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Ecological Drivers of Brown Pelican Movement Patterns and Reproductive Success in the Gulf of Mexico

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ECOLOGICAL DRIVERS OF BROWN PELICAN MOVEMENT PATTERNS AND REPRODUCTIVE SUCCESS IN THE GULF OF MEXICO

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ABSTRACT

The effects of environmental change on vast, inaccessible marine ecosystems are often difficult to measure and detect. As accessible and highly visible apex predators in marine environments, seabirds are often selected as indicators for studying the effects of disturbance at lower trophic levels, although data are restricted both temporally and spatially. For example, studies of seabirds have historically been limited to the breeding season, with limited data being available throughout the remainder of the annual cycle. Additionally, understanding of habitat associations and behavior of seabirds in the marine environment comes primarily from pelagic seabirds, whose habitat year-round is generally in remote marine areas removed from anthropogenic development, while similar data from nearshore seabirds are less common. Such data gaps limit our understanding or life-history traits among seabirds, one of the most imperiled avian groups globally, and subsequently our ability to inform conservation and marine spatial planning. My goal was to examine ecological relationships of diet, breeding biology, and movement patterns of a nearshore tropical seabird, the Eastern brown pelican, in the Gulf of Mexico, one of the most anthropogenically developed marine ecosystems worldwide. While my results supported previous findings that nutritional conditions are a key driver of seabird reproductive success and recruitment, they differ in suggesting that prey availability and delivery rates are more important to reproductive rates than energetic value of prey species. Since direct measurement of reproductive rates is time-consuming and difficult to collect, I also tested an integrated measure of nutritional stress during development, feather corticosterone, as a predictor of nestling survival and fledging rates.

Corticosterone predicted 94% of inter-colony variation in fledging success and was also correlated with post-fledging survival, making it a powerful tool for measuring demographic patterns in this species. To measure adult movement patterns, I deployed bird-borne biologgers to collect highly accurate spatial data from pelicans throughout the annual cycle. I found that individual breeders quickly returned to normal behavior after capture and tagging. GPS tracking also indicated that pelicans were highly mobile, ranging over large areas during the breeding season and migrating up to 2,500 kilometers during non-breeding. Movement patterns were influenced by local conspecific competition during both breeding and migration, such that birds from larger colonies moved longer distances year-round compared to those from smaller colonies. I also found a high degree of spatial, temporal, and individual variation in exposure to surface pollutants across the population. I recorded a high degree of individual variation in movement, which interacted with pollutant exposure to create a complex and varying distribution of risk throughout the northern Gulf metapopulation of brown pelicans. Understanding the factors driving this variation will inform future monitoring, conservation, and mitigation efforts for this species.

DEDICATION

To Dr. Farish Jenkins

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CHAPTER ONE

INTRODUCTION

As the global demand for energy increases, marine systems are increasingly being proposed or developed as sources of energy through wind and tidal harvest (Pelc and Fujita 2002) and petroleum extraction (Freudenberg and Gramling 1994). However, the rapid progress of energy extraction and development has often outpaced scientific understanding of its effects on marine systems and the organisms that inhabit them (Ward *et al.* 1979, Burke *et al.* 2012). Studies conducted following the installation of offshore energy projects have documented that effects on marine species, whether positive or negative, can be more significant than anticipated (Boesch and Rabalais 1987, Daan and Mulder 1996, Sammarco *et al.* 2004). The impacts of energy extraction can occur through direct adult mortality, as well as indirectly through pathways including compromised condition due to contaminants exposure, altered availability or distribution of prey, altered behavior, or reduced reproductive output (Haney 2014).

Marine birds have proven to be useful models to study the impacts of threats such as offshore development on the broader marine ecosystem (Furness and Greenwood 1993). Not only are seabirds relatively accessible compared to other marine vertebrates, but their wide-ranging migratory and foraging behavior increases the opportunities for them to interact with energy installations (Weise and Jones 2001). Seabirds also rely on a variety of above- and below-water habitats including both terrestrial breeding colonies and pelagic foraging grounds (Hunt 1990, Pinaud and Weimerskerch 2005), and as top-level marine predators they are particularly vulnerable to bioaccumulation of

contaminants (Walker 1990, Perez *et al.* 2008) and may provide indications of perturbations at lower trophic levels (Thompson *et al.* 1998, Weise and Jones 2001). Understanding the effects of existing development and predicting the impacts of future development on seabirds requires, however, a thorough understanding of seabird population dynamics, behavior, and habitat use under baseline conditions (Ballance 2008, Soanes *et al.* 2013). In reality, such information is often not collected until after development or contamination has altered baseline processes. Additionally, the direct contribution of anthropogenic stressors to demographic parameters in the marine environment varies widely and can be difficult to estimate (Burger 1993, Uhlmann *et al.* 2005).

The Gulf of Mexico contains a high density of oil infrastructure and coastal development, as well as a rich assemblage of nearshore seabirds, wading birds, migratory waterfowl, and shorebirds (Duncan and Havard 1980). The region is of year-round importance to Atlantic seabirds, including both local breeding populations and breeders from distant locations which winter along the Gulf Coast (Mikusa *et al.* 1998, Montevecchi *et al.* 2012, Haney *et al.* 2014). Many terrestrial areas of known importance to breeding, migrating, and wintering waterbirds have been designated for protection at state and federal levels. However, the marine environment of the Gulf, including offshore foraging and migratory habitat remains open to oil development, ship traffic, fishing, and contaminants release (Davis *et al.* 2000).

Given its distribution patterns, behavior, and known sensitivity to chemical and oil contaminants exposure (Blus 1982, King *et al.* 1985, Shields 2014), the brown pelican

(*Pelecanus occidentalis*) may be a good indicator of species-level effects of interaction with coastal and marine development (Wilkinson *et al.* 1994). However, despite the species' long history as a focus for conservation and restoration efforts, much of the information required to understand pelican population dynamics and habitat requirements, including adult and fledgling mortality, dispersal, site fidelity, diet composition, foraging behavior, migration patterns, and nonbreeding habitat use, remains unknown or poorly understood (Shields 2014, but see Wood *et al.* 1995 for colony site fidelity of brown pelicans in Florida; Schreiber and Mock 1988 for survival rates of *P. o. californicus*; and Briggs *et al.* 1981 for habitat use of *P. o. californicus*). For example, in the wake of the 2010 *Deepwater Horizon* oil spill, some preliminary tracking data collected from brown pelicans captured in the northern Gulf of Mexico indicated that local populations previously thought to be non-migratory or for which migratory paths were unknown vacate breeding areas to winter along the Yucatan Peninsula, northern Central America, and the Florida Gulf coast (Jodice *et al.*, unpublished data).

Summary of dissertation content

The principal objective of this dissertation is to investigate the ecological factors contributing to variation in pelican movements, behavior, and population dynamics throughout the northern Gulf of Mexico under baseline conditions.

Chapter 2 assesses the validity of using GPS tagging to study brown pelican movements. Individual tracking studies are a powerful means of assessing the effects of environmental change on movement patterns and interaction with affected areas, but their

usefulness depends on the assumption that individuals fitted with tracking devices are representative of the population as a whole. Since tagging has the potential to change behavior, I first compared the behavior of individuals fitted with GPS transmitters to untagged individuals in a captive setting in the hours following tag attachment. I then assessed the behavioral responses of tagged and untagged breeding pelicans in a field setting in the days following attachment, as well as the breeding success of individuals carrying GPS transmitters.

Chapter 3 uses data obtained from GPS transmitters to compare the year-round movement patterns of brown pelicans from colonies of varying sizes. I tested the hypothesis, previously documented in other seabird literature, that breeders from larger colonies would forage over larger areas during the breeding season in response to density-dependent competition in marine foraging habitat. I further expanded this hypothesis to include migratory patterns, and tested whether breeders from larger colonies traveled further from their breeding sites during winter months. Year-round responses to colony size have the potential to affect population-level patterns of spatial distribution in seabirds under baseline conditions, and the inclusion of migration in density-dependent movement patterns is a unique line of inquiry in the seabird literature.

Chapter 4 tests two physiological measures of nestling health to assess their utility in predicting and comparing colony-level reproductive success. As a key factor in population dynamics, reproductive success could be an informative metric for evaluating the effects of environmental perturbations at the population level; however, collecting these data is a difficult, expensive, and invasive process, and no program is currently in

place for long-term monitoring of reproductive success in brown pelicans. I tested the relationship of two physiological measurements of nestlings, body condition and stress hormone levels, to colony-wide reproductive success, individual survival to fledge, and post-fledging survival.

Chapter 5 examines how variation in the rate of energy delivery by pelican adults to nestlings both reflects underlying environmental conditions and influences nestling survival. Optimal foraging theory dictates that central-place foragers, such as nesting seabirds, should minimize their own energy expenditure in capturing prey and delivering it to nestlings while maximizing the amount of energy delivered. In brown pelicans, which can capture a large volume of prey in a single dive, the overall energy-maximizing strategy may not involve pursuing the most energy-dense prey available. I tested the variation in energy density between common prey species, as well as analyzing which components of energy delivery (energy density, provisioning rate, or meal mass) contributed most significantly to nestling survival. Understanding prey conditions and provisioning is a necessary first step to predicting how factors that influence prey distributions are likely to affect population dynamics.

Chapter 6 uses a combination of several modeling approaches to define the environmental characteristics driving habitat associations of brown pelicans, how these habitat associations vary between local and long-distance movements, and how the risk of encounters between pelicans and oceanic pollutants differ spatially, temporally, and individually. By assessing the distributions of both pelican populations and pollutant concentrations throughout the year, my data provide insight into the distribution of risk

across the metapopulation of pelicans in the northern Gulf as well as the breeding locations likely to be affected by future contamination events.

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CHAPTER TWO

SHORT-TERM BEHAVIORAL AND REPRODUCTIVE EFFECTS OF BIRD-BORNE DATA LOGGER ATTACHMENT ON BROWN PELICANS (*PELECANUS OCCIDENTALIS*)

Abstract

Although the use of bird-borne data loggers has become widespread in avian field research, the effects of capture and transmitter attachment on behavior and demographic rates are not often measured. Tag- and capture-induced effects have the potential to influence the degree to which transmitter data represent the behavior of the wider population, as well as to impact survival and reproduction. I measured the short-term behavioral and reproductive effects of handling and GPS transmitter attachment on brown pelicans under both captive and field conditions. In the captive population, I observed increased preening behavior among tagged individuals 0-2 hours after capture, with a corresponding reduction in time spent resting. However, in observations of free-living individuals 1-3 days post-capture, I found that these effects did not persist and that behavior of tagged breeding pelicans resembled that of untagged neighbors. I also followed tagged individuals through a full breeding season to assess whether transmitter attachment during breeding resulted in nest abandonment or breeding failure. The majority (88%) of tagged breeders remained at the same nest location for at least 48 hours and bred for an average of 49 days after capture. The remainder either re-nested elsewhere or abandoned and did not re-nest. Overall, 51% of GPS-tagged pelicans attended nests after hatch and were assumed to successfully fledge young. Breeding success was driven primarily by variation in location. Sex and handling time also

influenced probability of breeding success in tagged pelicans, suggesting that individual characteristics and the capture process itself can affect sensitivity to transmitter attachment in this species. I conclude that, although an adjustment period immediately following capture should be taken into account when analyzing spatial data, GPS transmitters have minimal effects and are a viable technique for studying behavior and demographics in this species.

Introduction

Traditionally, investigation of seabird foraging and wintering habitat has relied on ship-based surveys (reviewed in Ballance 2008), color-marking (Calvo and Furness 1992) or band recoveries (Schreiber and Mock 1988). Recently, individual tracking has become more commonplace due to its flexibility, ease of access, and broad applicability in the marine environment (Wakefield *et al.* 2009). Unlike survey or mark-recapture techniques, telemetry-based studies (Boyd *et al.* 2004) integrate year-round habitat use by known individuals, offer individual- and colony-specific information on preferred foraging and wintering habitat, and identify marine areas of particular conservation importance that might not otherwise be recognized (Tancell *et al.* 2013). At the same time, telemetry studies have potential drawbacks, including high costs, small sample sizes, and the need to accurately represent individual and geographic variation when scaling up to population-level patterns (Hebblewhite and Haydon 2010).

One important, though often overlooked, component of interpreting telemetry data is assessing the extent to which carrying a payload (*i.e.*, tracking device) impacts the

survival, behavior, and reproduction of individual birds (reviewed in Barron *et al.* 2010). Tag effects have the potential to restrict inferences drawn from tracking data if the activities of tagged birds differ from the baseline behavior of untagged individuals (Igual *et al.* 2005). Tagging also has the potential to reduce breeding success or increase mortality rates, which are of particular concern in sensitive species (Carey 2009). For long-lived seabirds, which generally raise only 1-2 young per year, short-term changes in adult condition or breeding success can have disproportionate long-term implications for population dynamics (Fredricksen *et al.* 2008). Despite these concerns, most tracking studies do not directly assess the impacts of the tags on the behavior or reproduction of seabirds (Vandenabeele *et al.* 2011). As the effects of both handling and tagging may vary among and within species (Carey 2009, Barron *et al.* 2010), it is important to understand how and whether individual tracking data might be impacted by tag-induced behavioral changes.

Brown pelicans (*Pelecanus occidentalis*) have long been a focal species for coastal conservation due to their sensitivity to contaminants exposure (Blus *et al.* 1979) and, in particular, to their high mortality and morbidity during oil spills (Jernelöv and Lindén 1981, Anderson *et al.* 1996, Haney *et al.* 2014). These factors, combined with their large population sizes and visibility, make them a strong indicator species for studying short- and long-term effects of anthropogenic alterations of nearshore marine systems, and they are often cited as targets for research and mitigation after spill events (Levy and Gopalakrishnan 2010). In comparison to other seabirds, brown pelicans are generally considered unusually sensitive to human disturbance during breeding

(Anderson 1988). Colony-based research efforts, including tagging studies, have thus been limited, and therefore most data on pelican movement comes from marking and banding studies (*e.g.* Schreiber 1976, Schreiber and Mock 1988). However, recent studies (*e.g.* Sachs and Jodice 2009, Eggert *et al.* 2010) have demonstrated that research can be conducted on nestling pelicans at breeding colonies without inducing nest abandonment or negatively impacting breeding success. This raises the possibility of collecting individual data on pelican breeding biology and movement ecology as a baseline for studying the impacts of future perturbations.

To date, GPS tracking of adult brown pelicans has been limited to non-breeding individuals and conducted away from breeding colonies (Croll *et al.* 1986, Evers *et al.* 2011, King *et al.* 2013) with the exception of a recent study conducted by Walter *et al.* (2014) in which breeding adult pelicans were captured at nests. In this latter example, 74% of nests of tagged individuals failed soon after tagging, and many subsequently relocated to different breeding colonies to re-initiate nesting. The reasons for this large-scale failure were unclear, and, beyond the observation of nest abandonment rates, effects of capture and tagging on adult behavior were not quantified. However, the failure of GPS-tagged pelicans to continue breeding normally after transmitter attachment indicates that the capture and tagging process may alter individual behavior.

To better understand how capture and tagging affects brown pelican behavior and breeding activity, I conducted behavioral observations of adult pelicans tagged with GPS transmitters, both in a captive setting (rehabilitation center) and in the field. In the captive portion of this research, I compared GPS-tagged and untagged individuals immediately

before and after transmitter attachment. In the field portion, I observed behavioral states of GPS-tagged nesting pelicans relative to untagged neighbors in the days following transmitter attachment, and quantified subsequent nesting duration and inferred success. This study provides an opportunity to assess the impacts of a common research practice (*i.e.*, individual tagging) on a species of conservation concern and also provides a template for designing field- and captive-based studies of tag impacts on free-ranging and rehabilitated seabirds.

Methods

Captive trial

On 11 June 2015, five adult California brown pelicans (*P. o. californicus*) were fitted with 65 g platform terminal GPS transmitters (GPS-PTTs: NorthStar Science and Technology) at the Los Angeles Oiled Bird Care and Education Center rehabilitation facility in San Pedro, California. These individuals had been oiled during the Refugio Oil Spill on 19 May 2015, had undergone cleaning and rehabilitation, and were being prepared for release at the time of transmitter attachment. Transmitters were attached dorsally between the wings using a backpack-style Teflon ribbon harness (Dunstan 1972; Figure 2.1). Transmitters were constructed with sloped fronts, to minimize resistance while diving, and ranged from 1.5 – 1.7% of individual body mass (M = 1.6%), below the 3% threshold generally considered acceptable for seabirds (Phillips *et al.* 2003). All GPS-tagged pelicans were released into a 6 × 13 × 5 m outdoor net enclosure containing a large pool and several perches 4 m in elevation, and filmed for 142 minutes pre- and 167

minutes post-transmitter attachment, for a total of approximately five hours (309 minutes) per individual and 25 total observation hours. The birds were sexed by culmen length. Four additional adult pelicans that did not receive transmitters, which had also been cleaned and rehabilitated following oiling in the Refugio spill, were housed in the same enclosure and filmed during the same period of time served as behavioral controls. Sex of control pelicans was not determined.

I used EthoLog 2.2 software (Ottoni 2000) to record behaviors of all pelicans during the pre- and post-attachment phases. Behaviors included six mutually exclusive state events (resting, ground loafing, perched loafing, preening, swimming, and flying) and nine instant events (walking, flapping, stretching, scratching, eating, shaking, bathing, diving, and interacting with other individuals). To minimize observer bias, all coding was done by the same observer (JSL). I standardized the frequencies of observed behaviors by dividing the duration (state events) or number (instant events) by total observation time in seconds. I then subtracted pre-attachment from post-attachment values to calculate the difference in each behavior by individual. Finally, after visually assessing the data to ensure that assumptions of normality were met, I compared differences in values between tagged and untagged individuals using one-way analysis of variance tests (ANOVAs).

Field trial

I captured and attached GPS transmitters to 85 breeding adult Eastern brown pelicans (*P. o. carolinensis*) at nest sites in six colonies throughout the northern Gulf of

Mexico (Figure 2.2). Sixty pelicans were captured between 26 April and 3 July 2013, and 25 between 26 April and 29 May 2014, with a maximum of one adult captured per nest. Of the 85 transmitters deployed, 74 recorded at least one full breeding season of GPS data (Figure 2.2) and only these were included in subsequent analyses of reproductive success. All adults were captured on nests using leg nooses during the late incubation and early chick-rearing stages. During the adult's absence, a plastic laundry basket was placed over the nest to protect nest contents from weather and predation. Median handling time was 17.5 minutes from capture to release and included blood sample collection, transmitter attachment, and standard physiological measurements. GPS-PTTs (65 g, NorthStar Science and Technology) were constructed with sloped fronts and attached as in the captive trial. Transmitters ranged from 1.5-2.9% of individual body mass (M = 1.9%). At the time of capture, I also collected DNA samples (~ 0.1µL metatarsal blood on filter paper), which I later used to determine the sex of all captured adults via PCR (Itoh *et al.* 2001).

During the 1– 3 days following capture, I conducted 3-hour behavioral observations on all adults present at nests during return visits to the colony (N = 35 individuals; 105 observation hours). The remaining individuals were not present during return visits, either due to nest abandonment (see Results) or because their mates were attending the nest at the time. Before beginning the observation, I selected a nearby (≤ 2 m distance) nest at the same phenological stage as each focal nest (*i.e.*, incubation, small chick-rearing, or large chick-rearing) to act as a control for comparison of behaviors. During the observation, I recorded the behavior of the tagged and control adults at 5-

minute intervals, classifying behaviors as resting, preening, alert (moving nest material, interacting with chicks or neighboring birds; comparable to loafing behavior in the captive trials), or agitated (alert and exhibiting signs of stress). For each individual observed, I calculated the percent of time spent in each behavior. I then separated the data by behavior and used paired t-tests to compare frequency of each individual behavior between GPS-tagged and untagged individuals.

Using transmitter data, I recorded the duration in days of subsequent nest attendance by all GPS-tagged individuals. Nests were considered active for as long as adults continued to visit the nesting colony at least once a day. I inferred approximate hatching dates from nest stage at date of capture, and, for the purposes of this study, considered breeding successful if adult attendance continued for at least 60 days after hatch. This represents the minimum age at which nestlings are likely to fledge (Shields 2014). For pelicans that re-nested following capture, I interpreted the start of attendance at the new site as the beginning of incubation and used a 90-day cutoff for successful breeding, incorporating 30 days of incubation time (Shields 2014) in addition to the 60-day fledging period. To assess post-capture nest survival and breeding success, I used a generalized linear modeling framework to model the probability that parents would attend the nest for at least 60 days after hatch, which I interpreted as likely brood success (binomial function, Bernoulli with logit link). To test which factors most influenced post-capture nest persistence and reproductive success I included handling time, nest stage, sex, body condition index (BCI: residual of the linear relationship between mass and culmen length), capture date, and capture location (*i.e.*, breeding colony) as predictor

variables. I used a Hosmer-Lemeshow Goodness of Fit test to assess the fit of the global model and compared models using Akaike's Information Criterion (AIC) values. Models were preferred if they resulted in a decrease in AIC of ≤ 2 relative to the best-fitting model, while models with Δ AIC of 4-7 were considered weakly supported (Burnham and Anderson 2004). I estimated means-parameterized model-averaged coefficients over the suite of preferred models, weighted by AIC weights.

Results

Captive trial

Relative to the untagged group, GPS-tagged individuals spent significantly more time preening ($p = 0.04$, $F_{(1,7)} = 6.41$) and less time resting ($p = 0.05$, $F_{(1,7)} = 5.62$) immediately post-tagging than prior to tagging. Tagged and control pelicans spent similar amounts of time resting prior to tagging (23% for each group). After capture, handling, and tag attachment, tagged pelicans spent 11% less time resting and 4% more time preening, while controls spent 17% more time resting and 12% less time preening. Differences between groups in swimming, flying, loafing, and perching behavior were not significant ($p > 0.05$ for each; Figure 2.3a). I did not find significant differences in frequency between the tagged and control groups for any of the instant events I quantified ($p > 0.05$ for each; Figure 2.3b).

Field trial

I did not observe any differences between the proportion of observation time spent in preening (t_{31} = -0.59, p = 0.56), resting (t_{31} = -0.88, p = 0.38), alert/loafing (t_{31} = 1.60, p = 0.12), or agitated (t_{31} = -1.42, p = 0.17) behavioral states between GPS-tagged individuals and untagged neighbors in the field 1 – 3 days post-tagging (Figure 2.4).

Overall, GPS-tagged pelicans (N = 74) continued attending nests for an average of 50 (SD ± 34; Range 0 – 113) days after capture. The majority (88%) continued breeding at their original nest sites following capture. The remaining adults either abandoned the breeding colony within one day of capture and did not re-nest that season (N = 3), re-nested at the same breeding colony but at a different nest site (N = 3), or re-nested at different breeding colonies between 30 and 65 km from the original nesting colony (N = 3) (Table 2.1). Successful breeders attended nests for an average of 83 days after hatch (SD ± 13 days) while unsuccessful breeders attended on average 18 days (SD ± 14.7 days). Both pelicans that re-nested and pelicans that remained at their original nest sites bred successfully (Table 2.1).

The global model was a good fit for the observed data (X^2_8 = 1.85, p = 0.99). The four best-performing models for breeding success included capture location (Table 2.2). Breeding success appeared lower in the Central and Western regions compared to the Eastern region (*i.e.*, the Eastern region was set as the reference level; Figure 2.5a). The model-averaged coefficient estimates (± SE) for location were -0.40 ± 0.64 for the Central region and -2.69 ± 0.72 for the Western region. Two of the top models also included handling time (-0.64 ± 0.54), and two included sex (0.66 ± 0.56). Phenological

variables (capture date and nest stage) and physical condition (BCI) were not included in the best-performing models for breeding success. Handling time at capture was significantly longer in unsuccessful than successful breeders ($t_{55} = 1.7$, one-tailed $p = 0.047$), with a significant decrease in breeding success among birds that were handled for more than 20 minutes (Figure 2.5b: Fisher's Exact Test, one-tailed $p = 0.045$). Sex did not differ significantly between successful and unsuccessful breeders (Figure 1.5c: Fisher's Exact Test, one-tailed $p = 0.33$), but females were more likely than males to abandon or re-nest within one day of capture (Fisher's Exact Test, one-tailed $p = 0.045$).

Discussion

I observed short-term behavioral effects of transmitter attachment in the captive setting 1-2 hours post-release, but not in the field setting 1-3 days post-release. Although captive and free-ranging groups were observed under different conditions and had different histories, both were observed relative to control individuals in similar conditions that had been disturbed due to capture of nearby individuals but not GPS-tagged. The fact that behavioral changes of captive birds immediately after transmitter attachment were not observed in free-ranging birds at nest locations within several days of capture suggests that behaviors indicative of stress or discomfort in this study, whether due to the attached device, the harness, the capture process, or any combination of the above, diminished rapidly.

Immediately after transmitter attachment, I observed differences in two behavioral states in tagged captive birds: time spent preening (increased) and time spent resting

(decreased). Since both handling and harness attachment may disrupt plumage and reduce waterproofing, increased preening behavior suggests an attempt to restore feather structure and represents a potential short-term increase in energy expenditure following handling and transmitter attachment. Other behaviors (swimming, perching, flying, loafing, and instantaneous events) did not increase or decrease following transmitter attachment, although flying, swimming, and perching opportunities were restricted by the small size of the enclosure. As swimming and flight are particularly critical to foraging, provisioning chicks, and escaping predators, changes in these behaviors might suggest an increased risk of mortality or breeding failure following transmitter attachment. My results suggest that such behaviors continued normally after capture. However, my observations are limited to captive birds in a small enclosure, and I did not measure foraging movements or flight and swimming behavior in the field. Free-ranging GPS-tagged individuals appeared to fly and swim normally after release (personal observation).

All supported models for breeding success included capture location as a predictor variable, indicating regional differences in breeding success among GPS-tagged adults. Currently, there are limited data on factors affecting productivity in brown pelicans throughout their range. However, Walter *et al.* (2014) also reported strong regional differences within the state of Louisiana in failure rates of nests of brown pelicans following capture and GPS-tagging, suggesting that rates of nesting success may vary widely depending on prey distribution, habitat availability, and environmental conditions. Apparent brood success of brown pelicans measured at colonies throughout

the study area in 2014 and 2015 ranged from 20% to 84%, with an average of 62% (N = 565 nests; Lamb, unpubl. data). This indicates that rates of breeding failure in tagged individuals fell within the range observed under natural conditions in the region.

Handling time appeared in two of the top models for breeding success. Longer handling periods resulted in a decrease in breeding success, with sharply reduced breeding success among birds that were handled for more than 20 minutes. Longer handling times may result in the captured bird reducing attendance, thus increasing the likelihood of eggs and chicks being lost to weather and predation. Effects of increased handling time have also been observed by Jodice *et al.* (2003) for black-legged kittiwakes. Sex also appeared as a predictor in two of the four top models, although again with a coefficient estimate not significantly different from zero. Although I did not observe a significant difference in breeding success between tagged male and female pelicans, my results indicate that females may be more likely than males to abandon immediately after being captured and fitted with GPS transmitters. As pelicans are sexually dimorphic, the percentage of body weight represented by a transmitter is higher for females (M = 2.2 ± 0.2%) than for males (M = 1.7 ± 0.1%). However, transmitter weight represented < 3% of body mass for all individuals included in this study, which is generally considered an acceptable payload for seabirds (Phillips *et al.* 2003, although see Vandenabeele *et al.* 2012 for discussion of the limitations of this rule). There is limited evidence that females of some seabird species may take longer than males to recover from disturbance (Weimerskirch et al 2002).

I did not observe the high rates of nest failure previously reported in GPS-tagged brown pelicans in the northern Gulf of Mexico following transmitter attachment (Walter *et al.* 2014). This study included pelicans from a much broader geographic range, but among breeders from the central region of this study, comparable to the Louisiana study area in Walter *et al.*, I also observed a lower rate of relocation and nest failure (48% in this study, vs. 94% in Walter *et al.*), a lower rate of abandonment within 48 hours of tagging (19% vs. 44%), and a longer duration of nesting for failed breeders that remained on their original nest sites (40 ± 9 days in this study, vs. 7 ± 10 days in Walter *et al.*). I took steps to reduce handling time and protect nest contents while captured adults were absent from the nest, which may have contributed to higher rates of nest persistence in this study. Future tracking studies of nesting brown pelicans might include such precautions, at a minimum, to ensure that nest contents are protected during the tagging process and to improve the likelihood of successful breeding by tracked adults.

My study suggests that capture and GPS-tagging in brown pelicans results in short-term behavioral effects, but that these effects do not persist into the days following transmitter attachment. Since GPS transmitters appear to have minimal effects on brown pelicans, data obtained from bird-borne loggers is a viable technique for studying behavior and demography in this species. Behavioral changes due to the transmitter attachment process can be accounted for by excluding locations obtained during the first 24 hours after transmitter attachment in order to avoid biased inference in GPS data analysis. Since this study included only the breeding season following capture, I did not assess long-term effects of transmitter attachment on adult survival or lifetime fitness.

While reproductive and survival values are key to understanding the demographic effects of perturbations such as researcher disturbance, baseline data on these parameters are lacking in this and many seabird species. Future studies are needed on long-term impacts of carrying a GPS transmitter on site fidelity, survival, and reproductive success in the years following transmitter attachment in this and other seabirds.

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Table 2.1. Nest persistence and breeding success of GPS-tagged pelicans in the northern Gulf of Mexico, 2013-2014. Breeding success defined as adults attending nests for at least 60 days post-hatching for the purposes of this study.

	N	Mean days attending nest after hatch (*SD*)	% successful
Total	74	50 (34)	51
Remained at original site	65	49 (33)	52
Re-nested (same colony)	3	57 (22)	67
Re-nested (different colony)	3	47 (24)	67
Abandoned	3	0	0

Table 2.2. Candidate models for breeding success of brown pelicans in the northern Gulf of Mexico, ranked in order of increasing AIC values with model weights (w_i), cumulative weights (Σw) and relative likelihoods (L_i). Models above the dashed line were considered strongly preferred (Δ AIC < 2) and models in dark grey were not supported. Terms used in models are defined in Methods. Numbers in parentheses represent model IDs.

Model ID	Terms	AIC	Δ_i (AIC)	w_i (AIC)	Σw	L_i (AIC)
8	location	85.75	0	0.27	0.27	1
14	handling + location (7 + 8)	86.2	0.45	0.22	0.49	0.80
11	sex + location (2 + 8)	86.3	0.55	0.20	0.69	0.76
17	sex + handling + location (2 + 7 + 8)	86.9	1.15	0.15	0.84	0.56
13	phenology + location (6 + 8)	88.81	3.06	0.06	0.90	0.22
16	sex + phenology + location (2 + 6 + 8)	89.46	3.71	0.04	0.94	0.16
18	phenology + handling + location (6 + 7 + 8)	90.15	4.4	0.03	0.97	0.11
19	global (2 + 4 + 7 + 8)	90.91	5.16	0.02	0.99	0.08
9	sex + phenology (2 + 4)	95.29	9.54	< 0.01		< 0.01
6	phenology (nest stage + capture date)	95.45	9.7	< 0.01		< 0.01
15	sex + phenology + handling (2 + 6 + 7)	96.69	10.94	< 0.01		< 0.01
12	phenology + handling (6 + 7)	96.73	10.98	< 0.01		< 0.01
4	nest stage	97.8	12.05	< 0.01		< 0.01
10	sex + handling (2 + 7)	103.2	17.45	< 0.01		< 0.01
7	handling time	103.4	17.65	< 0.01		< 0.01
2	sex	103.9	18.15	< 0.01		< 0.01
5	capture date	104.5	18.75	< 0.01		< 0.01
20	null model	104.5	18.75	< 0.01		< 0.01
1	BCI	105.1	19.35	< 0.01		< 0.01
3	individual (BCI + sex)	105.6	19.85	< 0.01		< 0.01

Figure 2.1. Positioning of GPS transmitter and harness dorsally (L) and ventrally (R). Los Angeles Oiled Bird Care and Education Center, San Pedro, California, 11 June 2015 (J. Lamb).

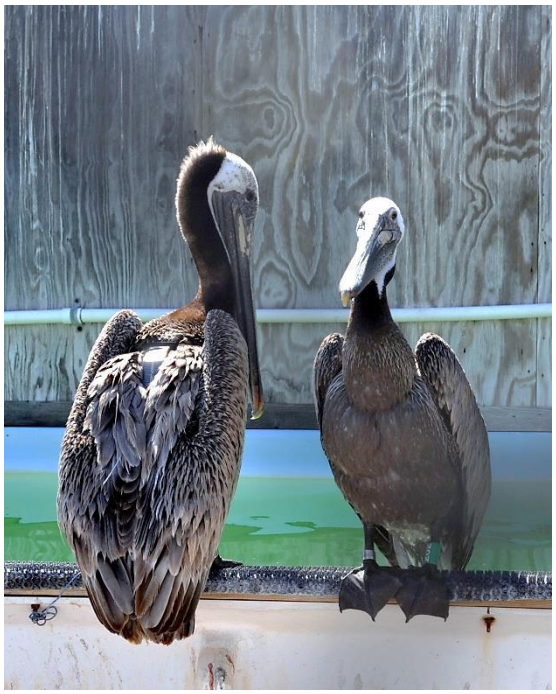


Figure 2.2. Map of colony locations of brown pelicans fitted with GPS transmitters. Number of birds tracked through the end of the breeding season from each colony is indicated in parentheses. Eastern, Central, and .Western study regions are delineated by dashed lines as defined by the U.S. Bureau of Ocean Energy Management.

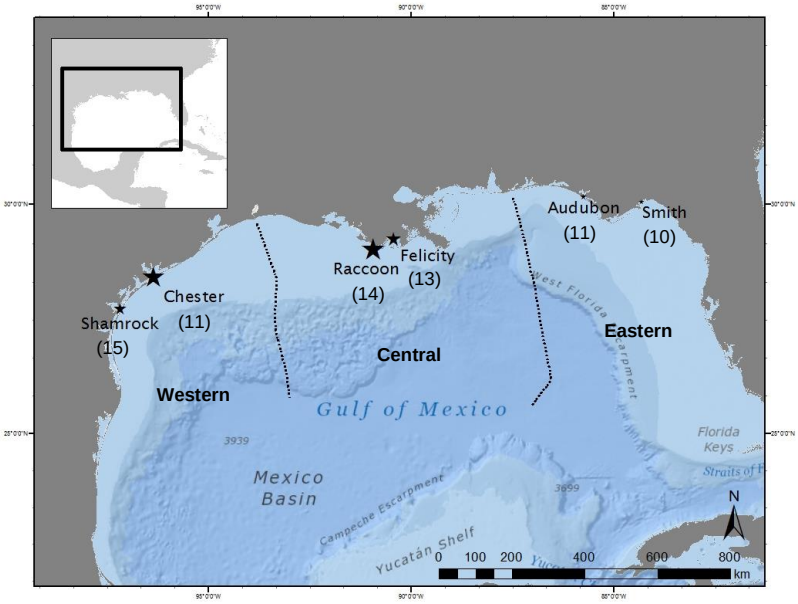
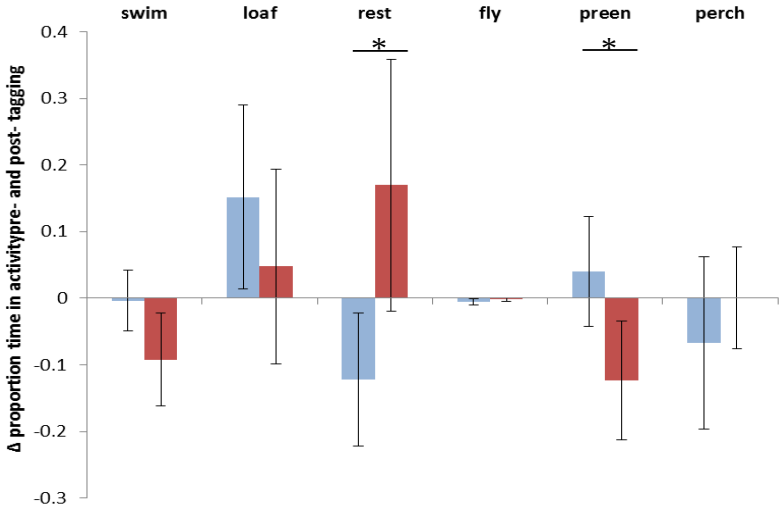


Figure 2.3. Change between time engaged in behaviors pre- and post-tagging for brown pelicans in a captive holding facility in (a) proportion of time spent in each behavioral state and (b) frequency of instant events. Positive values indicate an increase after tagging; negative values indicate a decrease. Blue bars represent the tagged group, red bars represent the untagged group, and error bars represent 95% confidence intervals. * = $p < 0.05$; all other differences are non-significant ($p > 0.05$).

