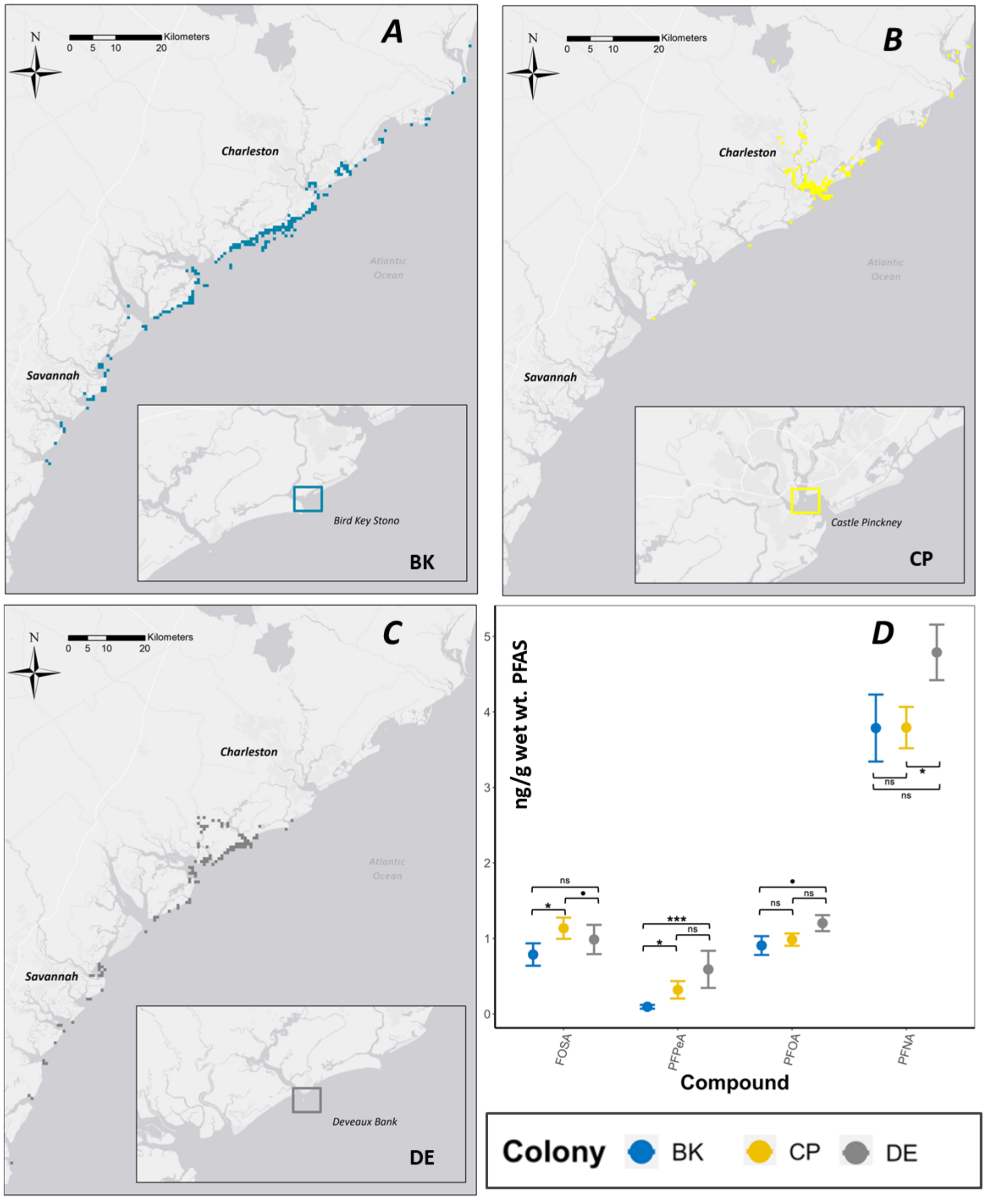


Figure 3.4. High-use areas of adult brown pelicans actively nesting on three colonies near Charleston, South Carolina, USA determined via GPS tracking. Blue squares represent high-use areas of birds from Bird Key Stono (A), yellow squares represent Castle Pinckney (B), and grey squares represent Deveaux Bank (C). Open boxes indicate colony locations following the same color scheme. Panel (D) shows points representing arithmetic means stratified by habitat, with whiskers denoting standard error. Differences between group means were determined using Dunn's test of multiple comparisons, with "ns" equal to "not significant", while * indicates $p < 0.05$, *** indicates $p < 0.001$, and • representing $p < 0.1$. BK, CP, and DE signify Bird Key Stono, Castle Pinckney, and Deveaux Bank, respectively.



CHAPTER FOUR

OIL SPILL MODELING INDICATES DIFFERENTIAL RISK TO FORAGING BROWN PELICANS

Abstract

Coastal seabirds are often among the species most heavily impacted by the accidental release of petroleum products into marine environments. Although spills from tankers have been decreasing over the past three decades, oil releases from general shipping activities has increased. Predicting where spilled oil may overlap with wildlife species of concern, however, is challenging due to the often complex nature of coastal marine hydrography and the difficulty of accurately assessing animal movement patterns. Among seabirds, brown pelicans (*Pelecanus occidentalis*) have historically been a species significantly affected by oil spills. On the Atlantic coast of the United States, the largest breeding colonies of brown pelicans are located near Charleston, South Carolina. Charleston Harbor is an important regional port for commercial shipping activity, and may further increase shipping traffic as a result of deepening its main channel. We used a publicly-available, no-cost toolkit for predicting oil spill trajectories (GNOME) constructed specifically for Charleston Harbor to identify the factors most likely to contribute to the potential overlap of spilled oil with foraging adult brown pelicans nesting on two nearby colonies. Using a matrix of 64 unique oil spill scenarios, results indicated that spills occurring within the boundaries of the harbor tended to produce low overlap with GPS tracked pelicans from both colonies as a result of relatively fast beaching times (70.3% of spills produced zero overlap). In contrast, spills occurring in the nearshore environment outside of the harbor displayed much higher rates of overlap and presented greater relative risk to foraging adult pelicans. Results from a zero-inflated generalized linear model indicated significant effects of spill size and pelican colony of origin on relative risk exposure, as well as interactions between month of spill and spill location. Pelicans nesting inside Charleston Harbor were at greater risk of exposure to surface oil than those nesting at a nearby colony located outside of the harbor, and risk was also positively associated with spill volume. Finally, risk tended to be elevated during the middle of the breeding season (June – July) for spills outside of the harbor, with potential consequences for reduced reproduction as a result.

Introduction

The unintended release of oil and other petroleum products into the environment continues to represent a substantial threat to wildlife as the global economy remains reliant upon fossil fuels as a primary source of energy (Chilvers & Battley 2019, Knol & Arbo 2014, Yaghmour 2019). Releases into marine and coastal systems are of particular concern due to the ability of spilled oil to travel long distances, remain in the environment for extended periods of time, exhibit stochastic dispersal patterns, and cause an array of primary and secondary effects to exposed individuals at even comparatively small concentrations (Maggini *et al*. 2017, Monson *et al*. 2000, North *et al*. 2011, Powers *et al*. 2013). For example, spilled oil can induce negative fitness effects, both lethal (Haney *et al*. 2014) and sublethal (Fallon *et al*. 2018), on contaminated individuals and alter populations at the regional scale long after the spill has occurred (Peterson *et al*. 2003, Votier *et al*. 2005, Walter *et al*. 2014).

Sources of spilled oil include wells and other infrastructure as well as vessels. With increases in safety-related infrastructure, governance, and navigational abilities, the number of spills originating from oil tankers has generally decreased since the 1990s even while the global volume of shipped oil has increased (Chen *et al*. 2019). The number of oil spills resulting from general shipping activities (i.e., cargo, bulk carriers, cruise ships, military, and fishing vessels), however, has consistently increased over the same period (Chilvers *et al*. 2021). The majority of these releases are comparatively small when examined next to high-profile disasters such as the *Exxon Valdez* spill or *Deepwater Horizon* blowout, yet still have the potential to cause significant ecological damage (e.g., Goldsworthy *et al*. 2000). Therefore, providing stakeholders and relevant agencies with predictive oil spill models can address current gaps in knowledge related to ship-based oil releases, especially when located near sensitive or protected ecological zones.

A significant challenge related to oil spill preparedness is the ability to reliably predict the spatial distribution of spilled oil, where it is most likely to interact with wildlife populations of interest, and the factors most likely to influence the spatial and temporal dynamics of these interactions (Chilvers & Battley 2019). Oil spills are more likely to occur in coastal areas, which tend to be highly biodiverse while also complex physically and hydrodynamically (Cakir *et al*. 2021, Marta-Almeida *et al*. 2013). This predictive challenge may be further compounded for wildlife managers and ecologists who may lack the hydrographic or technical expertise required to create realistic oil spill simulations. Conversely, those familiar with oil modeling techniques may be unequipped to analyze and interpret spatially-explicit wildlife data. Therefore, our goal was to bridge these two disciplines to create an accurate assessment of potential risk to a wildlife species demonstrated to be vulnerable to released oil in multiple regions, and to do so at a spatial and temporal scale that was locally-relevant to interested stakeholders.

Over the past two decades, the National Oceanic and Atmospheric Association (NOAA) Office of Response and Restoration has developed a publicly-available and easy-to-access toolkit for simulating oil spill trajectories based on realistic hydrodynamic conditions. This toolkit, known as the General NOAA Operational Modeling Environment (GNOME), allows users to generate fatalistic models of surface oil based on a suite of relevant input variables corresponding to both intrinsic (e.g., oil type and quantity) and extrinsic (e.g., wind speed, wind direction, water temperature) factors (Beegle-Krause 2001). Critically, location-specific modeling environments have been created within the GNOME framework that correspond generally to ports or regions with high levels of oil shipping activity, nested within five regions (Arctic, Atlantic, Gulf of Mexico, Pacific, and International). These localized modeling environments contain prepackaged information about the shorelines, tides, and currents of each particular place at scales more resolute and precise than the general GNOME toolkit. As these modeling environments are publicly available, at no cost, it is possible for interested parties to quickly and easily generate realistic oil spill scenarios locally matched to their location of interest.

We employed the GNOME toolkit to investigate the potential risk of ship-based oil spills in the Charleston Harbor, South Carolina, USA region to foraging adult brown pelicans (*Pelecanus occidentalis*). Charleston, one of the location-specific environments available in GNOME, is a particularly appropriate location to study the predictive overlap between oil spill scenarios and brown pelican distribution. First, there are several large and robust pelican colonies in the area, located at varying distances from both the port entrance and the main shipping channel (Jodice *et al*. 2007). Secondly, the U.S. Army Corps of Engineers is in the process of deepening the shipping channel by several meters within the harbor to accommodate the largest class of commercial vessels (Carse & Lewis 2020, Gourdin 2019). While allowing Charleston to expand its commercial port and increase shipping traffic, it also potentially elevates the risk of an oil spill into the nearby environment. Finally, the pelican population in this area is of high regional importance for the species, regularly hosting the largest breeding colonies on the Atlantic coast of the US (Jodice *et al*. 2013, Sanders *et al*. 2021).

To assess the potential for an oil spill in the harbor to impact brown pelicans, we used a matrix of 64 unique oil spill scenarios combined with GPS tracking data from adult brown pelicans from two nearby colonies. We sought to determine which macroscale factors influenced the relative risk to foraging adult pelicans of encountering surface oil in the Charleston Harbor region and to assess the importance of data gaps that may improve the models. Our modeling effort also provides an opportunity to assess the application of this readily-available toolkit to the determination of potential risk to coastal marine wildlife. We used broad-scale comparisons between the significant factors determining oil risk as modeled with the GNOME toolkit and observed outcomes of a documented oil accident in Charleston Harbor as a test of general agreement between GNOME simulations and actual spill events. Extensive or sensitively-located spills impacting high-use coastal habitat have been shown to have detrimental effects above the individual level, possibly contributing to regional declines for effected species (Carter *et al*. 2003, Piatt & Anderson 1996, Velando *et al*. 2005). This may be especially true for a species like brown pelicans, one of the seabird species most heavily impacted by the 2010 Deepwater Horizon event (Haney *et al*. 2014).

Methods

Oil spill modeling

All oil spill scenarios were simulated using the WebGNOME application (accessed August 2021; https://gnome.orr.noaa.gov), selecting the "Charleston Harbor, SC" location file. The spatial boundary for this location file is approximately a polygon encompassed by the coordinates (33°04.05 N, 80°10.71 W), (33°04.05 N, 79°37.71 W), (32°36.95 N, 79°37.71 W), and (32°36.95 N, 80°10.71 W). As spill location is often one of the most important factors determining exposure to wildlife (Chilvers *et al*. 2021), we used vessel-based Automatic Identification System (AIS) data to develop a probabilistic spatial grid based on actual vessel densities for selecting realistic spill locations *sensu* Brown *et al*. (2019). AIS data were obtained for the months spanning the approximate reproductive period of brown pelicans in the region (May - August) from the NOAA and Bureau of Ocean Energy Management online repository (MarineCadastre.gov; accessed

July 2021). We chose the reproductive period as this time of the annual cycle represents intense use of the harbor environment by foraging pelicans. We additionally chose to acquire AIS data from the year 2019 as it represents the latest year for which shipping data were available prior to the global coronavirus pandemic, which may have altered local shipping patterns (Millefiori *et al*. 2020). Briefly, AIS positional data were converted into vessel-specific track lines using the AIS Track Builder Pro 1.0 toolbox in ArcGIS Pro v 2.7.0. Track lines were then imposed on a 0.5 km x 0.5 km grid matched to the spatial boundaries of the GNOME location file. We then randomly selected two grid cells as locations for oil release to be used in subsequent modeling, with grid cell selection weighted by number of vessels (i.e., grid cells containing more vessel tracks were more likely to be selected as modeled spill locations). We also constrained selection such that one spill location was to occur within Charleston Harbor and one spill location was to occur in the nearshore waters outside of the harbor, with the purpose of discriminating the relative importance of spill location with respect to the harbor boundaries on the overlap of oil with adult pelicans (Fig. 4.1).