(a)



(b)

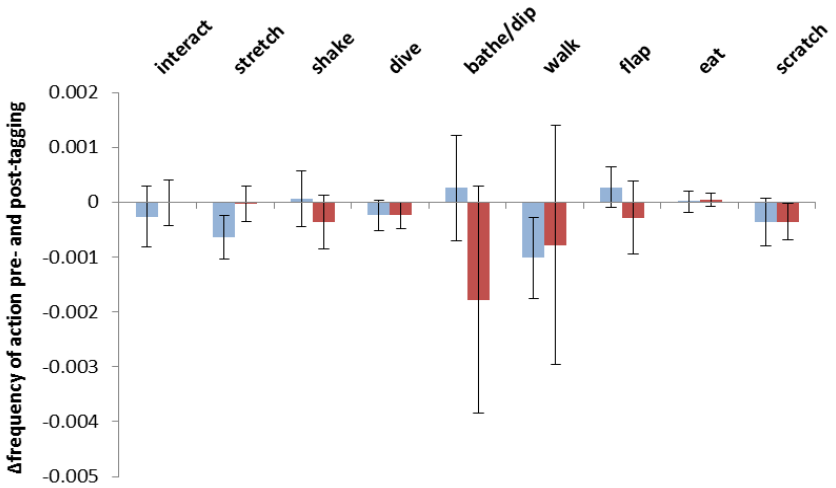


Figure 2.4. Percentage time spent of brown pelicans in different behavioral states for tagged individuals (blue) and untagged neighbors (red) 1-3 days after capture in field trials in the northern Gulf of Mexico. Error bars represent 95% confidence intervals. All differences between tagged and untagged individuals were non-significant ($p > 0.05$).

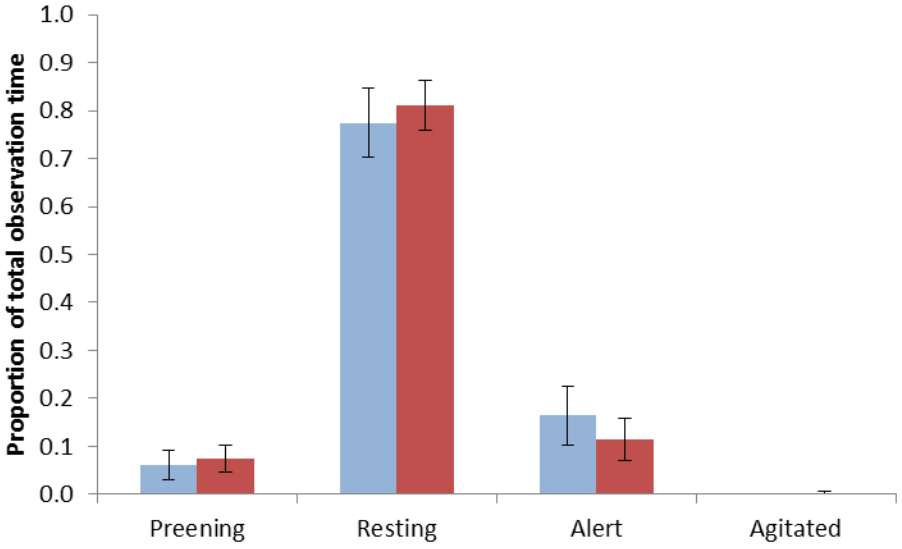
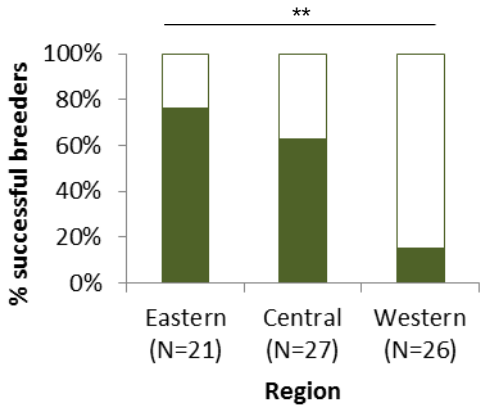
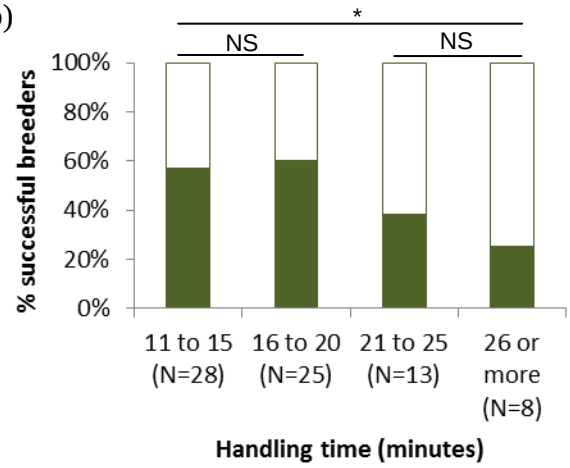


Figure 2.5. Influence of (a) capture location, (b) handling time, and (c) sex on probability of successful breeding in GPS-tagged adult pelicans. Filled bars represent successful breeders. *N* = number of tagged individuals. ** = $p < 0.001$ * = $p < 0.05$.

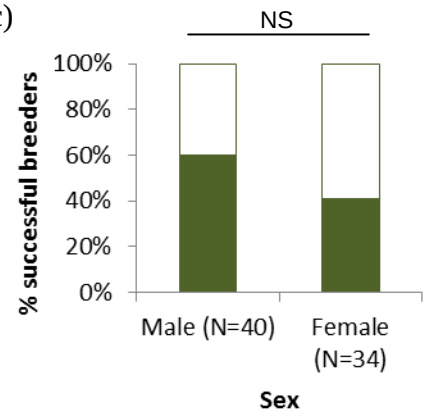
(a)



(b)



(c)



CHAPTER THREE

EVIDENCE FOR DENSITY DEPENDENCE IN FORAGING AND MIGRATORY BEHAVIOR OF A SUBTROPICAL NEARSHORE SEABIRD

Abstract

Density-dependent competition for food resources influences both foraging ecology and reproduction in a variety of colonial animals. These effects have been particularly well-studied in seabirds, and the concept that increasing numbers of breeders create increasingly large zones of prey depletion around breeding sites in colonial central-place foragers, commonly referred to as Ashmole's halo, was originally developed based on observations of tropical seabirds. To date, however, most of the support for this phenomenon originates from high-latitude, pelagic seabird populations. Little is known about how intraspecific competition affects movement in tropical and subtropical seabirds, which forage in less productive waters than temperate populations, or in nearshore seabirds, which experience a higher degree of intraseasonal variability in their foraging areas than pelagic species. I studied the effects of density dependence (breeding colony size) on year-round movement patterns of a nearshore colonial seabird, the brown pelican, originating from six breeding colonies in the subtropical northern Gulf of Mexico. I found evidence for density-dependent effects on foraging behavior during the breeding season, as total foraging area used by breeding adult pelicans increased linearly with colony size. Contrary to my predictions, however, larger foraging ranges did not result in either decreased condition or increased stress in nestlings, both of which parameters showed an inconsistent relationship to colony size. Since brown pelicans in

this region are partially migratory, I also tested the influence of breeding colony size on migratory behavior. I found that individuals from larger colonies were more likely to migrate, and traveled longer distances, than individuals from smaller colonies, indicating that the influence of density-dependent effects on spatial patterns persists into the non-breeding period. I conclude that density-dependent competition is an important driver of both the extent of foraging ranges and the degree of partial migration exhibited by brown pelicans colonies this region. However, its relationship to breeding success, and ultimately population regulation, remains uncertain.

Introduction

Colonial animals experience both costs and benefits of colony membership, and the optimal size of a colony is one that maximizes lifetime reproductive success for individual colony members by providing the largest possible ratio of benefits to costs (Brown and Orians 1970, Brown *et al.* 1990). However, the mechanisms by which colony size affects individual fitness can be difficult to quantify directly (Danchin and Wagner 1997). One aspect of colony size that provides both benefits and costs to individual members is its relationship to foraging behavior. A positive relationship between foraging success and colony size could result from the use of social information to locate and harvest food resources more quickly and efficiently (Brown and Brown 1996, Donaldson-Matasci *et al.* 2013). Alternately, larger colony sizes could negatively impact foraging success by intensifying localized competition for food resources, which imposes increased foraging costs through direct resource depletion, conspecific interference, or

altered prey behavior (Lewis *et al.* 2001, Kuhn *et al.* 2014). The resulting pattern of density-dependent reduction in resource availability around colony sites is commonly referred to as Ashmole's halo (Gaston *et al.* 2007, Hemerik *et al.* 2014). Since Ashmole (1963) first proposed density-dependent prey depletion as a stabilizing mechanism for avian colony size, extensive research has focused on testing its various predictions in natural systems. In addition to directly measuring prey abundance and behavior around colony sites (Birt *et al.* 1987, Ainley *et al.* 2003, Bonal and Aparicio 2008), studies have also documented patterns of population growth (Ridgway *et al.* 2006), colony distribution (Furness and Birkhead 1984, Griffin and Thomas 2000), foraging efficiency (Møller 1987), and reproductive output (Hoi *et al.* 2002) consistent with the operation of density-dependent competition for food resources in colonial avian populations.

Seabirds, which breed almost exclusively in colonies, have frequently been the model system for studying the factors that regulate avian colony size (Coulson 2002). Since prey depletion is extremely difficult to measure directly in marine systems, efforts to quantify the effect of density-dependent competition on individual breeders have focused primarily on indirect measures, principally adult foraging effort (*e.g.*, Ainley *et al.* 2004, Ford *et al.* 2007, Ballance *et al.* 2009). Foraging effort is expected to increase with colony size, and nestling condition (*e.g.*, Gaston *et al.* 1983, Hunt *et al.* 1986, Tella *et al.* 2001) is expected to decrease. The majority of these studies have been conducted on pelagic species breeding at temperate or polar latitudes, with very few examples from nearshore species and/or tropical and subtropical regions. Subtropical and tropical waters are generally less productive than temperate waters (Weimerskirch *et al.* 2004). As such,

resource depletion around seabird nesting colonies during breeding has the potential to be more acute in tropical regions compared to temperate or polar latitudes (Ashmole 1963). Furthermore, compared to pelagic systems, nearshore systems are characterized by greater temporal variability in environmental conditions, and more heterogeneous distribution of habitats (Erwin 1977, Suryan *et al.* 2006, Zamon *et al.* 2014). Thus, the effects of density-dependent factors on both foraging effort and chick condition in nearshore seabirds in (sub)tropical systems could be masked or dampened by the magnitude of underlying variation and complexity in local environmental conditions, prey distribution, climate, and anthropogenic activity (Chastel *et al.* 1995). Perhaps due to the complexity of these interacting factors, as well as limited baseline knowledge of foraging ecology in many tropical seabird species, few studies have tested Ashmole's predictions in either nearshore or subtropical seabirds (Table 3.S1).

Another gap in the study of density dependence as it relates to seabird colonies is the lack of data from throughout the annual cycle. Previous work describing effects of density-dependent resource competition on seabirds has occurred primarily during the breeding season, in which seabirds are obligate central-place foragers (Orians and Pearson 1979). Investigations during the migratory or wintering phase are lacking. Because some seabird species display partial migration (Lack 1944), in which some individuals migrate during non-breeding while others remain near the colony, decisions to undertake or forego migration may be linked to colony density. This is particularly true of nearshore systems, in which substantial changes in the distribution, abundance, and accessibility of forage fish over the annual cycle (Kaltenberg *et al.* 2010) result in

seasonal fluctuations in availability of coastal marine prey resources to top predators. Diamond (1978) tested colony-size relationships across several tropical species and found that species that bred in larger colonies were more likely to migrate than species with smaller average colony sizes. To date, this remains the only example testing the influence of density-dependent resource constraints on migratory patterns in seabirds, and it focused on species-wide patterns rather than individual strategies. However, recent advances in miniaturized tracking technologies (Wakefield *et al.* 2009) have made it possible to connect breeding-season foraging movements and reproductive parameters with non-breeding behavior on an individual scale, allowing for the study of migratory decisions within a single species or population.

I tested several predictions of the effects of density-dependent prey depletion on movement patterns and breeding in a nearshore seabird, the Eastern brown pelican (*Pelecanus occidentalis carolinensis*), nesting in the subtropical northern Gulf of Mexico. Unlike many nearshore seabird species, brown pelicans are large-bodied compared to other seabird species often nesting at the same colonies (*e.g.* terns), employ a plunge-diving rather than a surface-feeding foraging strategy, and in the northern Gulf of Mexico have few, if any, natural predators on the barrier islands where they nest. Both interspecific competition and predation are therefore limited, and hence prey availability may be the principal driver of breeding success. Moreover, brown pelicans are known to be partially migratory in this portion of their range (King *et al.* 2013), although winter locations for this species have not yet been linked to specific breeding colonies. I combined year-round GPS tracking of nesting adults from six breeding colonies of

various sizes with measurements of chick condition for the same colonies to test the influence of colony size on movement and reproductive parameters. Based on the body of research since Ashmole's predictions, I hypothesized that, at colony sites with comparable nearshore marine habitats, pelicans nesting in larger breeding colonies would 1) raise poorer-quality nestlings; 2) travel greater distances to forage during breeding; and 3) be more likely to migrate, and winter farther from their breeding sites, than those nesting at smaller colonies. Given the intensive pressure of anthropogenic activity on marine resources in the Gulf of Mexico, understanding the ecological drivers of distribution and demography of marine species is crucial to future marine planning.

Methods

Colony characteristics

I collected data on breeding adult and nestling pelicans at six colonies, including two colonies per region in the western, central, and eastern portions of the Northern Gulf of Mexico between 83° and 98° W and 27° and 31° N (Figure 3.1a). Within regions, colonies were 50 – 150 km apart, while colony groups in separate regions were 500 – 600 km apart. The number of breeding pairs at each study site was obtained from the most recent (*i.e.*, 2013) colonial waterbird censuses for each region (Texas Colonial Waterbird Survey, unpublished data; Colibri Ecological Consulting and R. G. Ford Consulting, unpublished data).

To compare underlying environmental conditions between colonies, I extracted environmental variables including two fixed parameters (bathymetry and bottom

substrate) and three seasonally-averaged parameters (salinity, sea surface temperature, and chlorophyll a) at distances of 10, 20, 50, and 150 km from the colony, bounded by the coastline and up to 50 km offshore (Figure 3.1b). I used a multivariate hierarchical clustering approach (K-means clustering: MacQueen 1967) to compare environmental characteristics between sites, and tested the resultant clusters using Multi-Response Permutation Procedure (MRPP) on a Euclidean distance matrix (McCune and Grace 2002). All statistical analyses were conducted in R (R Core Team, 2014).

Chick condition and stress

Between 3 and 26 June 2013, I measured the mass and culmen, tarsus, and wing lengths of 3-4 week-old chicks at the six colony sites at which I also tracked breeding adults (Figure 3.1a). I normalized culmen, tarsus, and wing length measurements and conducted a Principal Components Analysis (PCA) to generate a composite measure of skeletal size (*e.g.*, Benson *et al.* 2003). Using the first-axis PCA scores, I then regressed body mass on the index of skeletal size and fit a second-order polynomial regression equation to the data to describe the relationship between the two measures. Finally, I calculated the residual of each chick's body mass from the mass predicted by the regression function as an index of body condition (hereafter, BCI).

Since body condition provides a temporally limited measure of overall chick growth rates and nest conditions, I also used chick feathers sampled at the time of banding to assess levels of the stress hormone corticosterone over the course of development. As corticosterone levels in nestling tissues reflect nutritional stress during

the growth period (Will *et al.* 2014), this measurement provides an additional integrated index of overall nutritional conditions at a colony that might not be reflected by a one-time measurement of chick body condition. I measured corticosterone levels in feathers using a radioimmunoassay procedure similar to the one developed by Bortolotti *et al.* (2008). I used ANOVAs to compare colony-wide average BCI and feather corticosterone levels between the three regions samples, pairwise t-tests to compare values between colonies within each region, and linear models to assess the overall relationship between each parameter and colony size.

Adult tracking

To track movement patterns of adult pelicans, I used 65 g solar GPS Platform Terminal and Cellular Terminal transmitters (NorthStar Science and Technology) with a backpack-style Teflon ribbon harness attachment (Dunstan 1972). To elevate the transmitters and prevent feathers from covering the solar panels and antenna, I mounted each device on a 6 mm thick neoprene pad that also extended 6 mm beyond the perimeter of the transmitter in all directions. Transmitters were programmed to collect 12 fixes/day during breeding (April – August; every 90 minutes from 1030 to 0130 GMT), 10 fixes/day during pre- and post-breeding (September – October and February – March; every 90 minutes from 0700 – 0100 GMT), and 8 fixes/day during winter (November – January; every 120 minutes from 0700 – 0100 GMT). I obtained an average error estimate for GPS points from transmitters at known locations (N = 220) of 4.03 ± 2.79 meters.

I captured adults at nests using leg nooses in either the late incubation or early chick-rearing stage of breeding. All captured adults were weighed, measured, banded, and sampled for blood and feathers. I also calculated adult BCI as the residual of the linear relationship between culmen length and mass (Eggert *et al.* 2010). Since morphology is not always sufficient to determine sex in brown pelicans, adults were later sexed via PCR using collected DNA samples (Itoh *et al.* 2001). Total handling time from capture to release averaged 19 minutes (±6.5 minutes). Since individual characteristics may influence pelican foraging movements during breeding (Walter 2014), I used two-sample t-tests to compare individual characteristics of tracked adults (Table 3.1) between colonies.

Adult breeding season home ranges

All adults were captured while attending nests, and were therefore in breeding mode at the time of capture. Nest contents were recorded, including number and age of chicks present and number and status of eggs present (typically clutch size for this species is 2-3 eggs, and brood size is 1-2 chicks; Shields 2014). Given the high resolution of GPS data, nest attendance could be inferred from subsequent locations of adults, and the breeding season was presumed to continue until the adult ceased regular visits to the colony. All data points collected between transmitter attachment and the date that the adult discontinued regular nest attendance were considered breeding-season movements. Breeders that attended nests for at least 60 days after inferred hatch date were presumed successful (Shields *et al.* 2014). For adults that remained resident on the colony after the

breeding period had ended, I imposed a cutoff for breeding-season movements at 90 days after inferred hatch date. In these cases, the similarity between adult breeding and non-breeding movements resulted in home range estimates that were not significantly different among the different cutoff dates. Although GPS tags collected data over multiple years for some individuals, I included only the first year of data for each individual to maximize sample size and improve comparisons among individuals. GPS data were visually assessed and outliers (*i.e.*, points that required flight speeds in excess of 65 km per hour: Schnell and Hellack 1978) manually removed. I determined 50 and 95% kernel density estimate (KDE) home ranges for each individual using the 'ks' package in R (Duong 2015) with a plugin bandwidth estimator (Wand and Jones 1994, Gitzen *et al.* 2006). Finally, I calculated the areas included within the 50% (core) and 95% (full) KDE contours using Albers Conic Equal-area projections centered on each region. I used ANOVAs to compare core and full home range sizes between the three regions samples, one-tailed pairwise t-tests to test whether home range sizes were greater at the larger colony within each region, and a linear model to assess the overall relationship between colony size and home range size.

Adult migratory movements

To classify adults as migratory or non-migratory, I defined winter home ranges as all points between the last sustained linear post-breeding movement (in fall/winter) and the return to the breeding colony the following spring. Using only these locations, I approximated individual winter home ranges using 95% minimum convex polygons

(MCPs). Since individuals are not attached to a fixed central location during non-breeding, I chose the MCP approach to fully represent winter habitat without differentially weighting areas of more frequent use. If an individual's breeding-season home range (95% KDE) overlapped its winter home range, I classified the individual as non-migratory (Cagnacci *et al.* 2016). All other individuals were classified as migratory. I calculated migration distances using the linear distance between an individual's breeding colony and its winter MCP centroid. I compared average migration distance (t-tests) and the proportion of migratory individuals (Fisher's exact tests) between larger and smaller colonies within each region, and used linear models to assess the relationship between colony size and migration distance and between colony size and proportion of migrants.

Results

Colony characteristics

Each of the three regions sampled included two colonies of different sizes, with the larger colony containing between 2.4 and 2.6 times as many breeding pairs as the smaller colony (Table 3.1). Overall, eastern colonies were smaller than those in the central and western regions by an order of magnitude. Both the larger and the smaller colonies in the central region were of similar size (± 20%) to those in the western region. Colonies contained a mixture of pelicans and other species, principally herons and egrets (Ardeidae), Black skimmers (*Rhynchops niger*), terns (Sternidae), and Laughing gulls (*Leucophaeus atricilla*). Since these species use different foraging habitats and strategies,

and target different size classes of prey, than do brown pelicans, I did not consider them to be depleting the same resources and did not include their numbers in assessing colony size (see Discussion).

Environmental characteristics were relatively homogenous within each region but differed between regions. Colonies in the Central region were characterized by marine habitats with low salinity, high summer sea surface temperatures, and predominantly muddy substrates. Eastern colonies had predominantly sandy substrates and higher winter sea surface temperatures, while Western colonies had higher spring sea surface temperatures. Cluster analysis identified three distinct clusters, corresponding to the three regions (Figure 3.2). Dissimilarity in environmental characteristics was significantly greater between regions than within each region (MRPP: $A = 0.42$, $p < 0.001$).

Chick condition and stress

Nestling BCI differed at the regional level (ANOVA: $F_2 = 12.2$, $p < 0.001$). BCI was highest at Eastern colonies, lower in Central colonies, and lowest in Western colonies (Figure 3.3a). Nestling BCI did not differ between the smaller and larger colonies in either the Eastern ($t_{29} = 0.48$, $p = 0.31$) or Central ($t_{37} = -0.44$, $p = 0.32$) regions. In the Western region, the larger of the two colonies had a marginally lower average nestling BCI than the smaller colony ($t_{45} = -1.35$, $p = 0.09$). The slope of the linear relationship between colony size and mean chick BCI was not significantly different from zero ($F_4 = 2.68$, $p = 0\pm7$); however, a second-order polynomial closely fit the shape of the data ($y = 0.00004x^2 – 0.22x + 279$, $R^2 = 0.79$).

Mean nestling corticosterone levels did not differ between regions (ANOVA: F_2 = 0.98, p = 0.38). Within regions, values were marginally higher at the smaller colony in the Central region (t_{37} = 1.51, p = 0.07), significantly higher at the larger colony in the Western region (t_{45} = -2.87, p = 0.003), and significantly higher at the smaller colony in the Eastern region (t_{29} = 3.39, p = 0.001) (Figure 3.3b). The linear relationship between colony size and corticosterone levels was not significantly different from zero (F_4 = 0.23, p = 0.65).

Adult tracking

The number of birds captured at each colony ranged from nine to 14 (Table 3.1). Sex ratios of captured adults varied by colony, but did not differ significantly within each region (Fisher's Exact Test; Eastern: p = 0.64; Central: p = 1; Western: p = 0.39). Body size of captured adults also did not differ significantly between regions (ANOVA; Mass – F_2 = 0.81, p = 0.45; Culmen – F_2 = 0.71, p = 0.93) or colonies (Two-tailed T tests; Mass – Eastern: t_{19} = 0.25, p = 0.80; Central: t_{23} = 0.69, p = 0.50; Western: t_{23} = 0.93, p = 0.36. Culmen – Eastern: t_{20} = -0.37, p = 0.79; Central: t_{24} = 0.27, p = 0.78; Western: t_{24} = 0.74, p = 0.47), while body condition differed between (ANOVA; F_2 = 3.83, p = 0.03), but not within (Two-tailed T tests; Eastern: t_{19} = -0.87, p = 0.39; Central: t_{24} = -0.70, p = 0.49; Western: t_{22} = 0.72, p = 0.48), regions.

Adult breeding season home ranges

Mean breeding season core (50% KDE) and full (95% KDE) home ranges (N = 73 individuals) were smallest in the Eastern region and larger in Western and Central colonies (Figure 4; ANOVA; 50% KDE – $F_2 = 3.00$, $p = 0.06$; 95% KDE – $F_2 = 9.84$, $p < 0.001$). Within each region, the larger of the two colonies had greater mean core and full home range areas than the smaller colony, although these differences were not significant (One-tailed T tests; 50% KDE – Eastern: $t_{14} = 0.85$, $p = 0.21$; Central: $t_{18} = 0.86$, $p = 0.20$; Western: $t_{16} = 1.83$, $p = 0.04$; 95% KDE – Eastern: $t_{12} = 0.94$, $p = 0.18$; Central: $t_{22} = 1.66$, $p = 0.09$; Western: $t_{22} = 1.22$, $p = 0.12$). Overall, the linear relationship between colony size and breeding season home range size was significantly positive for both core and full home ranges. For each increase of 100 breeding pairs at a colony, mean core home range size of individual breeders increased by approximately 3 km^2 ($y = 0.03x + 43.5$, $SE = 25.7$, $R^2 = 0.82$, $p = 0.01$; Figure 3.4a) and mean full home range size increased by approximately 19 km^2 ($y = 0.19x + 393$, $SE = 103$, $R^2 = 0.93$, $p = 0.002$; Figure 3.4b). I did not find evidence for spatial segregation of breeding home ranges in neighboring colonies (Figure 3.5).

Adult migratory movements

Both the proportion of migrants and distance traveled to winter site were lowest among Eastern breeders and higher among Central and Western breeders (Figure 3.6). Within each region, breeders from the larger of the two colonies were more likely to migrate, and traveled further from the colony to winter, than did breeders from the

smaller colony, although intra-regional differences were significant only for migration distance (Proportion – Fisher's Exact Tests, $p > 0.20$ for all regions. Distance – one-tailed T tests; Eastern: $t_{17} = 1.97$, $p = 0.03$; Central: $t_{24} = 0.74$, $p = 0.23$; Western: $t_{17} = 1.95$, $p = 0.03$). For each increase of 100 pairs at the breeding colony, individuals were 1% more likely to migrate ($y = 0.0001x + 0.43$, $SE = 0.13$, $R^2 = 0.69$, $p = 0.04$; Figure 3.6a), and wintered approximately 16 km further from their breeding sites ($y = 0.16x + 344$, $SE = 186$, $R^2 = 0.75$, $p = 0.03$; Figure 3.6b).

Discussion

Density dependence is one of several factors potentially influencing breeding ecology, foraging distances, and migratory movements of colonial seabirds. To date, studies examining the relationship among colony size, foraging effort, and reproductive success in seabirds have typically focused on pelagic species, which experience less short-term and fine-scale variation in foraging habitat than do nearshore species (Becker and Beissinger 2003). Previous studies examining density-dependent effects on nearshore seabirds have generally been constrained by limited numbers of colonies, small sample sizes, and/or high variability in environmental conditions between colony sites (*e.g.*, Grémillet *et al.* 2004, Walter *et al.* 2014). I isolated the effects of colony size on movement patterns of nearshore seabirds by comparing both nesting parameters and tracking data from individual adults, and by using replicate colonies with similar marine habitat characteristics that differ primarily in the number of breeding pairs present, a proxy for intraspecific competition.

Two issues that might potentially confound the results of any assessment of colony size on foraging and reproductive ecology are interspecific competition and differences in resource availability among study colonies. Here, I discuss how I accounted for each.

For the purposes of this study, I included only the number of conspecifics present at a colony (*i.e.*, intraspecific competition) rather than the overall number of nesting birds present (i.e, interspecific competition). I did so based primarily on weak or indirect interspecific interactions during foraging. The other species nesting at the breeding colonies included in this study (*i.e.*, herons, egrets, terns, and skimmers) use different foraging habitats, employ different feeding, strategies and target different sizes and species of prey than do brown pelicans (De Graaf *et al.* 1985). Therefore, their effects on distribution and behavior of brown pelican prey are likely to be minimal. The only species present at these colonies that could potentially influence brown pelican foraging and breeding parameters is the Laughing Gull, a kleptoparasitic feeder. Accurate census numbers are unavailable for this species; however, since Laughing Gulls were present in similar densities at all but the smallest Eastern colony, it is unlikely that increased pelican foraging due to kleptoparasatism was generally biased toward larger or smaller breeding colonies.

Underlying resource availability, which is difficult to fully account for in marine systems, may also vary between colonies and hence confound an assessment of the influence of colony size on seabird behavior. For example, Gulf menhaden (*Brevoortia patronus*), which comprises a large portion of pelican diets in the Northern Gulf of

Mexico (Shields 2014), are concentrated in the central portion of the Gulf from the Florida Panhandle to the central Texas coast. Colonies in both the Eastern and Western regions were at the edges of the range of Gulf menhaden and therefore may have experienced lower availability of this particular prey item. Nevertheless, in both the Eastern and Western regions, the colony located furthest from core menhaden habitat (*i.e.*, Smith and Shamrock Islands: Figure 3.1) was also the smaller colony, and hence the predicted effects of menhaden shortages would counteract rather than enhance those of density-dependent prey depletion. Supplemental feeding from both mobile fishing vessels and stationary mainland locations (docks, piers) is also likely to contribute to pelican diets (*e.g.*, Wickliffe and Jodice 2010); however, distribution of fishing activity is relatively uniform throughout the study region (Levesque 2011), and I do not have reason to believe that these opportunities differ systematically between large and small colonies in the three regions I studied. Furthermore, I analyzed marine habitat characteristics at multiple scales and did not find any significant within-region differences in habitat characteristics between large and small colonies.

In this study, I addressed three principal predictions related to the operation of density-dependent prey depletion:

Hypothesis 1: Individuals nesting in larger breeding colonies will raise poorer-quality nestlings

Neither of the chick health metrics I tested (body condition index or feather corticosterone) showed a consistent relationship with colony size, either within or

between regions. Body condition showed a non-linear overall decline with colony size, suggesting a potential negative trend; however, this trend was not consistent between the larger and smaller colonies within each region. The relationship between colony size and various metrics of nestling provisioning and condition appears to be inconsistent based on previous studies of sea- and terrestrial birds (Brown and Brown 1996, Ainley *et al.* 2004, Gaston *et al.* 2007), which have suggested that reduced prey availability resulting from increased colony size may be counterbalanced by other factors, particularly adult foraging effort, to avoid negative effects on nestling health.

This study differs from previous studies of the effects of colony size on seabird behavior by focusing on nearshore seabirds in subtropical waters instead of pelagic seabirds in higher latitudes. Both the life-history strategies of nearshore compared to pelagic seabirds and the characteristics of the nearshore compared to the pelagic environment may underlie the inconsistent relationship I observed between colony size and chick condition. For example, nearshore seabirds tend to have a more variable clutch and brood size compared to pelagic seabirds and hence may be more capable of making reproductive tradeoffs in response to changes in local prey availability. Nearshore seabirds may also be able to buffer against the effects of prey depletion by varying foraging effort or specializing on different habitats, both of which are more readily accomplished in the more heterogeneous and proximal nearshore system compared to more distant pelagic systems. Similarly, increased availability of resources within forging range of the colony in nearshore environments may allow nearshore seabirds to increase foraging distances without reaching an energetic threshold (Ballance *et al.* 2009), thus

avoiding the need to reduce rates of prey delivery to an extent which would cause measurable declines in chick condition. Therefore, relationships between intraspecific resource competition and chick condition among colonies may be confounded by life history and environmental characteristics, particularly in complex nearshore systems (Suryan *et al.* 2006).

Hypothesis 2: Individuals nesting in larger breeding colonies will travel greater distances to forage during breeding

I found a strong linear increase in the size of both core and full home ranges of individual breeders with the size of the breeding colony. This relationship held true among as well as within each of the three Gulf regions, with individuals at the larger of the two colonies in each region traveling farther from the colony to forage than individuals at the smaller colony. The high comparability of environmental conditions within regions, and the lack of consistent individual differences between tracked birds from neighboring colonies, suggests colony size as the major factor driving foraging radius. This adds to a growing body of evidence that colonial birds consistently increase their foraging radius in response to localized density-dependent prey depletion (*e.g.*, Brown and Brown 1996, Lewis *et al.* 2001, Ainley *et al.* 2003, Ford *et al.* 2007, Bonal and Aparicio 2008, Elliott *et al.* 2009).

Since most work to date has concentrated on pelagic seabirds breeding at temperate latitudes, this study adds a new perspective to the understanding of the relationship between colony size and foraging distance in seabirds. In contrast to several

previous studies (*e.g.*, Grémillet *et al.* 2004, Wakefield *et al.* 2013), I did not document distinct spatial segregation in foraging ranges between closely neighboring colonies. In pelagic marine environments, prey resources are patchily distributed across large, relatively homogenous areas of habitat and concentrate around transient oceanographic structures (Tew Kai *et al.* 2009). In contrast, prey concentrations in nearshore environments may occur predictably in and around stationary coastal features including headlands, river mouths, and upwelling zones, but with a greater degree of within-season temporal variation than in pelagic habitats (Becker and Beissinger 2003). Thus, the overlap I observe between neighboring colonies may represent common exploitation of prey-concentrating features that are spatially predictable but temporally variable.

Hypothesis 3: Individuals nesting in larger breeding colonies will be more likely to migrate and will travel farther from the colony during non-breeding

I found positive correlations between breeding colony size and both the proportion of individuals in a breeding colony that migrated away from the colony during nonbreeding and the distance traveled by migrants. Partial migration in seabirds has been little-studied and, to the best of my knowledge, a relationship between migratory strategies of individual breeders and breeding colony size has not previously been observed in either nearshore or pelagic seabirds. While a variety of individual characteristics (*e.g.*, body size, sex, social status) can drive patterns of partial migration (Chapman *et al.* 2011), density dependent competition for resources may present a significant obstacle to remaining resident in the subtropical northern Gulf of Mexico.

During winter months, prey populations here migrate offshore, and shallow waters may freeze during periods of extreme cold, hence reducing availability of prey. Juvenile and adult mortality also appears to increase during winter around colonies. Partial migration may provide a potential solution to the problem of reduced resource availability during winter by reducing predation pressure.

Previous research on density-dependent population regulation in seabirds has focused almost exclusively on foraging movements and nesting health during the breeding season. The study of migratory behavior in relation to conspecific prey depletion due to density dependence has been less common, and has primarily been limited to species-level patterns (Diamond 1978). In contrast, investigations of relationships between colony size and migratory behavior within a single species have been rare. Previous evidence has indicated a complex migration strategy in brown pelicans (King *et al.* 2013), but has not offered any insight into how migratory behavior varies throughout the population or what drives individual migration patterns. My results offer insight into the ecological underpinnings of migratory decisions, suggesting that local intraspecific competition is a significant driver of partial migration, and that changes to brown pelican breeding distribution in the northern Gulf could result in corresponding shifts in migratory behavior and nonbreeding locations.

Conclusions

While predictions resulting from Ashmole's hypothesis of density-dependent population regulation in seabirds have been widely tested, the volume of data required to

make comparisons between breeding colonies, as well as the difficulty of controlling for underlying variation, has limited research to a fairly small number of species over a narrow range of geography and life history traits. As miniaturization of remote tracking devices continues to open new avenues of inquiry into the decisions and movements of individual birds from a greater variety of species and locations, it will become increasingly feasible to isolate and assess the influence of density-dependent resource competition on individual behavior and to scale these effects up to the population level. Like previous studies, my research indicates that adult movement patterns during the breeding season are more consistently related to colony size than are measures of chick condition and provisioning rates (Lamb, unpublished data). The lack of an observed detrimental effect of increased foraging area on chick health suggests that, dependent on species and habitat characteristics, birds may be able to adjust foraging effort in response to reduced prey availability without negative consequences for nestling health. Measurements of energetic expenditure by foraging adults could elucidate the foraging mechanisms by which some species may be more effective than others in buffering against reduced prey availability. Ultimately, testing Ashmole's predictions of the effects of intraspecific competition for prey resources and density-dependent prey depletion is secondary to testing prey depletion itself. Brown pelicans in the northern Gulf of Mexico provide an excellent system for studying a nearshore, subtropical seabird with a variety of colony sizes across a range of environmental conditions. Understanding the underlying prey distribution that drives observed patterns would be helpful in elucidating the

immediate causes of observed relationships between colony size and movement patterns in this species.

In contrast to foraging behavior, partial migration remains little-studied, particularly in seabirds. At the same time, migratory and non-breeding movements are widely recognized as crucial drivers of population patterns, and may be critical to species' abilities to adjust to changing climatic and oceanographic conditions. Although colony size appears to be part of the mechanism driving partial migration, details of which individuals migrate, and why, remain unknown. Future research could address the role of colony size in relation to fixed and variable individual characteristics and geography in determining migratory strategies, and how these decisions impact distribution of mortality risk during non-breeding.

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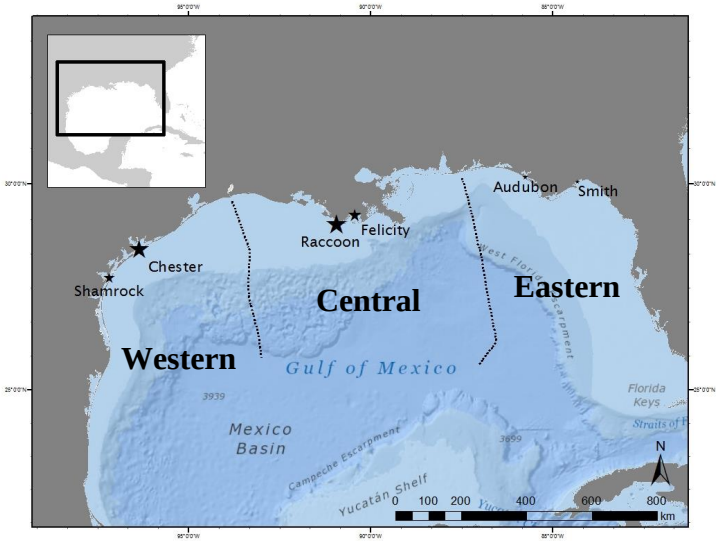
Table 3.1. Colony characteristics and measurements of tracked adults captured at six brown pelican breeding colonies in the northern Gulf of Mexico, 2013-2014. Measurements are reported as mean values, with standard deviations listed in parentheses.

	Eastern		Central		Western	
	Smith	Audubon	Felicity	Raccoon	Shamrock	Chester
Colony size	40	100	1800	4300	1400	3200
Adults tracked	9	11	12	14	11	10
% male	0.78	0.64	0.50	0.57	0.55	0.30
Mass (g)	3414 (432)	3414 (558)	3448 (369)	3546 (353)	3459 (562)	3070 (508)
Culmen length (mm)	322 (22)	315 (21)	313 (23)	316 (23)	321 (25)	309 (19)
Body Condition Index	-141 (273)	-241 (205)	77 (195)	121 (263)	-19 (306)	-147 (281)

Figure 3.1. (a) Locations of brown pelican study colonies in the Gulf of Mexico, 2013-2014. Sizes of stars represent comparative colony sizes. Dashed lines indicate relative boundaries between planning regions as defined by the U.S. Bureau of Ocean Energy Management. (b) An example of colony buffer zones (10, 20, 50, and 150 km) used to calculate environmental conditions for Shamrock Island, Texas.

(a)



(b)

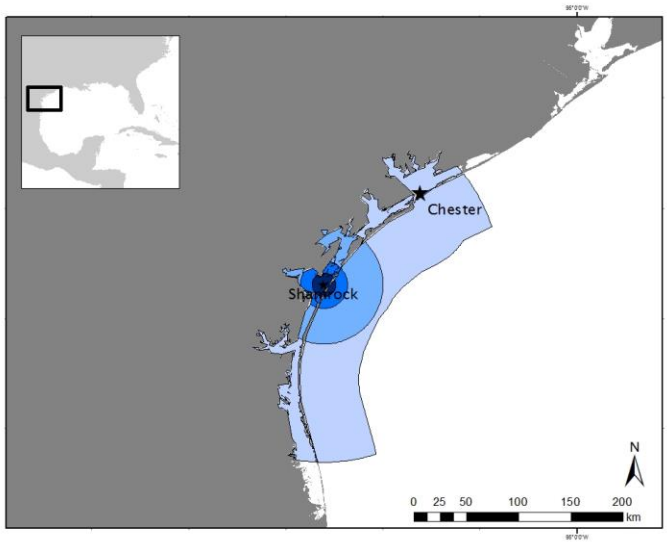


Figure 3.2. Environmental characteristics surrounding brown pelican study colonies in the northern Gulf of Mexico. Site codes contain the colony (Audubon: AU; Smith: SM; Felicity: FE; Raccoon: RA; Shamrock: SH; Chester: CH) and radius (10, 20, 50, or 150 km) at which environmental variables were calculated. Dashed hulls indicate clusters of sites in environmental covariate space, and solid vectors indicate directions of increasing values for individual covariates.

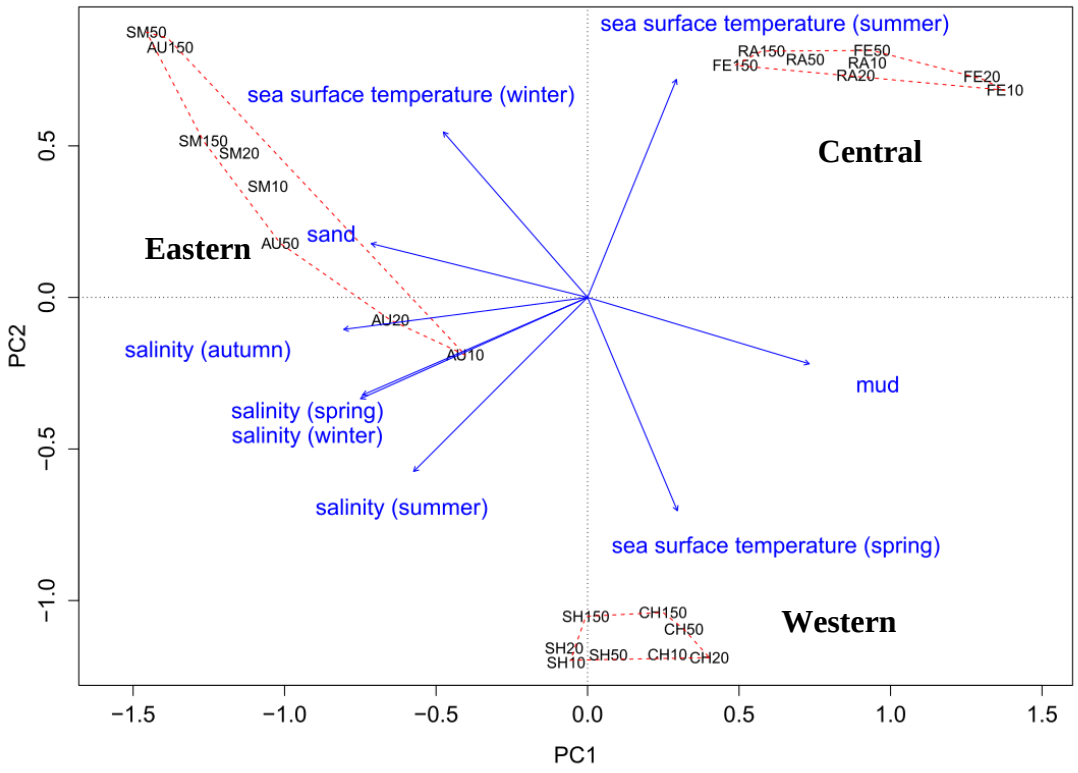


Figure 3.3. Brown pelican nestling (a) body condition index and (b) corticosterone levels in the Northern Gulf of Mexico, 2013-2014. Symbol shapes represent regions, and the larger colony in each region is indicated by an open symbol. Error bars represent 95% confidence intervals.

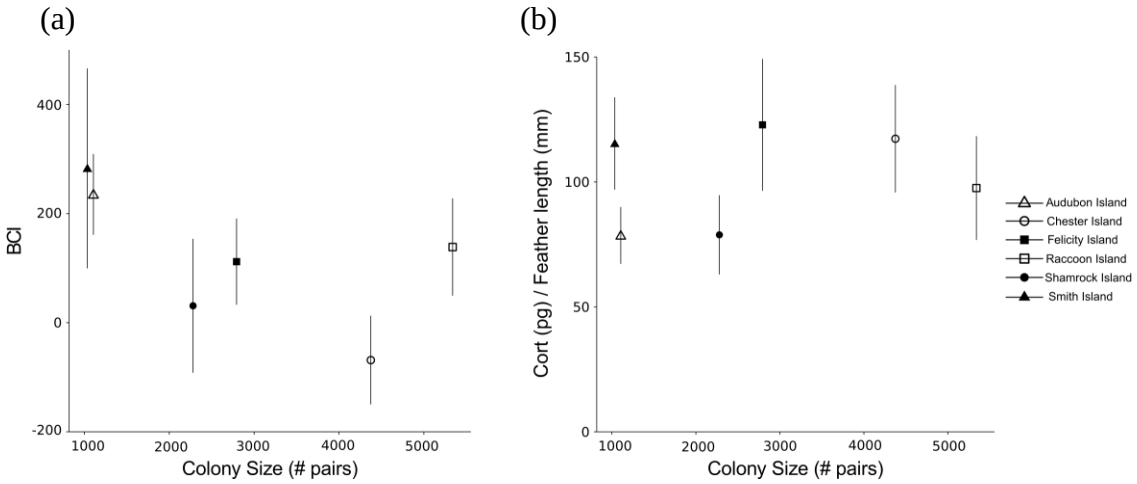


Figure 3.4. Mean 50% kernel density estimate (a) and 95% kernel density estimate (b) breeding season home ranges of breeding adult brown pelicans at each study colony in the northern Gulf of Mexico, 2013-2014. Symbol shapes differ by breeding region (triangular: Eastern, square: Central, circular: Western), and open symbols indicate the larger colony in each region. Regression lines are shown with 95% confidence intervals (shaded).

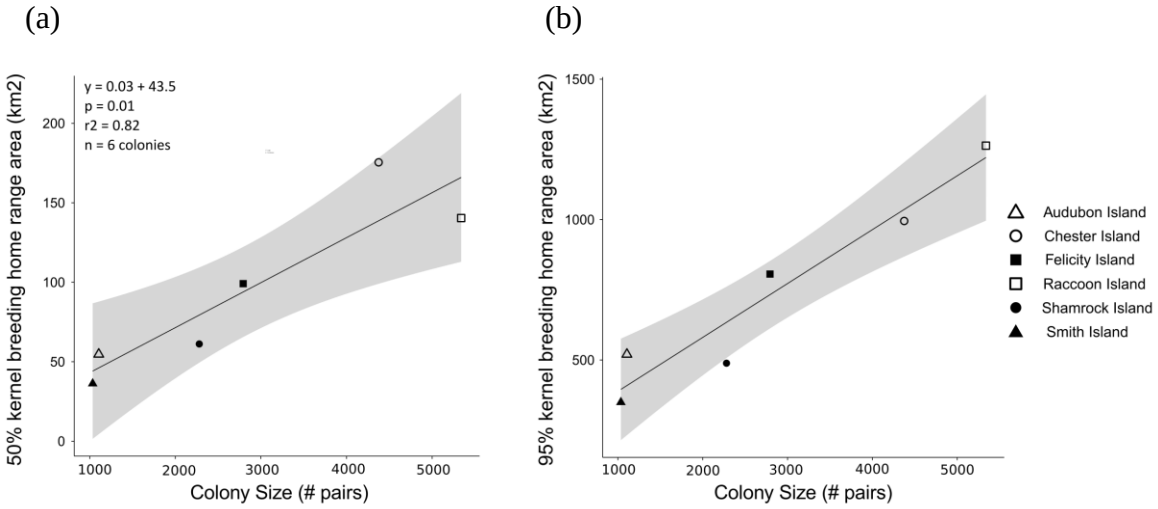
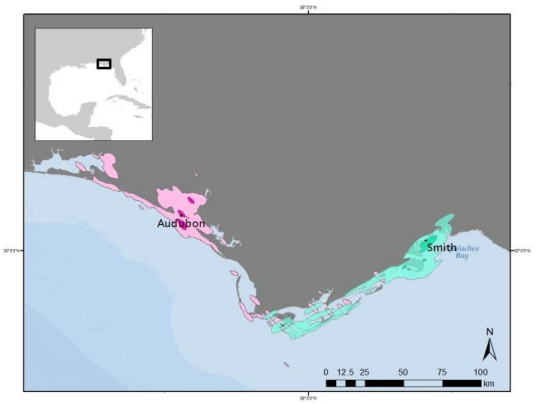
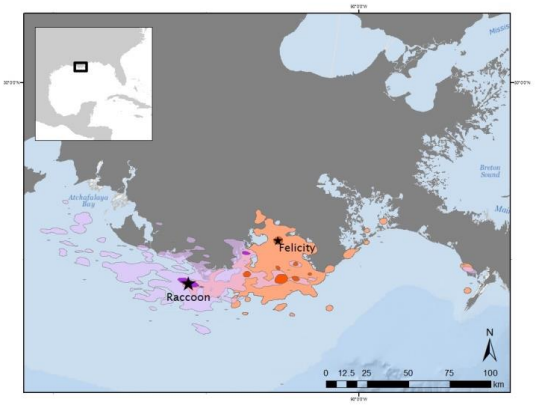


Figure 3.5. Brown pelican breeding home ranges by colony for the Eastern (a), Central (b), and Western (c) regions of the northern Gulf of Mexico, 2013-2014. Darker contours represent 50% kernel areas, and lighter contours represent 95% kernel areas.

(a)



(b)



(c)

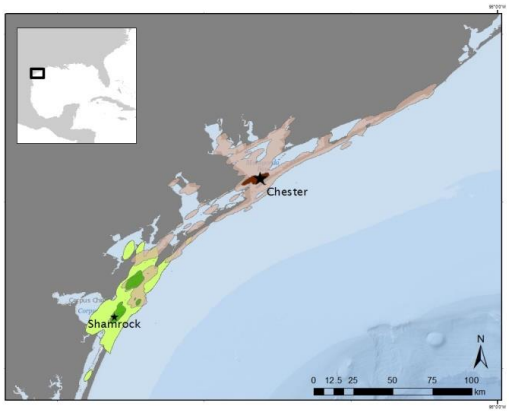


Figure 3.6. Proportion of migratory brown pelicans (a) and average distance between individual summer and winter home range centroids (b) at each study colony in the northern Gulf of Mexico, 2013-2014. Symbol shapes represent regions, and the larger colony in each region is indicated by an open symbol. Regression lines are shown with 95% confidence intervals (shaded).

(a) (b)

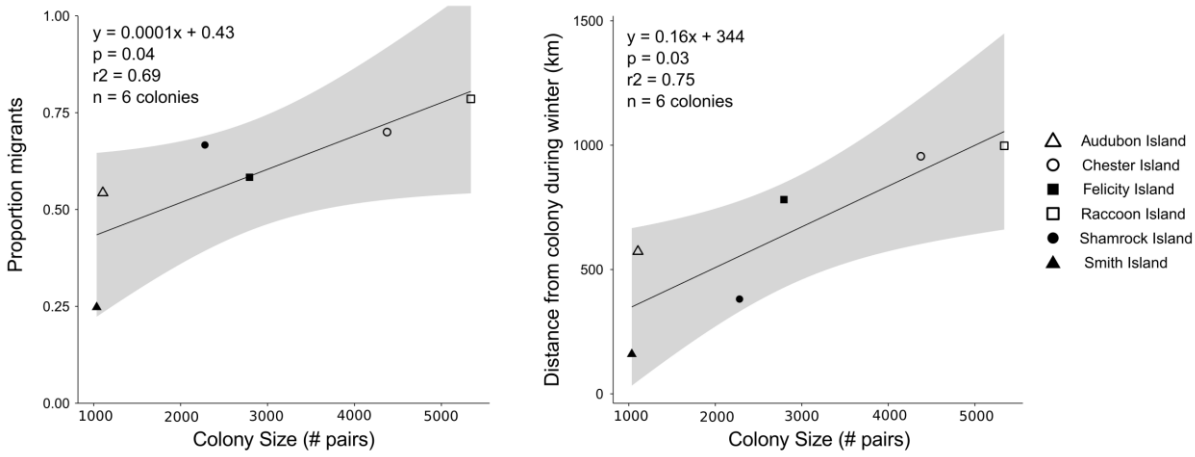


Table 3.S1. Previous studies of the relationship between avian colony size and resource competition.

	Species	Species group	Latitude	# Colonies	Metric	Relationship
Foraging						
Brown and Brown 1996	Cliff swallow	terrestrial songbird	41° N	16	foraging distance	positive
					foraging area	positive
Lewis et al 2001	Northern gannet	pelagic seabird	51° N	9	trip duration	positive
Ainley et al 2003	Black-legged kittiwake	pelagic seabird	60° N	3 clusters	foraging radius	positive
					foraging area	positive
					trip duration	positive
Ainley et al 2004	Adelie penguin	penguin	75° S	4	foraging distance	positive
					foraging area	positive
					trip duration	positive
Grémillet et al 2004	Cape gannet	pelagic seabird	32-33° S	2	foraging distance	positive[1]
					trip duration	positive
Ford et al 2007	Black-legged kittiwake	pelagic seabird	60° N	2	foraging radius	positive
Gaston et al 2007	Pelagic seabirds (4 species)	pelagic seabird		model	foraging radius	positive
Bonal and Aparicio 2008	Lesser kestrel	terrestrial raptor	39° N	56	foraging radius	positive
Ballance et al 2009	Adelie penguin	penguin	77° S	2	trip duration	positive
Elliott et al 2009	Common murre	pelagic seabird	62° N	1	foraging effort	positive[2]
					foraging radius	positive[2]
Wakefield et al 2013	Northern gannet	pelagic seabird	51° N	12	foraging area	positive
					foraging radius	positive
					trip duration	positive
Oppel et al 2015	Masked booby	pelagic seabird	8-16° S	2	foraging radius	positive
Energetics						
Brown and Brown 1996	Cliff swallow	terrestrial songbird	41° N	16	adult body mass variation	varies
Ainley et al 2004	Adelie penguin	penguin	75° S	4	adult body mass variation	none
Gaston et al 2007	Pelagic seabirds (4 species)	pelagic seabird		model	energy expenditure	positive
Ballance et al 2009	Adelie penguin	penguin	77° S	2	energy expenditure	positive

	Species	Species group	Latitude	# Colonies	Metric	Relationship
Distribution						
Furness and Birkhead 1984	4 species (pelagic)	pelagic seabird	51° N	12 – 27	colony distribution	negative
Cairns 1989	4 species (pelagic)	pelagic seabird	51° N	12 – 27	colony distribution	negative
Forbes et al 2000	Ancient murrelet, Cassin's auklet, Rhinocerous auklet	pelagic seabird	50-54° N	16 – 29	colony distribution	negative
Griffin and Thomas 2000	Rook	terrestrial corvid	54.6° N	18	colony distribution	negative
Lewis et al 2001	Northern gannet	pelagic seabird	51° N	9	colony growth rates	negative
Forero et al 2002	Magellanic penguin	penguin	43° S	29	colony distribution	negative
Ainley et al 2003	Black-legged kittiwake	pelagic seabird	60° N	3 clusters	colony distribution	negative
Grémillet et al 2004	Cape gannet	pelagic seabird	32-33° S	2	foraging locations	segregated
Dann and Norman 2006	Little penguin	penguin	39° S	28	colony distribution	negative
Ridgway et al 2006	Double-crested cormorant	nearshore seabird	45° N	37	colony growth rates	negative
Ford et al 2007	Black-legged kittiwakes	pelagic seabird	60° N	2	colony distribution	negative
Wakefield et al 2013	Northern gannet	pelagic seabird	51° N	12	foraging locations	segregated
Provisioning						
Snapp 1976	Barn swallow	terrestrial songbird	42.5° N	11	provisioning rate	none
Moller 1987	Barn swallow	terrestrial songbird	57° N	23	provisioning rate	negative
Brown and Brown 1996	Cliff swallow	terrestrial songbird	41° N	16	provisioning rate	positive
Ainley et al 2004	Adelie penguin	penguin	75° S	4	chick meal size	none
Bonal and Aparicio 2008	Lesser kestrel	terrestrial raptor	39° N	56	provisioning rate	negative
Breeding						
Snapp 1976	Barn swallow	terrestrial songbird	42.5° N	11	chick condition	negative
Wiklund 1982	Fieldfare	terrestrial songbird	67° N	8	breeding success	positive
Gaston et al 1983	Thick-billed murre	pelagic seabird	62° N	4	chick condition	negative
Hunt et al 1986	Pelagic seabirds (5 species)	pelagic seabird	56-57° N	2	chick growth rate	negative
					chick condition	negative
					clutch size	none
					breeding success	none
Moller 1987	Barn swallow	terrestrial songbird	57° N	23	brood size	none
Brown and Brown 1996	Cliff swallow	terrestrial songbird	41° N	16	chick condition	varies[3]
					chick survival	varies[3]
Tella et al 2001	Magellanic penguin	penguin	42-44.5° S	28	chick condition	negative
					chick immunocompetence	negative

	Species	Species group	Latitude	# Colonies	Metric	Relationship
Breeding (cont.)						
Forero et al 2002	Magellanic penguin	penguin	43° S	6	chick immunocompetence	none
					chick condition	negative
Hoi et al 2002	European bee-eater	terrestrial songbird	48° N	11	chick condition	negative
					chick survival	negative
Ainley et al 2004	Adelie penguin	penguin	75° S	4	chick growth rate	none
Bonal and Aparicio 2008	Lesser kestrel	terrestrial raptor	39° N	56	chick survival	negative
	Lesser kestrel	terrestrial raptor	39° N	56	chick condition	negative
Szostek *et al.* 2014	Common tern	nearshore seabird	47-53° N	3	chick survival	negative
Prey						
Snapp 1976	Barn swallow	terrestrial songbird	42.5° N	11	prey abundance	none
Birt et al 1987	Double-crested cormorant	nearshore seabird	47° N	2	prey density	depleted
Moller 1987	Barn swallow	terrestrial songbird	57° N	23	prey abundance	positive
					prey capture rates	negative
Forero et al 2002	Magellanic penguin	penguin	43° S	6	trophic levels of prey	negative
Ainley *et al.* 2003	Black-legged kittiwake	pelagic seabird	60° N	3 clusters	prey availability	negative
Bonal and Aparicio 2008	Lesser kestrel	terrestrial raptor	39° N	56	prey density	negative
					prey size	negative
Elliott et al 2009	Common murre	pelagic seabird	62° N	1	prey size	negative[2]
					trophic levels of prey	negative[2]
Wakefield et al 2013	Northern gannet	pelagic seabird	51° N	12	prey delivery rate	negative
Hemerik et al 2014	Unspecified seabird	pelagic seabird		model	prey density	negative
Interspecific						
Diamond 1978	Tropical seabirds (8 species)	nearshore and pelagic seabirds	0-10° S	9	foraging area	positive[5]
					migration	positive[5]
Gotmark 1982	Gulls (5 species)	nearshore seabird	58° N	1000	foraging radius	positive[5]
Jovani et al 2015	Seabirds (43 species)	pelagic seabird	45-75° N	28272	foraging radius	positive[5]

NOTES

[1] differing environmental conditions

[2] within breeding season for a single colony

[3] dependent on brood size

[4] no comparison between colonies

[5] comparison between species only

CHAPTER FOUR

PHYSICAL CONDITION AND STRESS LEVELS DURING EARLY DEVELOPMENT REFLECT NUTRITION AND PREDICT SURVIVAL IN A NEARSHORE SEABIRD

Abstract

The effects of acute environmental stressors on reproduction in wildlife are often difficult to measure due to the labor and disturbance involved in collecting accurate reproductive data. Stress hormones represent a promising option for assessing the effects of environmental perturbations on altricial young; however, it is necessary to first establish how stress levels are affected by environmental conditions during development and whether elevated stress results in reduced survival and recruitment rates. In birds, the stress hormone corticosterone is deposited in feathers during the entire period of feather growth, making it an integrated measure of background stress levels during development. I tested the utility of feather corticosterone levels in 3-4 week-old nestling brown pelicans for predicting survival rates at both the individual and colony levels. I also assessed the relationship of feather corticosterone to nestling body condition and nutritional stress. Chicks with higher body condition and lower corticosterone levels were more likely to fledge and to be re-sighted after fledge, while those with lower condition and higher corticosterone were more likely to be found dead. Feather corticosterone also predicted within-colony differences in survival between ground and elevated nest sites. Colony-wide, mean feather corticosterone was a stronger predictor than body condition of nest productivity, chick survival, and post-fledging dispersal, although these relationships were strongest before fledglings dispersed away from the colony. Both reproductive

success and nestling corticosterone were strongly related to nutritional conditions, particularly provisioning rates. I conclude that feather corticosterone is a powerful predictor of reproductive success and could provide a useful metric for rapidly assessing the effects of changes in environmental conditions, provided pre-existing baseline variation is monitored and understood.

Introduction

Impacts of acute or chronic environmental stressors on wildlife are typically quantified directly using mortality rates derived from carcass counts (Piatt *et al.* 1990, Burger 1993) or multi-year census data (Wiens *et al.* 1996, Yaukey 2012), which are then incorporated into demographic models to estimate the population-level effects of stressors (Haney *et al.* 2014). In addition to causing immediate mortality, however, stressors can also act sublethally through secondary pathways including reduced habitat quality (Cheng *et al.* 2009, Williams *et al.* 2010), compromised physical condition (Romero and Wikeski 2001), physiological and genetic modifications (Møller and Mousseau 2011), or increased susceptibility to existing threats such as disease or environmental fluctuation (Balseiro *et al.* 2005, Whitehead 2013). Many of these indirect and sublethal stressors subsequently impact demographic processes by reducing reproductive fitness in surviving individuals (Krebs and Burns 1977, Peterson 2001) but often are not explicitly or adequately addressed in demographic calculations and projections. Moreover, the breeding process itself is likely to compound impacts of environmental stress, since reductions in adult condition and habitat suitability make it

less likely for breeders to meet the energetic demands of territory defense, gestation, and provisioning young (Butler *et al.* 1988, Gannon and Willig 1994). Indeed, demographic models that do not accurately incorporate secondary effects of environmental stressors on breeding success and recruitment cannot accurately predict or quantify the complex population-level impacts of environmental perturbations (Peterson *et al.* 2003, Haney *et al.* 2014).

Despite widespread understanding of the capacity of sublethal environmental stress to negatively affect reproduction and recruitment, it can be difficult to determine the most appropriate endpoints for measuring these effects (Smits and Fernie 2013). In order for post-disturbance measurements to be informative, there must be a pre-existing understanding of the level of variation in reproductive parameters expected under baseline conditions (Teal and Howarth 1984, Velando *et al.* 2005). Such data are not always available for species of interest prior to catastrophic events (Eppley 1992). Moreover, the collection of reproductive data can be time- and labor-intensive and can involve researcher disturbance, which may make it difficult to implement rapidly in the wake of unexpected external change (Wiens *et al.* 1984). Snapshot measures of reproductive health (*e.g.*, Jakob *et al.*1996, Benson *et al.* 2003), which can be collected during a single visit and with minimal disturbance, allow for rapid data collection across large areas after disturbance events; however, their relationship to demographic parameters of interest (*e.g.*, reproductive success) must be evaluated in order to select appropriate metrics.

Stress hormone production offers a broadly applicable metric for assessing the impacts of environmental stressors on free-living wildlife populations (Romero and Wikelski 2001). Corticosterone (CORT) is the principal glucocorticosteroid stress hormones in birds, rodents, reptiles, and amphibians, and is frequently used as a measure of individual stress responses to environmental conditions and disturbance (*e.g.* Marra and Holberton 1998, Kitaysky *et al.* 2001, Blas *et al.* 2005, Bonier *et al.* 2007, Almasi *et al.* 2009). Stress hormones are upregulated in response to perceived stressors, prompting short-term behavioral and physiological modifications (McEwen *et al.* 1997). Over time, however, chronic elevation in CORT levels in response to chronic stress may negatively affect organism health by compromising immunosuppression, growth rates, body condition, and behavior (Sapolsky *et al.* 2000). CORT levels can be complicated by individual physiology (Angelier *et al.* 2007) and may change over life stages (Williams *et al.* 2008, Bonier *et al.* 2009). Within avian taxa, measuring corticosterone in altricial young controls for some of these influences, since their exposure to stress is localized and their range of behavioral responses is restricted (Kitaysky *et al.* 2003, Eggert *et al.* 2010). Since elevated stress in early life can result in severe developmental consequences (*e.g.* Kitaysky *et al.* 2003, Müller *et al.* 2009, Spencer *et al.* 2009, Butler *et al.* 2010), the corticosterone stress response can be used to test whether chick development, condition, growth, or survival are affected by acute or chronic environmental stress during nestling development, and to explore mechanisms underlying survival, reproductive performance, and population dynamics (Kitaysky *et al.* 2010).

While corticosterone levels in blood plasma can be elevated by short-term factors, such as stress resulting from capture (Love *et al.* 2003, Romero and Reed 2005), corticosterone in avian feathers provides a more sustained record of stress levels over days or weeks (Bortolotti *et al.* 2008, Harms *et al.* 2010). Feather corticosterone measurements allow for direct comparison of nestling condition between different breeding habitats, where variations in nutrition, contamination, predation, and parental attendance may affect chronic chick stress even if no physiological differences are apparent (Bortolotti *et al.* 2009, Harms *et al.* 2010). Recent laboratory and field studies have demonstrated that chronic nutritional stress elevates feather CORT levels in both captive and free-living seabirds (Will *et al.* 2015).

I assessed the utility of two snapshot nestling health measures, feather corticosterone concentration (feather CORT) and body condition index (BCI) for assessing reproductive success in the brown pelican (*Pelecanus occidenatlis*), a nearshore seabird with altricial chicks that frequently is subject to acute environmental stressors (Wilkinson 1994). I assessed the relationship of feather CORT and BCI to survival probability of individual nestlings, as well as to correlative population-based measures of nutritional stress, colony-wide fledging success and post-fledging dispersal. I predicted that a) levels of feather CORT in 3-4 week-old nestlings would be inversely related to nestling BCI measured simultaneously; b) probability of individual nestlings surviving to fledge would increase with increasing BCI and decreasing feather CORT measured at 3-4 weeks of age; c) colony-wide nest productivity would be highest at colonies with higher average BCI and lower feather CORT measured in 3-4 week-old chicks; and d) feather

CORT would increase and BCI decrease with increasing nutritional stress, measured by lower rates of energy delivery to nestlings.

Methods

Study species

The brown pelican is a large-bodied nearshore seabird and one of only two species of pelican to inhabit marine environments year-round (Shields 2014). Brown pelicans feed on schooling fish by plunge-diving, and can carry large masses of fish in a single pouch-load while feeding nestlings. They nest in large offshore colonies that can number several thousand individuals. Nest elevation can vary widely depending on available habitat, from open ground to tree sites up to 10 meters in elevation. Brown pelicans typically lay three sequentially-hatching eggs, which require an incubation period of ca. 30 days, and raise 1-2 young. Although nestlings can fly at ca. 60 days, they generally do not leave the nesting colony until 70-90 days after hatch. Brown pelicans exhibit biparental care and feeding throughout the nesting period. At least one parent attends at the nest at all times until chicks become mobile (~3-4 weeks), after which point parents are generally present at the nest site only when feeding chicks. Feedings may occur multiple times per day.

Study area

I conducted sampling between 2013 and 2015, throughout the northern Gulf of Mexico (Figure 4.1). I selected colony sites to represent the full geographic range of

pelican breeding areas in the region, with the exception of South Florida. In 2013, I collected physical measurements and feather samples from 3-4 week-old chicks (hereafter, chick sampling) at six colonies: two in the Florida panhandle, two in the Louisiana delta, and two along the central Texas coast. In 2014, I conducted chick sampling and monitored nest productivity at four colonies along the central and northern Texas coast. In 2015, I conducted chick sampling and monitored nest productivity at three colonies in the Florida panhandle and one in Alabama.

Nestling body condition

I selected 3-4 week-old nestlings for sampling based on either hatch dates (where known) or plumage development (fully-developed scapular contour feathers, remiges and rectrices in pin). Nestlings were readily captured by hand at or near nest sites. I collected physical measurements (culmen length, tarsus length, wing chord, and mass), checked for the presence of ectoparasites, and counted all ticks found on the underside of the left wing. I also banded each chick on the right tarsus with a uniquely numbered stainless steel US Geological Survey Bird Banding Lab leg band.

To calculate BCI, I ran a principal components analysis (PCA) on the three measures of skeletal size I collected: tarsus length, culmen length, and wing chord (Benson *et al.* 2003). Using each individual's score on the first principal components axis (PC1) as an index of overall skeletal size, I calculated the best-fitting regression equation for the relationship between mass and PC1 score. I chose a second-order polynomial to accurately represent the nestling growth process, which is initially linear but reaches a

peak and descends slightly prior to fledging. Finally, I calculated BCI as the standardized residual of actual body mass from the value predicted by the regression equation.

Feather corticosterone

At capture, I collected 3-4 scapular contour feathers from each nestling. Feathers were bagged and stored at room temperature until processing. I used random number generation to select 150 samples per year for CORT analysis, divided equally among study colonies. Following the recommendations of Lattin *et al.* (2011), I restricted the range of sample sizes analyzed by excluding from analysis samples that were extremely small (< 20 mg), and dividing samples larger than 160 mg into separate units for analysis.

I closely followed the methods for feather CORT extraction and analysis originally described by Bortolotti *et al.* (2008). Briefly, I removed the calamus from each feather, weighed and measured feathers individually, and prepared the sample for analysis by snipping feathers into small (< 0.5 mm) pieces with scissors and transferring the entire sample into a 16 mL test tube. Each sample received 7 mL of methanol and was placed in a sonicating water bath overnight at 30° C. I then pipetted the methanol into a separate 13 mL tube and conducted two additional washes, each with 2.5 mL methanol. The cumulative methanol sample, totaling 12 mL, was dried down under N_2, reconstituted in 200 µL buffer, and centrifuged to ensure that all accumulated corticosterone was dissolved in buffer. I conducted a radioimmunoassay (MP Biomedicals, LLC; ImmuniChem™ Double Antibody Corticosterone ^{125}I RIA Kit) on diluted samples. Simultaneous parallelism tests indicated that the assay accurately

detected CORT, and I used a standard sample with known CORT to measure intra-assay variation (1.7 – 1.9%) and subsampled a single feather sample to measure inter-assay variation (11%). I assessed feather CORT in a total of 365 chicks (2013: $N = 126$; 2014: $N = 144$; 2015: $N = 95$).

Since CORT concentrations may reflect feather quality as well as quantity (Patterson et al 2014), I divided the total amount of corticosterone detected in each sample by the total mass of all feathers in the sample (pg mg^{-1}), log-transformed values to meet assumptions of normality, and calculated feather mass per unit length (mg mm^{-1}) as an index of feather quality. Since feather mass and feather length were significantly negatively correlated ($p < 0.001$, slope = -1.14 ± 0.15), I calculated the residual of the best-fitting regression line between log-transformed CORT mg^{-1} and feather mass per unit length, de-trended the data by subtracting the regression line, and used the adjusted values in all analyses.

Nutritional stress

Nutritional stress in nestlings has three principal components: feeding rate (meals $nest^{-1}$ day^{-1}), meal mass (g $meal^{-1}$) and energy density of prey (kJ g^{-1}). Following field methods used in previous studies (*e.g.*, Jodice *et al.* 2006), I measured each of these metrics at the population level (breeding colony), and combined them to obtain an overall index of total daily energy delivery to nestlings (energy provisioning rate: EPR) for each study colony.

To measure feeding rates, I opportunistically selected groups of 15-20 nests at each colony visit and conducted 3-hour observations, recording arrivals and departure times of adults as well as any feedings observed. Although I did not attempt to associate feeding rates with specific nests used for productivity and chick condition analysis, I selected nest groups in the same areas of the colony to ensure that I was sampling the same population. I considered a feeding to have occurred when a nestling inserted its head into the adult's gular pouch and emerged with its throat engorged (Sachs and Jodice 2009). I did not observe extensive self-feeding by nestlings, and thus considered only direct feedings from adults to nestlings. To measure meal mass, I collected 8-10 regurgitated meals from nestlings at each colony every 5-7 days, varying the timing and location of collection opportunistically. I obtained regurgitates by approaching nestlings and collecting meals that were regurgitated voluntarily. All collected samples were stored in plastic bags and frozen for later analysis.

In the laboratory, I thawed each sample in a warm-water bath, dried off surface water using paper towels, then weighed, measured, and identified to species each individual fish. I classified each fish as whole (no visible damage), partial-whole (total length obtained, but some soft tissues missing), and partial (total length could not be obtained). For samples containing large numbers of fish (50 – 1000 items per sample; 26% of samples), I counted the total number of individuals of each species, weighed and measured a subsample of ten individual fish per species, and obtained a total weight and overall classification (whole, partial-whole, partial) for each species group. For samples containing extremely large numbers of fish (> 1000 items per sample; < 1% of samples),

I weighed and measured a subsample of ten fish per species, weighed the overall sample, and used the average weight per fish to approximate the total number of fish in the sample. I did not analyze samples for which the digestive process was too advanced to identify fish to species (< 1% of all samples collected). To estimate the mass of partial-whole and partial fish, I calculated the length-weight relationship as the best-fitting regression equation between log total length and log mass of whole fish for each species by year (Table S1). For partial-whole fish (*i.e.*, degraded fish for which I were able to measure total length), I used the regression line to estimate the corrected mass of the whole fish from its length. For partial fish (*i.e.*, degraded fish for which total length was not measurable), I used the mean total length of whole and partial-whole individuals collected from the same breeding colony on the same day to estimate a corrected mass from the regression equation.