For context, one of the few documented oil spills to occur within Charleston Harbor occurred in September 2002, involving the release of an estimated 300 barrels of #6 fuel oil from the containership *M/V Everreach* (McCay *et al*. 2006). While the cause of the spill is thought to have arisen after the vessel grounded on a submerged dredge pipe in the upper reaches of the Cooper River, oil release was relatively protracted and occurred while the vessel proceeded to the unloading terminal and again as it exited the harbor along the path of the shipping channel (McCay *et al*. 2006). Discriminating how spill origin influenced oil trajectories and subsequently wildlife exposure in this case is complex, however, as the *M/V Everreach* release was spatially transient and the release involved the oiling of nearly 50 km of shoreline both within and outside of the harbor (McCay *et al*. 2006). We therefore sought to provide further insights into how release location influences oil trajectories at the scale of the harbor by imposing the aforementioned fixed spatial constraints.

In order to provide realistic values for environmental inputs into the GNOME model, we obtained relevant data for wind speed, wind direction, and sea surface temperature (SST) spatially matched to Charleston Harbor (Table 4.1). Data for daily average wind speed and daily sustained wind direction were acquired from the NOAA National Centers for Environmental Information covering the years 2011 - 2020 (station WBAN:13880), and averaged for each month of the study period (May - August). In this way, we calculated a single value for each month of oil spill simulations representing the average decadal wind speed and average decadal wind direction for that month. SST data were similarly obtained at six-minute intervals from the NOAA National Data Buoy Center for each month of the study period (May - August) spanning 2015 - 2019 (station CHTS1 - 8665530 - Charleston, Cooper River Entrance, SC). An average monthly value was then calculated from these data representing the five-year average SST for each month of the study period to be used in subsequent modeling.

Dates and times for modeled oil spills were chosen with the intention of providing the greatest possible influence of tidal stage on oil dispersion (i.e., the most discriminatory scenarios). We selected as dates for the modeled oil spills the day in each calendar month of the study period (May - August 2019) on which the maximum net tidal range occurred (i.e., the greatest difference between high and low tide). We then simulated oil spills to occur at low, rising (calculated as halfway between low and high), high, and falling (calculated as halfway between high and low) tides (Table 4.1). Each spill was therefore modeled as a point release (i.e., instantaneous release of oil) occurring at the aforementioned time.

We investigated the influence of oil spill size on the potential overlap with foraging pelicans by replicating each oil spill using two different volumes of spilled oil. As designated by the International Tanker Owners Pollution Federation, ‘small’ oil spills were modeled as releases of 50 barrels and ‘large’ spills were modeled as releases of 5000 barrels (note that the *M/V Everreach* spill involved ~300 barrels). As the GNOME model employs Lagrangian elements to spatially represent paths of spilled oil (hereafter ‘splots’), and the number of splots input into the model affects their overall distribution regardless of the size of the oil spill (Xu *et al*. 2013), we matched the number of modeled splots to the size of the modeled oil spill in a 1:1 ratio. In this way, each splot generated by the GNOME model represented one barrel of oil. All oil spills were modeled using general Heavy Fuel Oil #6, as this oil type is one of the most commonly released in shipping and tanker accidents causing impacts to wildlife (Chilvers *et al*. 2021).

Each oil spill model was terminated on the first whole hour (i.e., 60 min interval) at which spilled oil first became beached on land. We chose this variable cutoff time to investigate how differences in the factors listed above affected the amount of time it took for oil to first make contact with land. For pelicans at sea, contamination is likely to occur with surface oil as a result of their foraging behavior. We made the assumption that the longer oil is present on the surface of the water, the greater the risk of foraging pelicans encountering it and becoming contaminated. We also sought to compare oil fate estimates from GNOME (i.e., time to first make contact with land) with hindcasted oil fates derived from the *M/V Everreach* accident.

Brown pelican tracking

Methods used for obtaining and analyzing pelican tracking data were similar to Wilkinson *et al*. (2021). We deployed 45 solar-powered GPS-PTT units (GeoTrak Inc., North Carolina, USA) annually from 2017 - 2020 on adult brown pelicans nesting at two colonies proximal to Charleston Harbor (Bird Key Stono, *n* = 25; Castle Pinckney, *n* = 20; Fig. 4.1). Deployments occurred during incubation or early chick-rearing (i.e., 2-4 weeks post hatch). Transmitters (~65g, 10 x 3.3 x 3 cm) represented ≤ 3% body mass of instrumented pelicans (range = 2475 - 4350 g). Pelicans were captured at the nest and equipped with the GPS unit in the field using a backpack-style harness (see Lamb *et al*. (2017a) for attachment details). Units were programmed to record positional fixes at 90 min intervals from 10:00-02:30 GMT (fixes limited by power availability). Unit error was assumed to be 4.03 ± 2.79 m (Lamb *et al*. 2017b)

As we were interested in determining oil overlap with foraging pelicans during the breeding season, we used recursive behavioral patterns to extract only movements that occurred while individual birds were actively nesting. Nest coordinates for each pelican were extracted using release locations, and a 250 m radius buffer was established around each nest location (Wilkinson *et al*. 2021). Regular nest attendance was then identified using the R package *recurse* (Bracis *et al*. 2018), and defined as the presence of locational fixes occurring within the 250 m buffer separated by ≤ 168 hrs. We then extracted all locations from deployment until the final day of nest attendance. As some individual pelicans remain near the nest site year-round, we imposed a 90-day cutoff for adults that were initially instrumented during chick-rearing and a 120-day cutoff for adults that were initially instrumented during incubation, corresponding the maximum number of days recorded to successfully raise offspring (Lamb *et al*. 2017b, Shields 2020).

Oil spill risk

We determined the relative risk of spilled oil to foraging adult pelicans by using a grid-based approach based on the spatial boundaries of the GNOME location file. All calculations of spatial overlap were conducted using ArcMap v 10.1 (ESRI, California, USA). Both pelican tracking data (separated by month and colony of origin) and oil spill splots outputted from the GNOME model (separated by unique spill scenario) were projected onto a 0.5 km x 0.5 km grid using a WGS 1984 Web Mercator Auxiliary Sphere projection. We then used the *spatial join* function to search for grid cells in which both ≥ 1 pelican location and ≥ 1 oil splot occurred. To determine a relative risk score for each oil spill scenario unique to each pelican colony, we developed the following metric

$$R = (p/n) \times g$$

where R is the relative risk score, p is the number of unique pelicans from the colony of origin which overlapped with at least one oil splot for a given scenario, n is the total number of unique pelicans from the colony of origin tracked for the given oil spill scenario, and g is the total number of splots (i.e., barrels of oil) that occurred in the grid cells which contained pelican locations. In this way, our relative risk score represents the percentage of pelicans that overlapped with spilled oil out of the total number of pelicans that were tracked from each colony for each scenario (i.e., affected versus available), multiplied by the number of barrels they interacted with, to account for differences in sample sizes of pelicans between months and colonies. We included the multiplier g as a way to incorporate spill size into the measure of risk, as we assumed that the more oil occurred in a given cell with a tracked pelican, the more likely the pelican would be to actually encounter the spilled oil in a real-life setting. The number of barrels g was summed across all pelicans p such that if an individual pelican occurred in more than one grid cell containing oil, all barrels were added to the final total g while each individual was only counted once in the total p (i.e., an individual pelican could only be counted once in p but contribute all encountered oil across multiple grid cells to g).

Statistical analysis

Factors significantly influencing the relative risk score of oil contamination to foraging adult pelicans were assessed using a zero-inflated generalized linear model specified with a logit link Gamma error distribution. Due to the high number of zeroes present in the data, we specified both an intercept-only zero-inflated model for assessing the occurrence of non-zero data and a conditional model for assessing significant factors influencing relative risk score (i.e., a hurdle model) using package *glmmTMB* in program R (Brooks *et al*. 2017). Variables included in the global model were colony of origin, spill location, month of spill, tidal stage, and spill size. Variable significance was assessed using iterative removal, with model comparison following stepwise selection evaluated using Akaike's information criterion (AIC) values. Those variables which did not improve AIC were discarded. Two-way interaction terms for those variables which initially improved model AIC were added to the final model. The most appropriate model was then selected as that with the lowest overall AIC value.

Results

A total of $n = 64$ unique oil spill scenarios were generated in GNOME (2 size spills x 4 tidal stages x 2 starting location x 4 months), generating 128 relative risk scores (each scenario generated two risk scores, one for pelicans from Bird Key Stono and one for pelicans from Castle Pinckney). The number of tracked pelicans per month ranged from 5 - 20 individuals, generating 382 - 3632 points per month (Table 4.2).

Tracked pelicans from Castle Pinckney tended to use habitats both within and highly proximal to Charleston Harbor more consistently than pelicans from Bird Key Stono, which also included individuals that occupied coastal habitats further south along the coast to Savannah, Georgia (Fig. 4.2). Pelicans from both colonies, however, were rarely found > 5km offshore, instead using nearshore environments.

On a broad (km-level) scale, distribution of spilled oil depended largely upon the location of the release. According to the GNOME models, there were no scenarios where oil initially released inside the harbor exited the harbor, instead tending to quickly beach either on nearby Crab Bank or on the surrounding shoreline of the harbor (Fig. 4.3). Conversely, oil spilled outside of the harbor tended to be distributed to the northwest of the spill site in nearshore waters, rarely entering the mouth of the harbor, and this nearshore area is where most interactions with pelicans occurred (Fig. 4.4). Relative risk scores across all spill scenarios ranged from 0 - 1517 ($\bar{x} = 72.92$, median = 0.49).

In total, 70.3% of spill scenarios occurring inside the harbor did not have any overlap with GPS-tracked brown pelicans (i.e., no overlap in the aquatic environment). For the majority of these scenarios with zero overlap (62.2%), all oil beached before the first 60-min interval had passed (i.e., all oil spilled reached shore in less than one hour) thus providing very limited opportunities for spatial overlap with foraging pelicans. Relative risk scores for oil spilled inside the harbor ranged from 0 - 170 ($\bar{x} = 10.19$, median = 0.00). In contrast, nearly all spill scenarios occurring outside of the harbor had at least some overlap with foraging pelicans (92.2%). Relative risk scores for oil spilled outside the harbor ranged from 0 - 1517 ($\bar{x} = 135.64$, median = 6.41). Note that the highest possible relative risk score using our formula is 5000 (i.e., every available bird overlapping every barrel of oil for a large spill scenario).

Among complementary spill scenarios (i.e., all other factors equal), oil first beached significantly faster when released inside the harbor ($\bar{x} = 1.0$ hr) compared to outside of the harbor ($\bar{x} = 11.9$ hrs; paired Wilcoxon signed rank test, $Z = -7.38$, $p <$

0.001). In addition, large spills first reached shore significantly faster ($\overline{x} = 6.1$ hrs) than small spills ($\overline{x} = 6.8$ hrs; paired Wilcoxon signed rank test, $Z = 0.95$, $p < 0.01$). There were no significant effects of tidal stage (Kruskal-Wallis rank sum test, $X^2 = 0.31$, $p > 0.05$) or month (Kruskal-Wallis rank sum test, $X^2 = 1.94$, $p > 0.05$) on the amount of time for oil to first reach shore.

The most appropriate conditional model as assessed via AIC included colony of origin, spill size, and the interaction between month of spill and spill location (ΔAIC = 24.3) Model results indicated that pelicans from Castle Pinckney experienced significantly higher relative risk scores than pelicans from Bird Key Stono, and that spills of larger size produced greater relative risk scores (Table 4.3). Spills which occurred in the months of June and July and which occurred outside of the harbor were also significantly positively associated with relative risk score (Table 4.3).

Discussion

Oil and other petroleum products released into the environment pose a significant threat to coastal and nearshore wildlife (Votier *et al*. 2005). A key challenge in designing mitigation strategies that are relevant at local scales is predicting where oil and wildlife are likely to interact, and identifying what factors are likely to enhance the probability of those interactions (Chilvers & Battley 2019). We leveraged a publicly-available, user-friendly toolkit developed for the purpose of modeling location-specific oil trajectories in combination with wildlife telemetry data to identify macroscale risk factors associated with ship-based oil spills to foraging adult pelicans in Charleston, South Carolina, USA.

The results of this modeling exercise demonstrate the importance of spill location in influencing overlap with coastal and marine wildlife while they are occurring on the surface of the water. For example, ~75% of modeled spills occurring inside Charleston Harbor did not overlap with pelicans during foraging. This relatively high proportion of non-overlap was driven in large part by significantly faster beaching times of oil spilled from within the harbor (~ 1 hr to beaching and oil being unavailable for interactions with wildlife on the water surface) compared to spills originating outside of the harbor. We also identified different risks associated with temporal aspects of the spill and size of the spill, with spills occurring during the midst of pelican breeding and spills with larger volumes of oil released producing more risk to foraging pelicans. Lastly, our results also suggest that pelicans nesting inside Charleston Harbor are more at-risk for interacting with surface oil compared to pelicans nesting at a colony located more distally to the harbor, even for spills which also occur outside of harbor.

Modeling the spatial fate of spilled oil is a difficult task, particularly in coastal environments with complex hydrography (Balogun *et al*. 2021). Especially for those with limited expertise in hydrodynamic modeling, developing realistic predictions about where wildlife may be most at-risk to encountering unintentionally released oil can represent a significant gap in knowledge. This is further compounded at local scales, as important factors affecting the distribution of spilled oil tend to operate over relatively short spatial or temporal intervals and in ways that can vary greatly among locations (Balogun *et al*. 2021, Gurumoorthi *et al*. 2021). To help address this gap, GNOME was developed to provide accessible oil spill modeling tools available at localized scales to users with potentially limited hydrodynamic experience. Importantly, GNOME has been validated to simulate realistic oil trajectories based on hindcasting actual spills (Marta-Almeida *et al*. 2013, Prasad *et al*. 2018, Xu *et al*. 2013). Selecting values for environmental variables (i.e., wind speed, wind direction, and sea surface temperature) that accurately represent past conditions, however, is critical for hindcast modeling in GNOME (MacFadyen 2017). By extension, the selection of environmental variables also likely plays an outsized role in determining the realism of hypothetical spill scenarios.

As we were interested in making generalized conclusions about the most likely distribution of oil to occur during the breeding season of brown pelicans, we used as environmental inputs decadal and 5-year averages of wind and sea variables, respectively, suited to each month of the study period. While these values represent prevailing conditions that would be most likely to occur given a spill during these months, local surface winds can dramatically alter oil trajectories (Gurumoorthi *et al*. 2021, Zhu *et al*. 2020), and so our modeled spills should not be interpreted as finalized oil distributions for all spills occurring in or near Charleston Harbor. We instead acknowledge the critical role of wind and other local conditions on the distribution of surface oil during release events, and have rather attempted to identify macroscale factors that could alter the risk of wildlife-oil interactions in the area by selecting average values for highly dynamic environmental variables. Local stakeholders should therefore consider how wind conditions during an actual spill differ from long-term averages, and adjust any assessments of risk to foraging pelicans accordingly.

In addition to local conditions, spill location is also an important factor in determining the extent of overlap with wildlife populations (Chilvers *et al*. 2021). We used AIS data collected from vessels within the study area to select spill locations that reflected actual vessel densities, with the assumption that spills are more likely to occur where vessels occur (Renner & Kuletz 2015). The vessel density grid constructed highlighted the location of the main shipping channel inside the harbor, as well as the primary approach in nearshore waters (Fig. 4.1). Indeed, both locations selected as spill origins were located in this distinct channel. Shipping accidents often occur in channels (e.g., NTSB 2021), and oil spill risk assessments frequently choose channels and/or anchorages as release locations for spilled oil (Azevedo *et al*. 2016, Kankara *et al*. 2016). We also chose to follow this probabilistic approach based on the number of vessels transiting within a given area, as many ship-based accidents occur as a result not of faulty navigation but of human-related errors (Fan *et al*. 2020). Furthermore, the *M/V Everreach* accident of 2002 released oil largely along the shipping channel, supporting our use of a vessel density grid for selecting likely spill locations.

As demonstrated by the vessel density grid, the portion of the shipping channel inside of Charleston Harbor is located near the northern shoreline, often approaching to < 1 km. Importantly for seabirds, it also passes nearby two breeding colonies. The first, Castle Pinckney, is located to the south of the shipping channel and has hosted ~240 breeding pairs of pelicans annually since 2000 (Jodice *et al*. 2007, SCDNR unpub data). The other breeding colony, Crab Bank, is located on the northern edge of the shipping channel. Crab Bank historically hosted ~625 pairs of pelicans annually, but in recent years has been devoid of nesting seabirds due to erosion to the island (Jodice *et al*. 2007, SCDNR unpub data). However, Crab Bank is currently undergoing sediment renourishment using dredge spoils from the deepening of the Charleston shipping channel, with the goal of restoring the island as a breeding location for nearshore seabirds including pelicans (U.S. Army Corps of Engineers 2018). Due to the proximity of Crab Bank to Castle Pinckney (~2.5 km), we assume that oil impacts may be similar for pelicans from both colonies but also acknowledge that could change, particularly if increases on Crab Bank alters pelican foraging behavior via density dependence effects.

While we expected that foraging pelicans from Castle Pinckney would interact to a large extent with spills originating inside the harbor due to spatial proximity, we instead found generally very low overlap between pelican GPS data during foraging and modeled oil. This low overlap also extended to pelicans from Bird Key Stono foraging within the harbor. Instead of remaining on the surface of the water, spilled oil inside the harbor beached quickly, typically within 60 min. For the purposes of our modeling exercise, this meant that most oil splots were gathered on proximal shorelines and unavailable for overlap with at-sea locations of foraging pelicans. While it is possible that some foraging pelicans could interact with surface oil within an hour of being spilled, we instead suggest that the primary environmental threat resulting from spills occurring inside the harbor may be to the neighboring shorelines and intertidal areas which support an abundant and diverse community of coastal birds throughout this portion of the year (Eggert 2012). Critically, at least some oil made landfall on Crab Bank for the majority of simulations occurring inside the harbor (62.5%). While trajectories of oil beaching on

Crab Bank were heavily influenced by both wind and proximity to the hypothetical spill site, results nevertheless suggest that seabirds inside the harbor may be exposed to oil to a lesser extent on the surface of the water compared to the threat of beached oil impacting physical colony or loafing/roosting locations. Oil which makes landfall in highly estuarine marsh environments, such as those surrounding Charleston Harbor, may also resuspend several weeks later where it once again becomes available for interactions with foraging pelicans (King *et al*. 1979).

Results of modeling efforts also suggested that pelicans nesting within the harbor on Castle Pinckney had significantly greater relative risk scores than pelicans nesting outside of the harbor on Bird Key Stono. Pelicans from Castle Pinckney tended to consistently use nearshore waters surrounding the mouth of Charleston Harbor, and importantly this area was used by a relatively higher percentage of tracked individuals from Castle Pinckney than for individuals from Bird Key Stono. In contrast, while some pelicans from Bird Key Stono were observed to use the mouth of the harbor and surrounding nearshore waters, many individuals also did not use this area and were instead distributed more homogeneously along the coastline, leading to lower relative risk scores (Fig. 4.2). We therefore suggest that while fewer individual pelicans breed on Castle Pinckney, a greater percentage may be vulnerable to surface oil than for nearby colonies which host larger numbers of individuals. In our study area, a sizable colony also occurs ~ 40 km north and outside of Charleston Harbor (i.e., Marsh Island) and ~ 37 km south of Charleston Harbor (i.e., Deveaux Bank; Jodice *et al*. 2013). However, tracking data of individuals from both colonies indicate negligible use of habitats in or near the harbor. These results demonstrate the importance of individual tracking data to assessing the risk of a spill within a given location.

We also found evidence that spills occurring during the middle of the reproductive period (i.e., June and July) may produce more overlap with foraging pelicans than spills which occur near the start (May) or end (August) of the reproductive period, especially for spills which occur outside of the harbor. There may be several reasons for this increase, which are not mutually exclusive. The first is that seasonal changes in winds, currents, or temperatures altered the trajectories of oil between months. For example, the mean 5-year SST in May was on average 4.7 C° colder than the 5-year mean SSTs in other months. Decadal wind speeds in May were also on average 1.9 km/hr faster than decadal wind speeds in other months, which may have altered trajectories towards shore. Decadal wind directions were largely similar between months, however, primarily flowing from south to north. Taken together, it could be that seasonal changes in the local environment, although potentially slight, have the capacity to significantly alter exposure probability (e.g., Balogun *et al*. 2021).

Alternatively, seasonal changes in the local foraging ranges of pelicans could also lead to changes in exposure to surface oil. For example, Geary *et al*. (2020) documented reductions in the spatial footprint of foraging brown pelicans over the course of the breeding season associated with increased time spent foraging in quality habitats. Given the highly dynamic estuarine habitats present proximal to the mouth of Charleston Harbor, this area may represent high-quality habitat for foraging adult pelicans. If adults then forage for more time or restrict their foraging to these areas, which were also locations where surface oil tended to aggregate, exposure risk may also become elevated. Pelicans may also be drawn to nearshore waters surrounding the mouth of Charleston Harbor by shrimp trawlers, an industry that provides an anthropogenic food subsidy to brown pelicans in the form of discarded bycatch (Jodice *et al*. 2011, Wickliffe & Jodice 2010). The shrimp harvesting season typically commences in late spring or early summer (i.e. May or June), and may artificially congregate foraging pelicans in areas commonly used by trawlers as the breeding season progresses as well.

For reproductively-active pelicans, June and July typically correspond to the chick-rearing stage of the breeding cycle. As chicks age and become able to thermoregulate independently, adult pelicans typically spend greater time away from the nest (Sachs & Jodice 2009). While increased time spent away from the nest may not indicate increased foraging (Geary *et al*. 2020, Lamb *et al*. 2017c), it may nevertheless lead to changes in pelican behavior that could expose them to surface oil at higher probabilities (e.g. resting on water or transiting to loafing areas). Oiling of adult pelicans during this time has the potential to acutely disrupt reproduction, and impact assessments of spills that occur during times of active breeding may consider the potential loss of young associated with the oiling of parent birds (Evers *et al*. 2019).

Lastly, GNOME modeling indicated a significant effect of oil spill size on the relative risk scores to adult pelicans. While volume of oil spilled may indeed affect the extent of interactions with wildlife (e.g., carcasses found; Morgan *et al*. 2014), the spill location is generally regarded as a more critical factor than volume, as even very small spills can have large impacts to wildlife (Chilvers *et al*. 2021). While we found evidence that large spills produced higher risk factors to adult pelicans, this may have been an artifact of splot number and oil concentration compared to increased spatial overlap. When calculating risk scores, we included the multiplier *g* as a measure of interaction intensity under the assumption that a pelican would be more likely to interact with surface oil when a large volume of oil was present in a given cell compared to an equally-sized cell that contained less surface oil. This likely contributed to the higher risk scores for large-sized spills, and should be interpreted understanding the aforementioned assumption. Nevertheless, we contend that large spills would increase the likelihood of interactions with foraging pelicans possibly resulting from an increase in the spatial movement of surface oil. This is evidenced in the GNOME models by the significantly faster time to first beaching for large spills compared to small spills. As oil volume is increased, the possibility of oil becoming entrained into a higher variety of dispersing hydrodynamic currents may also be increased, thereby accelerating movement. However, these results should be interpreted with caution as it remains unclear how splot number may have affected beaching time as well within the construction of the GNOME models.

Comparisons between significant factors influencing pelican risk to oil as modeled by the GNOME toolkit and observations from the *M/V Everreach* accident yielded general agreement at a broad scale. For example, it was estimated that for the section of the spill which occurred inside the harbor (i.e., upon approach of the terminal), oil first beached within 40 mins of initial release (McCay *et al*. 2006). Additionally, < 1% of spilled oil was estimated to have remained on the surface of the water 3 hrs post-release (McCay *et al*. 2006). These observations support our conclusion from GNOME modeling that oil spilled inside the harbor tends to beach relatively quickly, and is only available for interaction with pelicans on the surface of the water for a comparatively short amount of time. Observational data of biological injuries as a result of the *M/V Everreach* spill also tentatively support our findings of increased risk to pelicans nesting inside the harbor. Of the 48 – 53 pelicans observed to have been oiled in the aftermath of the spill, all but three were documented on Crab Bank (McCay *et al*. 2006). At the time of observation, there were an estimated 200 pelicans using the island, meaning that ~25% of pelicans present appeared to have interacted with oil to some extent (McCay *et al*. 2006). Given the spatially protracted nature of the spill, it is difficult to determine exactly where interactions may have occurred, but our model suggests the nearshore environment outside of the harbor mouth (an area included in the *M/V Everreach* spill) may be a particular area of concern. Notably, there were not any reports of oiled pelicans at Bird Key Stono, but it unclear if this was the result of a true absence of oiling or a lack of observer effort. Finally, observers reported significant shoreline oiling at both Castle Pinckney and Crab Bank, as well as the estuarine complexes both to the north and east of the colonies (McCay *et al* 2006). While GNOME did not predict oiling at Castle Pinckney, our results did highlight both Crab Bank and the eastern edge of the harbor to be especially susceptible to beaching oil. Taken together, we were able to find several points of agreement between predictive GNOME modeling efforts and observational assessments of a documented oil spill in the Charleston Harbor area, supporting the potential use of GNOME for wildlife managers.