I measured proximate composition and energy densities in whole samples (purchased bait fish and undamaged chick regurgitates) of the most common prey fish species using extraction techniques as described in Anthony *et al.* (2000). Briefly, I dried fish to determine water content, extracted lipids from dried fish to determine lipid content, and ashed lean dry fish to determine protein content. Energy density for each prey item was then calculated as the sum of energy for lipid and protein. Species for which I was able to directly measure energy densities comprised 93% by biomass of all prey samples (Table 4.S2). For less-common species (7% of total biomass), I substituted either energy density values from other species within the same family or, if no comparable values were available in my data or in the literature, biomass-weighted

averages of all other prey species. I calculated total energy content of sampled meals based on mean energetic values for each prey species multiplied by biomass, then averaged over the total meal mass to obtain a value of kJ g^{-1}. For a complete description of methods used in analysis of nestling meals, please see Chapter 5 of this dissertation.

Nest productivity and nestling survival

I visited nesting colonies close to the end of the incubation period and selected 3-4 groups of focal nests per colony, each group containing 20-30 nests. In colonies containing both elevated and ground nests, I selected closely-spaced groups such that each contained nests of one type or the other to allow for comparison. On my initial visit, I recorded nest contents, assigned an identifying number to each nest, and photographed the nest group from marked observation points that could be accessed without disturbance to focal nests. On return visits, I identified nests using the numbered photograph and checked the contents of each nest from the observation point. Once nestlings reached 3-4 weeks of age, concurrent with measurements and feather sampling, I banded nestlings on the left tarsus with a permanent plastic band (Haggie Engraving: 2014—green; 2015—blue) engraved with a three-digit white alpha code to aid in re-sighting.

Once nestlings began to disperse away from nest locations, I searched the surrounding areas of the colony with binoculars for banded chicks and recorded all bands observed. I continued observations until chicks reached at least 60 days of age. Beginning approximately 8 weeks after hatch, I also conducted regular searches of the colony for

dead banded chicks and recovered all bands found. To determine nest productivity (fledglings $nest^{-1}$), nestlings that were observed alive at least 60 days after hatch and disappeared from the colony, but were not found dead, were presumed to have successfully fledged (Shields 2014). I calculated plot- and colony-wide fledge success as the number of chicks fledged from observation nests, divided by the total number of nests observed.

To determine survival post-fledging, I relied on opportunistic re-sighting of banded chicks by colony monitors and birders along the coast of the Gulf of Mexico. I received band re-sightings and recoveries reported to the Bird Banding Lab, as well as directly to me through a dedicated web portal. Sightings and recoveries were obtained throughout the United States Gulf Coast and from Mexico through January 2016.

Statistical analyses

I visually assessed frequency distributions of measured variables, and where necessary used log transformations to meet assumptions of normality. To evaluate CORT and BCI as predictors of individual survival to fledge, I conducted logistic regression with a binary outcome (fledged/died) on each metric and assessed the fit of the resulting models. To assess the utility of CORT, BCI, and nest- specific factors as predictors of individual survival, I ran independent generalized linear models, each with a binary outcome (fledged/died; resighted alive/recovered dead) and logit link. I used CORT, BCI, nest elevation (ground or elevated), nesting colony, date, hatch order, and number of siblings as fixed factors.

To calculate colony-wide survival rates, I used a joint live recapture – dead recovery model (Burnham 1993). I assessed survival rates at two time steps: survival to fledge (3 months after hatch) and post-dispersal survival (6 months after hatch). Dead individuals were recovered in the intervals between time steps, and individuals were considered to have survived to a new time step if they were re-sighted alive after that period ended. Since resightings and recoveries took place across the entire range of the population, I fixed dispersal parameters (F) at 1 (*i.e.*, 100% probability that banded individuals remained in the sampling area). I derived parameter estimates for survival (S), recovery (r), and resighting (p) during each time interval using Markov chain Monte Carlo estimators with a burn-in of 1000 samples, followed by 4000 tuning samples and 10000 runs.

To compare the relative value of different metrics (CORT and BCI) for predicting aggregate nest productivity and survival rates, I used a generalized linear modeling framework (Gamma, log link) with fledge success as the response variable and average CORT, average BCI, and the interaction of CORT with BCI as predictor variables. I computed AIC_c values to account for the small sample sizes that resulted from using colony as the sampling unit and used these values for model comparison. Models were considered to receive strong support if they resulted in a $\Delta\ AIC_c \leq 2$, and moderate support if they resulted in a $\Delta\ AIC_c$ of between 2 and 4 (Burnham and Anderson 2004).

To assess nutritional stress by colony, I calculated meal mass (g $meal^{-1}$), nest-specific provisioning rate (meals $nest^{-1}$ $hour^{-1}$), and energy density of meals (kJ g^{-1}) for each colony. These three components together form the energy provisioning rate (EPR: g

nest^{-1} hour^{-1}, Jodice *et al.* 2006). To obtain a combined measure of EPR by colony, I modeled energy-days for each colony by randomly selecting (with replacement) 100 values for provisioning rate (meals day^{-1}) from the set of measured values. The model then chose at random (with replacement) a mass and an energetic value for each meal, multiplied meal mass by energy density to obtain total energy content per meal, and summed total energy across all meals for each modeled day to obtain a set of energy provisioning rates (kJ day^{-1}). I calculated the mean and standard deviation of EPR for each colony by averaging values obtained from 1000 runs of the model. I chose to calculate EPR on a per-nest basis rather than a per-chick basis, to avoid the confounding relationship between higher provisioning rates and improved longevity of second- and third-hatched chicks. I used generalized linear models (Gamma, log link) to assess the relationships of EPR and its component metrics to chick health parameters and nest productivity.

Results

Individual survival

For individual nestlings, feather CORT concentrations were significantly negatively correlated to BCI (linear model: coefficient = -194 ± 31.6, $F_{1,364} = 37.7$, $p < 0.001$, $R^2 = 0.09$). Chicks that died before fledging had lower body condition ($F_{1, 239} = 6.1$, $p = 0.01$) and higher feather CORT ($F_{1, 239} = 24.7$, $p < 0.001$) at 3-4 weeks of age than chicks that were presumed fledged (*i.e.*, survived until at least 60 days after hatching) (Figure 4.2). Of the other covariates I tested, only nest height (linear model,

ground relative to elevated: coefficient = -2.79 ± 0.80, Z_{109} = -3.76, $p < 0.001$) and body size (linear model: coefficient = 1.25 ± 0.43, Z_{109} = 2.88, $p = 0.004$) were significant predictors of fledging success. Nestlings from ground nests had significantly lower BCI (ground: M_{74} = -97.2 ± 479; elevated: M_{117} = 72.0 ± 363; $F_{1,191}$ = 7.74, $p = 0.006$) and higher feather CORT (ground: M_{74} = 2.08 ± 0.71; elevated: M_{117} = 1.72 ± 0.64, $F_{1,191}$ = 17.8, $p < 0.001$) than nestlings from elevated nests. I did not find a significant effect of colony, region, year, sampling date, hatch order, or number of siblings on fledging probability (linear models: $p > 0.10$ for each).

Survival probabilities of individual nestlings > 60 d post hatch were negatively related to feather CORT and positively related to BCI (Figure 4.3). Chicks found dead post-fledging had significantly lower body condition (ANOVA: $F_{1,40}$ = 11.4, $p = 0.002$) and significantly higher feather CORT (ANOVA: $F_{1,40}$ = 18.4, $p < 0.001$) at 3-4 weeks after hatch than did chicks that were resighted alive after fledge (Figure 4.2).

Colony-specific nest productivity and chick survival

Within breeding colonies, feather CORT levels were correlated with nest productivity at individual observation plots. Nest productivity and nestling feather CORT (Figure 4.4a-b), but not nestling BCI (Figure 4.4c), differed significantly between ground and elevated subplots at two of the four colonies with both ground and elevated nests. Overall, colony-wide productivity rates were significantly correlated with average feather CORT (coefficient = -0.88 ± 0.15, t_5 = -5.77, $p = 0.002$; Figure 4.5a) and BCI (coefficient = 0.42 ± 0.15, t_5 = 2.80, $p = 0.04$; Figure 4.5b) of sampled chicks. The

strongest model predicting colony-specific nest productivity as a function of chick health parameters, which was also the only model supported by comparison of AIC_c values, contained feather CORT alone (Table 4.1). The top model explained 84% of the observed deviance (null = 1.91; residual = 0.31).

Modeled chick survival to fledge (3 months after hatch) at individual colony sites was significantly correlated with average feather CORT (coefficient = -0.23 ± 0.03, t_5 = -6.91, $p < 0.001$; Figure 4.6). BCI was also moderately correlated with survival to fledge (coefficient = 0.109 ± 0.047, t_5 = 2.31, $p = 0.069$). The strongest model predicting chick survival to fledge as a function of chick health parameters, which was also the only model supported by comparison of AIC_c values, contained feather CORT alone (Table 4.1). The top model explained 91% of the observed deviance (null = 0.144; residual = 0.013).

Modeled post-dispersal survival (to 6 months after hatch) at individual colony sites was moderately correlated with average feather CORT (coefficient = -0.07 ± 0.03, t_5 = -2.37, $p = 0.064$; Figure 4.6). BCI was not correlated to post-dispersal survival (p = 0.25). Both the feather CORT-only model and the null model were supported as predictors of post-dispersal survival, although the former was 1.7 times as likely as the latter to be the best model (Table 4.1). The top model explained 54% of the observed deviance (null = 0.026; residual = 0.012).

Nutritional stress

Energy provisioning rate had a significant positive relationship to BCI (linear model, coefficient = 0.22 ± 0.07, t_5 = 3.28, p = 0.02; Figure 4.7a) and a significant negative relationship to feather CORT (linear model, coefficient = -0.0005 ± -0.0001, t_5 = 3.88, p = 0.01; Figure 4.7b). The two biomass components of EPR, feeding frequency (meals nest^{-1} day^{-1}, M = 4.18, N = 142) and meal mass (g meal^{-1}, M = 157.6, N = 583) had similarly high levels of overall variation (CV frequency = 0.67; CV mass = 0.76), while energy density of meals (kJ g^{-1}, M = 4.34, N = 583) was less variable (CV = 0.10). EPR explained 72% of observed variance in colony-wide average feather CORT and 68% of observed variance in colony-wide average BCI (Figure 4.7). Of the separate components of EPR (Table 4.2), meal delivery rate explained the largest portion of variation in each of the two chick health metrics (CORT: 30.1%; BCI: 48.2%), followed by meal mass (CORT: 23.7%; BCI: 2.9%) and energy density (CORT: 3.2%; BCI: 0.9%). EPR was significantly correlated to nest productivity (linear model, coefficient = 0.00043 ± 0.00004, t_5 = 10.03, $p < 0.001$, R^2 = 0.95) and nestling survival to fledge (linear model, coefficient = 0.00015 ± 0.00002, t_4 = 4.30, p = 0.008, R^2 = 0.81); however, there was no correlation between EPR and post-fledging survival rates (linear model, p = 0.27).

Discussion

I found that corticosterone in nestling feathers, which represent an integrated measure of developmental stress during feather growth, was highly correlated with traditional measures of reproductive success (fledglings per nest) and nestling health

(BCI) at individual, subcolony, and colony-wide scales. Moreover, my results indicate that measuring feather corticosterone in young chicks can reveal differences in chick health, fledging success, and post-fledging survival that are not captured by body condition alone.

My first objective was to assess the relationship between feather CORT and a more traditional measure of nestling health, BCI (Benson *et al.* 2003), as predictors of nestling survival. In accordance with recent work on other avian taxa, I found that nestling feather CORT was negatively correlated to both body condition (Fairhurst *et al.* 2013, López-Jiménez *et al.* 2015) and fledging probability (Fairhurst *et al.* 2013, Lodjak *et al.* 2015) at the individual level. Although both feather CORT and BCI were significantly correlated to chick survival to fledge, feather CORT slightly outperformed BCI in predicting the fates of individual nestlings. At the colony level, models containing only feather CORT were favored over models containing BCI with and without feather CORT as predictors of nest productivity, survival to fledge, and post-dispersal survival. Additionally, feather CORT predicted within-colony differences in fledge success by habitat type that were not apparent in comparisons of BCI. These differences in explanatory power could result from the time scales sampled by the two metrics. BCI is likely to be more sensitive than feather CORT to short- term variation in nutritional stress; *e.g.*, at one of the colonies included in this study (Shamrock Island), average chick mass was 2,660 g and average meal mass was 181 g, or about 7% of body weight. This level of short-term variation could substantially elevate BCI of a recently-fed pelican chick compared to a chick that had not been fed in several hours. Since meal delivery

rates and the size of meals in relation to chick mass can vary by more than an order of magnitude both among and within avian species (Ricklefs *et al.* 1985, Anderson and Ricklefs 1992), the use of BCI as a measure of nestling condition requires consideration of how these short-term factors may influence its utility in describing long-term patterns of chick condition. Feather CORT integrates a longer time series of conditions (Bortolotti *et al.* 2008) and thus may be less susceptible than BCI to short-term variation. The fact that I measured feather CORT early in development (about 20-30 days into a 60-90 day fledging period) and found a strong relationship to fledging probability further indicates that feather CORT can serve as an accurate predictor of long-term conditions that persist through the breeding season.

I also assessed the relationship between feather CORT and variation in local (site- and nest-specific) conditions. Although nestling feather CORT is strongly correlated to environmental conditions during development (*e.g.*, Harms *et al.* 2010, Will *et al.* 2015, Lodjak *et al.* 2015), site and nest-specific factors can still confound the environment-stress relationship (Fairhurst *et al.* 2012, Lodjak *et al.* 2015). I did not find a significant influence of either hatch order or number of siblings on feather CORT. A previous study of plasma CORT in brown pelican nestlings (Eggert *et al.* 2010) also found no effect of brood size or hatch order on stress levels; however, sibling dynamics have been found to affect feather CORT levels in nestling raptors (Yosef *et al.* 2013, López-Jiménez *et al.* 2015). I did find an influence of microhabitat characteristics (elevated vs. ground nest location) on feather CORT. Nestlings at elevated nests may benefit from improved passive thermoregulation, reduced energy expended in movement, and reduced

aggressive interactions with neighboring adults and nestlings that subsequently act to maintain lower levels of feather CORT. This study concurs with data on brown pelican nest productivity in Louisiana (Walter *et al.* 2013) suggesting that nestlings from elevated nests tend to survive longer than nestlings from ground nests, contributing to increased nest productivity at elevated sites. If elevated nest sites offer improved fledging success, positive reinforcement may occur at these sites if experienced or dominant breeders then choose elevated over ground nesting sites.

Finally, I tested the relationship between nestling health metrics, nutritional stress (energy provisioning rate), and breeding success. My results indicated that both nestling feather CORT and nestling BCI were highly correlated to EPR, and that EPR explained 95% of the variation in nest productivity between the colonies I studied. Of the components of EPR, meal delivery rate explained a larger portion of the variation in survival metrics and nestling health than did meal mass or energy density of prey. Meal mass was also correlated with nestling feather CORT, although not with BCI or survival, while energy density had no significant linear relationships with nestling health or survival metrics. The low correlation between nestling health and energy density in this system is in contrast to previous studies of seabirds (reviewed in Österblom *et al.* 2008) that have suggested prey quality as a key driver of nestling survival. Information regarding energy content of prey in the Gulf of Mexico suggests that differences in quality may not be as variable between species as it is in other marine systems (Stickney and Torres 1989, Anthony *et al.* 2000). In addition, pelicans in this system rarely experience nest predation, human disturbance, or extreme weather events at colony sites

during breeding, meaning that few factors are likely to confound the relationship between developmental stress and chick mortality. Once nestlings fledged, EPR at the natal colony was no longer a strong predictor of survival probability, indicating that differences in the quantity of food during development are not a dominant driver of survival after dispersal. However, both feather CORT and BCI were correlated to post-fledging survival, which suggests that developmental nutritional stress may continue, via indirect effects on physiology, to influence the probability that individuals will survive to recruit back into the breeding population once they have fledged. The demographic effects of negative feedbacks between developmental stress and recruitment have been documented in other seabird species (*e.g.*, Kitaysky *et al.* 2010). Although the short time scale (6 months after hatch) of my analysis limited my ability to draw conclusions, linking these parameters is a necessary step toward understanding the long-term demographic consequences of perturbations in the developmental environment.

Although measuring feather corticosterone requires more post-collection laboratory analysis than traditional reproductive success and chick health metrics, its advantages include minimal disturbance at breeding colonies, ease of collection and storage, and the ability to sample multiple colonies in a short time. In order to draw inferences at broader spatial scales (*e.g.*, between colonies or regions), however, sampling regimes would need to account for the influence of varying habitat characteristics. Several recent feather CORT studies, particularly Fairhurst *et al.* (2014) and Lodjak *et al.* (2015), and López-Jiménez *et al.* (2015), have described the context-dependence of the stress-environment relationship and its sensitivity to local-scale habitat

quality and climactic variation. My results indicate that, while sibling dynamics do not confound variation in feather CORT in this species, nest height can affect both physiology and survival and should be taken into account when sampling so as to accurately reflect overall colony characteristics. These differences highlight the importance of understanding how different site- and individual-specific factors contribute to underlying variation in measured parameters, and how these factors could interact cumulatively or multiplicatively with environmental conditions to mask or exaggerate the effects of perturbations on reproduction.

I found both inter- and intra-regional variation in colony-specific nestling health and reproductive success under baseline conditions across the northern Gulf of Mexico. The foraging environment experienced by breeding wildlife depends on a variety of biotic and abiotic factors that can change across a species' range as well as between and within breeding seasons. Distinguishing the effects of environmental perturbations requires that the effects of short-term changes to foraging conditions be distinguished from the background noise of pre-existing variation. Endpoints that can be measured consistently across space and time offer a potential basis for the kind of long-term monitoring projects that would allow baseline variation to be measured and compared to post-disturbance conditions. This study provides evidence that feather CORT can be used to detect differences in underlying nutritional quality and predict reproductive parameters in a free-living seabird population, making it an appropriate basis for long-term monitoring of population-wide reproductive health and, ultimately, detection of the indirect demographic effects of environmental change.

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Table 4.1. Candidate models for brown pelican nest productivity and nestling survival in the northern Gulf of Mexico as a function of colony-average body condition (BCI) and feather corticosterone (CORT) of 3-4 week-old chicks, ranked in order of increasing AIC values with model weights (w_i), cumulative weights (Σw) and relative likelihoods (L_i). Models in bold were considered strongly supported.

	Terms	AIC_c	Δ_i (AIC_c)	w_i (AIC_c)	Σw	L_i (AIC_c)
Productivity						
	CORT	**4.17**	**0**	**0.94**	**0.94**	**1.00**
	BCI	11.14	6.97	0.03	0.97	0.03
	BCI + CORT	11.40	7.22	0.02	0.99	0.02
	Null model	13.06	8.88	0.01	1.00	0.01
Post-banding survival						
	CORT	**-17.66**	**0**	**0.96**	**0.96**	**1.00**
	BCI + CORT	-10.70	6.87	0.03	0.99	0.03
	BCI	-6.34	11.32	< 0.01	1.00	< 0.01
	Null model	-5.40	12.27	< 0.01	1.00	< 0.01
Post-dispersal survival						
	CORT	**-19.80**	**0**	**0.55**	**0.55**	**1.00**
	Null model	**-18.74**	**1.06**	**0.32**	**0.87**	**0.59**
	BCI	-16.53	3.27	0.11	0.98	0.19
	BCI + CORT	-13.00	6.81	0.02	1.00	0.03

Table 4.2. Mean values (± standard deviation) for brown pelican nest productivity, chick health metrics, and energy provisioning metrics by colony in the northern Gulf of Mexico 2014-2015.

	Colony	Productivity	BCI	CORT	Meals day^{-1}	g meal^{-1}	Energy g^{-1}	EPR
2014	Shamrock	0.51 ± 0.66	-499 ± 446	2.47 ± 0.52	2.23 ± 1.28	181 ± 114	4.66 ± 0.50	2574 ± 1618
2014	Chester	0.68 ± 0.79	-136 ± 372	2.44 ± 0.54	3.10 ± 2.80	147 ± 116	4.53 ± 0.61	2902 ± 2548
2014	Galveston	0.94 ± 0.86	-251 ± 472	2.09 ± 0.60	5.68 ± 3.08	98 ± 70	3.99 ± 0.63	2995 ± 1804
2015	Smith	0.30 ± 0.64	-189 ± 209	3.02 ± 0.38	4.21 ± 3.08	80 ± 36	4.35 ± 0.39	1977 ± 1286
2015	Ten Palms	1.64 ± 0.95	193 ± 291	1.56 ± 0.37	5.84 ± 3.14	159 ± 96	4.59 ± 0.35	4876 ± 2722
2015	Audubon	1.42 ± 0.85	325 ± 379	1.41 ± 0.28	5.32 ± 2.33	156 ± 146	4.33 ± 0.38	4845 ± 2554
2015	Gaillard	1.06 ± 0.85	150 ± 272	1.30 ± 0.46	3.84 ± 1.89	151 ± 72	4.69 ± 0.36	3574 ± 1928

Figure 4.1. Location of brown pelican colonies sampled in the northern Gulf of Mexico. Marker sizes represent relative colony size (75 – 5000 nesting pairs). Nestling health samples were collected from all colonies, and nutrition and productivity data were also collected from colonies outlined in red. Locations of other brown pelican nesting colonies in the northern Gulf of Mexico by this study are indicated in yellow

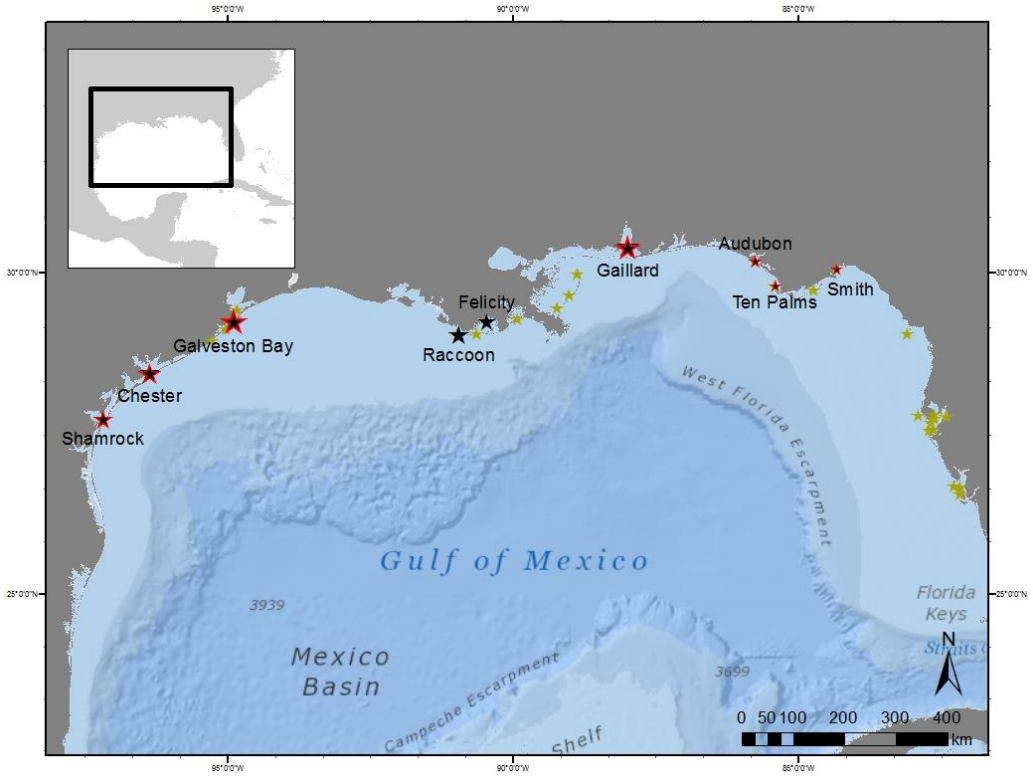
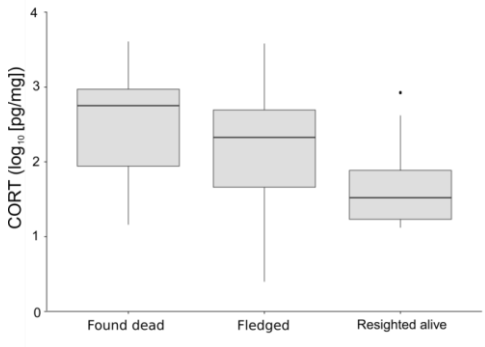


Figure 4.2. Distribution of individual measurements of (a) feather CORT and (b) BCI at 3-4 weeks post-hatch for brown pelicans nestlings later found dead after banding, presumed fledged, and resighted alive after leaving the breeding colony in the northern Gulf of Mexico, 2013-2015.

(a)



(b)

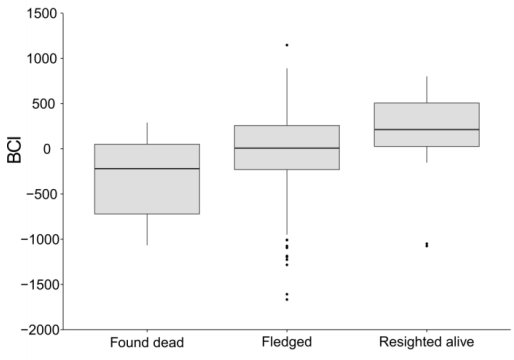


Figure 4.3. Probability of individual brown pelican nestlings being found dead (0) or resighted alive (1) after fledging, as a function of (a) CORT and (b) BCI, northern Gulf of Mexico, 2014-2015. Modeled survival probability (binomial logistic regression) is represented by the red curve, and observation frequencies are represented by grey bars (*e.g.*, two dead birds [bottom left bar panel a] had CORT measures between -0.6 and -0.4 while six live birds top left bar panel a] had CORT measures of that same value).

(a) (b)

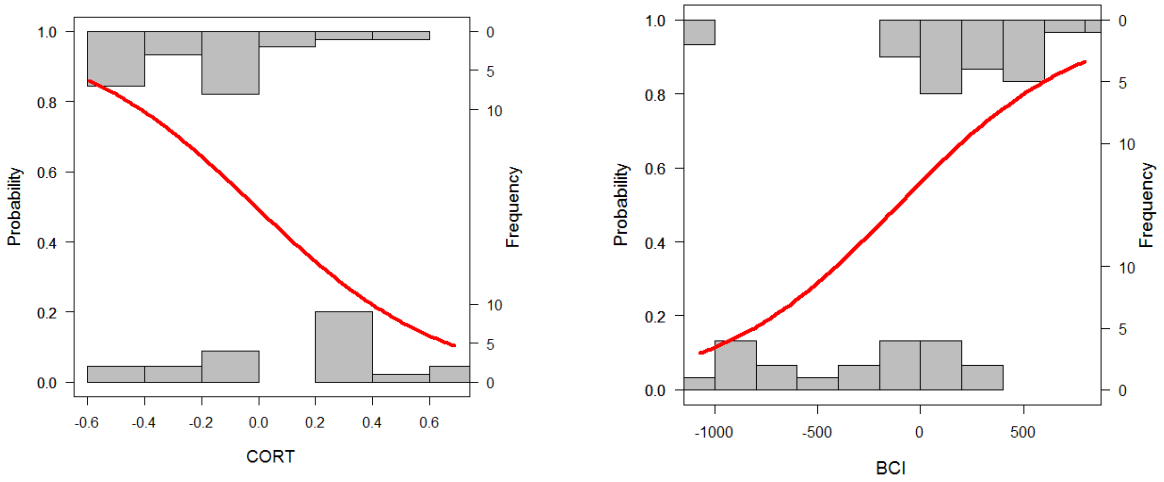
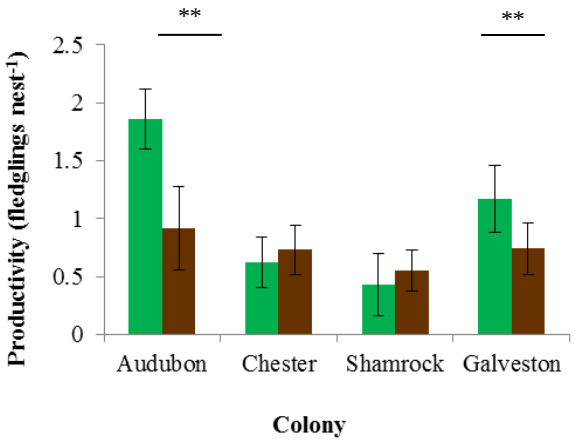
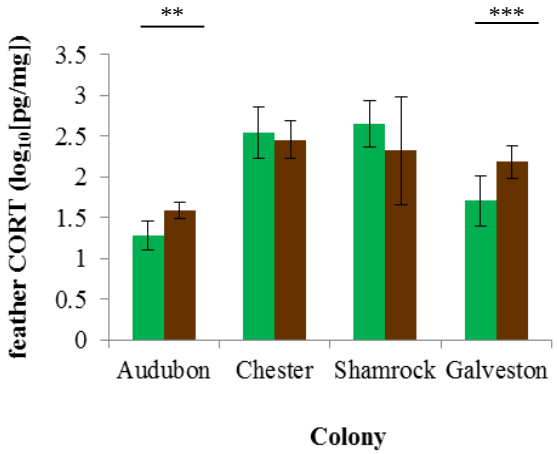


Figure 4.4. Mean values for brown pelican (a) nest productivity, (b) CORT, and (c) body condition of nestlings in elevated (green) and ground (brown) nest plots at colonies containing both nest types in the northern Gulf of Mexico (2014-2015). Significant within-colony differences are indicated by asterisks (ANOVA: *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$); for all other differences, $p > 0.05$. Error bars represent 95% confidence intervals of the mean.

(a)



(b)



(c)

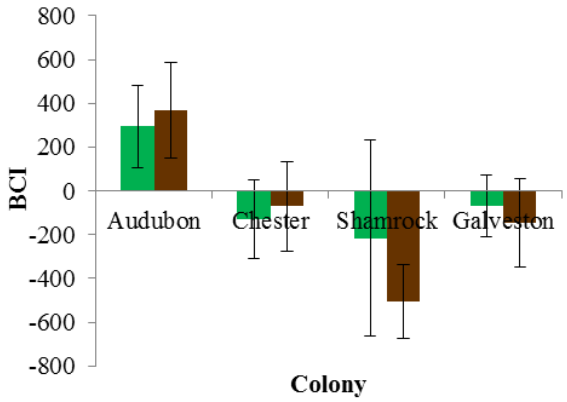
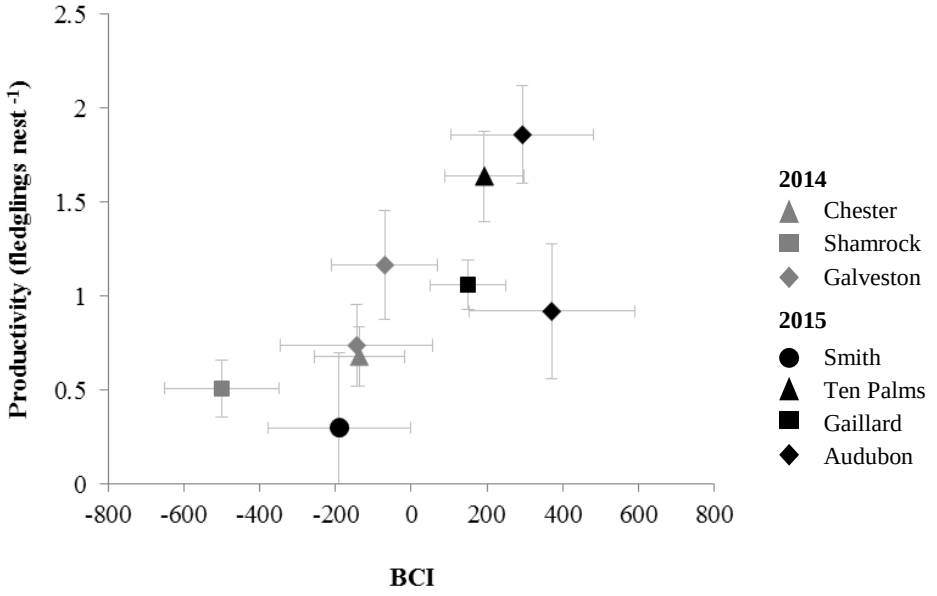


Figure 4.5. Correlation of mean brown pelican nest productivity to (a) chick condition and (b) feather CORT for colonies in the northern Gulf of Mexico, 2014 – 2015. Points represent colony-wide averages except where different habitat types differed significantly in productivity, in which case mean values are separated by habitat type. Error bars represent 95% confidence intervals.

(a)



(b)

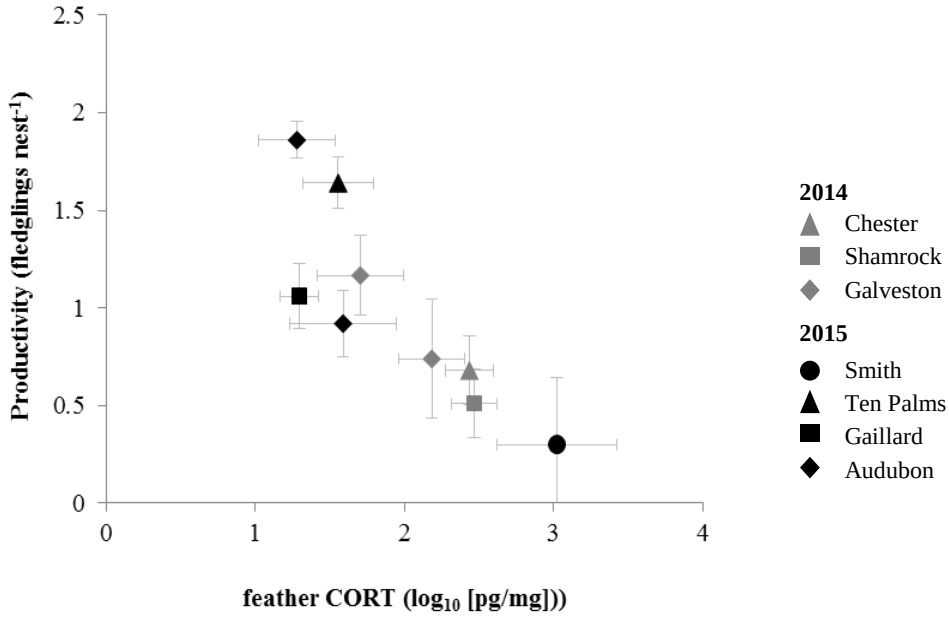


Figure 4.6. Relationship of brown pelican nestling feather corticosterone to probability of survival to fledge (filled circles, solid line) and post-dispersal survival (open squares, dashed line) in the northern Gulf of Mexico, 2014-2015.

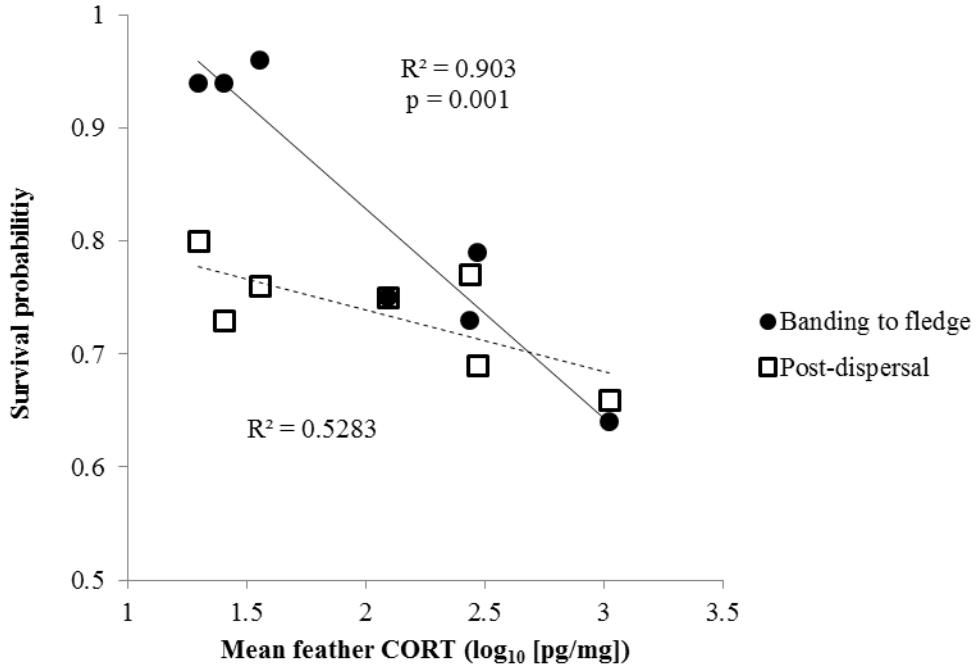
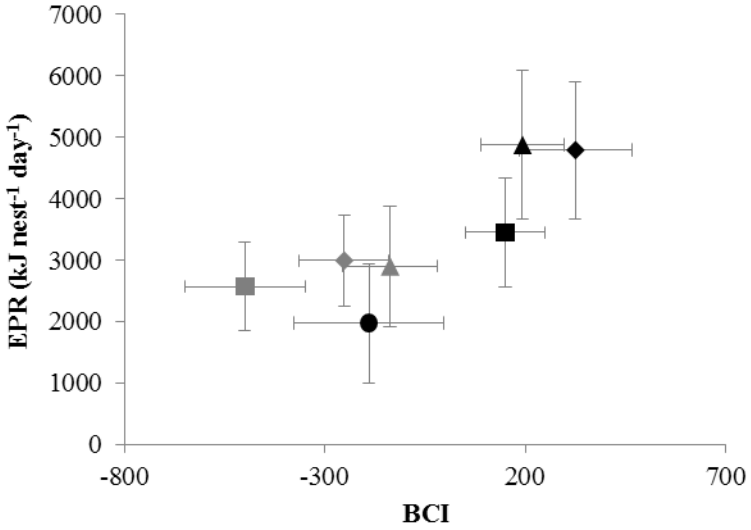


Figure 4.7. Relationship of energy provisioning rate (EPR) to brown pelican chick health parameters (a) BCI and (b) feather CORT by colony, 2014 – 2015, northern Gulf of Mexico. Points represent colony-wide mean values, and error bars represent 95% confidence intervals.