Conclusion

We found that oil spill location is likely the most important macroscale factor determining the relative risk to foraging adult brown pelicans in the Charleston Harbor region to encountering surface oil, which is in general agreement with the prior literature (Chilvers *et al*. 2021). Oil released inside the harbor tended to beach quickly, where it may represent a significant threat to intertidal habitats on pelican colonies, but produced low relative risk to pelicans while foraging. Spills occurring outside of the harbor presented greater risks to pelicans while in the nearshore environment, especially in large volumes and during the middle of the reproductive period. Additionally, pelicans from Castle Pinckney were at greater risk than pelicans from Bird Key Stono. Given the proximity of Crab Bank to Castle Pinckney, we suggest that pelicans attempting to recolonize Crab Bank may be at a similarly elevated risk to shipping-based oil spills in the Charleston region, as highlighted by the events of the 2002 *M/V Everreach* accident (McCay *et al*. 2006).

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Table 4.1. Relevant input variables into the GNOME environment for generating oil spill scenarios. Dates represent the day of the calendar month with the greatest range between tidal maxima and minima, with approximate times of tidal events (Eastern Standard Time). SST represents the 5-year average for the given month. Wind speed and wind direction represent the decadal average for each variable in each given month.

	May	June	July	August
Date	17 May 2019	4 June 2019	31 July 2019	30 August 2019
Low Tide	13:36	15:25	13:57	14:35
Rising Tide	16:48	18:33	17:07	17:43
High Tide	20:01	21:41	20:18	20:51
Falling Tide	23:13	00:49	23:29	23:59
SST (°C)	24.5	28.2	29.8	29.7
Wind Speed (km/hr)	13.0	11.9	11.1	10.3
Wind Direction (°)	190	181	181	175

Table 4.2. Sample sizes of GPS-tracked pelicans from each study colony separated by month, with the total number of pelican locations used for each oil spill scenario.

	May	June	July	August
No. of Tracked Pelicans				
Bird Key Stono	13	17	13	9
Castle Pinckney	6	20	9	5
No. of Points				
Bird Key Stono	1531	2622	3260	1740
Castle Pinckney	382	3632	3576	1796

Table 4.3. Summary results of the conditional zero-inflated generalized linear model selected by AIC showing factors significantly related to relative risk exposure. Symbol † = p-value < 0.05, * = p-value < 0.001.

Model parameter	Coefficient Estimate	SE	Z-score	p-value
Intercept*	2.624	0.548	4.785	< 0.001
Month (June)†	-1.649	0.675	-2.443	0.014
Month (July)	-0.457	0.665	-0.686	0.493
Month (August)	0.443	0.616	0.720	0.472
Location (Outside)	-0.293	0.589	-0.498	0.619
Colony (C. Pinckney)*	1.812	0.187	9.676	< 0.001
Spill Size (Small)*	-4.474	0.184	-24.270	< 0.001
Month (June) x Location (Outside)*	4.103	0.725	5.663	< 0.001
Month (July) x Location (Outside)*	2.512	0.719	3.493	< 0.001
Month (August) x Location (Outside)	0.819	0.686	1.194	0.233

Figure 4.1. Map of Charleston Harbor, South Carolina, USA, showing the main shipping channel and approach. Lines represent vessel-based AIS data from ships entering the harbor from May-August 2019. Vessel tracks are overlaid on a 0.5 km x 0.5 km grid representing vessel density (warmer colors indicate higher vessel counts per grid cell). Yellow triangles represent the two randomly-chosen spill locations based on vessel density. Open squares indicate brown pelican colony locations.

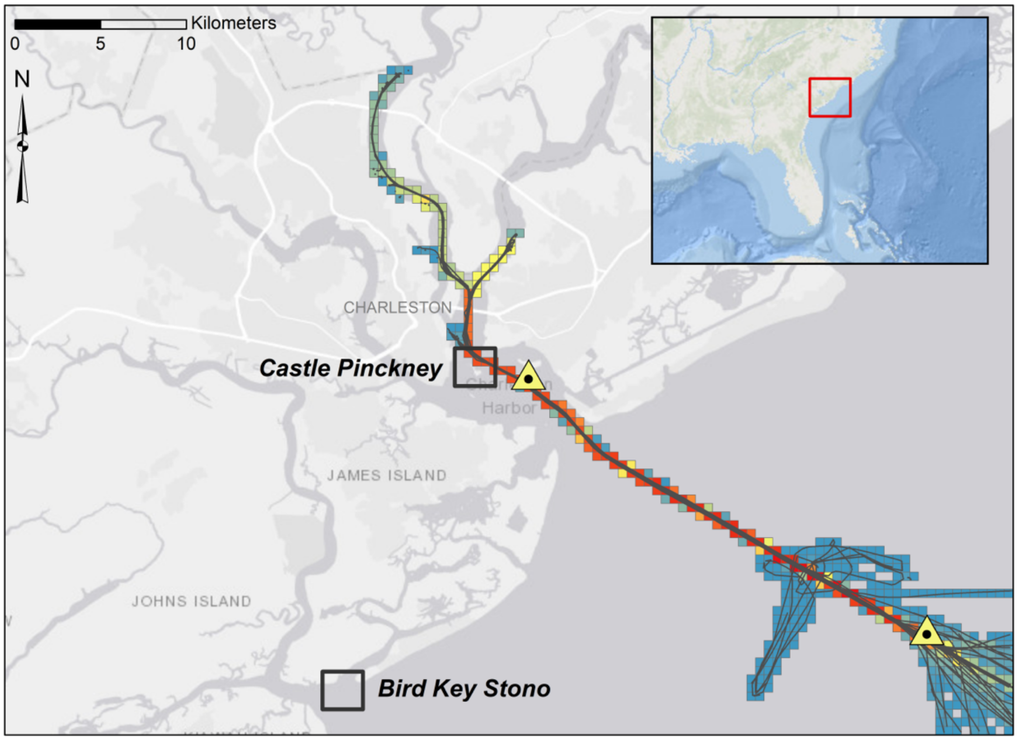


Figure 4.2. Kernel density maps indicating the utilization distributions of brown pelicans from A) Castle Pinckney and B) Bird Key Stono. Stars indicate breeding location for each colony, respectively. Note differences in scale between maps, with individuals from Bird Key Stono moving further south than individuals from Castle Pinckney. Darker colors indicate higher-use areas.

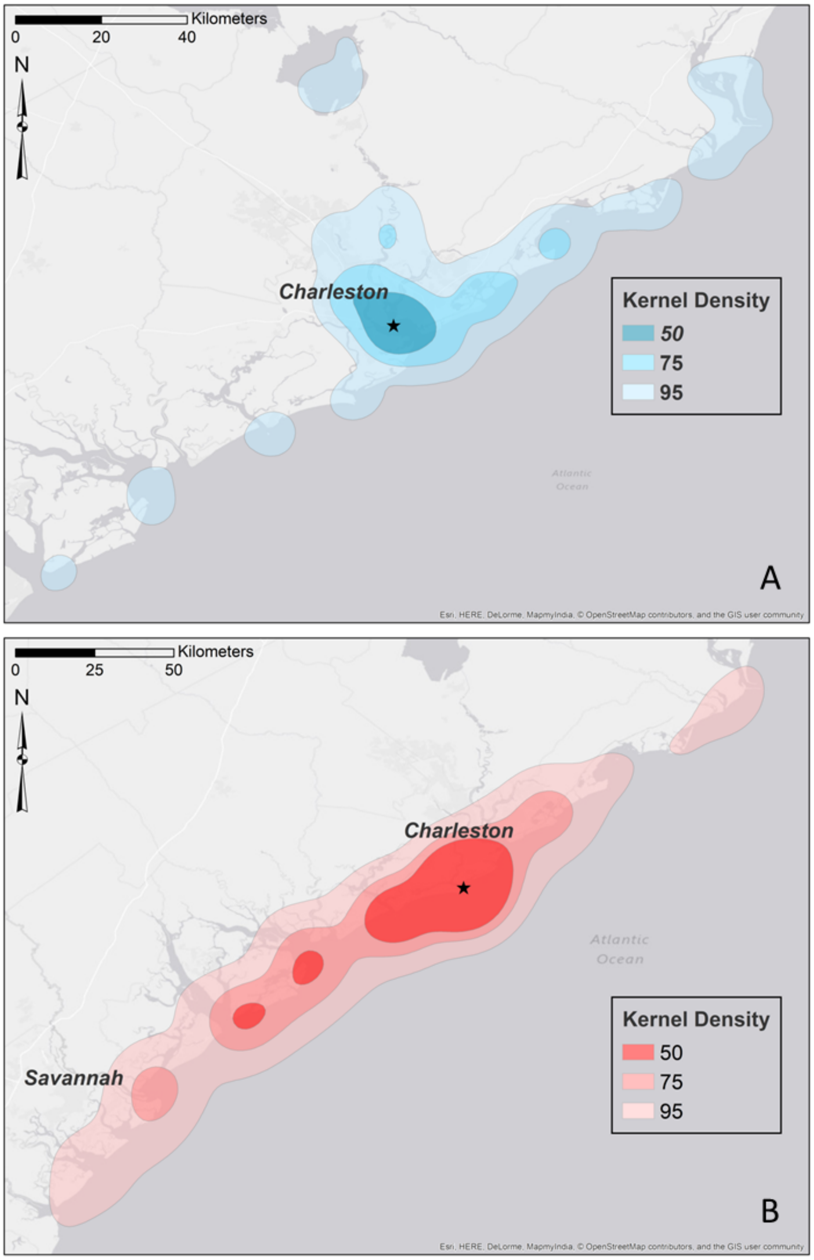


Figure 4.3. Example output of oil splots from the Charleston Harbor specific location file developed in the GNOME toolkit representing modeled oil spill scenarios. A) represents a modeled spill of small size (50 barrels) occurring in May on a rising tide. B) represents a modeled spill of small size (50 barrels) occurring in June on a low tide. Crosses indicate beached oil and dots indicated surface oil (note an absence of surface oil in A due to beaching times of < 1 hr). Spill locations are designated by the yellow triangle. Open squares represent colony locations.