(a)



(b)

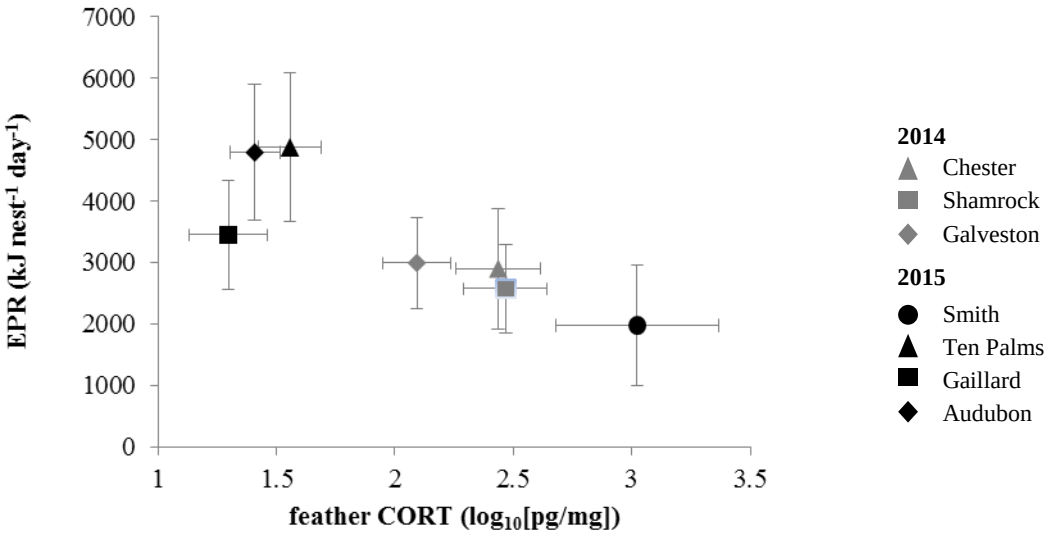


Table 4.S1. Length-weight relationships of common fish species in brown pelican diets, northern Gulf of Mexico, 2013-2015.

Species	Equation	Intercept	Slope	R^2	*p*
Brevoortia patronus	mass = $e^{-12.233} * \text{length}^{3.138}$	-12.23	3.14	0.99	< 0.001
Micropogonius undulatus	mass = $e^{-11.298} * \text{length}^{2.926}$	-11.30	2.93	0.83	< 0.001
Leiostomus xanthurus	mass = $e^{-11.324} * \text{length}^{2.976}$	-11.32	2.98	0.98	< 0.001
Trichiurus lepturus	mass = $e^{-16.051} * \text{length}^{3.278}$	-16.05	3.28	0.97	< 0.001

Table 4.S2. Prey-specific proportions of diet (percent total biomass) and mean energy densities (kJ g^{-1} wet mass) used in calculating energy provisioning rate. Values for species in the first column are calculated from laboratory measurements of prey samples, while values in the second column are based on measured or published values for similar species.

Species	% of total	kJ g^{-1}	Species	% of total	kJ g^{-1}
Brevoortia patronus	0.57	4.52	*Cynoscion nebulosus*	0.01	3.48
Anchoa mitchilli	0.10	4.12	*Chloroscombrus chrysurus*	0.01	3.60
Mugil cephalus	0.04	3.95	*Lutjanus campechanus*	0.01	4.44
Anchoa lyolepis	0.04	4.38	*Menticirrhus americanus*	0.01	4.05
Trichiurus lepturus	0.03	5.05	*Bairdiella chrysoura*	<0.01	4.33
Micropogonius undulates	0.03	5.24	*Diplectrum formosun*	<0.01	4.45
Lagodon ehavior	0.03	4.65	*Scomberomorus maculatus*	<0.01	3.60
Opisthonema oglinum	0.03	4.67	*Bagre marinus*	<0.01	4.95
Leiostoma xanthurus	0.02	4.83	*Decapterus punctatus*	<0.01	3.60
Anchoa hepsetus	0.02	4.88	*Symphurus urospilus*	<0.01	4.00
Unknown	0.01	4.45	*Cyprinodon variegatus*	<0.01	4.21
Cynoscion arenarius	0.01	3.48	*Peprilus paru*	<0.01	3.42
Sciaenops ocellata	<0.01	4.54	*Citharichthys spilopterus*	<0.01	4.00
ehavior .	<0.01	4.36	*Sybodus foetens*	<0.01	4.16
Harengula jaguana	<0.01	5.18	*Scomberomorus cavalla*	<0.01	3.60
Farfantepenaeus duorarum	<0.01	4.16	*Hemiramphus brasiliensis*	<0.01	3.92
			Tylosurus crocodilus	<0.01	3.92
			Peprilus burti	<0.01	3.42
			Diodon holocanthus	<0.01	4.16
			Chicken	<0.01	4.60
			Lolligunculla brevis	<0.01	4.25
			Orthopristis chrysoptera	<0.01	4.88
			Gobioides broussonetii	<0.01	4.81
			Selene setapinnis	<0.01	3.60
			Larimus fasciatus	<0.01	4.54
			Prionotus tribulus	<0.01	4.63
			Hemicaranx amblyrhynchus	<0.01	3.60
			Isopod	<0.01	2.59
			Menidia beryllina	<0.01	4.80
			Fundulus majalis	<0.01	4.21

CHAPTER FIVE

INFLUENCE OF DIET COMPOSITION AND PROVISIONING RATES ON REPRODUCTIVE SUCCESS IN A SUBTROPICAL NEARSHORE SEABIRD

Abstract

Understanding how both quality and quantity of prey affect marine predator population dynamics is a crucial step toward predicting the effects of environmental perturbations, including overfishing, pollutants, invasive species, and climate change, on population-level processes. However, the comparative roles of prey availability, prey size, and prey quantity in the foraging ecology and reproductive success of marine predators can vary widely depending on characteristics of both species and ecosystems. The Junk Food Hypothesis, which posits that a lack of high-energy prey species may negatively affect reproductive capacity of marine top predators even when abundant prey resources are available, has been proposed as a mechanism by which changes in prey populations could affect predator populations; however, little work has been done to test whether this mechanism operates in tropical systems. I collected three years of data on brown pelican (*Pelecanus occidentalis*) nestling diets and provisioning from nine breeding colonies in the tropical waters of the northern Gulf of Mexico. I assessed meal species composition, meal mass, feeding frequency, energy densities of common prey items, and reproductive success. Both feeding frequency and meal mass were significantly correlated to energy provisioning rates and nestling survival, while energy density of meals had little effect on either metric. Compared to previous results from cold-water systems, I found that energy density of common prey items was lower (4.4 kJ

g^{-1}, vs. 5.2 – 6.5 kJ g^{-1} in other studies) and encompassed a narrower range of values. Lipid content, which drove much of the observed variation in this study, was also lower (9% dry mass, vs. 16 – 23% in other studies) and less variable than in high-latitude systems. While Gulf menhaden (*Brevoortia patronus*) was the most common prey species at all colonies, its prevalence varied with underlying distribution, and the proportion of menhaden fed to nestlings was not strongly correlated to fledging success. I conclude that availability and accessibility of prey, particularly smaller and younger age classes, is the main driver of brown pelican reproductive success, while prey quality varies little between species in this region. I posit that similar mechanisms may operate in other tropical and subtropical systems, where lipid reserves of common fish species tend to be lower than at temperate latitudes. Furthermore, I suggest that environmental disturbances that limit survival of larval fish, such as catastrophic oil spills and climate change, have the potential to substantially impact reproductive success of brown pelicans by reducing the availability of numerous small prey in subsequent breeding seasons.

Introduction

The ability of marine top predators to survive and reproduce depends primarily on the production of sufficient food resources at lower trophic levels to meet the energetic requirements of both adults and young (Frederiksen *et al.* 2006). Both the quantity and quality of available prey can influence survival, reproduction, and population dynamics in apex predators, and the Nutritional Stress Hypothesis (NSH) posits that reductions in either prey availability or quality can affect demographic parameters (Trites and

Donnelly 2003, Jodice *et al.* 2006, Hjernquist and Hjernquist 2010). However, a switch to nutrient-poor prey may cause reduced fitness even if abundant prey is available (Rosen and Trites 2000). This observation has given rise to the Junk Food Hypothesis (JFH), which posits that prey quality is the ultimate driver of demographic parameters, regardless of availability (Österblom *et al.* 2008). Both experimental (Rosen and Trites 2004, Romano *et al.* 2006) and field (Golet *et al.* 2000, Kadin *et al.* 2012, Cohen *et al.* 2014) studies have found that switching high-lipid prey for lower-energy alternatives can result in measurable reductions in breeding parameters, even when the amount and rate of delivery are unchanged. Most of the support for JFH comes from cold-water systems, where prey species are likely to have higher lipid reserves on average than warm-water species (Stickney and Torres 1989). Few data are available from tropical systems (waters $\geq$ 23°C average temperature: Ballance and Pitman 1999), in which the relatively low variation in lipid levels among fish species may reduce the range of energetic values in prey species available to top predators.

Even in a prey community with limited interspecific variation in energy density, however, differences in prey quality may still exist. Optimal foraging theory (MacArthur and Pianka 1966) takes into account not only the energy a predator obtains from prey, but also the energy it expends in finding, capturing, handling, and digesting prey. An optimal forager is expected to maximize the net energy gain, calculated as the difference between energy obtained from prey and energy expended in foraging. Thus, differences in both predator foraging strategies and prey behavior could result in variation in the amount of energy predators obtain from different prey types, even among prey species with similar

energy content. Marine predators employ a wide variety of foraging strategies, which allow them to exploit different prey types and forage in different sections of the water column (Ashmole 1971, Spear and Ainley 1998). Tropical seabirds, which are typically limited to foraging near the water's surface, compete for limited prey resources using a variety of capture techniques including skimming, surface-plunging, surface-seizing, plunge-diving, and, occasionally, pursuit-diving (Ballance and Pitman 1999). While the various modifications of surface-feeding techniques allow some partitioning of prey, species at tropical latitudes do not partition prey species as extensively as high-latitude species, which forage at a wider variety of depths and often specialize on different prey items. Thus, the definition of junk food should include not only the energy density of prey but also how readily prey can be captured given the foraging techniques employed by the species of interest. Differences in availability between prey species reflect both abundance, which is an absolute measure, and accessibility, which can differ from predator to predator both within and among species.

Unlike most seabird species, the plunge-diving brown pelican (*Pelecanus occidentalis*) is able to capture and transport a large volume of prey items simultaneously, using a feeding method and jaw morphology more closely analogous to that of rorqual whales (Balaenopteridae) than that of other seabirds (Field *et al.* 2011). While single-prey loaders foraging optimally will act to maximize net energy delivery on an item-by-item basis (*e.g.*, Bugge *et al.* 2011), a species that captures several prey items at a time would optimally seek to maximize the energetic value of the entire prey load. This logically results in a feeding strategy that prioritizes spatial aggregations of prey, even if individual

prey items are of relatively low energetic value, as long as the net energy obtained is greater than the energy available from feeding on less-aggregated resources. Thus, a prey species encountered individually or in small groups might be perceived as inferior by a multiple prey loader, even if the energetic value of individuals of that species is high; conversely, prey that are easily captured in large schools might offer higher net energy gains regardless of their individual energetic value. Indeed, whales tend to specialize on lower-energy prey than do cetacean species that pursue and capture individual prey items (Spitz *et al.* 2012).

Studies of brown pelicans in the tropical waters of the Gulf of Mexico have suggested reliance on a single prey species, Gulf menhaden (*Brevoortia patronus*), which can constitute over 95% of biomass in diet samples in the central northern Gulf (Arthur 1919). The Gulf menhaden is one of the most abundant forage fish species in the region and supports the second-largest in the United States (Vaughan *et al.* 2007). Samples collected from eastern portions of the species' Gulf range, where menhaden are naturally less abundant than in the central and western portions of the Gulf, show a decreasing trend in the predominance of menhaden in pelican diets (Fogarty 1981). Although this suggests that relative availability plays a role in the frequency of menhaden in pelican diets, it is unclear how or whether this underlying variation in diet composition affects demographic parameters, nor how menhaden compares energetically to other available alternatives. Given the role of brown pelicans as an indicator species for assessing the effects of contamination and oil pollution in the region (Shields 2014), understanding

underlying dietary and demographic variation provides a crucial reference point for quantifying the effects of environmental stressors.

Over three years, I assessed the species composition, energy density, mass, nestling provisioning rate, nest productivity, and adult foraging distances of brown pelicans along natural gradients of Gulf menhaden availability in the Eastern and Western Gulf of Mexico. Based on predictions of the Junk Food Hypothesis, I would expect to measure lower nest productivity at colonies with lower overall energy density of prey items, regardless of feeding rates or meal mass. Based on the predictions of the Nutritional Stress Hypothesis, I would expect to find that all three factors contribute to nest productivity. Finally, a relationship between nest productivity and species composition of the diet without an accompanying difference in species-specific energy density would suggest that prey-specific factors other than energy content (*e.g.*, behavior, accessibility) contribute to prey quality, supporting the idea that prey characteristics aside from energy density contribute to perceptions of prey quality by top predators in this system.

Methods

Focal species and study area

The brown pelican is a large-bodied nearshore seabird and one of only two species of pelican to inhabit marine environments year-round (Shields 2014). Pelicans feed on schooling fish by plunge-diving, and can carry large masses of fish (up to 9.6 L total volume or 300% of body volume: Field *et al.* 2011) in a single pouch-load while

feeding nestlings. They nest in large offshore colonies that can number several thousand individuals. Brown pelicans typically lay three sequentially-hatching eggs, which require an incubation period of ca. 30 days, and raise 1-2 young. Although nestlings can fly at ca. 60 days, they generally do not leave the nesting colony until 70-90 days after hatch. Brown pelicans exhibit biparental care and feeding throughout the nesting period. At least one parent attends the nest at all times until chicks are able to thermoregulate and become mobile and (~3-4 weeks), after which point parents are generally present at the nest site only when feeding chicks. Feedings may occur multiple times per day (Sachs and Jodice 2009).

I was primarily interested in the interaction of two species, the brown pelican and the Gulf menhaden; therefore, I chose to focus on brown pelican breeding colonies within the range of Gulf menhaden, which extends along the northern Gulf coast from the Florida Panhandle in the east to the central Texas coast in the west (Figure 5.1). Gulf menhaden spawn offshore during winter, and adults and larvae enter estuaries around February and remain there through October, with juveniles moving offshore into progressively deeper and more saline waters as they grow to adult size (Ahrenholz 1991). Juveniles reach adult size by the end of their first summer and migrate offshore with the adult population in the fall. Juveniles are distributed primarily within the core range of the species in the central northern Gulf, while adults range further to the east and west (Figure 5.1).

Since Gulf menhaden abundance varies throughout the region, I selected sampling locations to represent the underlying range of prey availability. In Year 1 (2013), I

sampled colonies from eastern, central, and western portions of the northern Gulf coast. In Years 2 and 3 (2014-2015), I focused on the western (Corpus Christi Bay to Galveston Bay, TX; Year 2: 2014) and eastern (Mobile Bay, AL to Apalachee Bay, FL; Year 3: 2015) sections of the coast and sampled colonies both within and outside the core range of Gulf menhaden (Figure 5.2).

Diet composition

In Year 1 (2013), I collected meals opportunistically. In years 2-3 (2014-2015), I visited each study colony regularly (every 5-7 days). To obtain meals from nestlings, I selected recently-fed nestlings, based on either having seen a feeding occur or observing that the nestling had a visible bolus or engorged throat. I approached the nest from the colony edge and waited for the nestling to voluntarily regurgitate the meal. If the target nestling did not regurgitate, I selected a different nestling and repeated the process until I had obtained ca. ten complete meals. To limit disturbance to individual nests, I targeted different areas of the colony on subsequent visits; I also varied the time of day at which samples were collected. I collected meals throughout the chick-rearing period, from hatch (late April) through fledging (early August). To limit variation in chick age within each sample, I targeted nestlings at the same stage of feather development, indicating similar hatch dates, and recorded overall nestling age for the sample as estimated from feather growth (*sensu* Walter *et al.* 2013). I did not collect samples from recently-hatched nestlings (one week old or less), both to limit disturbance and because pelican nestlings do not consume whole fish until several days after hatch (Sachs and Jodice 2006).

Additionally, since nestlings regurgitated food less readily as they reached adult size, I were not able to sample chicks older than approximately ten weeks of age. Samples were stored frozen until analysis.

In the laboratory, I thawed each sample in a warm-water bath, removed it from plastic, dried off surface water using paper towels, then weighed, measured, and identified to species each individual fish. Species identifications were based on descriptions in McEachran and Fechhelm (2010). I also classified each fish as whole (no visible damage), partial-whole (total or standard length obtained, but some soft tissues missing), and partial (length could not be obtained). For samples containing large numbers (50-1000) of small fish of the same species (26% of samples), I counted the total number of individuals of the species, weighed and measured a subsample of ten individual fish, and obtained a total weight and overall classification (whole, partial-whole, partial) for each species group. For samples containing extremely large numbers (> 1000) of small fish (<1% of samples), I weighed and measured a subsample of ten fish per species, weighed the overall sample, and used the average weight per fish to approximate the total number of fish in the sample. For samples in which individual fish were no longer intact, I counted the number of heads and tails present in the sample and used the larger of the two numbers as an approximate count. I did not analyze samples for which the digestive process was too advanced to identify fish to species (< 1% of all samples collected).

Where needed, I corrected standard lengths of fish to total lengths using the best-fitting regression equation between standard and total length for that species calculated

from whole samples (Table 5.S1). To estimate the mass of partial-whole and partial fish, I calculated the length-weight relationship as the best-fitting regression equation between log total length and log mass of whole fish for each species by year (Table 5.S1). For partial-whole fish (*i.e.*, degraded fish for which I was able to measure total length), I used the regression line to estimate the corrected mass of the whole fish from its length. For partial fish (*i.e.*, degraded fish for which total length was not measurable), I used the mean total length of whole and partial-whole individuals collected from the same breeding colony on the same day to estimate a corrected mass from the regression equation. Finally, I totaled the corrected masses of individual fish within each meal to obtain a total corrected meal mass.

Meal delivery rate

To assess meal delivery rates, I conducted 3-hour nest observations during each colony visit throughout the chick-rearing period (*i.e.*, every 5-7 days from hatch through fledging, late April to early August). I selected groups of 15-20 nests, varying both the location within the colony and the time of day of observations. During each three-hour period, I recorded all direct feedings in which a nestling's head enters an adult's throat and the nestling's throat is subsequently engorged. Indirect feedings (Sachs and Jodice 2009) appeared to take place only within the first few days after hatch. Since chicks are brooded by adults during this time and are hidden from view, the frequency of such feedings is difficult to quantify; thus I excluded recently-hatched nests from observation.

I calculated meal delivery rates on a per-nest basis. This measure reflects the rate of provisioning by adults, but not necessarily the rate at which each individual nestling consumes food. Pelicans can raise up to three young, hence meals delivered to a nest may be shared among as many as three nestlings. However, each nestling may not receive an equal share, since nestlings that hatch earlier can often consume a larger share of feedings based on superior competitive ability (larger body size, more advanced muscle development and mobility) or preferential feeding by adults. Since I was not able to consistently distinguish first, second, and third-hatched chicks in the field throughout the extended chick-rearing period and subsequently allocate feedings to individual chicks, I chose to assess delivery rates by nest with number of chicks as a covariate. I standardized delivery rates to a 15-hour day, representing the average day length (civil twilight) during the study period. Pelicans are visual foragers and are considered not to forage at night (Shields 2014), and my observations also suggest that adult activity diminishes shortly after sunset.

Energy density of meals

I measured proximate composition and energy density of common prey species using methods as described by Anthony *et al.* (2000). Briefly, I dried fish to a stable mass in a 60° C oven and homogenized samples using a mortar and pestle. I then extracted lipids from the sample using a Soxhlet apparatus with a 7:2 (v:v) hexane: isopropyl alcohol solvent. Following the 10-hour extraction, the sample was left to dry for 24 hours and re-weighed to determine lean mass. I then extracted proteins from the sample by

ashing at 600° C for 12 hours. The mass of the remaining skeletal ash was subtracted from the pre-ashing mass to determine the ash-free lean dry mass, which is composed primarily of proteins (94%: Anthony *et al.* 2000). I then multiplied the lipid and protein contents by standard energetic values based on their relative assimilation efficiencies (lipids: 39.5 kJ/g; proteins: 17.8 kJ/g: Schmidt-Nielsen 1997) to obtain the overall energy density of the sample.

I measured energy densities in both regurgitated fish identified as whole during processing and bait fish purchased live or freshly-caught from fishing suppliers close to study colonies. For the three most common prey species (Gulf menhaden, Atlantic croaker *Micropogonius undulatus*, and pinfish *Lagodon rhomboides*), I ran ANOVAs to determine whether energy content differed between regions or sample types (bait fish vs. regurgitated fish). Because energy values for one of the three species, Atlantic croaker, differed significantly between the eastern and western regions (Table 5.1), I chose to calculate energy densities separately for the two regions where possible. However, I did not find differences in energy content between bait and regurgitated samples, and therefore combined all samples within each region during further analysis. One species, Gulf menhaden, had an apparent difference in energy content between bait samples and regurgitated fish ($p = 0.056$). In this case, regurgitated fish were higher in energy than bait samples, so I chose to use only regurgitated samples to determine energy content for this species. I also tested for differences in energy density between locations within regions, and over time, in two species (Atlantic croaker and Gulf menhaden) and found that energetic content did not differ within regions and did not change as the season

progressed (Table 5.1). Therefore, I considered energy density of prey to be consistent throughout the breeding season and within each region. Since Gulf menhaden were the only prey species to show a bimodal size distribution, I measured energy content of juveniles (< 110 mm total length: Ahrenholz 1991) and adults (> 110 mm) separately.

To determine meal-specific energy density, I multiplied the total mass of each prey species in the meal by the mean energetic value of that species. For species for which I did not measure energy density directly, I obtained energetic values for the same or closely-related species from published literature (Table 5.2). Species for which I was able to directly measure energy content accounted for 93% of total biomass, while species for which I inferred values from closely-related species measured directly (4%) and values obtained from scientific literature (3%) constituted the remaining 7%. I then summed the energy derived from each individual species and divided by the total meal mass to obtain an energetic value (kJ g^{-1}) for the full meal. I calculated meal-specific lipid content using the same process.

Fledging success

In Years 2 and 3 (2014-2015), I visited nesting colonies close to the end of the incubation period and selected 3-4 groups of focal nests per colony, each group containing 20-30 nests. In colonies containing both elevated and ground nests, I selected closely-spaced groups such that each contained nests of one type or the other to allow for comparison. On my initial visit, I recorded nest contents, assigned an identifying number to each nest, and photographed the nest group from marked observation points that could

be accessed without disturbance to focal nests. On return visits, I identified nests using the numbered photograph and checked the contents of each nest from the observation point. Once nestlings reached 3-4 weeks of age, concurrent with measurements and feather sampling, I banded nestlings on the left tarsus with a permanent plastic band (Haggie Engraving, MD: 2014 – Green; 2015 – Blue) engraved with a unique three-digit white alphanumeric code.

Once nestlings began to disperse away from nest locations, I searched the surrounding areas of the colony with binoculars for banded chicks and recorded all bands observed. I continued observations until chicks reached at least 60 days of age. Beginning approximately 8 weeks after hatch, I also conducted regular searches of the colony for dead banded chicks and recovered all bands found. To determine apparent fledging success (fledglings $nest^{-1}$), nestlings that were observed alive at least 60 days after hatch and disappeared from the colony, but were not found dead, were presumed to have successfully fledged (Shields 2014). I calculated plot- and colony-wide fledge success as the number of chicks fledged from observation nests, divided by the total number of nests observed. Since detectability of fledglings is high in this species and habitat, I considered this method to accurately represent overall fledging success.

Statistical modeling

To assess nutritional stress by colony, I compared values of meal mass (g $meal^{-1}$), nest-specific provisioning rate (meals $nest^{-1}$ $hour^{-1}$), and energy density of meals (kJ g-1) for each colony using ANOVAs with post-hoc Tukey's Honestly Significant Difference

(HSD) tests. The product of these three components is the energy provisioning rate (EPR: g nest^{-1} hour^{-1}, Jodice *et al.* 2006). To obtain a combined measure of EPR by colony, I modeled energy-days for each colony, similarly to Jodice *et al.* (2006), by randomly selecting (with replacement) 100 values for provisioning rate (meals day^{-1}) from the set of measured values. The model then chose at random (with replacement) a mass and an energetic value for each meal, multiplied meal mass by energy density to obtain total energy content per meal, and summed total energy across all meals for each modeled day to obtain a set of energy provisioning rates (kJ day^{-1}). I calculated the mean and standard deviation of EPR for each colony by averaging values obtained from 1000 runs of the model. I chose to calculate EPR on a per-nest basis rather than a per-chick basis, to avoid the confounding relationship between higher provisioning rates and increased longevity of second- and third-hatched chicks (Jodice *et al.* 2006). I then evaluated the relationships of individual provisioning metrics to EPR using ANOVAs on nested sequential linear models. Finally, to assess the relationship between species composition and rate of energy delivery to nestlings, I conducted non-metric multidimensional scaling (NMDS) on proportional composition of meals by species, and overlaid provisioning metrics on the resulting ordination.

Results

Diet composition

Over three years, I collected a total of 641 chick meals (Year 1: N = 27; Year 2: N = 423; Year 3: N = 191), containing 98,036 g of prey. I identified 46 prey species

representing 25 families (Table 2). Thirty-six of the prey species represented less than 1% each of biomass collected; of these, 16 species represented less than 0.05% each of biomass collected (Table 5.2). Gulf menhaden was the most common prey species by weight overall, as well as at each individual study site. The proportion of menhaden in total biomass varied by colony, with higher proportions of menhaden closer to the center of the Gulf (Figure 5.2). Other common prey species did not show a consistent pattern of abundance in meals across sites, except for anchovy (*Ancho sp.*, 3 species), which increased from the western to the eastern Gulf (Figure 5.3). The majority of meals (76%) contained a single fish species. 12% contained two species, 5% contained three species, 4% contained four species, and the remaining 3% contained between five and seven species.

Proximate composition and energy density

Energetic content varied by species from 3.3 to 5.5 kJ g^{-1}, averaging 4.38 ± 0.98 kJ g^{-1} wet mass across all samples (Figure 5.4). Protein content of dry mass had low variation across measured samples (M = 76.9 ± 6.4% dry mass, CV = 8%) and correlated weakly with energy density per wet gram of fish (linear model, coefficient = 2.00 ± 0.42, $F_{1,217}$ = 22.3, $p < 0.001$, R^2 = 0.09), while lipid content was variable both between and within species (M = 9.8 ± 7.3% dry mass, range = 2.6 – 16.8, CV = 75%) and was highly correlated with energy density (linear model, coefficient = 0.12 ± 0.03, $F_{1,217}$ = 1929, $p < 0.001$, R^2 = 0.90). Species-specific mean lipid content ranged from 2.6 to 20.3% dry mass, with mean values for most species falling between 3 – 14%. Total length of prey

fish was positively correlated with, but weakly explained, energy density per gram wet mass of fish (linear model, coefficient = 0.004 ± 0.006, $F_{1,217} = 29.1$, $p < 0.001$, $R^2 = 0.12$). First-year menhaden had significantly lower energy densities and lower lipid content than adult menhaden in both sampling regions (ANOVAs: Western, total energy: $F_{1,50} = 5.96$, $p = 0.02$, percent lipids: $F_{1,50} = 4.59$, $p = 0.04$,; Eastern, total energy: $F_{1,8} = 6.25$, $p = 0.04$, percent lipids: $F_{1,8} = 7.18$, $p = 0.03$) (Figure 5.4).

Biomass and energy provisioning rates

Average meal mass, meal delivery rate, and energy density of meals varied significantly among colony sites, but not did not show a consistent pattern between regions (Figure 5.5). The two biomass components of EPR, feeding frequency (meals nest^{-1} day^{-1}, $M = 4.32$, $N = 137$) and meal mass (g meal^{-1}, $M = 157.6$, $N = 583$) had similarly high levels of overall variation (CV frequency = 0.67; CV mass = 0.76), while energy density of meals (kJ g^{-1}, $M = 4.34$, $N = 583$) was less variable (CV = 0.10). Relative to range-wide averages, individual colony sites showed a generally opposing pattern between meal mass and meal delivery rates (Figure 5.6a). Colonies with below-average meal delivery rates tended to have above-average meal masses, and conversely. Energy densities followed a similar pattern to meal masses, but did not deviate more than 10% from the overall mean. Site-specific variation in all three provisioning metrics tended to covary (Figure 5.6b), with below-average variability toward the central and eastern Gulf and higher variability in the west.

Mean biomass provisioning rate (BPR) to nests varied by colony from 454 ± 294 to 1106 ± 587 g day^{-1} (Figure 5.7). Mean energy provisioning rate (EPR) varied by colony from 1977 to 4876 kJ day^{-1}. BPR and EPR were highly correlated (linear model: coefficient = 4.48 ± 0.34, $F_{1,5} = 168$, $p < 0.001$) and increased from west to east with the exception of the easternmost colony, Smith Island. Of the individual provisioning covariates measured at each colony, meal delivery rate alone explained 38% of variance in energy provisioning rate, followed by meal mass (24%) and energy density of meals (1%). Both feeding frequency and meal mass improved model fit when added sequentially to the intercept-only model, but adding energy density did not significantly improve the fit of the model (Table 5.4).

Meal delivery rates increased with increasing proportions of menhaden and anchovy, which were also associated with decreasing energy density of meals (Figure 5.8a). By comparison, meals containing higher proportions of spot (*Leiostomus xanthurus*), croaker, and pinfish were associated with lower delivery rates and higher energy densities (Figure 5.8b-d). Meal masses were highest for meals containing striped mullet (*Mugil cephalus*) or Atlantic cutlassfish (*Trichiurus lepturus*) and lowest for meals containing anchovies (Figure 5.8c). The proportion of biomass represented by small size-class fish (< 110 mm total length) at individual colonies correlated to feeding frequency (linear model: $F_{1,5} = 7.18$, $p = 0.04$, $R^2 = 0.59$, coefficient = 0.108 ± 0.04) but not to meal mass (linear model: $F_{1,5} = 0.16$, $p = 0.7$) or energy density (linear model: $F_{1,5} = 1.82$, $p = 0.24$).

Fledging success

Average fledging success (chicks nest^{-1}) was strongly correlated to mean energy provisioning rate at the colony level (Figure 5.9). Of the individual components of EPR, feeding frequency explained the largest portion of variance in nest productivity (49%, null deviance = 1.397, residual deviance = 0.714), followed by meal mass (15%, residual deviance = 1.181) and energy density of meals (0.1%, residual deviance = 1.395). Both feeding frequency and meal mass significantly improved the fit of a null model for average fledging success by colony, while energy density did not improve model fit (Table 4). Diet composition (% menhaden) did not correlate to fledging success (linear model, $F_{1,5} = 0.89$; $p = 0.39$).

Discussion

The Junk Food Hypothesis (Österblom *et al.* 2008) makes three key assumptions: first, energy content varies sufficiently between prey species to make some species significantly higher-quality than others; second, differences in energy intake for predators feeding on different prey species result primarily from interspecific differences in energetic content; and third, population-level demographic patterns are driven primarily by the energetic content of prey regardless of their availability. I will examine these assumptions in turn in the context of brown pelicans provisioning nestlings in tropical waters of the northern Gulf of Mexico.

Energetic content of prey items varied within a narrow range, with energy densities of most measured species falling between 3 and 5 kJ g^{-1} wet mass. Compared to

results from previous work in temperate and polar systems (*e.g.* van Pelt *et al.* 1997, Anthony *et al.* 2000, Meynier *et al.* 2008), average energetic content of fish species in this study was lower and varied less widely between species. Lipid values in this study, which generally fell between 2 – 14% of dry mass, were considerably lower than lipid values reported from cold-water systems, while protein values were slightly higher (Table 5.5). However, my observations accord with previous work on mesopelagic fish species in the Gulf of Mexico (Stickney and Torres 1989) and the South Atlantic Bight (Jodice *et al.* 2011), which suggest that fish species within the Gulf of Mexico and at similar latitudes along the southeastern coast of the U.S. have relatively higher protein levels, lower lipid reserves, and lower overall energetic values than species at northern and southern latitudes characterized by cooler oceanic temperatures and higher interseasonal variability. Overall energy density of prey items increased with prey total length, resulting in a higher energetic content per gram for larger items; however, this relationship was not consistent within all prey species. Despite the wide longitudinal variation of my sampling area and the variation in prey species composition relative to prey distribution, energetic content of meals fed to pelican chicks varied little between colonies. Furthermore, colony-specific energy provisioning rates closely reflected a combination of meal mass and frequency of meal deliveries (*i.e.*, the BPR), but did not relate to energy content of meals. This suggests that the Junk Food Hypothesis may not be appropriate to describe foraging behavior or population patterns in this region, given that the first two assumptions (significant interspecific variation in prey energy content,

and energy intake values that reflect differences in prey species composition) appear not to apply to brown pelicans this system.

I tested the final assumption (demographic rates are driven by energy content of prey) by relating colony-wide reproductive success to nutritional parameters. I found that biomass provisioning rate (meal mass + meal delivery rate) explained over 90% of variation in nest productivity, while energy density of meals alone did not relate to fledging rates. The fact that nestling mortality due to predation is limited in this system (Walter *et al.* 2013) further supports my observation that most of the variation in fledging success can be explained by provisioning metrics alone. It is interesting to note the apparently opposing relationship between meal delivery rates and meal mass, the two primary drivers of nest productivity. In general, as meal delivery rates increased, meal masses decreased on a colony-wide basis. The relative magnitude of variation in these two metrics provides a useful basis for assessing how foraging conditions and strategies differ from site to site, indicating that there may be a trade-off between prey load maximization and time spent foraging.

While meal mass and delivery rates are clearly correlated to fledging success, the lack of a relationship between energy density of meals and nestling survival reinforces that the Junk Food Hypothesis is not supported in this context of existing prey composition. My results are similar to those of several previous studies that have found biomass provisioning metrics to be considerably better predictors of fledging success than energetic content of food items (*e.g.* Jodice *et al.* 2006, Hjernquist and Hjernquist 2010). Österblom *et al.* (2008) suggest that the negative influence of lower-energy food

items is particularly pronounced in certain species of seabirds, especially species specialized to carry single prey items or small masses of prey, species with energetically expensive foraging strategies, and species with low digestive efficiency. Although plunge-diving is energetically demanding, pelicans are able to capture and carry large volumes of prey, which may allow them to buffer the effects of reduced prey quality by increasing prey quantity without minimal added foraging effort. My results additionally suggest that prey communities in warm-water systems such as the Gulf of Mexico present top predators with a limited range of energetic options, which may contribute to the fact that all support for the Junk Food Hypothesis to date has come from cold-water systems at northern latitudes (Österblom *et al.* 2008).

Although brown pelicans in the Gulf of Mexico are presumed to consume primarily Gulf menhaden (Shields 2014), the extent of their dependence on menhaden as a food source has not been studied in detail across the region. I found that Gulf menhaden was the most common prey species by mass at all colony sites; however, its prevalence in pelican diets varied among sites. Menhaden constituted 60 – 84% of pelican nestling diets in colonies at the core of its range, (*i.e.*, the central northern Gulf of Mexico) but less than 40% of diets in colonies at the eastern and western margins of its range. Similarly, first-year menhaden (individuals hatched during the previous winter), which are confined primarily to estuaries in the central Gulf during summer months (Ahrenholz 1991), represented 56% of nestling pelican diets at the colony closest to the core of their range and 3% or less outside the range margins. These results support previous observations of the importance of menhaden in brown pelican diets (*e.g.*, Arthur 1919, Fogarty *et al.*

1981); however, they also indicate that the proportions of menhaden consumed by pelicans vary depending on underlying distribution and inferred availability. Where menhaden are naturally less prevalent, other prey species, principally anchovy, spot, croaker, and pinfish, contribute more significantly to nestling diets. Both among study colonies and more generally, pelican colony size tended to follow a similar trend to menhaden proportion in diets. While colonies with higher proportions of non-menhaden species did not experience reduced nest productivity, it is important to note that colonies located at the range margins or outside the core range of Gulf menhaden were generally smaller than those located closer to the center of the range by several orders of magnitude.

The factors driving productivity rates, meal delivery rate and meal mass, do not explicitly account for differences in species composition between meals; however, both parameters reflect the availability and accessibility of prey within foraging range to the colony, which varies by species. I examined how these parameters vary across diet composition and found that they do not covary. Higher percentages of menhaden, Atlantic thread herring (*Opisthonema oglinum*), and anchovies (order Clupeiformes) in nestling diets were related to both higher provisioning rates and generally lower meal masses, while species including spot, croaker, and pinfish (order Perciformes) corresponded to lower feeding rates and moderate meal masses. Clupeiformes are typically schooling fish and occur in large aggregations in clear and relatively shallow water, while Sciaenidae, the family to which most of the Perciformes observed in pelican diets belong, are bottom-dwellers that do not school and avoid waters where visibility is

high (Nelson 1994). For a multiple-prey loader that can capture several prey items at once, targeting highly concentrated prey resources regardless of energetic content could be a means of maximizing biomass delivery. The prevalence of juvenile menhaden, which form schools in shallow estuarine waters but move offshore as they grow to adult size (Ahrenholz 1991), suggests that pelicans target accessible prey aggregations without regard for energetic content, since first-year menhaden were among the least energy-rich prey items observed in both the northeastern and northwestern regions of the Gulf. Overall, I found that the proportion of diet biomass composed of small fish, including both juvenile stages of larger species and species with mature size less than 110 mm total length, correlated positively with meal delivery rates but did not correspond to reduced meal masses, indicating that small prey items can be captured at a higher frequency without reducing biomass. Large-bodied species such as striped mullet were associated with the highest meal masses I observed, although given the infrequency of these species in nestling pelican diets it is difficult to determine the role they play in overall provisioning.

The potential importance of high-availability, lower-energy prey, such as young-of-the-year menhaden, to brown pelican reproductive output is of potential conservation interest. Recruitment rates in Gulf menhaden are highly sensitive to temperature and precipitation, with warmer and wetter winters producing comparatively fewer recruits in the next year class (Deegan 1990). Given that winter temperatures and precipitation are expected to rise under current climate change projections (Biasutti *et al.* 2012), the availability of larval fish (*e.g.*, Muhling *et al.* 2010) could become more limited or more

variable in future climactic conditions. Additionally, pollution events such as the 2010 *Deepwater Horizon* oil spill significantly depress larval fish survival (Incardona *et al.* 2014) and could have indirect effects on prey dynamics that compound the direct effects of oil exposure to predators.

My study suggests that in this system, energetic content of prey does not vary sufficiently for differences in species composition to directly impact demographic rates through their effects on energy provisioning, as posited by the Junk Food Hypothesis. I found a strong correspondence between biomass provisioning rates, energy provisioning rates, and nest productivity, suggesting that the amount, rather than the type, of food delivered to brown pelican nestlings predicts their survival to fledging. Tropical marine systems have thus far been underrepresented in tests of the relative influence of prey quality and prey quantity on the demographics of marine top predators, and many features of this system, particularly the moderate energetic values and limited variation in energy content of common prey species, are likely to exist elsewhere in warm-water tropical and subtropical systems. In similar contexts, an understanding of comparative prey quality that incorporates behavior, accessibility, and spatial distribution, in addition to energetic content, would have greater power to explain the relationship between diet composition and demography of marine predators.

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Table 5.1. Results of ANOVAs comparing measured energy densities of three common prey species between sample types (bait vs. regurgitated), sampling dates, and sampling locations.

	Between sample types		Between regions		Within regions		Seasonal	
	P	F (df)	p	F (df)	p	F (df)	p	F (df)
Micropogonius undulatus	0.95	0.43 (1,37)	**< 0.001**	**51.3 (1,39)**	0.29	1.29 (2,30)	0.65	0.21 (1,37)
Lagodon rhomboids	0.31	1.20 (1,7)	0.97	0.01 (1,18)	n/a	n/a	n/a	n/a
Brevoortia patronus	0.06	3.86 (1,37)	0.37	0.81 (1,34)	0.13	2.24 (2,25)	0.72	0.13 (1,37)

Table 5.2. Fish species occurring in the diets of brown pelican chicks in the northern Gulf of Mexico, 2013-2015. An asterisk (*) in the biomass column denotes less than 0.05% of total biomass.

Order	Family	Species	Common name	Year	% biomass
Atheriniformes	Atherinidae	*Menidia beryllina*	Inland silverside	1,2,3	0.1
Aulopiformes	Synodontinae	*Sybodus foetens*	Inshore lizardfish	1,2	*
Beloniformes	Belonidae	*Tylosurus crocodilus*	Houndfish	3	*
	Hemiramphidae	*Hemiramphus brasiliensis*	Ballyhoo halfbeak	1,2	0.1
Clupeiformes	Clupeidae	*Brevoortia patronus*	Gulf menhaden	1,2,3	61.0
		Harengula jaguana	Scaled sardine	1	0.3
		Opisthonema oglinum	Atlantic threadfin herring	2,3	1.7
	Engraulidae	*Anchoa hepsetus*	Striped anchovy	2,3	1.5
		Anchoa lyolepis	Dusky anchovy	3	2.2
		Anchoa mitchilli	Bay anchovy	1,2,3	7.5
Cyprinodontiformes	Cyprinodontidae	*Cyprinodon variegatus*	Sheepshead minnow	2	0.2
		Fundulus majalis	Striped killifish	2	*
Decapoda	Penaeidae	*Farfantepenaeus duorarum*	Pink shrimp	2,3	*
Mugiliformes	Mugilidae	*Mugil cephalus*	Striped mullet	2,3	4.8
Perciformes	Carangidae	*Caranx crysos*	Blue runner	1	0.1
		Chloroscombrus chrysurus	Atlantic bumper	1,2,3	0.6
		Decapterus punctatus	Round scad	3	0.1
		Hemicaranx amblyrhynchus	Bluntnose jack	2	*
		Selene setapinnis	Atlantic moonfish	2	*
	Gobiidae	*Gobioides broussonetii*	Violet goby	2	*
	Haemulidae	*Orthopristis chrysoptera*	Pigfish	1,2	*
	Lutjanidae	*Lutjanus campechanus*	Red snapper	15	0.3
	Sciaenidae	*Bairdiella chrysoura*	Silver perch	1,2	0.4
		Cynoscion arenarius	Sand seatrout	2,3	1.2

Order	Family	Species	Common name	Year	% biomass
Perciformes (cont.)	Sciaenidae (cont.)	*Cynoscion nebulosus*	Spotted seatrout	2,3	1.1
		Larimus fasciatus	Banded drum	2	*
		Leiostomus xanthurus	Spot	1,2,3	2.9
		Menticirrhus americanus	Southern kingfish	2	0.7
		Micropogonias undulatus	Atlantic croaker	1,2,3	3.8
		Sciaenops ocellata	Red drum	2,3	0.5
	Scombridae	*Auxis thazard*	Frigate mackerel	3	0.2
		Scomberomorus cavalla	King mackerel	2	0.1
		Scomberomorus maculatus	Spanish mackerel	2	0.3
	Serranicae	*Diplectrum formosun*	Sand perch	3	0.2
	Sparidae	*Calamus proridens*	Littlehead porgy	1	*
		Lagodon rhomboides	Pinfish	1,2,3	2.4
		Stenotomus caprinus	Longspine porgy	1	*
	Stromateidae	*Peprilus burti*	Gulf butterfish	2,3	0.1
		Peprilus paru	American harvestfish	2	0.1
	Trichiuridae	*Trichiurus lepturus*	Atlantic cutlassfish	1,2,3	3.6
Pleuronectiformes	Cynoglossidae	*Symphurus urospilus*	Spottail tonguefish	3	0.1
	Paralichthyidae	*Citharichthys spilopterus*	Bay whiff	2,3	0.1
Scorpaeniformes	Triglidae	*Prionotus tribulus*	Bighead searobin	2,3	*
Siluriformes	Ariidea	*Bagre marinus*	Gafftopsail catfish	1,2,3	0.3
Tetraodontiformes	Diodontidae	*Diodon holocanthus*	Longspine porcupinefish	2	*
Teuthida	Loliginidae	*Lolligunculla brevis*	Atlantic brief squid	1,3	*
Other			Isopod	3	*
			Bait (chicken)	3	*
			Unknown		1.2

Table 5.3. Regional mean energy density values (kJ g^{-1}) and lipid values (% dry mass) used in calculating energy densities of meals fed to brown pelican nestlings, 2014-2015.

Species	Biomass	% of total	Energy density	% lipids	*N*	Source
Northwestern Gulf of Mexico (Galveston Bay – Corpus Christi Bay, Texas)						
Gulf menhaden	42157	67.2				
Adult	23201	37.0	4.77	13.7	39	1a
First-year	18956	30.2	3.53	4.7	9	1a
Striped mullet	4020	6.4	3.95	6.9	6	1a
Atlantic croaker	2818	4.5	3.75	5.0	39	1a
Atlantic cutlassfish	2798	4.5	5.05	13.9	12	1a
Spot	2260	3.6	4.83	13.5	9	1a
Bay anchovy	1648	2.6	4.12	8.6	20	1b
Pinfish	1065	1.7	4.63	9.6	9	1a
Spotted seatrout	973	1.6	3.48	2.6		Sand seatrout (1a)
Unknown	873	1.4	4.16	2		All samples (1a)
Sand seatrout	787	1.3	3.48	2.6	9	1a
Southern kingfish	638	1.0	4.05	2.6		Sand seatrout (1a)
Red drum	485	0.8	4.54	8.1	1	1a
Silver perch	384	0.6	4.33			Yellow perch (2)
Spanish mackerel	303	0.5	3.60	2.6		3
Gafftopsail catfish	300	0.5	4.95			Flathead catfish (4)
Atlantic bumper	191	0.3	3.60	2.6		Spanish mackerel (3)
Striped anchovy	174	0.3	4.88	10.2	9	1b
Sheepshead minnow	156	0.3	4.21			Gulf killifish (5)
Atlantic harvestfish	145	0.2	3.42	1.6		Atlantic butterfish (6)
Anchovy sp.	80	0.1	4.28	8.4		All anchovies (1b)
King mackerel	65	0.1	3.60	2.6		Spanish mackerel (3)
Ballyhoo halfbeak	51	0.1	3.92	1.2		Black needle (7)
Gulf butterfish	48	0.1	3.42	1.6		Atlantic butterfish (6)
Porcupinefish	43	0.1	4.16	9.3		All samples (1a)

Species	Biomass	% of total	Energy density	% lipids	*N*	Source
Atlantic threadfin herring	42	0.1	5.46	20.3	2	1a
Chicken (bait)	39	0.1	4.60	3.0		8
Pigfish	36	0.1	4.88			9
Pink shrimp	35	0.1	4.16	5.2	4	1a
Violet goby	34	0.1	4.81			Black goby (10)
Bay whiff	13	< 0.05	4.00			Winter flounder (11)
Striped killifish	13	< 0.05	4.21			Gulf killifish (5)
Bighead searobin	13	< 0.05	4.63	3.6		Red searobin (12)
Atlantic moonfish	12	< 0.05	3.60	2.6		Spanish mackerel (3)
Inland silverside	11	< 0.05	4.80			Brook silverside (4)
Inshore lizardfish	11	< 0.05	4.16	9.3		All samples (1a)
Bluntnose jack	10	< 0.05	3.60	2.6		Spanish mackerel (3)
Banded drum	4	< 0.05	4.54	9.3		Red drum (1a)
Sardine sp.	2	< 0.05	5.18	3.61	2	1b
Northeastern Gulf of Mexico (Mobile Bay, Alabama – Apalachee Bay, Florida)						
Gulf menhaden	15817	49.6				
Adult	14985	47.0	4.80	12.7	12	1b
First-year	827	2.6	3.36	4.0	4	1b
Bay anchovy	5052	15.8	4.12	8.6	20	1b
Dusky anchovy	2189	6.9	4.38	5.2	1	1b
Atlantic threadfin herring	1633	5.1	4.67	7.7	6	1b
Striped anchovy	1221	3.8	4.88	10.2	9	1b
Pinfish	1165	3.7	4.65	13.2	12	1a
Atlantic croaker	819	2.6	5.24	16.8	6	1a
Striped mullet	684	2.1	3.95	6.9	8	1b
Atlantic cutlassfish	657	2.1	5.05	13.9	12	1a
Atlantic bumper	394	1.2	3.60	2.6		Spanish mackerel (3)
Sand seatrout	313	1.0	3.48	2.6	9	1a
Red snapper	307	1.0	4.44	3.9		13
Spot	279	0.9	4.83	13.5	9	1a

Species	Biomass	% of total	Energy density	% lipids	*N*	Source
Unknown	268	0.8	4.45	10.7		All samples (1b)
Anchovy sp.	184	0.6	4.36	8.1		All anchovies (1b)
Frigate mackerel	183	0.6	3.60	2.6		Spanish mackerel (3)
Sand perch	150	0.5	4.45	10.7		All samples (1b)
Spotted seatrout	131	0.4	3.48	2.6		Sand seatrout (1a)
Scaled sardine	103	0.3	5.18	11.3	2	1b
Round scad	93	0.3	3.60	2.6		Spanish mackerel (3)
Spottail tonguefish	90	0.3	4.00			Winter flounder (11)
Bay whiff	52	0.2	4.00			Winter flounder (11)
Inshore lizardfish	35	0.1	4.45	10.7		All samples (1b)
Houndfish	23	0.1	3.92			Black needle (7)
Bighead searobin	21	0.1	4.63			Red searobin (12)
Atlantic brief squid	18	0.1	4.25			Squid (10)
Gafftopsail catfish	13	< 0.05	4.95			Flathead catfish (4)
Pink shrimp	5	< 0.05	4.16	5.2	4	1a
Inland silverside	4	< 0.05	4.80			Brook silverside (4)
Gulf butterfish	3	< 0.05	3.42			Atlantic butterfish (6)
Isopod	0.5	< 0.05	2.59			

1) This study (a: Eastern, b: Western); 2) Hartman and Brandt 1995; 3) Jodice *et al.* 2011; 4) Eggleton and Schram 2002; 5) Wedge *et al.* 2015; 6) Roth *et al.* 2008; 7) Fernandes *et al.* 2014; 8) USDA; 9) Adams 1976; 10) Karpouzi 2005; 11) Plante *et al.* 2005; 12) Eder and Lewis 2005; 13) Schwartzkopf 2014

Table 5.4. Nested models for colony-specific mean brown pelican nestling energy provisioning rates and nest productivity based on feeding rate, meal mass, and energy density of meals, northern Gulf of Mexico, 2014-2015. Terms are added sequentially, and a p-value of < 0.05 indicates a significant improvement in fit compared to the previous model.

Terms	Residual df	Residual deviance	df	deviance	F	*p*
Energy provisioning rate						
Intercept only	6	7236805				
+ feeding rate	5	4498564	1	2738240	24.79	0.016
+ meal mass	4	379699	1	4118866	37.3	0.009
+ energy density	3	331316	1	48383	0.44	0.56
Nest productivity						
Intercept only	6	1.397	1			
+ feeding rate	5	0.714	1	0.683	47.83	0.006
+ meal mass	4	0.056	1	0.658	46.12	0.007
+ energy density	3	0.043	1	0.896	0.90	0.41

Table 5.5. Mean energy density and proximate composition values for forage fish species from this study compared to values reported from other regions.

Location	Lipid fraction (% dry mass)		Protein fraction (% dry mass)		Water (% wet mass)		Energy density (kJ g^{-1} wet mass)		Source
	M	(range)	*M*	(range)	*M*	(range)	*M*	(range)	
Gulf of Mexico	9	(3-20)	77	(65-87)	73	(68-77)	4.4	(3.4-5.5)	This study
Gulf of Alaska	18	(3-53)	75	(40-89)	77	(62-87)	5.2	(2.4-8.5)	Anthony *et al.* 2000 Van Pelt *et al.* 1997
Campbell Plateau	17	(3-37)	61	(45-68)	69	(67-80)	6.5	(3.8-8.5)	Meynier *et al.* 2008
Eastern Bering Sea	23	(6-60)	69	(38-85)	78	(65-91)	5.7	(3.4-10.3)	Payne *et al.* 1999
Bay of Biscay	16	(2-36)	67	(25-88)	75	(60-92)	5.4	(0.7-10.2)	Spitz *et al.* 2010

Figure 5.1. Locations of brown pelican colonies (study colonies: white; other: green) and Gulf menhaden range (summer, yellow; winter, blue; filled, major; hatched, minor) (Love *et al.* 2013) in the northern Gulf of Mexico. Dashed outlines represent menhaden egg/larvae distributions (red, summer; blue, winter). Pelican colony marker sizes proportional to colony size during this study (75 – 5000 breeding pairs).

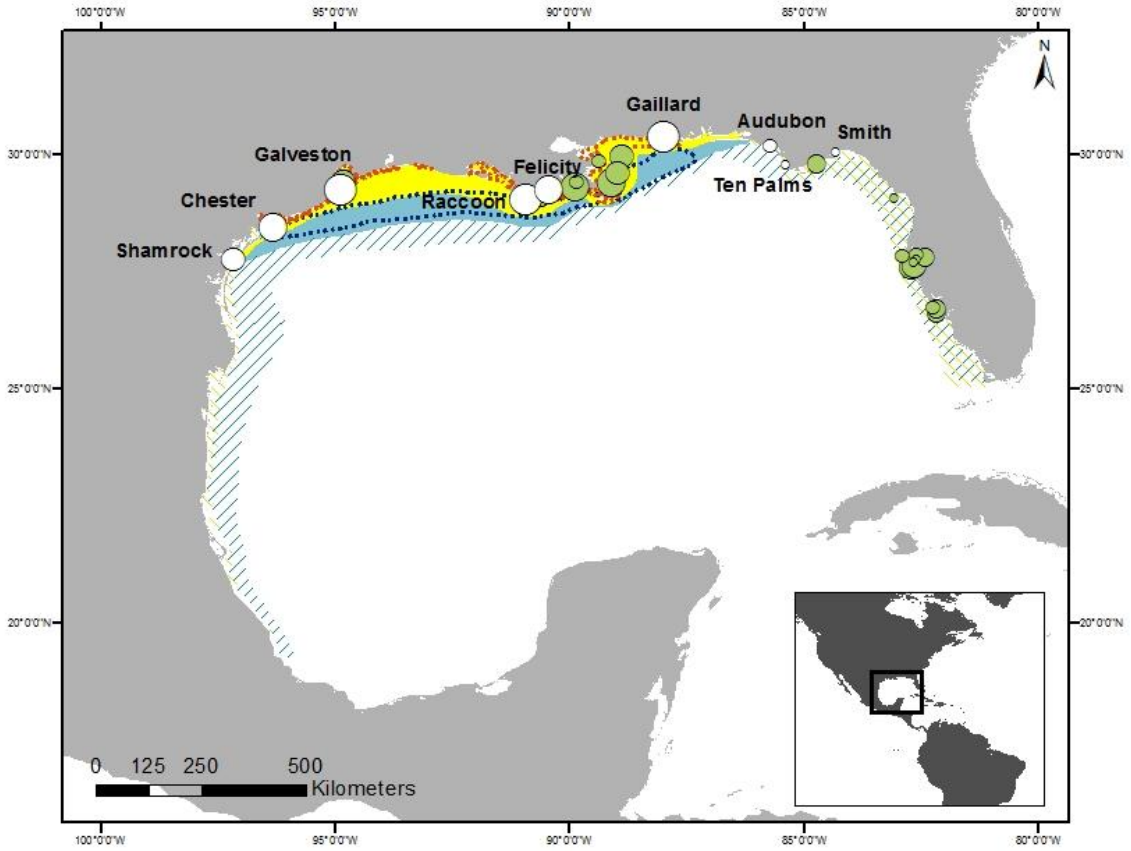


Figure 5.2. Percentage of menhaden in brown pelican chick diets in the northern Gulf of Mexico, 2013-2015. Pies represent the portion by biomass of adult menhaden (dark grey), first-year menhaden (medium grey) and other prey species (light grey) in chick diets. Shaded areas indicate the summer distributions of adult (solid – major; hatched – minor) and first-year (dashed outline) menhaden (Love *et al.* 2013).

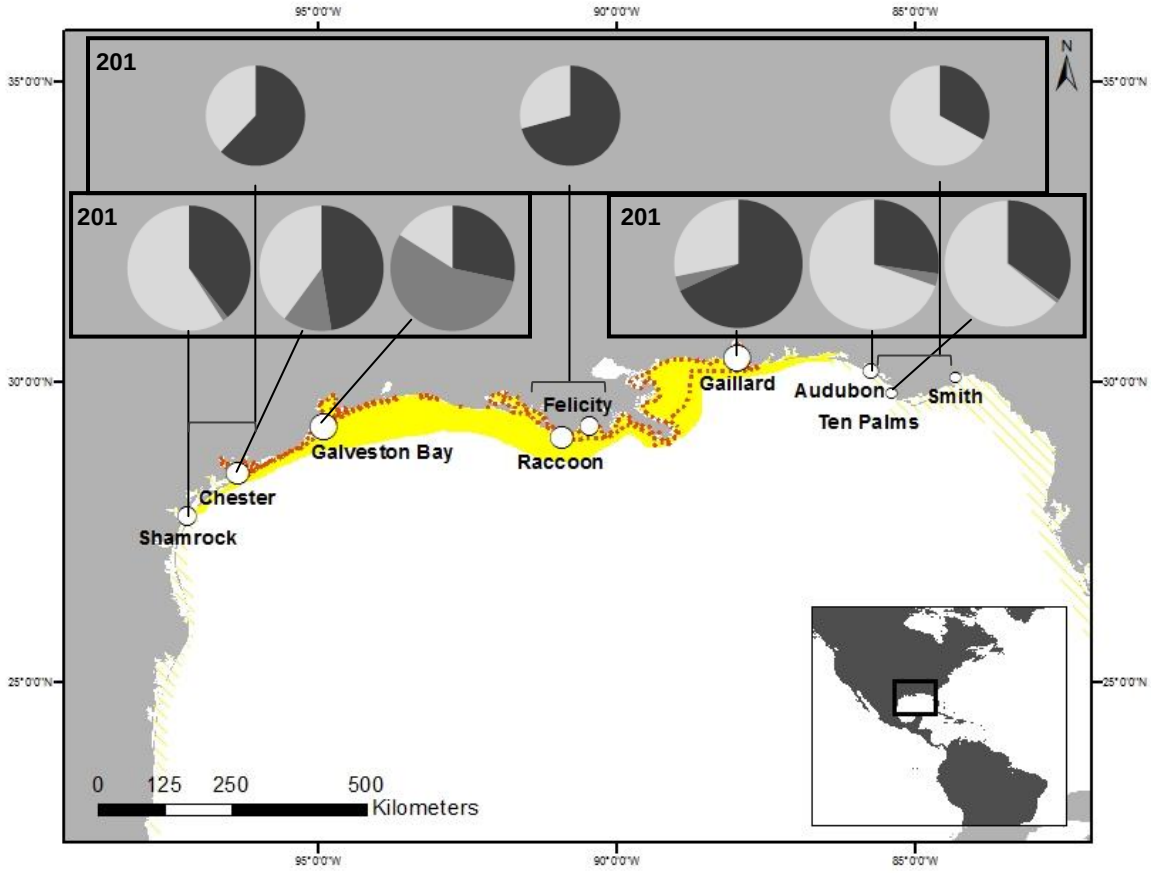
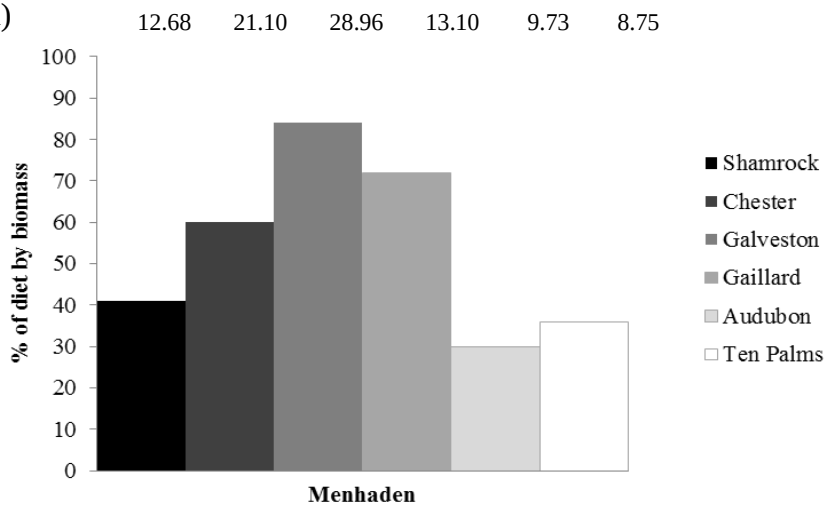


Figure 5.3. Portion of brown pelican nestling diet biomass represented by (a) Gulf menhaden, and (b) other major prey species (*i.e.*, species comprising more than 1% of overall nestling diet biomass collected) in the northern Gulf of Mexico, 2014-2015. Colonies are ordered from westernmost to easternmost. Sample size (total mass of recovered meals, kg) for each colony is listed above panel (a).

(a)



(b)

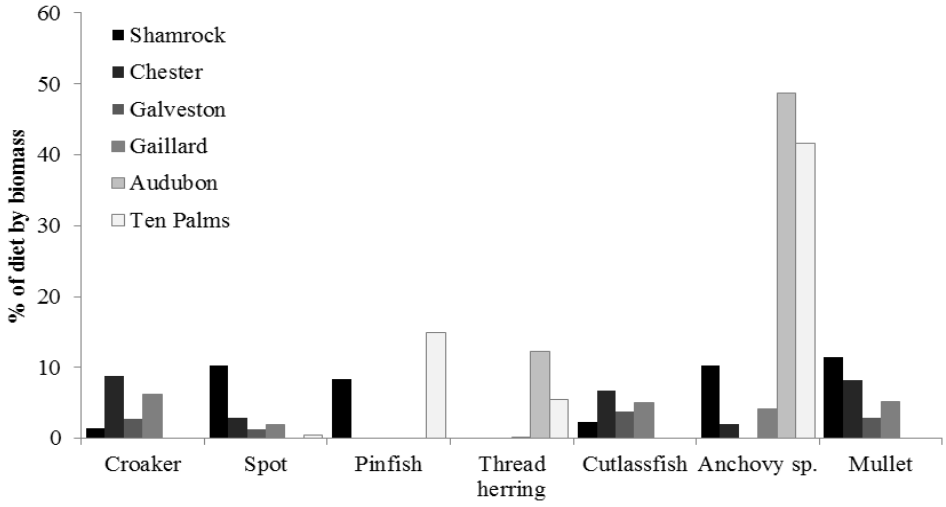


Figure 5.4. Mean energy densities of brown pelican prey species (each > 1% of total biomass) from northwestern (Corpus Christi Bay – Galveston Bay, TX: solid bars) and northeastern Gulf of Mexico (Mobile Bay, AL – Apalachee Bay, FL: patterned bars), 2014-2015. Error bars represent 95% confidence intervals.Sample sizes are listed in parentheses.

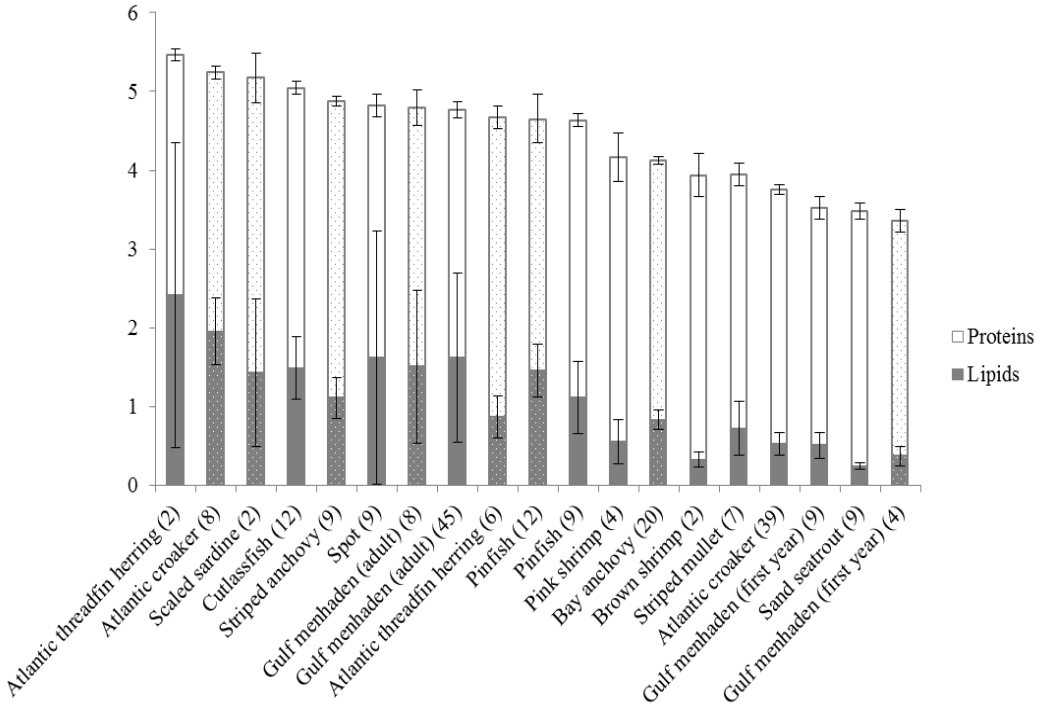


Figure 5.5. Comparison of average (a) meal mass, (b) provisioning rate, and (c) energy density of meals between brown pelican colony sites, northern Gulf of Mexico, 2014-2015. Letters denote Tukey post-hoc groups, error bars are 95% confidence intervals of means, and dashed lines are global mean values.

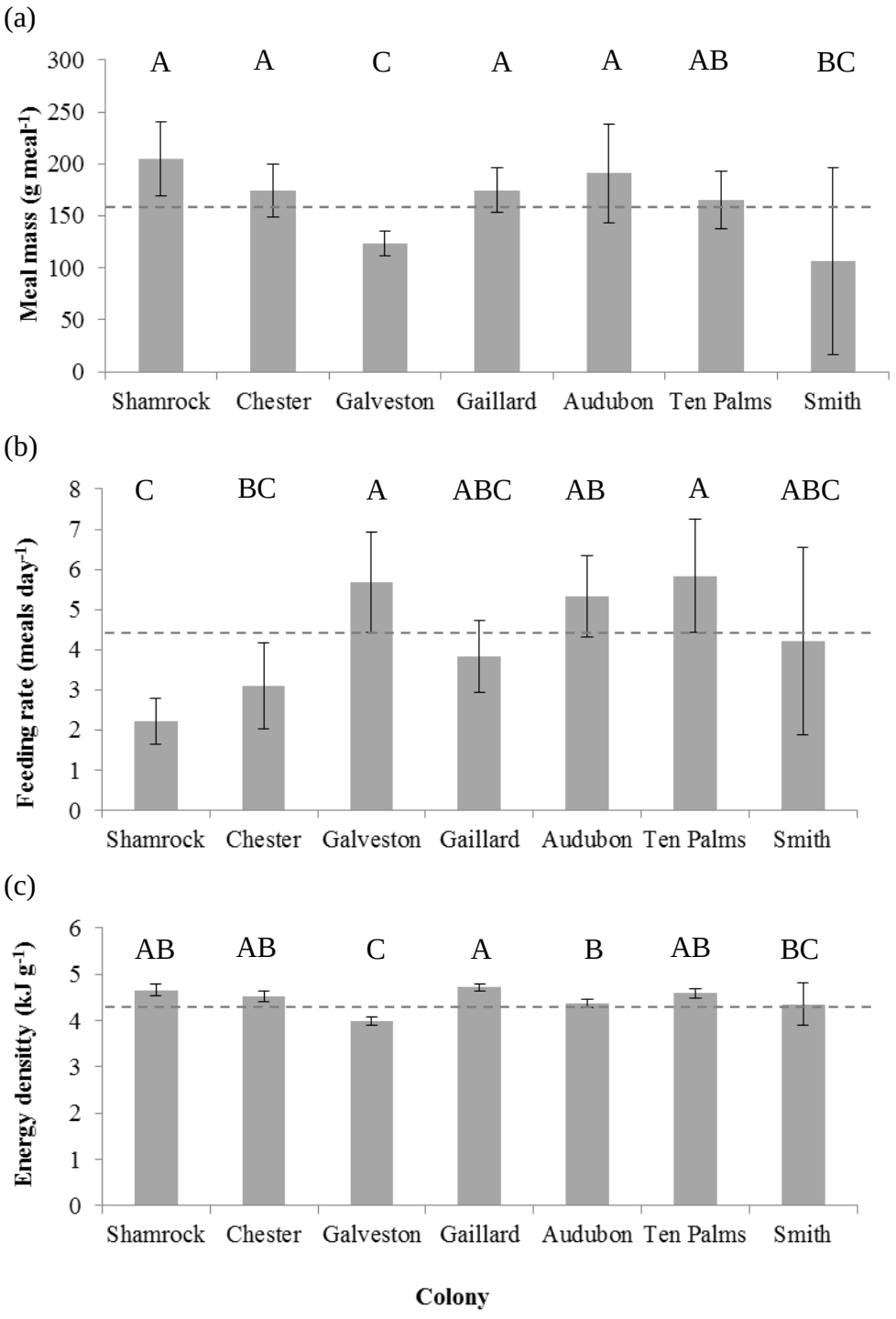
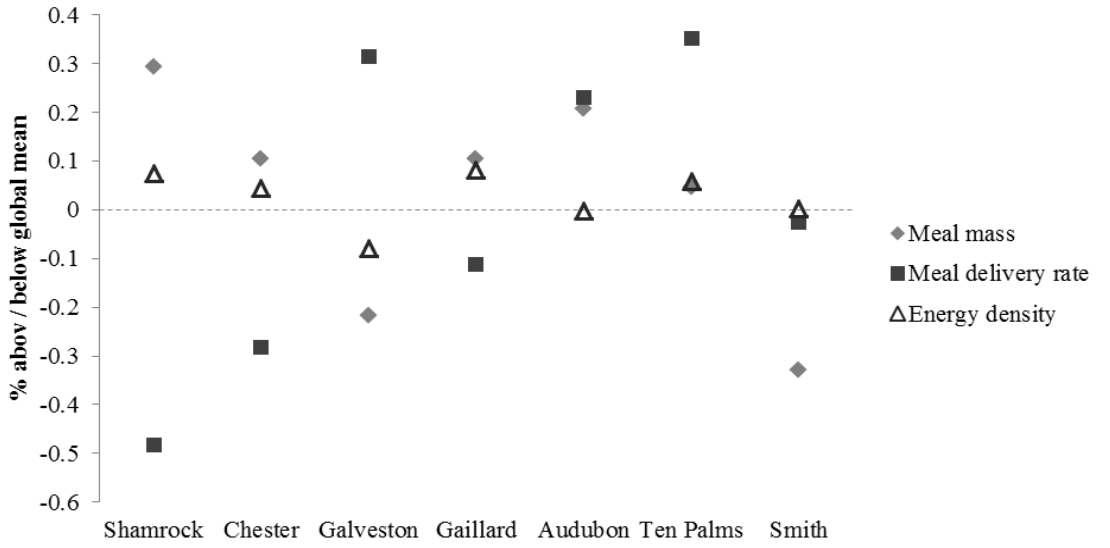


Figure 5.6. Drivers of between-colony variation in (a) mean values of provisioning metrics and (b) coefficients of variation for brown pelican colonies in the northern Gulf of Mexico, 2014-2015. The mean value for each metric across all samples is set at zero, and individual points represent deviation from the global mean (as a percentage of global mean) at that colony site.