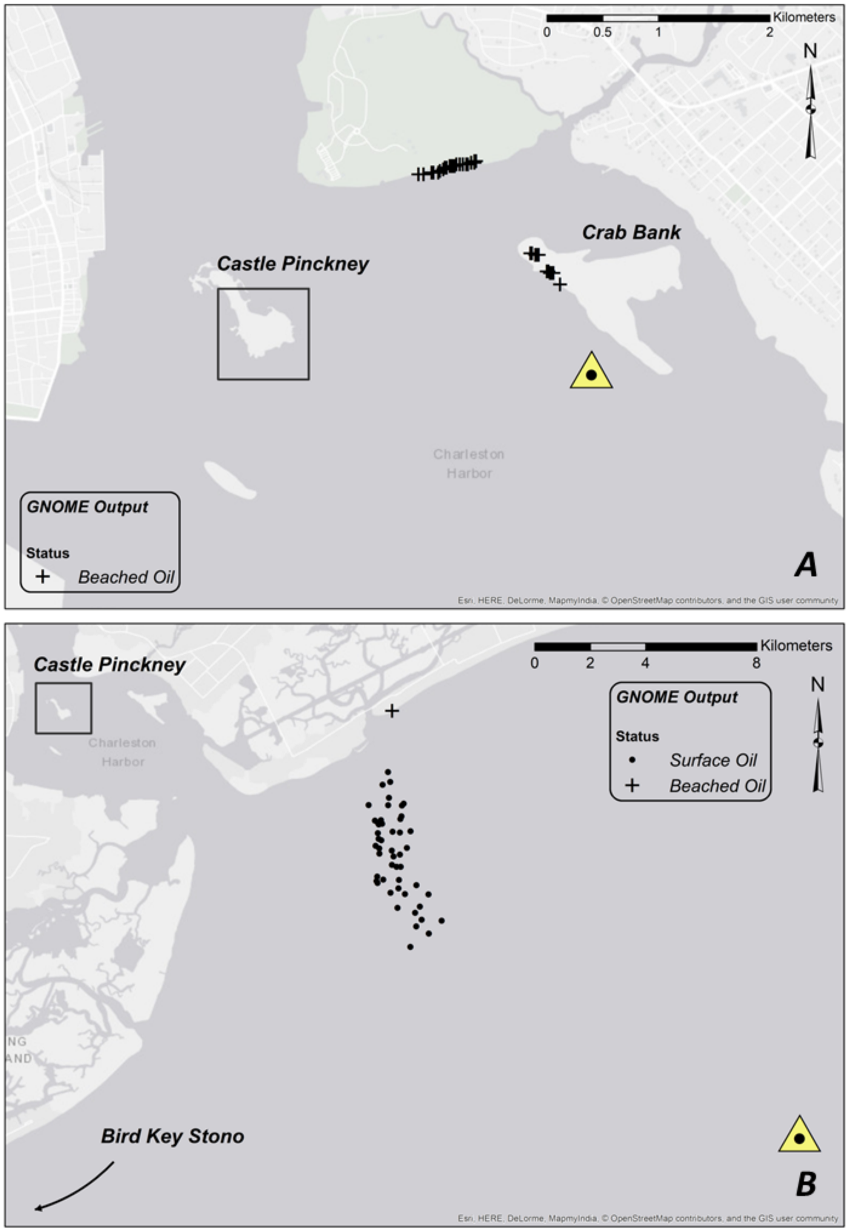
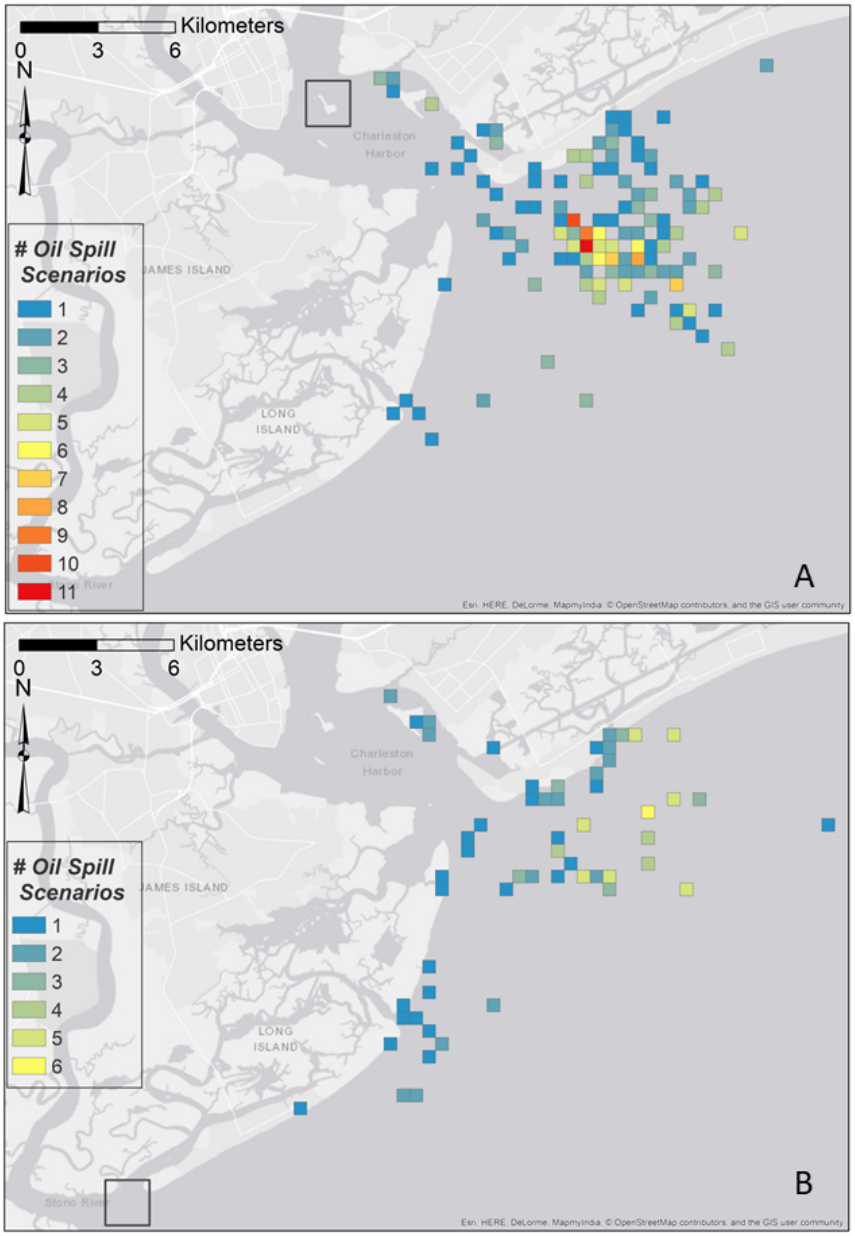


Figure 4.4. Locations of surface oil and brown pelican overlap as determined by GNOME modeling and GPS tracking data, respectively, for all oil spill scenarios across months (May – August). A) depicts overlap for pelicans from Castle Pinckney. B) depicts overlap for pelicans from Bird Key Stono. Grid cells are colored by the frequency with which an overlap between surface oil and at least one pelican occurred (*n* = 64 scenarios). Open squares represent colony locations.



CHAPTER FIVE

SUPPORT FOR THE FASTING ENDURANCE HYPOTHESIS OF PARTIAL MIGRATION IN BROWN PELICANS

Abstract

Partial migration occurs when only a certain fraction of a population or species migrates instead of all individuals. Considered an evolutionary precursor, understanding why some individuals choose to undertake migration while others do not may serve to inform general migratory theory. While several hypotheses currently exist for explaining the maintenance of partial migration, empirical support for many is limited. To address this gap, we analyzed telemetry data acquired from individual brown pelicans (*Pelecanus occidentalis*; *n* = 74), a partially migratory seabird, nesting on six colonies in the South Atlantic Bight over the course of four autumn migrations using a Cox's proportional hazards model. We estimated that approximately 74% of pelicans nesting within the study area may be migratory on an annual basis, with the remainder staying within the surrounding marine ecoregion year-round. Mean date of migration initiation was 9 November, although movements occurred from September – December. Modeling results indicated significant effects of rising sea-surface temperatures and decreased body condition on migration rate. We suggest that the ontogenetic migration of the primary forage species of brown pelicans from estuarine to pelagic environments causes a seasonal reduction in prey, and that individuals in poor body condition are unable to meet the energetic demands potentially associated with this decrease in prey availability (i.e., the fasting endurance hypothesis of partial migration). Although we did not find evidence

for a density-dependent migratory response, the effects of intraspecific competition on migration in pelicans should also be considered.

Introduction

Seasonal migrations are a common adaptive behavior of vagile organisms resulting in increased growth, survival, or reproduction across space and time (Shaw 2016). Migration may allow individuals to avoid unfavorable conditions (Bartel *et al*. 2011, Poulin *et al*. 2012, Xu & Si 2019), access habitats advantageous for reproduction distinct from primary foraging areas (Semlitsch 2008, Stewart & DeLong 1995, Weimerskirch *et al*. 2017), or track specific resources such as seasonal vegetation growth or prey (Furey *et al*. 2018, Sergeant *et al*. 2015). Both internal and external factors may initiate migration (Jachowski & Singh 2015). For example, physiological condition may act as one of several internal drivers (Hegemann *et al*. 2019). Often, external drivers for the onset of migratory movements take the form of environmental cues such as seasonal changes in light or temperature, especially when these signals indicate resource availability either locally or at the migratory destination (Ramenofsky *et al.* 2012, Winkler *et al*. 2014).

At the population level, migration may be undertaken seasonally by all individuals (obligate migration) or by some fraction (partial migration) (Dingle & Drake 2007, Terrill & Able 1988). Although the evolutionary drivers of each form are poorly understood, partial migration is more common, especially among avian taxa, and thought to be a precursor to obligate migration (Berthold 1999, Hegemann *et al*. 2019, Pulido

2011). Several competing hypotheses exist explaining the mechanisms underlying the maintenance of partial migration, and by extension the development of obligate migration (Chapman *et al*. 2011). For example, the competitive release hypothesis posits that dominant individuals will tend to be sedentary while subordinate individuals will tend to migrate to alleviate the effects of intraspecific competition (Gauthreaux 1978, Chapman *et al*. 2011, Bai *et al*. 2012). Migration to avoid intraspecific competition is often characterized by a positive density-dependent response (Lamb *et al*. 2017a). An alternative is the fasting endurance hypothesis, which posits that a seasonal reduction in foraging opportunities or food availability triggers migratory behaviors for those individuals unable to meet energetic demands (Chapman *et al*. 2011, Gow & Wiebe 2014). Individuals at a greater risk of starvation (i.e., in poor condition and/or with limited food resources) are more likely to migrate compared to those with greater resource abundance and/or better body condition. The thermal tolerance hypothesis suggests that individuals unable to incur the cost of enduring thermal extremes at the nesting area will migrate (Belthoff & Gauthreaux 1991, Palacín *et al*. 2009, Chapman *et al*. 2011). Under this hypothesis, individuals of either small or large body size (depending on thermal intolerance to cold or hot, respectively) or those experiencing more extreme ambient conditions (e.g., at the edges of geographic ranges) will tend to migrate to areas that are less likely to have conditions that exceed an intrinsic thermal tolerance threshold.

Importantly, extrinsic factors influencing the decision-making process of individuals within a partially migratory population may be relatively stochastic both spatially and temporally (Fieberg *et al*. 2008, Pratt *et al*. 2017). An emergent line of research is focused on intrinsic genetic controls of migration, and how environmental conditions may intersect with genetics to determine the migratory potential of populations. The respective portions of resident and migratory individuals within a population may therefore be variable on an interannual basis based on prevailing environmental conditions, especially if the individuals that make up the population possess varying genetic liabilities for migratory decision-making based on intrinsic factors (i.e., the threshold model of migration; Pulido 2011).

Much of the current understanding related to extrinsic drivers of migration has been derived from studies of temperate terrestrial species, especially birds (Shaw 2016). Notably, research has tended to focus on species which exhibit well-defined migrations between relatively sessile breeding and non-breeding periods (e.g., neotropical migratory passerines or migratory shorebirds). Within this avian framework, the majority of published research has focused on the phenology of spring migration, when individuals return to breeding grounds (Haest *et al*. 2019). Comparatively less focus has been given to autumn migration, frequently called the 'neglected season' (Gallinat *et al*. 2015), even though changes in autumnal conditions can alter species distributions, regulate reproductive capacity, modulate ecological dynamics among interacting species, and modify the net productivity of ecosystems (Gallinat *et al*. 2015). These data gaps concerning drivers of autumn migration are further compounded by research biases associated with ecosystem study. Arctic and temperate systems have disproportionately contributed to our understanding of partial migration, leading to calls for research in less-studied tropical and subtropical systems (Sekercioglu 2010). Whereas higher-latitude systems have relatively predictable peaks and troughs of resource abundance, lower-latitude systems may have much more subtle, unpredictable, or heterogeneously-distributed resources across space and time accompanying less-defined boundaries of seasonality (Lisovski *et al*. 2017).

Coastal and nearshore systems in particular are characterized by dynamic and variable resource abundances (Knip *et al*. 2010). Acting as the interface between terrestrial and marine domains, estuarine-influenced habitats within coastal ecosystems are some of the most productive yet complex environments globally (Kennish 2002). This is in part due to the wide variety of input variables determining productivity within estuaries, including freshwater discharge and nutrient load, sunlight availability, wind regimes, tidal action, and oceanic factors such as sea surface temperature, sea surface salinity, and sea surface height (Boyer *et al*. 1993, Janzen & Wong 2002, Morris *et al*. 1990, Torregroza-Espinosa *et al*. 2021). Estuarine systems provide critical breeding and early life-stage habitat for many species of marine fish that subsequently are key components of complex food webs. These forage fish often time their own ontogenetic or seasonal movements with localized shifts in primary productivity. It may therefore be adaptive for upper-trophic-level predators, especially those with mobile capabilities, to be responsive to the same or similar environmental cues as their primary prey, even when the predator is not directly affected by the environmental change (e.g., tracking interannual changes in ocean temperature as a measure of prey abundance; Szesciorka *et al*. 2020).

The Eastern brown pelican (*Pelecanus occidentalis carolinensis*) is an apex predator in nearshore systems that is distributed widely from tropical to temperate waters of the western North Atlantic. The breeding range for this species extends throughout the US coast of the Gulf of Mexico and on the Atlantic coast from southern Florida to Chesapeake Bay. This range spans approximately 21 degrees of longitude and 14 degrees of latitude and encompasses a diversity of nearshore ecosystems. While early investigations using band recoveries suggested an annual movement of adults away from breeding colonies (Schreiber & Mock 1988), the advent of bird-borne satellite tracking technology confirmed a partial migration strategy for populations both in the northern Gulf of Mexico and in the South Atlantic Bight (King *et al*. 2013, Lamb *et al*. 2017a, Poli 2015). While several studies exist examining drivers of movement within the breeding season (Geary *et al*. 2018, Geary *et al*. 2020, Walter *et al*. 2014), relatively little attention has been paid to factors causing large-scale movements outside of the reproductive period. An exception is Lamb *et al*. (2017a), which documented a significant and positive density-dependent effect on both autumn migration strategy and migration distance for pelicans in the northern Gulf of Mexico consistent with the competitive release hypothesis. Drivers of partial migration are complex, however, and may not be homogenous among populations for species with expansive ranges, such as the brown pelican. Hypotheses of partial migration are also not mutually-exclusive, and several mechanisms could be operating simultaneously. The aim of the current study is therefore to leverage tracking data collected from pelicans breeding in the South Atlantic Bight, a more latitudinally expansive system compared to the northern Gulf of Mexico, to examine drivers of partial migration during the post-breeding season.

Methods

Study area and focal species

The South Atlantic Bight (SAB) is generally defined as the extent of Atlantic coastal North America from the Cape Fear River Basin to Cape Canaveral (~34° - 28° latitude). It is characterized by a complex geomorphology dominated by estuarine systems, salt marshes, and barrier islands. There are ca. 15 pelican colonies active in any given year within the SAB, as not every colony is active every year (Jodice *et al*. 2013). Colony sizes range from < 100 to nearly 4000 pairs, with the largest colonies centered near Charleston, South Carolina (32.8° N, Fig. 5.1) . Brown pelicans in this region typically cease nesting activity by late August, after which a portion of individuals from any given colony may undertake movements away from the breeding area that may manifest as short-range dispersal movements or long-distance migrations.

Encompassing the SAB and approximating its borders is the Carolinian marine ecoregion (Spalding *et al*. 2007, Fig. 5.1). Dominated by the interaction of the Gulf Stream with the relatively broad continental shelf, which determines much of the large-scale oceanography of the area, the Carolinian ecoregion is subject to seasonal shifts in productivity in both nearshore and pelagic waters (Voulgaris 2013). Together with the Northern Gulf of Mexico marine ecoregion, this area forms the Warm Temperate Northwest Atlantic marine province (Spalding *et al*. 2007). To the south exists the

Floridian marine ecoregion, encompassing much of southern Florida and the Keys (Spalding *et al*. 2007). Part of the Tropical Northwestern Atlantic marine province, the Floridian ecoregion exhibits markedly less seasonal fluctuations in oceanography and is more closely aligned with the Caribbean (Longhurst 2007).

Data collection

We deployed 65 g solar GPS Platform Terminal transmitters (GeoTrak Inc., North Carolina, USA) on brown pelicans (*n* = 86) during the reproductive periods of 2017 - 2020 at six colonies within the SAB. Briefly (see Lamb *et al*. 2017b for details), adult pelicans were captured on the nest while chick-rearing (May - August) via either neck or leg lasso. Transmitters (10 x 3.5 x 3 cm) were attached dorsally via a backpack-style harness individually constructed using Teflon ribbon, and weighed ≤ 3% body mass of instrumented birds (range = 2475 - 4350 g). Transmitters were programmed to record locations at 90 min intervals between 11:30 - 01:00 GMT (i.e., 10 locations/day) from September - November, and to record locations at 120 min intervals between 12:00 - 02:00 GMT (i.e., 8 locations/day) from November - March to conserve battery power during seasons with lower sunlight availability. Unit error was assumed to be similar to that of Lamb *et al*. (2017a), i.e., 4.03 ± 2.79 m.

We measured the tarsus, culmen, and mass during capture, and collected 3-4 body feathers from the dorsal side of the pelican above the uropygial gland. DNA from feathers was then extracted and developed via PCR for sex determination (Animal Genetics Inc., Florida, USA). Total handling time averaged 15 mins (± 3 mins).

To estimate adult physical condition, we developed a body condition index (BCI) following Lamb *et al*. (2017a). Assuming a linear relationship between culmen length (a proxy for skeletal size) and body mass, a best-fit regression equation was calculated to generate predicted body mass based on culmen length. BCI was then defined as the difference between measured body mass and predicted body mass, with negative values indicating an individual in relatively poorer condition and positive values indicating an individual in relatively better condition. Regression equations were calculated separately for each sex to account for inherent sexual dimorphism in the species (Shields 2020). We also tested whether BCI was correlated with date of capture, as condition was only measured once at deployment and may be hypothesized to vary with phenology. Finally, colony-specific estimates of the number of breeding pairs of pelicans were obtained following counts of colonial waterbirds in each state (Table 5.1).

Data processing

Erroneous GPS locations were removed via a combination of visual inspection and speed filtering at ≥ 65 km/h (Schnell & Hellack 1978). To reduce computational time, and because we were interested in regional-scale movements, GPS data were reduced to a single location per day by taking the daily mean of all recorded fixes for each individual. As the latest date of initial transmitter deployment during the study was 10 August, we removed all locations preceding that date. This allowed for the movement track of each individual to commence on the same date regardless of year, ensuring that, in subsequent modeling, the observation period for each individual would begin simultaneously.

To distinguish between migratory and resident behaviors at the individual level, we examined daily locations of pelicans from the beginning of the observation period as defined above until either the track ended or 1 March of the subsequent year, whichever occurred first. In rare instances, GPS locations were transmitted after the unit had become detached from the bird or the individual had perished. In these cases, the end of the track was determined via visual inspection for the cessation of 'regular' movements (i.e., no movement recorded for several consecutive days). We used the spatial boundary of the Carolinian marine ecoregion for categorizing migratory and resident pelicans. Migratory individuals were defined as those which departed the marine ecoregion at some point during the observation period, while resident individuals were defined as those remaining within the boundary of the ecoregion throughout the duration of the observation period. We chose to use the marine ecoregion boundary as a migratory threshold because, unlike purely distance-based metrics, the boundaries of the marine ecoregion are inherently meaningful ecologically. Pelicans may depart the area surrounding the breeding colony, for example, yet remain within an ecologically-similar environment throughout the annual cycle. The focus of this study was to determine drivers of movement across large-scale environmental gradients, without being confounded by more local movements away from, but still relatively proximate to, the location of breeding. For this reason, pelicans labeled in the current study as residents may not have actually remained at the breeding colony year-round, but were instead residents of the same ecological environment throughout the annual cycle. To validate this choice, the tracks of migratory pelicans were also examined for maximal distance travelled from the breeding colony. On average, pelicans that were labelled as migratory travelled a maximum distance of 977 ± 301 km from their colony of origin, which is approximately five times the average maximum distance travelled by pelicans labelled as resident (196 ± 137 km). As colonies of origin averaged 422 ± 87 km from the border of the ecoregion, migratory pelicans tended to continue traveling an additional ~550 km further once exiting, underscoring the large-scale movements undertaken by these individuals (Fig. 5.1).

For those individuals that migrated (i.e., departed the ecoregion), we used the package *migrateR* in the R statistical framework to determine the day on which migratory behavior commenced (Spitz 2019). As we were only interested in determining uni-directional movements (i.e. autumn or outward migration only), and tracks did not include return movements in the spring, we fit only 'resident' and 'dispersal' models to each track. Models are based on net-squared displacement, with the 'resident' model showing no change and the 'dispersal' model showing an increase in displacement over time with a distinct movement period (see Spitz *et al*. 2017 for details). The most appropriate model was then selected via AIC, and an estimation of the starting date of migratory movements was extracted. The behavior of all pelicans classified as migratory under the marine ecoregion threshold were also best approximated by the 'dispersal' model in the *migrateR* framework, further validating our decision.

Environmental covariates

We selected environmental variables that both matched hypotheses of partial migration outlined in Chapman *et al*. (2011) and that were also comparable to Lamb *et al*. (2017a). For example, the thermal tolerance hypothesis suggests that individuals unable to incur the cost of enduring thermal extremes at the nesting area will migrate. We therefore downloaded spatially and temporally explicit ambient air temperatures from the Movebank Environmental Data Automated Track Annotation System (Env-DATA) for each daily-averaged pelican location. Air temperature data (2 m above surface level) was provided at a resolution of 0.25° and recorded at 12:00 EST for each day. To approximate the fasting endurance hypothesis, which states that seasonal reductions in foraging opportunities drive the need to migrate for those individuals unable to meet energetic demands, we included environmental variables that influence the abundance and distribution of Atlantic menhaden (*Brevoortia tyrannus*), the primary prey of pelicans in the SAB (Shields 2020). While we were unable to directly measure menhaden abundance, sea surface temperature (SST) and chlorophyll-*a* (chl-*a*) concentrations may serve as local proxies for relative menhaden availability in the environment (Geary *et al*. 2020). We also chose to include a daily index of the North Atlantic Oscillation (NAO), which can modulate menhaden abundance in the SAB on larger climactic scales (Roberts *et al*. 2019). Spatially and temporally explicit measures of SST and chl-*a* were obtained using the R package *rerddapXtracto*. Daily Multi-scale Ultra-high Resolution SST was provided by the NASA Jet Propulsion Laboratory GHRSST at 0.01° resolution. Chl-*a* concentrations were downloaded from the Aqua MODIS satellite as an 8-day composite at 4 km resolution, as daily and 3-day composites contained too many cells of missing data to successfully incorporate into subsequent time-to-event modeling. Daily NAO indices were downloaded from the NOAA Climate Prediction Center (https://www.cpc.ncep.noaa.gov, accessed 18 March 2021). Finally, we also downloaded estimated measures of the meridional (north - south) wind component at 10 m above ground level. As the migratory movements of pelicans in the SAB are largely latitudinal, we hypothesized that individuals may choose to depart under favorable (tailwind) conditions. Meridional wind was obtained from the Env-DATA system at a spatial granularity of 0.25° and recorded at 12:00 EST for each day.

Statistical analysis

We used time-to-event modeling to investigate the influence of intrinsic and extrinsic factors on the migratory decisions of brown pelicans. Specifically, covariates were fit using Cox's proportional hazards model (CPHM), a form of survival modeling that can be applied to specific biological events that are single-occurrence (Rivrud *et al*. 2016, Sherril-Mix *et al*. 2008). Underlying the CPHM is the hazard function, which is the modeled rate of occurrence of the specific event through time. As hazards are rates, not probabilities, in the current application the hazard represents the instantaneous potential for migration to occur at time *t* per unit time (e.g., the rate of daily migration decreases by a factor of *x* for every unit increase in variable y).

Several advantages exist for applying CPHMs to animal telemetry data. Often, tracking data contain incomplete information for individuals that experience tag failure or mortality before the event of interest occurs. Non-optimal strategies for handling censored individuals include discarding collected data or crafting assumptions about subsequent behavior. CPHMs are instead robust to censored data, and therefore allow the user to incorporate all collected data from the observation period into the model. This is both methodologically and ethically preferable, especially when considered in the context of animal-borne telemetry. CPHMs also allow for time-dependent covariates, without requiring a specific underlying distribution function of the hazard. The CPHM does assume that a baseline hazard exists, and that the effects of the covariates on the hazard are proportional (i.e., a given covariate influences the risk of migration in each individual equally over time and are additive on one scale). A CPHM then estimates the multiplicative effect of the covariates on the baseline hazard.

Each individual pelican was represented in the model by a single year of tracking, although four pelicans were tracked for > 1 year. This was done to not bias the model towards an individual strategy. We chose to use tracking data in the model from the first observation period that ended in either residency or migration (i.e., to eliminate censored data when complete data was available). No pelican tracked for > 1 year switched strategies between years.

Model selection was undertaken using an information theoretic approach. We first fit a global model containing the static variables of sex, BCI, culmen length, and colony size, and the time-dependent variables of NAO, SST, chl-*a*, ambient air temperature, and meridional wind component. Variables were then removed via stepwise selection using Akaike's information criterion (AIC), with those not improving AIC iteratively discarded. The subsequent model with the lowest AIC value was therefore selected as the most appropriate. Interactions between variables selected in the best-performing model were also examined for subsequent improvement of fit. We also investigated potential lag effects by calculating 7, 10, and 13-day rolling averages of SST and iteratively adding to the best supported model.

Results

Movement data (*n* = 7717 daily observations) were collected for 74 brown pelicans within the observation period, beginning 10 August and ending 1 March each year (Table 5.1). We classified 47 individuals as migratory (Fig. 5.2), with an average migration initiation date of 9 November ± 24 days (range = 2 September - 28 December). A total of 10 individuals were confirmed as residents of the SAB throughout the observation period. The remaining 17 individuals provided censored data, with dates of censorship ranging from 20 August - 19 February (median = 20 October). In order to approximate the percentage of pelicans that may be migratory from the SAB in any given year, we compared the number of confirmed migrants to confirmed residents (i.e., censored individuals were not included). Because a GPS transmitter would need to remain functional for a longer period of time to confirm residency (i.e., transmit from 10 August to 1 March, *n* = 203 days) versus indicating migration (i.e., latest initiation of migration was 28 December, *n* = 140 days), we chose to compare the number of individuals that both migrated and had transmitters that were operational for the full observation period (*n* = 29) to the number of confirmed residents (*n* = 10). Using this approximation, we therefore estimate that ~74% of pelicans breeding within the SAB may migrate out of the ecoregion on an annual basis. This estimate remains unchanged if instead the total number of migrants ($n = 47$) is compared to the number of birds (both resident and censored) which did not migrate by the latest recorded migratory date (28 December; $n = 16$).

Tracks from migratory individuals indicated a variety of destinations upon exiting the Carolinian marine ecoregion (Fig. 5.1). Frequently used areas included the southern Florida peninsula, especially the Florida Keys, as well as the northern coast of Cuba. The southern coast of Cuba and the Yucatan Peninsula of Mexico were also used, although this was less common. Northward movements were comparatively rare. Two individuals exited the Carolinian marine ecoregion to the north, reaching Chesapeake Bay; because both movements were followed by a return to the SAB before 1 March, they were not considered to represent migratory events for the purposes of this study. One individual returned south after its northward trip and exited the Carolinian marine ecoregion to overwinter in southern Florida (treated as a migratory individual). The transmitter of the second individual ceased to operate soon after arrival back in the SAB and was therefore treated as censored data. Pelicans that remained within the SAB primarily used the coasts of Georgia and southern South Carolina, rarely moving north of Charleston.

BCI was not significantly correlated with date of capture ($r(72) = 0.03$, $p > 0.05$). AIC stepwise selection indicated the proportional hazards model with the best fit included the static term BCI and time-dependent terms SST, NAO, and chl-*a*. The remaining variables examined did not improve model fit and were excluded. Interactions between BCI and the selected time-dependent terms also did not approve model fit.