(a)



(b)

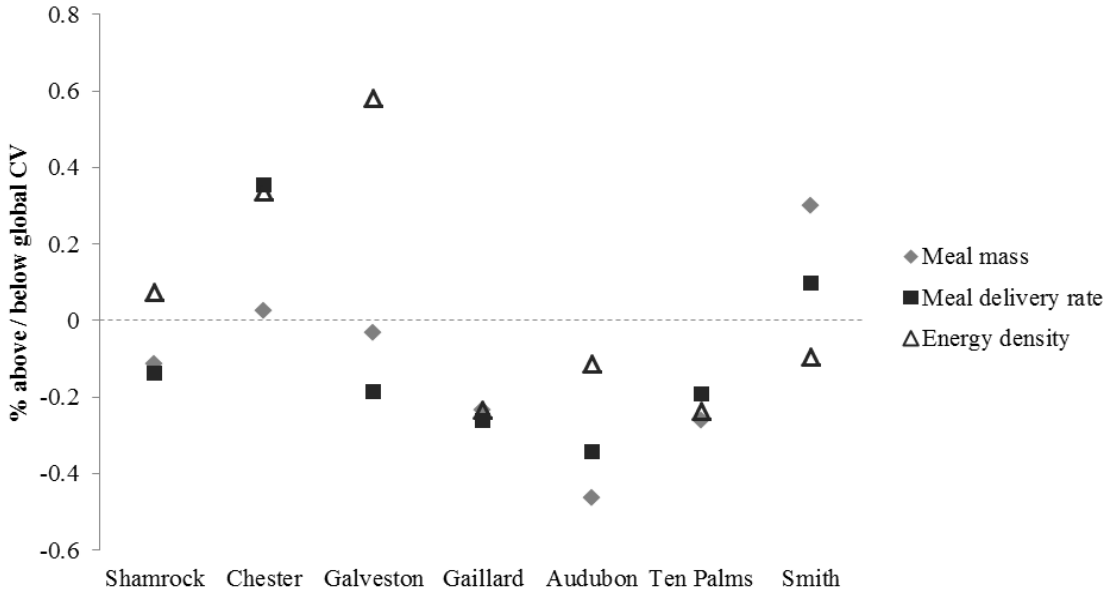
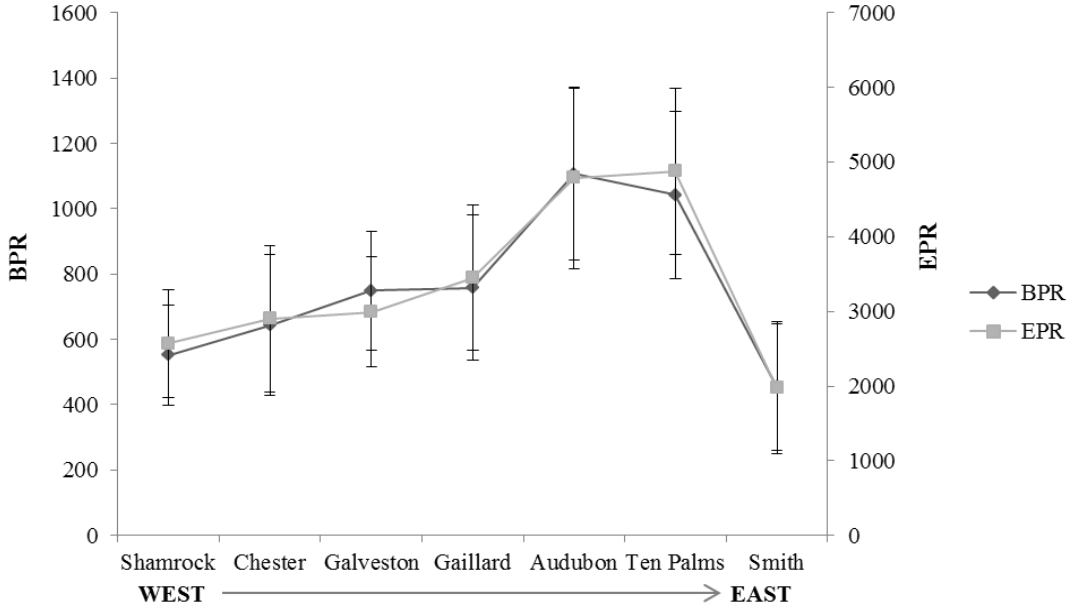


Figure 5.7. Comparison of (a) biomass provisioning rates (BPR:dark grey) and energy provisioning rates (EPR: light grey), and (b) fledging success, at brown pelican colonies across the northern Gulf of Mexico, 2014-2015. Error bars represent 95% confidence intervals.

(a)



(b)

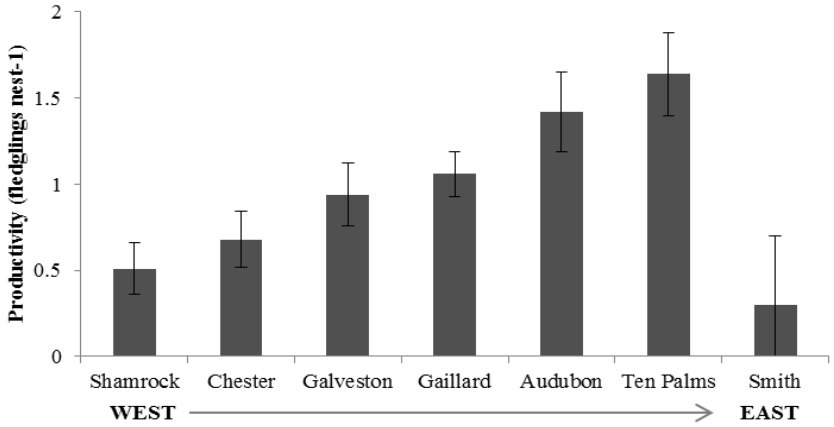


Figure 5.8. Non-metric multidimensional scaling plots showing the distribution of species composition of individual meals (grey dots) collected from brown pelican nestlings in the northern Gulf of Mexico, 2014-2015. (a) includes three components of energy provisioning rate (feeding frequency, MDR; meal mass, MASS; energy density, ED) overlaid as vectors showing increasing values (direction) and strength of association (magnitude); (b-d) are surface plots of the three components of energy provisioning rate (b: MDR, c: mass; d: ED) showing isoclines and direction of increase in ordination space.

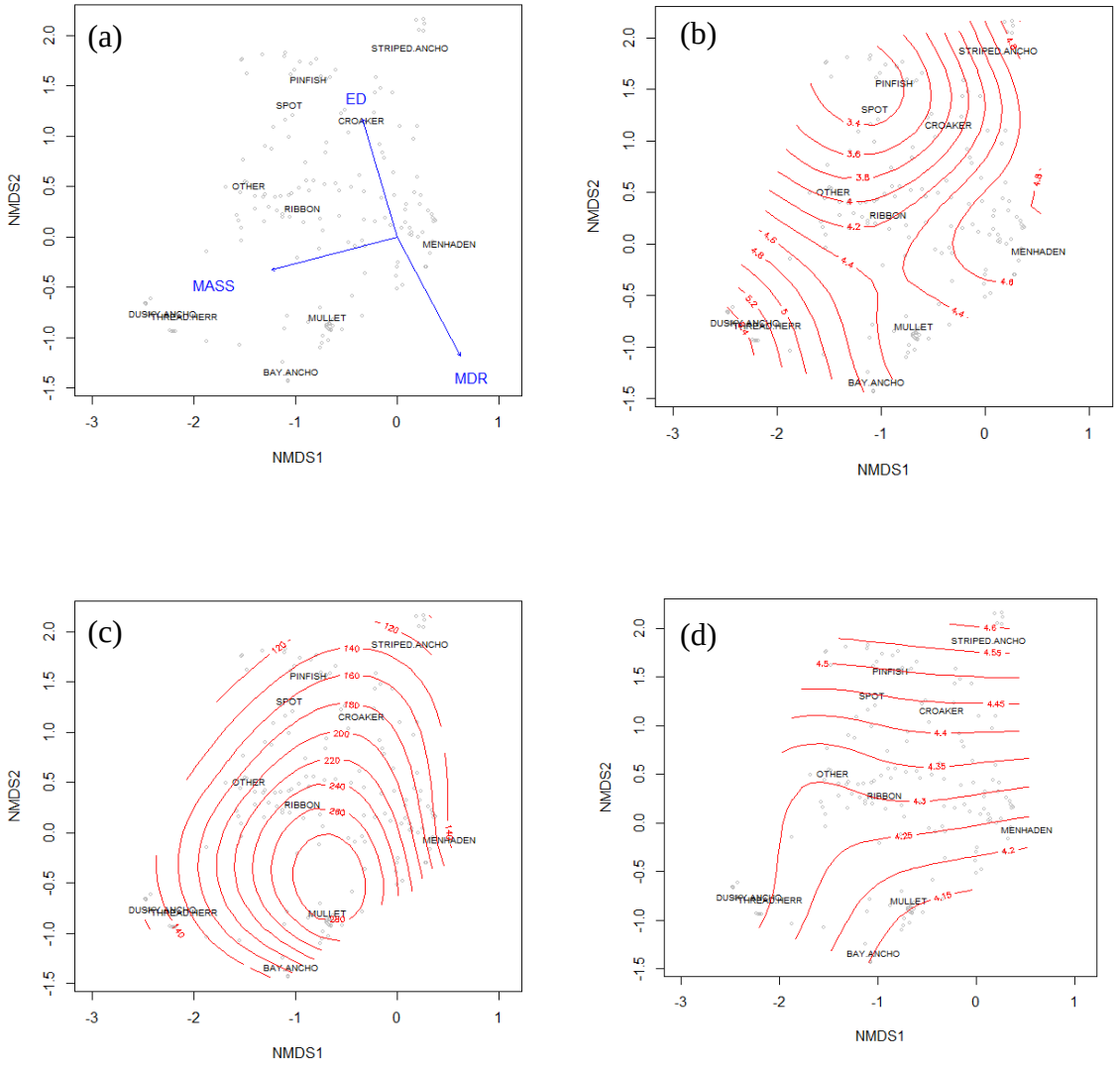
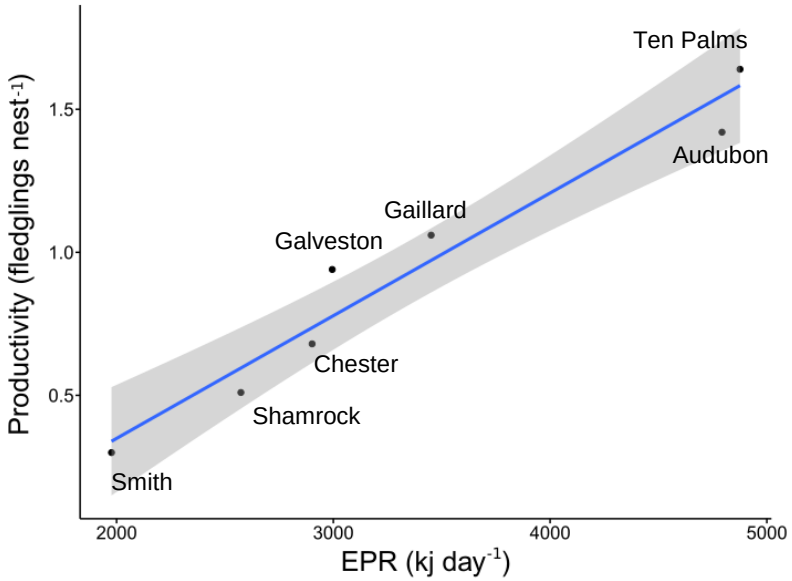


Figure 5.9. Linear relationship between (a) energy provisioning rate and nest productivity (Equation: y = 0.0004 x – 0.508; R^2 = 0.952), and (b) biomass provisioning rate and nest productivity (Equation: y = 0.0019 x – 0.535; R^2 = 0.943) at brown pelican nesting colonies in the northern Gulf of Mexico, 2014-2015. 95% confidence interval of the regression line is shaded.

(a)



(b)

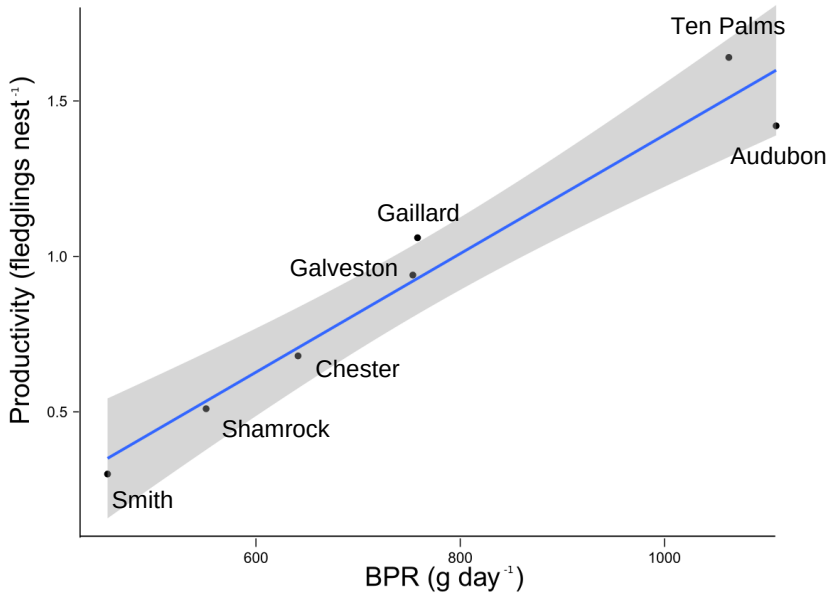


Table 5.S1. Corrections used in calculating mass of partial and damaged samples of common fish species in pelican chick diets, northern Gulf of Mexico, 2013-2015. Equations are derived from intact samples and describe the relationships between standard length (SL) and total length (TL), and between total length and mass (a: Western region; b: Eastern region).

Species		Equation	R^2	p
Standard length (SL) to total length (TL)				
Brevoortia patronus[b]		TL = 1.251 SL + 0.547	0.99	< 0.001
Micropogonius undulatus[b]		TL = 1.167 SL + 6.531	0.99	< 0.001
Leiostoma xanthurus[b]		TL = 1.259 SL – 1.118	1	< 0.001
Lagodon rhomboides[b]		TL = 1.118 SL + 12.029	0.96	< 0.001
Anchoa mitchilli[b]		TL = 1.117 SL + 4.387	0.95	< 0.001
Anchoa lyolepis[b]		TL = 1.192 SL + 0.203	0.96	< 0.001
Anchoa hepsetus[b]		TL = 1.114 SL + 4.060	0.97	< 0.001
Opisthonema oglinum[b]		TL = 1.284 SL – 2.198	1	< 0.001
Total length (TL) to mass				
Brevoortia patronus				
	a	log(mass) = 3.138 log (TL) – 12.233	0.99	<0.001
	b	log(mass) = 3.10 log (TL) – 12.233	0.98	<0.001
Micropogonius undulatus				
	a	log(mass) = 2.926 log (TL) – 11.928	0.83	< 0.001
	b	log(mass) = 2.630 log (TL) – 9.862	0.92	<0.001
Leiostomus xanthurus[a]		log(mass) = 2.976 log (TL) – 11.324	0.98	< 0.001
Lagodon rhomboides[b]		log(mass) = 2.763 log (TL) – 9.980	0.97	<0.001
Anchoa mitchilli[b]		log(mass) = 2.641 log (TL) – 10.470	0.86	<0.001
Anchoa hepsetus[b]		log(mass) = 2.223 log (TL) – 8.603	0.88	<0.001
Opisthonema oglinum[b]		log(mass)= 3.001 log (TL) – 11.553	0.97	<0.001
Trichiurus lepturus[a]		log(mass) = 3.278 log(TL) – 16.051	0.97	< 0.001

CHAPTER SIX

USING INDIVIDUAL MOVEMENT PATTERNS TO EVALUATE BEHAVIORAL STATES, HABITAT ASSOCIATIONS, AND SURFACE POLLUTANT EXPOSURE IN A NEARSHORE SEABIRD

Abstract

Conservation of highly mobile species requires an understanding of habitat requirements and connectivity across a broad, often international landscape. In marine environments, where animal movements usually occur far from land and out of sight, remote tracking data can serve to define not only movement but behavior, refining current understanding of both how individuals are distributed across the landscape and how they interact with landscape features and risk factors. I collected three years of GPS-tracking data from brown pelicans nesting in the northern Gulf of Mexico, and used a Hidden Markov Model to define separate resident behavioral states, defined by slow movement through limited areas of habitat, from transient states in which animals moved quickly across large areas. I then described characteristics of preferred habitat using a marginality analysis of remotely sensed environmental variables. Finally, I weighted locations by behavioral states and overlaid preferred habitat with an index of surface pollution concentration in order to evaluate spatial, temporal, and individual variation in pollutant exposure. I found that pelicans selected similar habitat characteristics, including below-average salinity and above-average primary production, in both resident and transient activity periods throughout the year. Characteristics of occupied habitats varied through the annual cycle, particularly in the north central Gulf. Although previous studies have suggested that nearshore seabirds are influenced by both temperature and

productivity of oceanic waters, salinity is an unusual component of seabird habitat selection and may be driven in this system by an abundance of estuarine-dependent prey. Exposure to surface pollution varied annually, as well as between individuals. During the breeding season, central Gulf breeders were exposed to higher pollution rates than either eastern or western Gulf colonies; however, breeders from different regions overlapped on non-breeding grounds, leading to similar levels of pollution exposure during post-breeding and migratory periods. Males also experienced higher pollution exposure than females during non-breeding. This study offers insight into habitat features selected by nearshore seabirds in a subtropical marine environment, and provides a baseline for determining likelihood of contaminants exposure across a regional metapopulation.

Introduction

Animals use habitat for a variety of different needs including obtaining food, sheltering from predators, thermoregulating, raising young, and moving between other habitat patches (Börger *et al.* 2008, Morrison *et al.* 2012). Since each of these needs involves a specific set of habitat characteristics and features, an animal's interactions with its environment may vary depending on both its location on the landscape and its fine-scale movement and behavioral patterns (Garthe and Hüppop 2004). Evaluating the effects of environmentally heterogeneous stressors on mobile wildlife requires understanding not only the spatial and temporal overlap between individuals and threats, but also the extent of risk individuals encounter in relation to adverse effects based upon their habitat use and behavior (Desholm and Kahlert 2005, Jaeger *et al.* 2005, Beaudry *et*

al. 2010). Increases in the spatial and temporal resolution of individual tracking technologies have resulted in a shift toward individual-based analysis of habitat requirements (Hebblewhite and Haydon 2010); however, habitat assessments derived from individual tracking data often incorporate only presence or absence across landscapes and do not account for behavior (Tremblay *et al.* 2009).

In wide-ranging pelagic and semi-pelagic seabirds, habitat use typically changes between the breeding season, when birds are central-place foragers based in terrestrial colonies, and the nonbreeding season, when birds rely primarily on marine habitats (Weimerskirch and Wilson 2000). Within each stage of the breeding cycle, habitat use also depends on individual characteristics (Bearhop *et al.* 2006), phenology (Catry *et al.* 2009), colony size and location (Lewis *et al.* 2001), and environmental features (Tew Kai *et al.* 2009). These factors all contribute to variation in individual energy requirements, resulting in differences in foraging strategies and habitat preferences (Daunt *et al.* 2006, Phillips *et al.* 2009). Compared to pelagic species, nearshore seabirds generally occupy smaller foraging ranges that extensively overlap human-dominated marine and coastal areas year-round (Thaxter *et al.* 2012). These areas contain a higher diversity of habitat features and prey species assemblages (Becker and Bessinger 2003) and respond to different oceanographic processes than do large marine ecosystems (Gray 1997). Despite these differences, many of the same individual, colonial, and environmental factors that influence habitat choice in pelagic species also operate within nearshore seabird populations (*e.g.* Erwin 1977, Suryan *et al.* 2000). Nearshore seabirds experience higher levels of human disturbance and habitat modification of breeding, resting, and foraging

grounds than pelagic species (Croxall *et al.* 2012), and habitat features that concentrate nearshore seabirds and their prey may also concentrate risk factors such as pollutants, bycatch, and anthropogenic disturbance. Temporal variation in habitat needs and movement patterns can contribute significantly to the likelihood of risk exposure, as well as the degree to which risk factors impact both individuals and populations (Beaudry *et al.* 2010). The effects of environmental perturbations on seabirds can strongly depend on temporal factors, such as breeding stage, that influence their behavior and use of affected areas (Eppley and Rubega 1990, Montevecchi *et al.* 2012).

Due to its large size and persistence along human-dominated coastlines, the brown pelican (*Pelecanus occidentalis*), represents one of the most visible nearshore seabirds for much of North and Central America. While pelicans in highly developed coastal areas may benefit from land- and ship-based supplemental feeding (Wickliffe and Jodice 2010) and aggregations of prey around offshore energy installations, they are also particularly vulnerable to contaminants. The species was reduced to near-extinction by DDT exposure during the mid-twentieth century (McNease *et al.* 1992) and continues to experience high mortality rates during oil spills (Haney 2014). In the Gulf of Mexico, data on brown pelican movements come from observations of a small number of marked and banded birds across limited geographic areas (Schreiber and Mock 1988, Stefan 2008, King *et al.* 2013, Walter *et al.* 2014). The discrete nature of existing data makes it difficult to reliably predict how, or at what spatial and temporal scales, individuals interact with acute and chronic contamination. Unpublished data collected following the *Deepwater Horizon* oil spill suggest that there may be significant overlap in the winter

and migratory ranges of pelicans from different breeding colonies; hence, relatively localized oiling events in certain areas during the non-breeding season could affect birds from multiple colonies and result in population-level impacts (Jodice *et al.*, unpubl. data). Moreover, while most threats associated with marine energy development affect offshore foraging grounds, efforts to restore damaged populations generally target individual colony sites (Campagna *et al.* 2011). Understanding year-round movements of brown pelicans throughout the region could improve targeted mitigation efforts by linking affected at-sea habitat to individual breeding colonies, as well as predicting which portions of the Gulf-wide metapopulation might be affected by contamination events.

Using a three-year set of tracking data from brown pelicans breeding across the northern Gulf of Mexico, I refined location data using estimates of behavioral states derived from a Hidden Markov Model and determined preferred habitat characteristics across behavioral states. I then evaluated spatial, temporal, and individual variation in surface pollution overlap as a factor of both location and behavioral state. My results are intended to inform future response efforts to contamination events, as well as provide a baseline understanding of the mechanism by which oceanographic features drive both habitat use and pollutant exposure risk in a prominent nearshore seabird.

Methods

Pelican locations

To track movement patterns of adult pelicans, I used 65 g solar GPS Platform Terminal and Cellular Terminal transmitters (NorthStar Science and Technology) with a

backpack-style Teflon ribbon harness attachment (Dunstan 1972). To elevate the transmitters and prevent feathers from covering the solar panels and antenna, I mounted each device on a 6 mm thick neoprene pad that also extended 6 mm beyond the perimeter of the transmitter in all directions. Transmitters were programmed to collect 12 fixes/day during breeding (April – August; every 90 minutes from 1030 to 0130 GMT), 10 fixes/day during pre- and post-breeding (September – October and February – March; every 90 minutes from 0700 – 0100 GMT), and 8 fixes/day during winter (November – January; every 120 minutes from 0700 – 0100 GMT). I obtained an average error estimate for GPS points from transmitters at known locations (N = 220) of 4.03 ± 2.79 meters.

Adults were captured at nests using leg nooses in either the late incubation or early chick-rearing stage of breeding. All captured adults were weighed, measured, banded, and sampled for blood and feathers. I also calculated adult body condition index (BCI) as the residual of the linear relationship between culmen length and mass (Eggert *et al.* 2010). Since morphology is not always sufficient to determine sex in brown pelicans, adults were later sexed via PCR using collected DNA samples (Itoh *et al.* 2001). Total handling time from capture to release averaged 19 minutes (±6.5 minutes). Since individual characteristics may influence pelican foraging movements during breeding (Walter *et al.* 2014), I used two-tailed t-tests to compare individual characteristics of tracked adults between colonies. Over three years, I fitted 85 individual pelicans with GPS transmitters, 77 of which recorded sufficient data for subsequent analysis (Table

6.1). Unless otherwise specified, all statistical manipulation of spatial data was conducted using the adehabitat family of packages (Calenge 2006) in R 3.2.3 (R Core Team 2014).

I manually identified and removed outliers using a speed cutoff of 65 km/hour between successive points, which is the maximum travel speed recorded for brown pelicans (Schnell and Hellack 1978). Cleaned locations for each individual were then interpolated to regular 90-minute intervals. Since location data were not collected overnight, I chose not to interpolate tracks between successive days, and I differentiated each day as a separate trajectory by cutting tracks between each set of two successive points separated by a gap of greater than 6 hours.

Movement states

To distinguish resident from commuting behavior, I fit a two-state Hidden Markov Model (HMM; Patterson *et al.* 2009) to the regularized movement trajectories using the moveHMM R package (Michelot *et al.* 2015). Hidden Markov Models are a particularly flexible and efficient way of characterizing behavioral states from precise and regularized tracking data (Langrock *et al.* 2012), and thus are a good fit for GPS tracking locations. Briefly, the model assumes *a priori* that observed movement data are driven by underlying movement "states," characterized by a distribution of step lengths (distance between successive points) and turning angles. A Markov chain is used to describe the state parameters and classify data according to its most probable state membership.

Since I intended to characterize patterns of movement between rather than within days, I fit the model to a reduced data set of one location per day, calculated as the centroid of all locations for that day. I began with the assumption that local movement would be characterized by short step lengths and sharp turning angles, and commuting movement by long step lengths and wide turning angles. Therefore, I set initial step length estimates at 5 (± 5) km for State 1 and 10 (±10) km for State 2. I estimated initial turn angles of π radians for state 1 and 0 radians for State 2, and initial angle concentrations of 1 for each state. In subsequent analyses, I assigned all points along the trajectory for a given day to the movement state associated with that day.

Environmental variables

I measured environmental characteristics of pelican habitat using seven habitat variables, four of which were constant year-round for any given point (distance to coastline, distance to river outflow, bathymetry, and bottom substrate), and three of which varied by month (net primary production, sea surface salinity, and sea surface temperature) (Table 6.2). I chose these variables to represent a suite of likely drivers of nearshore habitat variation, particularly the distribution of pelican prey populations (*e.g.*, Deegan 1990). Since limited data are available on fine-scale variation in oceanographic features such as currents and eddies, and since these features have a high degree of short-term variability in coastal areas (Kaltenberg *et al* 2010), I used the distance to physical features that influence the movement of water (coastline, river outflow) as proxies for these processes. Depth and bottom substrate can influence both prey distributions and

oceanographic characteristics. Net primary production, which integrates chlorophyll concentrations over a range of depths (Behrenfeld and Falkowski 1997), provides an index of oceanographic productivity that influences the distribution of consumers at higher trophic levels. Salinity and temperature also influence the distribution of aquatic prey species depending on their osmotic and thermal tolerances. Since some data were reported at finer spatial resolutions than others (Table 6.2), I standardized all variables to a resolution of 0.1 degree (approximately 10 km) grid squares. I calculated distance values as the distance from the grid square centroid to the feature of interest. For all other variables, I resampled the data using the mean value for each 0.1 degree grid square.

Habitat suitability and distribution

I mapped preferred habitat characteristics in ecological space using a multivariate ordination of all habitat variables using a Hill-Smith principal components analysis (Hill and Smith 1976), which allows the inclusion of both categorical and continuous variables. For each grid square, I calculated habitat suitability as the squared Mahalanobis distance of that point from optimal location of the species in the multivariate ordination (*i.e.*, higher distances indicate less suitable habitat) (Clark *et al.* 1993, Calenge *et al.* 2008). I projected habitat suitability as the probability of obtaining a higher squared Mahalanobis distance for that cell than the calculated value. Thus, in the final suitability scores, values closer to 1 indicate lower distance from the multivariate optimum location and higher habitat suitability.

To characterize individual responses to the measured habitat variables, I used an Outlying Mean Index (OMI) analysis (Dolédec *et al.* 2000). Briefly, OMI is an ordination technique that characterizes available sites based on a suite of environmental variables, sets the mean of all conditions at zero in n-dimensional space, then determines the axis that describes the maximum amount of marginality (difference from the mean) of individual animals or species in ecological space. Thus, the first axis of the OMI is the combination of environmental characteristics that best explains the position of animals across available resources. Similarly, the position of each habitat characteristic on the first axis of the OMI represents that variable's contribution to animal distributions; that is, the strength of selection on that characteristic. OMI does not assume specific resource selection functions, and allows differences in individual niche selection to be taken into account when describing the distribution of a group of animals. I conducted OMIs for each month on all individuals and habitat variables for each behavioral state, then averaged the scores of individuals on the first OMI axis to calculate niche location and breadth for groups within the population. I also examined spatial distribution of breeders from different regions. I determined 95% kernel density estimates (KDEs) for all individuals from each breeding region using the 'ks' package (Duong 2015) in R with a plugin bandwidth estimator (Wand and Jones 1994, Gitzen *et al.* 2006). I then used an Albers Conic Equal-area Projection to calculate the areas included within each region's 95% KDE contour, and to estimate the intersection areas between kernels from different regions.

Risk overlap

To calculate surface pollutant concentrations for each grid square, I created a combined index of potential pollutant sources including: an ocean pollution data layer generated from shipping traffic and port locations (Halpern *et al.* 2008), locations of oil drilling rigs and platforms, and locations of oil and gas pipelines (Bureau of Ocean Energy Management). Together, these sources account for the majority of acute and chronic pollution in this region (Emergency Response Division 2016). After restricting the dataset to active platforms and pipelines, I calculated oil infrastructure concentrations using values of platform counts and total lengths of pipeline per grid square. Since I assumed each layer to contribute equally to pollution risk, I summed evenly across the three pollutant layers and normalized the resulting values to create a combined surface pollutant and oil infrastructure data layer.

I calculated overall surface pollution overlap with potential brown pelican habitat by multiplying monthly habitat suitability values (Mahalanobis distance probabilities) by surface pollution scores for each grid square. For each interpolated individual location, I extracted the value of the surface pollution score at the corresponding grid cell. I then averaged the values of all points obtained from each individual by month to obtain a mean monthly pollution overlap index for that individual. To compare risk exposure between groups of individuals, I calculated the mean and standard deviations of individual overlap scores and tested for between-group differences using one-way ANOVAs. To assess the influence of behavioral states on exposure risk, I assigned resident points a weight of 1 and transient points varying weights of 1 (equal exposure

probability between states), 0.5 (exposure during rapid linear movement is half as likely as during slow movement), 0.1 (exposure probability is proportional to travel speed), and 0 (no exposure during rapid linear movement). I then multiplied the scores of transient squares by the range of potential weights and averaged across all locations for each individual.

Results

Pelican locations

After cleaning and interpolating all collected locations (N = ca. 180,000), I obtained a total of 169,990 GPS locations from 77 individual brown pelicans (mean per individual = 2237 ± 1688; range per individual = 34 – 7371). Sex ratios of captured adults varied by colony, but did not differ significantly within each region (Fisher's Exact Test; Eastern: $p = 0.64$; Central: $p = 1$; Western: $p = 0.39$). Body size of captured adults also did not differ significantly between regions (ANOVA; Mass – $F_2 = 0.81$, $p = 0.45$; Culmen – $F_2 = 0.71$, $p = 0.93$) or colonies (Two-tailed T tests; $p > 0.69$ for all), while body condition differed between (ANOVA; $F_2 = 3.83$, $p = 0.03$), but not within (Two-tailed T tests; Eastern: $t_{19} = -0.87$, $p = 0.39$; Central: $t_{24} = -0.70$, $p = 0.49$; Western: $t_{22} = 0.72$, $p = 0.48$), regions.

Movement states

The HMM converged on two distinct movement states. State 1 (resident) had a mean step length of 3.24 (± 3.57) km and mean turning angle of -3.11 (± 0.59) radians.

State 2 (transient) had a mean step length of 26.95 (± 30.44) km and a mean turning angle of 0.04 (± 0.30) radians. (Figure 6.2 a-b). Individuals were more likely to remain in their current state than transition to the other (transition probabilities, resident – resident: 0.94; transient – transient: 0.90). Both resident and transient points occurred throughout the Gulf of Mexico (Figure 6.2c) and within each individual trajectory (Figure 6.2d).

Overall, 61.5% of bird-days were classified as resident and 38.5% as transient (Figure 6.3). The proportion of time individuals spent in each state did not differ significantly by sex (ANOVA, $F_{1,76} = 2.12$, $p = 0.15$). Between breeding regions, individuals tagged in the eastern region spent relatively more time in the resident state ($M = 0.73 \pm 0.04$) than did individuals tagged in the central ($M = 0.53 \pm 0.03$) or western ($M = 0.65 \pm 0.05$) regions (ANOVA, $F_{2,74} = 6.61$, $p = 0.002$). Both states were observed year-round; however, resident behavior was relatively more common between December and March and between May and August, while transient behavior was the more frequently observed state during the remaining months. Niche position and breadth on measured habitat variables did not change depending on behavioral state (Figure 6.4).

Habitat suitability and distribution

The habitat variables most strongly associated with pelican residency year-round were net primary production (positive) and sea surface salinity (negative) (Figure 6.5). Sea surface temperature was negatively associated with residency during non-breeding, but the association diminished to near zero during the breeding season. Compared to seasonally-dependent variables, fixed factors were less strongly associated and less

variable in their relationship to pelican habitat use, and did not vary during the year. Bathymetry had a positive relationship with residency (*i.e.*, pelicans were more likely to occupy shallower waters), while distance to coastline and distance to river outflow were both negatively associated with use by pelicans.

Patterns of association with seasonally-dependent habitat variables varied between breeding regions (Figure 6.6). Pelicans breeding in the central region of the Gulf exhibited the highest degree of variation in environmental characteristics of selected habitat, and were more strongly associated with waters characterized by high productivity and low salinity during summer (breeding) than during winter (non-breeding). Pelicans from the central and eastern regions selected habitat with a lower degree of seasonal variation in environmental characteristics, although pelicans from all regions associated more strongly with sea surface temperature during breeding than during non-breeding.

Overall, areas of highest year-round habitat suitability (*i.e.*, highest probability of containing optimal habitat based on multivariate ordination) were located in the northern Gulf, particularly the central and western regions (Figure 6.7). During summer, the total area of preferred habitat was narrowly restricted to coastal areas of the northern Gulf; however during the fall and winter, suitable habitat characteristics also occurred from the nearshore region out to ca. 200 km offshore. In both summer and winter, habitat with optimal characteristics for brown pelicans closely followed the distribution patterns of Gulf menhaden *Brevoortia patronus* (Figure 6.8), the principal prey species of brown pelicans in this region (see Chapter 5 of this dissertation). Observed use areas of pelicans from the western, central, and eastern regions overlapped spatially throughout the Gulf

(Figure 6.9). Breeders from central Gulf colonies shared 41% of their total habitat with breeders from other locations, western Gulf breeders shared 36%, and eastern Gulf breeders shared 15%. Habitats shared by central and western breeders accounted for 94% of total shared habitat, and the area shared by all three regions represents 6% of total shared habitat.

Risk overlap

Hot spots of overlap between preferred pelican habitat and surface pollution (*i.e.*, areas of high overlap) were consistent throughout the year and included most of the central and western regions of the northern Gulf, particularly the Mississippi Delta and Galveston Bay (Texas) areas (Figure 6.10). Other hot spots varied seasonally in intensity and included Corpus Christi Bay (Texas), Tampa Bay (Florida), the Florida Keys, the mouth of the Apalachicola River (Florida), and locations along the Yucatan Peninsula (Mexico) and in the Caribbean.

Among individuals, pollutant exposure through the annual cycle varied by breeding location and sex (Table 6.3). Average overlap between individuals and pollution sources was lowest during nonbreeding, increased at the start of the breeding season, and reached a maximum during post-breeding (Figure 6.11a). Overlap rates differed significantly by breeding region (ANOVA: $F_{2,74} = 11.97$, $p < 0.001$). Breeders from the Eastern region experienced lower year-round exposure to surface pollutants, while central and western breeders had similar year-round exposure rates (Table 6.3). Exposure varied seasonally in both central and western breeders, while individuals breeding in the Eastern

region experienced lower overall exposure and seasonal variation (Figure 6.11b). Between sexes, males averaged higher exposure than females (ANOVA, $F_{1,75} = 4.48$, $p = 0.037$), which was driven by higher levels of overlap with surface pollutants during the non-breeding season (Figure 6.11c).

Down-weighting locations that were classified as transient generally reduced or removed the localized peak in pollutant exposure that occurred during the late fall (October – November) in most groups, and emphasized the downward trend in exposure risk from a peak at early breeding to a low during winter (Figure 6.11 a-c). Between-region differences in individual exposure probability were still significant after down-weighting transient points by 0.5 (ANOVA: $F_{2,74} = 5.93$, $p = 0.004$); however, between-sex differences were not (ANOVA: $F_{1,75} = 2.53$, $p = 0.11$).

Discussion

The principal goals of this study were to use locations and movement states of brown pelicans in the Gulf of Mexico, determined from individual tracking data, to better understand the species' marine habitat associations and subsequently assess individual risk exposure to spatially varying oceanic pollution. Despite the level of energy infrastructure in the northern Gulf of Mexico, and the importance of this region to nearshore seabirds and other coastal birds, this is the first such effort to develop an individual risk model for this suite of avian species in the region.