Additionally, model performance decreased with increasingly lagged average SST. Model diagnostics based on scaled Schoenfeld residuals indicated that assumptions of proportionality were met for each variable. Model concordance (0.735 ± 0.04 SE) indicated good predictive ability of the model, with likelihood ratio and Wald tests achieving high significance ($p < 0.001$). SST had a significant positive effect on the hazard, with a 79% (95% CI: 56 - 120%) increase in the daily departure rate for every 1°C increase in temperature (Table 5.2). BCI had a significant negative effect on the hazard, with a 0.23% (95% CI: 0.07 - 0.40%) decrease in the daily departure rate for every unit increase in condition (Table 5.2). NAO and chl-*a*, while included in the final model, did not reach statistical significance (i.e., CI of the hazard overlapped 1).

Discussion

Animal migration is both one of the most ubiquitous behaviors in ecology and also one of the most difficult to study and consequently least understood (Wilcove & Wikelski 2008). Particularly vexing is partial migration, whereby some individuals from a population may undertake energetically expensive and potentially risky long-distance movements while others will remain within the same explicit area over time. Here, we provide evidence that both intrinsic (body condition) and extrinsic (resource abundance) factors contributed to the migratory strategies of brown pelicans in a subtropical marine system. Instead of evaluating pre-existing and competing hypotheses *a priori* and subsequently fitting models to them, we followed a hypothetico-deductive approach which resulted in a model aligned with the fasting endurance hypothesis of partial migration (Chapman *et al*. 2011). Given the relative scarcity of literature empirically supporting this hypothesis, we posit that continued tracking of partially migratory species may be a key opportunity for testing the evolution of migratory behavior generally (Lundblad & Conway 2020).

Resource abundance (e.g., prey availability) is the primary extrinsic factor underlying partial migration under the fasting endurance hypothesis. For brown pelicans in the SAB, diet is largely composed of a single species, the Atlantic menhaden (Blus 1982, Sprunt 1925). Studies during the breeding season indicate that up to 95% of chick forage can be composed of menhaden (Baldwin 1946, Fogarty 1981), and that adults and chicks tend to share similar diets (Shields 2020). Although diet has not been well documented during the non-breeding season, we can assume that post-breeding pelicans would not undergo a seasonal shift in diet if menhaden remained available given the foraging efficiency this item provides (Lamb *et al*. 2017c). If so, then menhaden likely represent a critical resource for both migratory and resident pelicans while in the SAB. We therefore posit that pelican migration is linked to the availability of a specific, preferred size class of menhaden, and that this availability interacts with intrinsic factors (i.e., factors represented by our measure of BCI) to influence the probability of migration among individuals. Here we review diet preference, how this interacts with availability via menhaden ontogeny, and ultimately how these factors may then influence migration-related decisions.

Pelicans preferentially consume smaller, juvenile (0-1 y/o) menhaden compared to larger, adult fish when available (Lamb *et al*. 2017c). This age-related bias may be driven in part by ontogenetic habitat associations in developing menhaden (Lamb *et al*. 2017c). Adult menhaden spawn offshore in the mid-shelf region (20 - 60 m depth) primarily during the winter, and in the SAB typically in association with the western boundary of the Gulf Stream, beyond the expected foraging range of pelicans (Checkley *et al*. 1988, Checkley *et al*. 1999). Larvae then become dependent upon ocean circulation mechanisms to deliver them into estuarine complexes for development in the late winter or early spring (Hare *et al*. 1999, Lozano *et al*. 2012) where larval menhaden proceed to juvenile stages over the course of the summer months, taking advantage of the abundant resources available during this time and transitioning from capturing live zooplankton to planktonic filter-feeding (Friedland *et al*. 1996). Finally, each menhaden cohort will exit the estuaries in the autumn to join the offshore adult population, which are themselves at least partially migratory in nature, exhibiting a net southward movement during the winter months from the Northeast and Mid-Atlantic Bight to the SAB (Liljestrand *et al*. 2019).

Tracking of brown pelicans in the SAB has indicated that foraging adults rarely occur in waters further than 5 - 10 km offshore, instead relying on estuarine and nearshore environments rather than on pelagic systems for prey acquisition (Poli 2015, Wilkinson *et al*. 2019). These habitats are heavily favored by developing menhaden as nurseries, and within these systems menhaden appear to serve as a locally-abundant resource for pelicans while they are present (Glass & Watts 2009, Hartman & Brandt 1995). However, the availability of juvenile menhaden as a resource may decrease suddenly and rapidly during the seasonal transitions from summer to autumn due to their ontogeny. Therefore, the autumn migration of juvenile Atlantic menhaden from inshore, estuarine habitats to offshore, pelagic environments may represent a key change in resource availability for brown pelicans that subsequently acts as an extrinsic driver for their own migration from the SAB.

While we were unable to monitor menhaden abundance directly, we included in our models of pelican migration environmental variables that influence menhaden distribution and abundance (SST, chl-a, NAO; Geary *et al*. 2020, Roberts *et al*. 2019). The final model included each of these proxy variables for menhaden abundance, to the exclusion of other environmental variables such as ambient temperature or meridional wind component that might influence pelicans more directly (e.g., via thermal tolerance or flight energetics). Of these, SST was a highly significant and positive predictor of the rate of pelican migration. Pelicans that migrated appeared to have experienced a relative increase in SST that was preceded first by a variable period of depressed SSTs (Fig. 5.3). Juvenile menhaden are triggered to leave estuarine systems for the pelagic environment by periods of sustained, cool SSTs that occur seasonally during autumn. For example, Friedland & Haas (1988) documented consistent initiation of menhaden emigration from an estuarine complex in Virginia five days after the onset of SSTs below 24°C. Records from June & Chamberlin (1959) indicated that emigration in Delaware commenced once temperatures in the estuarine environment fell below that of the adjacent ocean. While it may be beneficial for pelicans to remain in the area during such menhaden emigration events, as the relative availability of juvenile menhaden may be temporarily enhanced through the movement of many individuals, following emigration there may be a significant decrease in menhaden abundance in the nearshore habitats that pelicans use for foraging. As SSTs undergo local rewarming, pelicans may then choose to migrate as menhaden movement ceases and abundances are depressed. The association of pelicans with cooler relative SSTs during the non-breeding season is further supported by Lamb *et al*. (2019), which documented a rangewide selection for low SSTs during the winter based on a habitat suitability analysis of tracked individuals. In addition, the relationship between elevated SST and migration rate did not change even when SST was calculated using rolling averages, suggesting that pelicans which are experiencing warmer temperatures on a broader temporal scale will tend to migrate compared to those experiencing cooler temperatures. However, it should be noted that models using lagged SST performed significantly worse than the non-lagged model, indicating that short-term SST fluctuations remain a better overall predictor of migration rate in this system.

A decrease in resource abundance, as may occur with menhaden emigration, may subsequently lead to a concomitant increase in intraspecific competition among pelicans (Duijns & Piersma 2014). Increased intraspecific competition could lead to changes in intrinsic factors that might also affect migration strategy. We found that BCI was significantly related to the migration hazard. For every unit increase in BCI, the hazard was decreased by 0.23%, indicating that those individuals in worse condition were more likely to exit the SAB given equal environmental conditions (Table 5.2). We posit that the annual emigration of juvenile menhaden out of estuarine systems drives local resource scarcity, thereby increasing competition among pelicans. Individuals in better body condition may be more competitive than individuals in poorer condition at acquiring limited resources, or they may be better able to withstand periods of resource shortages. For example, during the breeding season, Geary *et al*. (2018) found that higher-quality pelicans in better body condition were also more efficient in foraging and took more variable risks with higher energetic returns than individuals in poorer conditions, which tended to be more static in their foraging behavior (i.e. the rich get richer hypothesis). This suggests that individuals in good condition are more likely to be strong competitors or have the capacity to withstand food shortages compared to individuals which are in poor condition. However, individuals in poor condition may also choose to migrate regardless of prey availability, given the lack of a significant interacting term between BCI and SST within our selected model. It is important to note that skeletal body size was not supported in the final model of pelican migration, indicating that the decision to migrate was dependent more on the relative condition of the individual and less on absolute size. Interspecific competition for juvenile menhaden is likely to be of comparatively reduced importance, given the relatively low contributions of this species to the diets of other estuarine predators in the region (e.g. terns, gulls, dolphins; Aygen & Emslie 2006, McGinnis & Emslie 2001, Pate & McFee 2012).

In contrast to the fasting endurance hypothesis, where the primary driver of migration is individual physiology (i.e., the inability of individuals to withstand resource scarcity), density dependence is a main factor influencing migration under the competitive release hypothesis. However, Chapman *et al*. (2011) note that resource availability typically is density dependent, and untangling the nuances of physiology versus competition is likely difficult. For example, Lamb *et al*. (2017a) found evidence for density-dependent drivers of both migration strategy and migratory distance in pelicans nesting along the northern Gulf of Mexico. In that study, migratory behavior was positively related to colony size, with individuals from larger colonies being more likely to migrate and to migrate a longer distance than individuals from smaller colonies. Importantly, however, there was also an effect of skeletal body size, with larger individuals more likely to remain near the colony as residents. The conclusion reached was that intraspecific competition, driven by density-dependent factors, was the primary driver of partial migration for that population, which closely matches the competitive release hypothesis.

In contrast to Lamb *et al*. (2017a), we were unable to find evidence for colony size or skeletal body size as a predictor of pelican migration in the SAB. In addition to the inherent ecological difference between the Gulf of Mexico and the SAB, there also exist significant differences in colony structure between the two studies. Pelican colonies in Lamb *et al*. (2017a) were widely spaced along the entire United States coastline of the Gulf, generally separated by ≥ 100 km. Colonies in the current study were much more closely spaced, especially when considered within South Carolina and Georgia (~25 km, respectively). Given that colonies in each state were within the daily foraging range of individual pelicans, for the purposes of intraspecific density dependence they may better be considered as two clustered subpopulations rather than exclusive colonies. *De facto* individual colony size may therefore be less important as a driver of competition in this system than overall subpopulation size, unlike in the northern Gulf. In addition, Lamb *et* *al*. (2017a) collapsed all tested environmental variables into a single indexed score, possibly masking the influence of specific extrinsic drivers of migration such as SST, which we found to be significant. Lastly, differences in methodologies may also have contributed to differences in outcomes. For example, we used the borders of an ecologically-meaningful habitat (i.e., marine ecoregion) to classify migratory behaviors while Lamb *et al*. chose a distance-based metric better suited to the Gulf of Mexico, as well as time-to-event models in place of generalized linear models. While these conclusions are not mutually-exclusive, further study is warranted to make clear the role of intraspecific competition as a contributor to partial migration in this species (i.e., as a result of resource scarcity, density-dependence, or both). Brown pelicans may represent a model species on which to test hypotheses related to partial migration, given the relatively broad range of the species and the variety of marine ecosystems they inhabit.

Conclusion

Despite recent increases in animal-borne tracking capabilities, the fundamental ecology of migration for many species remains unclear. Particularly unresolved are the mechanisms underpinning the maintenance of partial migration. We provide support for the fasting endurance hypothesis of partial migration using telemetry data from post-breeding brown pelicans in the South Atlantic Bight. Time-to-event models indicated significant effects of SST and BCI on the migration rates of pelicans, and we suggest that pelicans in poor condition are more likely to migrate and that migration may be driven in part by seasonal reductions in prey availability. Further work should resolve the importance of intraspecific competition on migratory behavior for this population, and assess how climate change may impact pelican migration via the potential alteration of menhaden development and emigration.

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Table 5.1. Characteristics and sample sizes of GPS-tracked Eastern brown pelicans from six breeding colonies in the South Atlantic Bight, USA.

	Bird Island	Little Egg Island	Deveaux Bank	Bird Key Stono	Castle Pinckney	Marsh Island
Coordinates	31° 07' N 81° 26' W	31° 18' N 81° 16' W	32° 32' N 80° 10' W	32° 37' N 79° 59' W	32° 46' N 79° 54' W	32° 59' N 79° 33' W
# of tracked adults	6	5	19	22	16	6
Years	2020	2020	2017-20	2017-18, 2020	2017-20	2017
Mean colony size (pairs)	396[a]	421[a]	1107[b]	3019[b]	566[b]	713[b]
% male	33	20	37	59	38	83

Table 5.2. Output from the top-ranked Cox's proportional hazards model as applied to migratory pelicans in the South Atlantic Bight, USA. Hazard values > 1 indicate a positive effect, < 1 indicate a negative effect, and = 1 indicate no effect.

Variable	Coef	SE	Hazard	*z*-value	*P*-value
BCI	-0.002	0.001	0.998	-2.768	0.006
NAO	-0.449	0.253	0.638	-1.776	0.076
SST	0.585	0.103	1.794	5.658	< 0.001
Chl-*a*	0.084	0.080	1.087	1.046	0.295

Figure 5.1. Movements of migratory (left) and resident (right) Eastern brown pelicans tagged with GPS-PTT satellite transmitters in the South Atlantic Bight, USA. The shaded blue region represents the borders of the Carolinian marine ecoregion used to delimit migratory behaviors. Inset maps depict the locations of breeding colonies near Brunswick, GA, and Charleston, SC, respectively (BI = Bird Island; LEI = Little Egg Island; DE = Deveaux Bank; BKS = Bird Key Stono; CP = Castle Pinckney; MI = Marsh Island).

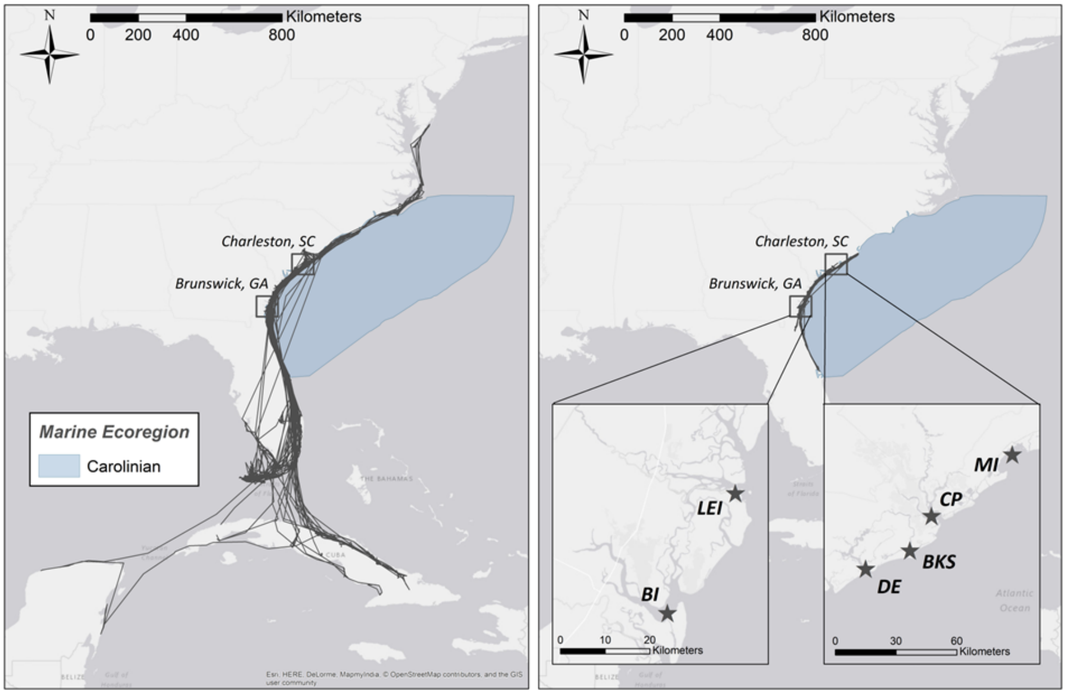


Figure 5.2. Cumulative migration probability (solid line) with 95% confidence interval (dashed line) throughout the observation period for Eastern brown pelicans in the South Atlantic Bight derived from the final Cox's proportional hazards model. Shaded grey region represents the temporal distribution of migration events (n = 47). Note the broad confidence interval near the end of the observation period, which reflects the occurrence of individuals remaining resident (i.e., within the ecoregion) for the entire observation period.

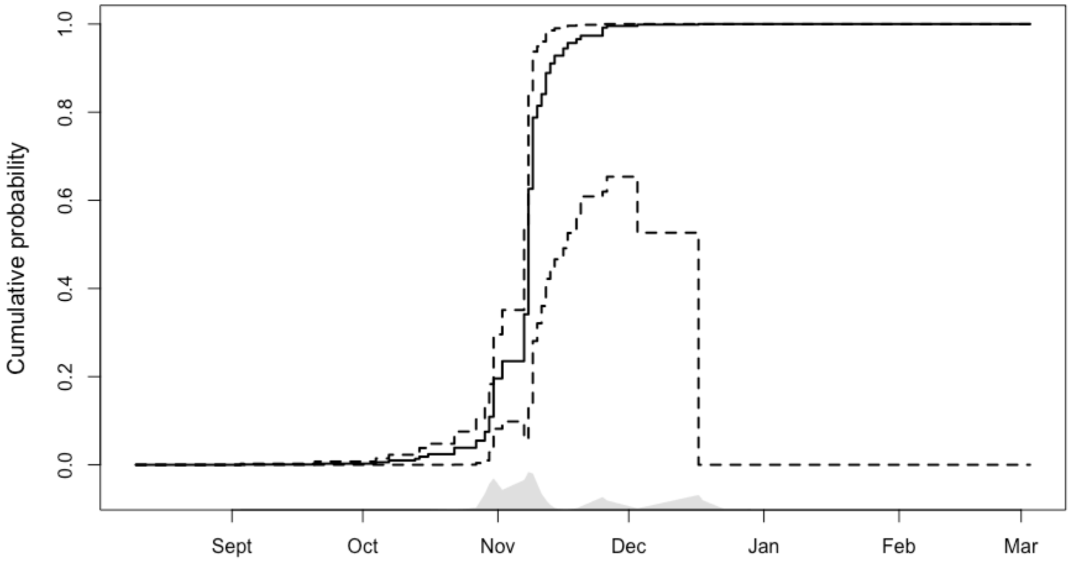
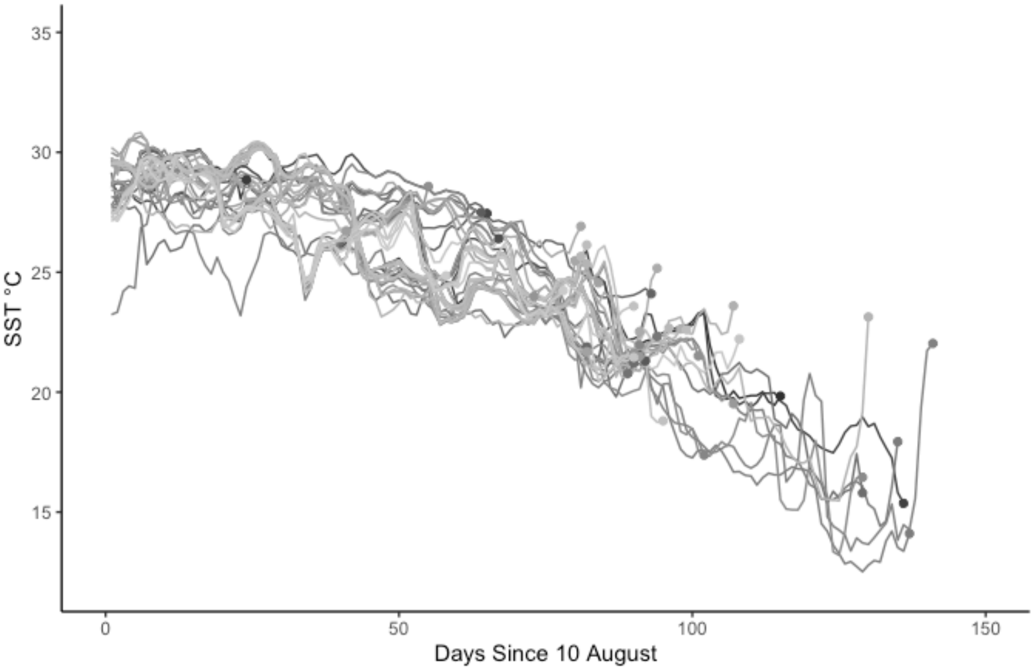


Figure 5.3. Sea-surface temperatures (SST °C) experienced by migratory (n = 47) GPS-tracked pelicans in the South Atlantic Bight over the study period, beginning 10 August. Lines are shaded by individual, with closed circles indicating the migration event.



CHAPTER SIX

CONCLUSION

This dissertation contains multiple studies connected by themes of spatial ecology, movement behavior, and conservation of brown pelicans (*Pelecanus occidentalis)* in the South Atlantic Bight. Although each study has relied fundamentally on individual-based movement data collected from brown pelicans via bird-borne telemetry, the lens through which those data have been analyzed has been modulated by both collected auxiliary data (e.g., eggs) and remotely-sensed data (e.g., environmental measures). In this way, I have been able to address key gaps in understanding related to the causes and consequences of movement behaviors in brown pelicans from this region.

Significant findings

Monitoring the behavior of coastal organisms during tropical cyclones is an inherently difficult task (Weimerskirch & Prudor 2019). From the limited studies that exist, two main strategies appear to be employed for increasing survival during these extreme weather events. The first strategy is to find shelter and remain relatively sedentary for the duration of the event (e.g., Liu *et al*. 2010) ; the second is to flee upon the approach of the storm (e.g., Udyawer *et al*. 2013) . By monitoring two cohorts of GPS-tagged brown pelicans during the passages of three tropical cyclones, I was able to derive measures of activity displayed by individual pelicans throughout the duration of cyclonic activity using a relatively novel behavioral classification algorithm, Expectation Maximization binary Clustering (Garriga *et al*. 2016). I demonstrated that pelicans tend to display a shelter-and-wait strategy, with reduced activity during peak cyclonic exposure. This reduction in activity was correlated with changes in barometric pressure and wind speed, two environmental characteristics strongly associated with extreme weather. Finally, I suggest that the maintenance of natural estuarine complexes may be important for coastal organisms enduring the passages of hurricanes within the South Atlantic Bight.

Seabirds are often regarded as effective sentinels of marine pollution, and the brown pelican specifically has historically been significantly affected by widespread environmental contamination (Wilkinson *et al*. 1994). Poly- and perfluoroalkyl substances (PFAS) represent a class of toxic chemicals of emergent concern capable of long-range transport and an extreme resistance to environmental degradation. PFAS have achieved a near-ubiquitous environmental presence, however, due to their widespread anthropogenic use and subsequent release (Armitage *et al*. 2009). Charleston, South Carolina, USA, has emerged as a location of concern for PFAS contamination nationally, with elevated concentrations of PFAS reported in predator species (e.g., dolphins; Fair Houde 2018), prey species (e.g., forage fish; Fair *et al*. 2019), and local substrates (e.g., sediment; White *et al*. 2015) from the region. Importantly, individuals which rely to a greater degree on urban habitats proximal to Charleston may display higher concentrations of PFAS compared to individuals which favor less urban habitats located at greater distances from the urban center. Through the collection of pelican eggs from three colonies located at increasing distance to urban Charleston, combined with colony-level estimates of urban habitat use derived from GPS tracking data, I demonstrate that pelicans nesting comparatively far from the urban environment and which rarely use urbanized habitats may nevertheless display elevated concentrations of PFAS. These findings imply that contaminant monitoring should include seabird colonies not only directly exposed to urbanized habitats but also colonies located at comparatively far distances from potential point sources of pollution. The need to resolve *income* versus *capital* breeding strategies for monitored seabird species is also highlighted. Finally, given the concentrations of PFAS reported in this study, future work should attempt to identify potential reproductive impacts to brown pelicans in the region.

Another marine pollution risk to coastal organisms is the unintended release of oil and other petroleum products into the environment. However, creating risk assessments for potentially impacted species can be difficult due to the complexities associated with developing realistic predictions regarding the likely trajectories of spilled oil (Chilvers & Battley 2019). I leveraged a publicly-available toolkit developed by the National Oceanic and Atmospheric Administration (NOAA) to construct a matrix of 64 unique oil spill simulations occurring in and around Charleston Harbor. I then overlapped the results of these spill simulations with pelican-derived tracking data from two nearby colonies to resolve the factors most associated with the risk of surface oil contamination to foraging pelicans. Results suggest that spill location, along with spill size and timing of the spill during the breeding season, were the most important factors determining pelican-oil overlap. Based on this study, foraging seabirds may be much more likely to encounter surface oil when it is released outside of the harbor compared to spills occurring inside the harbor, as spills inside the harbor may be more of a risk to nearby intertidal habitats due to relatively accelerated beaching times of spilled oil.

Partial migration occurs when some portion of a population chooses to migrate, while the other portion does not (Chapman *et al*. 2011). The mechanisms underlying partial migration are important to uncover, as this system is generally regarded as a precursor to full migration (Chapman *et al*. 2011). However, individuals are expected to migrate based on a variety of both intrinsic and extrinsic factors, and identifying which factors may be the most relevant to a given population can be difficult. Brown pelicans in the South Atlantic Bight exhibit a partial migration strategy, but the mechanisms influencing individual choice in migration are unclear. I applied a type of survival model, Cox's proportional hazards model, to pelican tracking data from both migratory and non-migratory individuals to assess which factors were most important for influencing migratory decision-making in this population. Results of this modeling were consistent with the fasting endurance hypothesis of partial migration, which states that individuals unable to endure reductions in foraging will migrate while those able to withstand foraging reductions will remain in place (Chapman *et al*. 2011). I suggest that the ontogenetic migration of juvenile Atlantic menhaden (*Brevoortia tyrannus*) from estuarine to pelagic habitats in the autumn results in a reduction in forage for brown pelicans, and that individual pelicans unable to cope with this reduction migrate from the region. There exists only limited empirical support for the fasting endurance hypothesis in the literature, and this study therefore represents an important work documenting this potential mechanism in driving migration generally.

Animal-borne telemetry represents a powerful tool for assessing ecological relationships. The movements of organisms are influenced by a wide variety of factors, and the behavioral decisions of individuals may in turn serve to act on the fitness of the organism. Understanding the interplay between movement drivers and the consequences of animal behavior are key to furthering ecological research and developing effective conservation strategies in the face of unprecedented anthropogenic activity.

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