Habitat suitability and distribution

Although extensive work has described the environmental factors driving at-sea habitat use by seabirds in pelagic waters (*e.g.*, Haney 1985, Pinaud and Weimerskirch 2005, Tew Kai *et al.* 2009), relatively little is known about the factors driving marine habitat use in nearshore seabirds particularly in the North Atlantic. For the most part, prior studies of habitat preferences in nearshore-foraging species have been conducted in northern temperate waters (*e.g.*, Day et al 2000, Becker and Beissinger 2003, Yen *et al.* 2006, McLeay *et al.* 2010). Similarly to results from these systems, I found that marine productivity was the most significant driver of habitat selection of brown pelicans in nearshore environments in the Gulf of Mexico. Also in concordance with previous results (Day *et al.* 2000, Becker and Beissinger 2003), I found that the influence of sea surface temperature on at-sea distribution was significant but highly variable over time. In a departure from previous assessments of habitat use of nearshore seabirds, which generally found little effect of salinity on habitat use, I found that salinity strongly influenced habitat use for brown pelicans. Although the effects of salinity have not been extensively documented on this species or other coastal seabirds, recent studies (*e.g.*, Zamon *et al.* 2014) have suggested that river plumes can be important nearshore foraging habitat for seabirds, concentrating prey in a manner analogous to oceanic fronts in pelagic systems. While distance to river outflow was only weakly related to pelican habitat suitability in this study, pelicans were often located in relatively large estuarine complexes and therefore may ultimately be responding to salinity gradients that exist even at a greater distance from river mouths.

Since the scale of movement that I observed was relatively small (on the order of tens of kilometers per day, rather than hundreds of kilometers as is commonly observed in pelagic seabirds), I chose environmental variables likely to relate to the distribution of prey rather than those that might facilitate long-distance movement (*e.g.*, prevailing winds) or visual identification of foraging areas (*e.g.*, ocean color).The influence of salinity in particular is correlated to the abundance and distribution of prey items. Brown pelicans in the Gulf of Mexico forage primarily on Gulf menhaden (see Chapter 5), which concentrate during the spring and summer in low-salinity estuarine environments (Deegan 1990). Both summer and winter distribution of preferred pelican habitat corresponded closely with Gulf menhaden distributions, indicating that pelicans select habitat principally as a function of prey concentrations. I did not find that the spatially fixed metrics I tested had a strong influence on habitat suitability (*e.g.* distance to coastline, distance to river outflow, bathymetry, or bottom substrate). Previous studies (*e.g.*, Suryan *et al.* 2012) have suggested that such metrics tend to provide a more consistent predictor of seabirds distributions than seasonally varying environmental characteristics. The lack of a strong relationship of pelican distributions to static marine features may result from the short timescale of this study, or may be a feature of the Gulf of Mexico which is dominated by silt and sand and has a highly dynamic coastal geography and bathymetry relative to rocky shores in more northern regions where most other studies have occurred (Britton and Morton 2014).

Another possible explanation for the lack of a strong relationship of pelican habitat suitability to static features may relate to the scale at which I conducted my

analysis. The spatial scale of the environmental data available (10 x 10 km) and the temporal resolution of the GPS data I collected (90 minute intervals) did not allow us to distinguish fine-scale foraging areas from commuting or resting habitat. Thus, I confined my observations to mesoscale movement patterns and habitat selection on a monthly timescale. The fact that seasonally varying parameters were more strongly related to habitat selection than physical oceanographic features is consistent with previous observations that mesoscale habitat use is likely to be driven by primary productivity, while physical features become more important at the micro (< 10 km) scale (Becker and Bessinger 2003). Habitat selection likely also occurs at finer scales than those described by this study (Kristan 2006), and may vary with daily or weekly changes in estuarine dynamics that alter distribution and concentrations of prey.

Besides general habitat associations, I examined specific habitat use by pelicans captured while breeding in colonies in three sections of the northern Gulf: the eastern (Florida panhandle), central (Alabama, Mississippi, and Louisiana coasts), and western regions. I observed a distinct separation between birds from eastern Gulf colonies and those in the central and western regions. While year-round habitat overlap between breeders from central and western colonies totaled 30 – 40%, eastern breeders shared only 15% of their total habitat area. Moreover, while central and western Gulf breeders extensively used the same set of nonbreeding areas in the southern Gulf along the east coast of Mexico and throughout the Yucatan Peninsula, eastern Gulf breeders typically migrated southward to the Florida Keys and Cuba. I did not observe overlap between the eastern breeding population and either the central or western groups in southern Gulf

wintering habitat. The only area in which breeders from all three regions overlapped was in the Mississippi Delta, in the central Gulf. The apparent separation between the eastern breeding colonies and the rest of the northern Gulf population is particularly interesting in light of the fact that translocations from eastern colonies were used to re-establish the central Gulf breeding population following DDT-related extirpation (McNease *et al.* 1984).

To date, studies of brown pelicans nonbreeding movements have been limited to information on band recoveries, typically from birds banded as juveniles (Schreiber and Mock 1988, Stefan 2008) and tracking data from individuals captured during non-breeding (King *et al.* 2013). This has limited the possibility of linking nonbreeding birds to breeding colonies outside the breeding season. Ours is the first study to incorporate individual data on year-round movements of pelicans from known breeding locations. Understanding the likelihood of overlap between different breeding populations in different regions of the Gulf helps to refine current understanding of the distribution of environmental risk among breeding populations, and to better identify which segments of the overall breeding population are affected by spatially explicit threats in the marine environment.

Risk overlap

Spatial distribution and habitat use of seabirds are often used in combination with threat distributions to assess exposure to risk (*e.g.* LeCorre *et al.* 2012, Tranquilla *et al.* 2013, Renner and Kuletz 2015); however, overlap models have generally accounted for

exposure only in terms of co-occurrence of birds and threats. The likelihood of threat exposure also varies depending on how birds interact with their environments, which can vary from species to species (Garthe and Hüppop 2004) or between phenological states within a species (Eppley and Rubega 1990). I used a Hidden Markov Model to distinguish resident behavior, in which individuals were restricted to limited areas of habitat, from transient behavior, which was characterized by more frequent and longer-distance movements. This technique can improve predictive risk models by incorporating *a priori* biological understanding of expected behavioral states (Patterson *et al.* 2009) to better predict the likelihood that co-occurrence of individual locations with threats will result in exposure.

I found the highest levels of overlap between preferred pelican habitat and surface pollution in the northern Gulf. Other hotspots of overlap were concentrated around large river outflows, which experienced high pollution pressure from ports and shipping as well as favorable pelican habitat characteristics (low salinity, high productivity). Overall exposure risk increased sharply at the start of the breeding season, when pelicans returned to the higher pollution levels of the northern Gulf to breed and environmental factors restricted suitable habitat to a very narrow range in the nearshore environment. Risk levels either remained constant or declined during the breeding season, then peaked again during autumn (September – November), which coincides with the annual molt in brown pelicans. The post-breeding, molt phase of the annual cycle represents a period of constrained resident behavior, since molting birds have limited flight capabilities. My model indicated that breeders from the western Gulf of Mexico, which supports less oil

infrastructure than the central region, experienced statistically similar levels of risk to pollutant exposure year-round compared to those from the highly developed central region. The similarity in risk despite the difference in exposure (*i.e.*, infrastructure and development) may be due in part to the fact that the major pelican breeding colonies in the western region are located near major shipping lanes, which are a significant source of pollutants, as well as to the use of highly polluted areas, such as the Mississippi Delta, by western Gulf breeders during non-breeding. My model suggested that female brown pelicans experienced lower year-round probability of pollution exposure. Female pelicans were more likely to migrate to the less-developed southern Gulf of Mexico, which had generally lower concentrations of surface pollutants during the non-breeding season, and usually departed the breeding colony immediately following breeding completion or failure.

The parameters I used to model risk could easily be modified to reflect future improvements in our understanding of pelican behavior or the spatio-temporal aspects of marine pollution risk. I assessed the effects of down-weighting transient points by 50%, by 90%, and completely removing them from the analysis, reflecting different levels of inferred interaction with surface pollutants during long-distance movement. Although the same general patterns in temporal pollution risk were not altered by lowering the assumed risk of pollutant exposure during long-distance movement, down-weighting transient points had the effect of reducing estimated peaks in exposure risk during the late-autumn migration and dispersal period. Further direct observations of pelicans outside the breeding season, especially during staging and molt, would help to refine

understanding of how behavior affects surface pollution exposure risk during periods of frequent long-distance movement. I chose to equally weight contributions of oil platforms and drilling rigs, oil pipelines, and ship- and port-based pollution to overall pollution risk; however, there are important differences between these factors. Pollution at ports and along shipping lanes is likely to be chronic and low-level, while pollution from oil infrastructure is more likely to be short-term and acute, although both can be sources of either acute or chronic pollution. This approach could be refined by monitoring the frequency, size, and location of pollutant spills and incorporating frequency and intensity of spills into analysis of pollution probability. Evaluating pollutant concentrations in tissues of brown pelicans from different breeding regions would also provide a useful test of my model's exposure risk predictions.

Conclusions

This study demonstrates that both seabird habitat preference and risk exposure have spatial, temporal, and individual components. In the past, efforts to respond to pollution events have been hampered by a lack of baseline understanding of exposure risk across the population. My results suggest that habitat needs of brown pelicans relate closely to those of their prey, and offer insight into year-round habitat preferences of a highly visible marine predator that can serve as an indicator of environmental perturbations at lower trophic levels in nearshore marine systems.

Incorporating behavioral state-space models into risk estimation offers a potential solution to the fact that overlap between animal movements and spatially heterogeneous

threats does not necessarily constitute exposure. Understanding the relationship between movement, behavioral states, and interaction with different threat types is a crucial refinement to threat exposure studies. Since this study focused on an ocean-borne threat type, surface pollution, I chose to preferentially weight individual locations that indicated higher residency in a particular marine environment and shorter flight distances. Such an approach might be appropriate for other threats that affect primarily resident or foraging individuals. For seabirds, this might include fisheries bycatch, plastic ingestion, and entanglement. However, there are other threats that would be more likely to impact transient or migratory individuals (*e.g.*, wind turbines for which the rotor-swept zone is above the species' typical foraging altitude), or to impact both migrants and residents individually (*e.g.*, severe weather). My approach is highly adaptable in that decisions to include different movement types, or to preferentially weight one movement type over another, can be made and adjusted according to prior understanding of behavior during different life history stages, and of which groups are likely to be most affected by the threat of interest.

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Table 6.1. Colony characteristics and measurements of tracked adults captured at six brown pelican breeding colonies in the northern Gulf of Mexico, 2013-2014. Measurements are reported as mean values, with standard deviations listed in parentheses.

	Eastern		Central		Western	
	Smith	Audubon	Felicity	Raccoon	Shamrock	Chester
Colony size	40	100	1800	4300	1400	3200
Adults tracked	9	11	12	14	11	10
% male	0.78	0.64	0.50	0.57	0.55	0.30
Mass (g)	3414 (432)	3414 (558)	3448 (369)	3546 (353)	3459 (562)	3070 (508)
Culmen length (mm)	322 (22)	315 (21)	313 (23)	316 (23)	321 (25)	309 (19)
Body Condition Index	-141 (273)	-241 (205)	77 (195)	121 (263)	-19 (306)	-147 (281)

Table 6.2. Environmental data layers used for habitat analysis.

Variable name	Layer name	Data source	Original resolution
Environmental variables			
Distance to coast	World Vector Shoreline, Intermediate Resolution	Global Self-consistent Hierarchical High-Resolution Geography Database, NOAA (Wessel *et al.* 1996)	1:25000
Distance to river outflow	North American Rivers and Lakes	North American Data Atlas (Center for Environmental Cooperation 2009)	1:100000
Bathymetry	2-minute Gridded Global Relief Data, (ETOPO2) v2	NOAA (National Geophysical Data Center 2006)	0.033
Bottom substrate	Dominant Bottom Types and Habitats	NOAA Gulf of Mexico Data Atlas (Jenkins 2011)	
Net primary production	Vertically Generated Production Model	Ocean Productivity, Oregon State University (O'Malley 2012)	0.083
Sea surface temperature	Sea Surface Temperature, Climatological Mean, 10 m depth	NOAA National Centers for Environmental Information (Boyer *et al.* 2011)	0.1
Sea surface salinity	Sea Surface Salinity, Climatological Mean, 10 m depth	NOAA National Centers for Environmental Information (Boyer *et al.* 2011)	0.1
Surface pollution variables			
Surface pollution	Ocean Pollution (Ship Traffic and Ports)	Global Map of Human Impact Project, National Center for Ecological Analysis and Synthesis (Halpern *et al.* 2008)	0.01
Platforms	Drilling Platforms – Gulf of Mexico	Bureau of Ocean Energy Management (2016)	NA
Pipelines	Oil and Gas Pipelines – Gulf of Mexico	Bureau of Ocean Energy Management (2016)	NA

Table 6.3. Description of the first axis of monthly Outlying Mean Index analyses of brown pelican locations and habitat variable scores in the Gulf of Mexico, 2013-2016. Eigenvalues of the first axis represent variance explained, and Proportion of Total is its proportional representation relative to the sum of eigenvalues for all axes. Habitat variable scores are the positions of measured habitat variables on the first axis, where zero is the mean of each variable across all habitat units.

	Month												
	1	2	3	4	5	6	7	8	9	10	11	12	Mean
Axis 1 Eigenvalue	9.88	12.97	12.71	23.73	20.07	13.12	17.32	18.57	18.25	15.32	9.41	10.82	15.18
Proportion of total	0.70	0.72	0.73	0.88	0.81	0.81	0.86	0.86	0.80	0.82	0.79	0.76	0.80
Habitat variable scores													
Distance to coast	-1.02	-1.06	-1.00	-1.05	-1.10	-0.96	-0.87	-0.92	-1.05	-1.07	-1.06	-1.04	-1.02
Bathymetry	0.49	0.53	0.48	0.51	0.54	0.47	0.43	0.47	0.52	0.53	0.50	0.52	0.50
Distance to river outflow	-0.73	-0.83	-0.66	-0.50	-0.57	-0.58	-0.42	-0.45	-0.64	-0.68	-0.80	-0.77	-0.64
Substrate	-0.08	-0.07	-0.14	-0.29	-0.32	-0.24	-0.26	-0.27	-0.24	-0.25	-0.20	-0.15	-0.21
Net primary production	1.83	2.66	2.40	2.66	2.56	2.25	2.53	2.94	2.85	2.25	1.43	1.83	2.35
Sea surface temperature	-1.61	-1.60	-1.71	-1.51	-1.59	1.02	1.23	1.14	-1.71	-1.82	-1.74	-1.61	-0.96
Sea surface salinity	-1.46	-1.12	-1.53	-3.56	-3.01	-2.35	-2.87	-2.70	-2.32	-2.24	-1.51	-1.70	-2.20

Table 6.4. Mean pollutants overlap for observed brown pelican locations in the Northern Gulf of Mexico, 2013-2016.

		M	Standard deviation	Number of individuals
Breeding region				
	Eastern	0.082	0.023	23
	Central	0.133	0.034	26
	Western	0.122	0.049	28
Sex				
	Female	0.102	0.043	33
	Male	0.123	0.041	44
Month				
	January	0.050	0.059	44
	February	0.041	0.056	31
	March	0.057	0.054	28
	April	0.119	0.068	27
	May	0.136	0.051	56
	June	0.127	0.048	63
	July	0.125	0.058	69
	August	0.115	0.053	64
	September	0.109	0.060	63
	October	0.119	0.063	60
	November	0.103	0.075	63
	December	0.074	0.076	51

Figure 6.1. Locations of brown pelican study colonies in the Gulf of Mexico, 2013-2016. Sizes of stars represent comparative colony sizes. Dashed lines indicate relative boundaries between planning regions as defined by the U.S. Bureau of Ocean Energy Management.

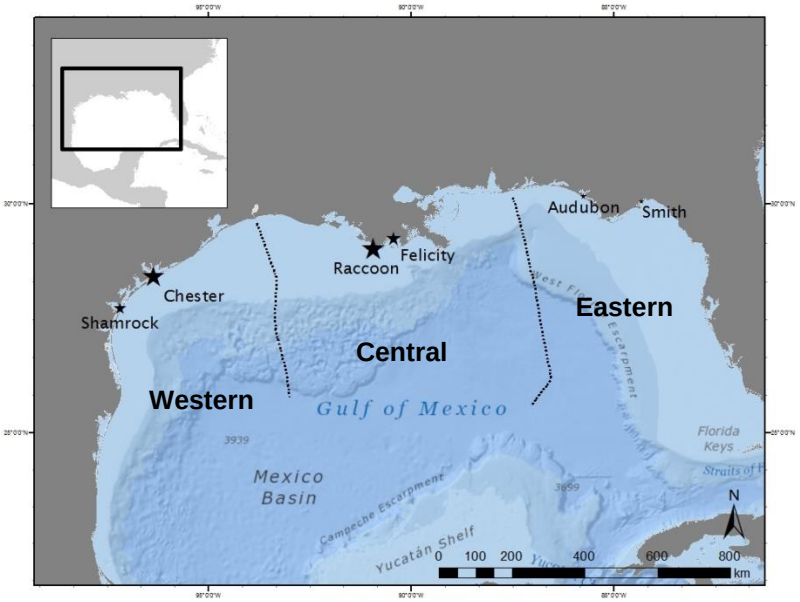


Figure 6.2. Characteristics of (a) step lengths and (b) turning angles, and (c) locations of resident (State 1) and transient (State 2) hidden Markov movement states derived from brown pelican GPS locations in the Gulf of Mexico, 2013-2016. Grey bars represent overall density distributions of variables, and colors represent states (red: resident; green: transient). (d) shows an example of a movement trajectory from a single individual with locations classified by model-assigned movement state.

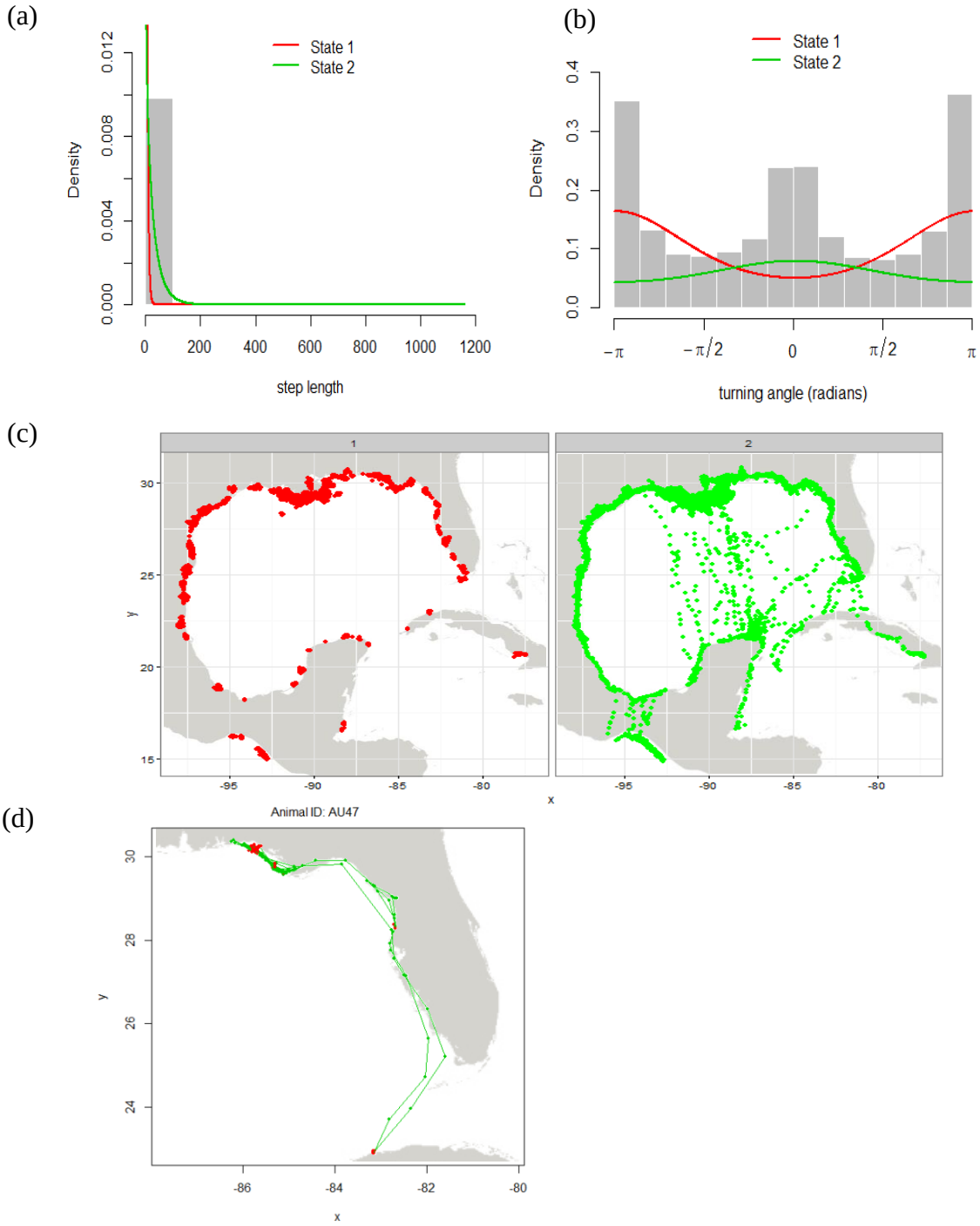


Figure 6.3. Deployment duration and behavioral states of GPS-tagged brown pelicans in the Gulf of Mexico, 2013-2016. Total numbers of GPS locations after cleaning and interpolation are listed to the right of each bar. Bar colors indicate behavioral states derived from Hidden Markov modeling (red: resident; green: transient).

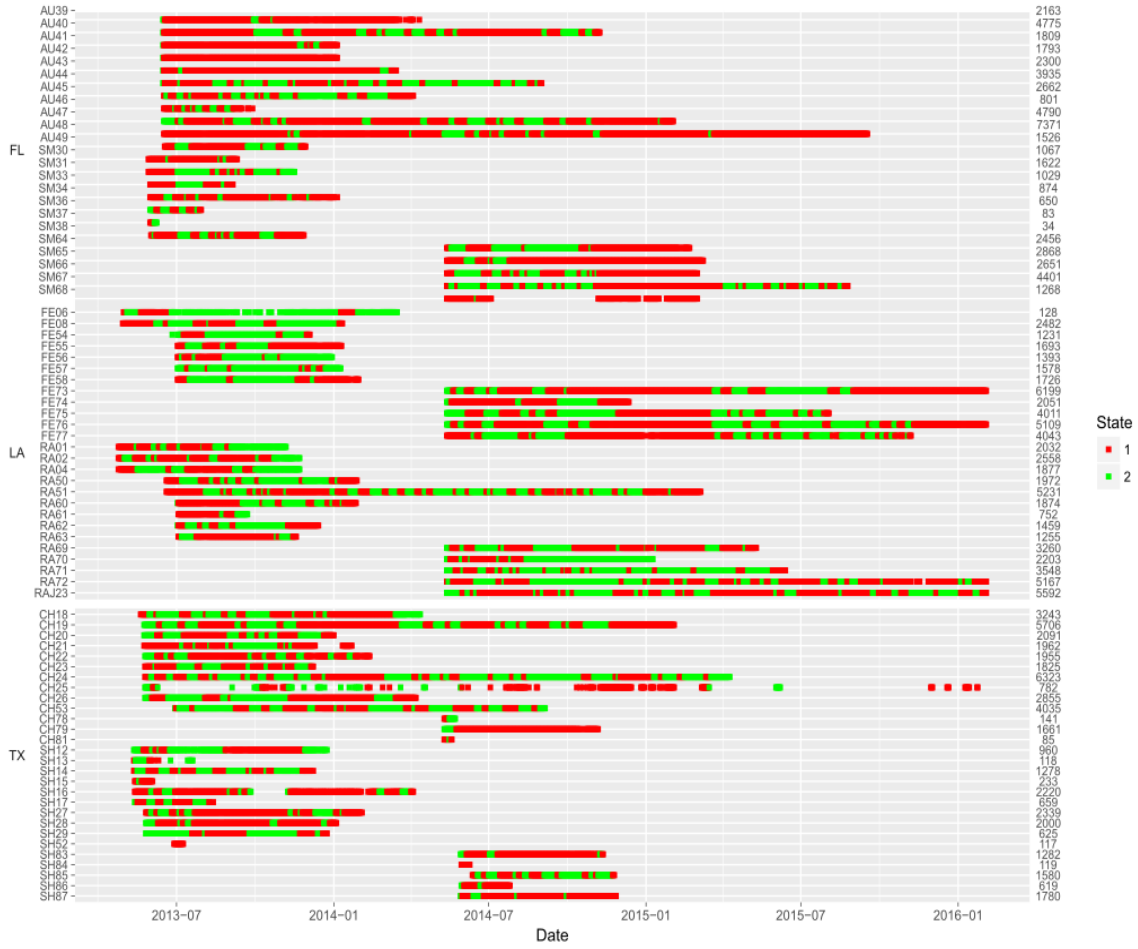


Figure 6.4. Niche center and breadth of resident (red) and transient (green) behavioral states of brown pelicans on measured habitat variables in the Gulf of Mexico, 2013-2016.

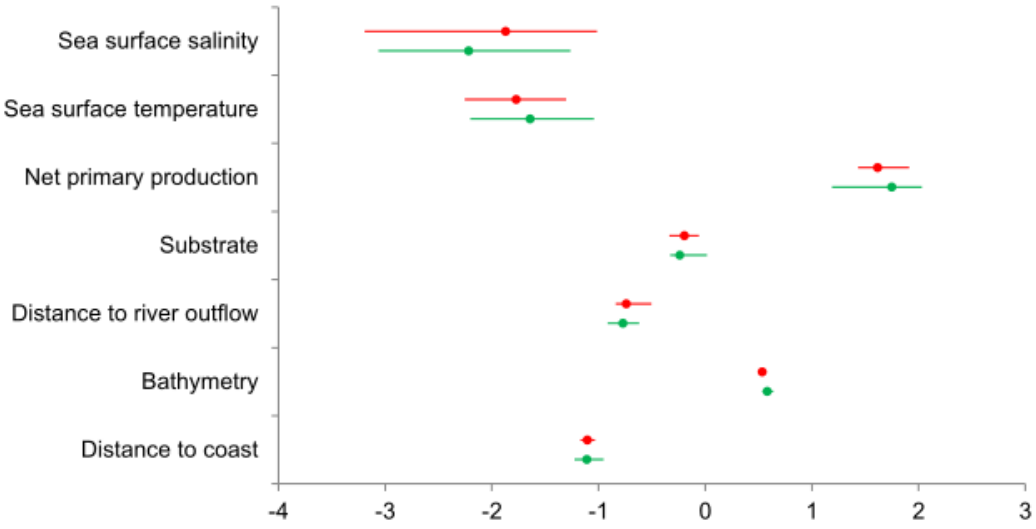


Figure 6.5. Annual patterns of strength and direction of selection .by brown pelicans on measured habitat variables, Gulf of Mexico, 2013-2016. Strength of selection (positive or negative) is generated from Outlying Mean Index and increases with distance from zero. Lines represent generalized additive model regressions (smoothing parameter = 1.3) of monthly averages for each variable, and grey bars are 95% confidence intervals of regression lines.

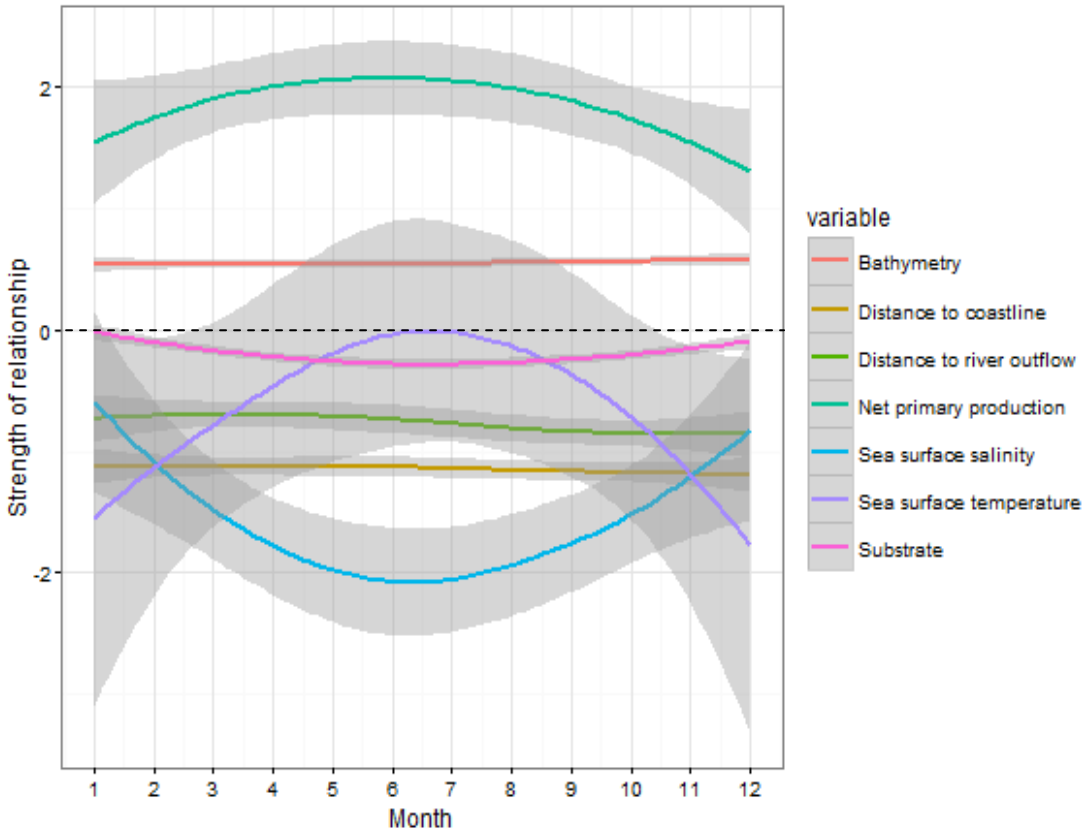


Figure 6.6. Annual patterns of strength and direction of selection by brown pelicans on seasonally varying habitat variables by breeding region, Gulf of Mexico, 2013-2016. Strength of selection (positive or negative) is generated from Outlying Mean Index and increases with distance from zero. Lines represent generalized additive model regressions (smoothing parameter = 1.3) of monthly averages for each variable, and grey bars are 95% confidence intervals of regression lines.

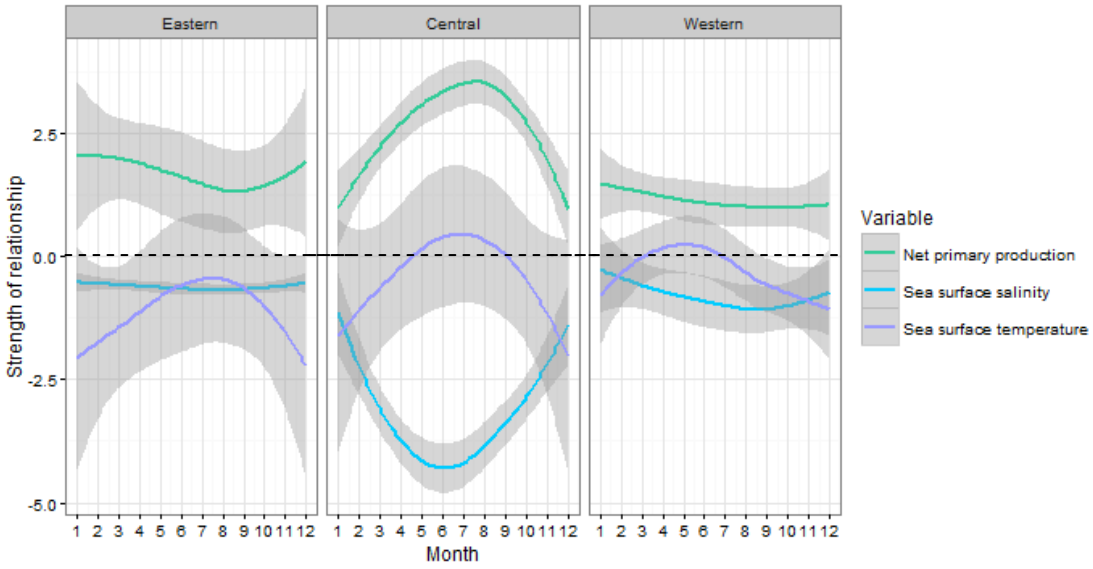


Figure 6.7. Suitability scores of available habitat for brown pelicans in the Gulf of Mexico based on Mahalanobis distances. Darker colors indicate higher suitability.

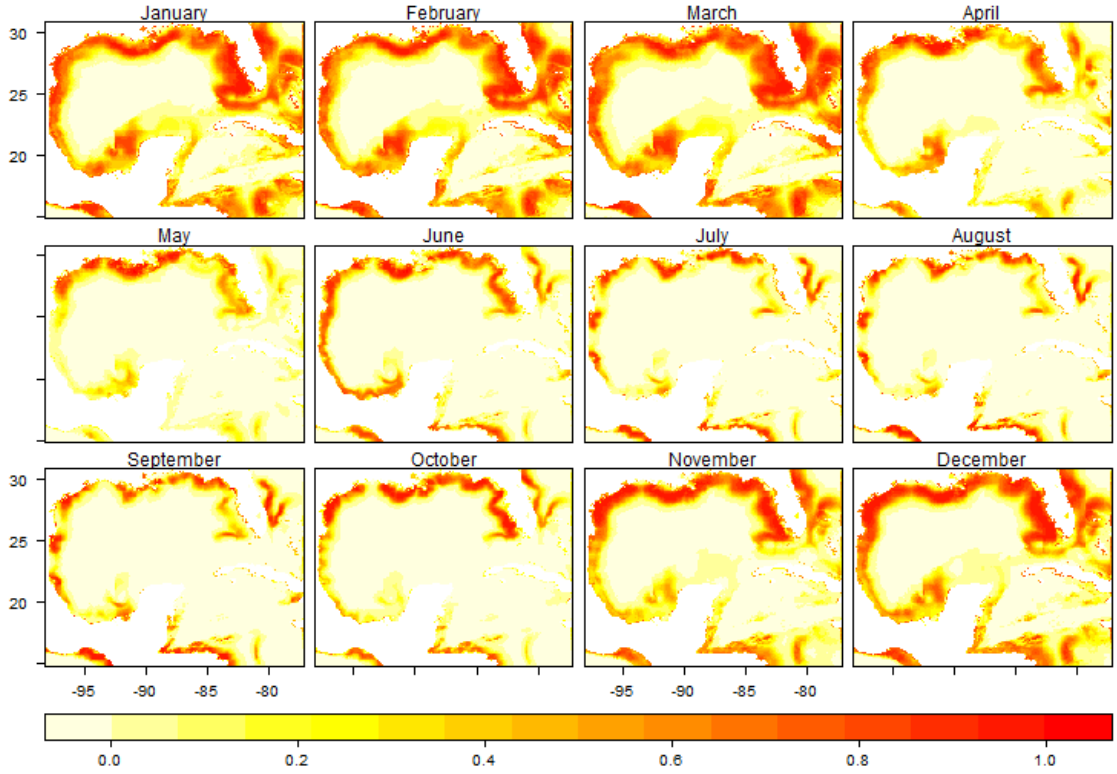
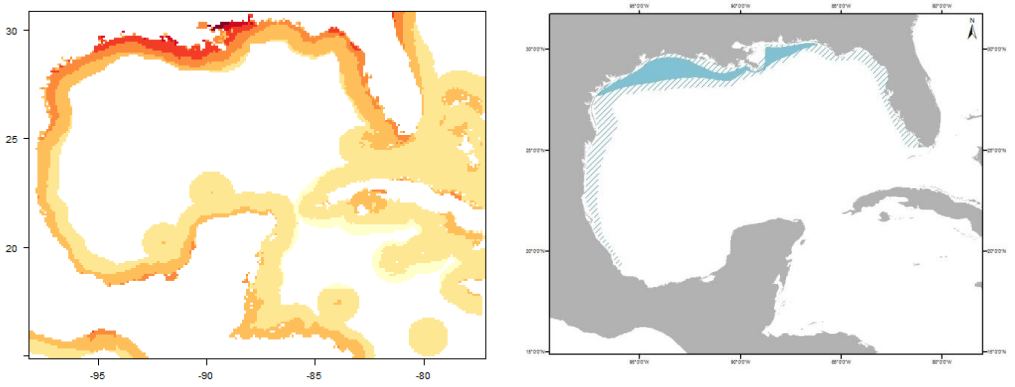


Figure 6.8. Distributions of preferred brown pelican habitat characteristics and Gulf menhaden range in (a) winter (January) and (b) summer (June). Darker colors represent higher habitat suitability for brown pelicans.

(a)



(b)

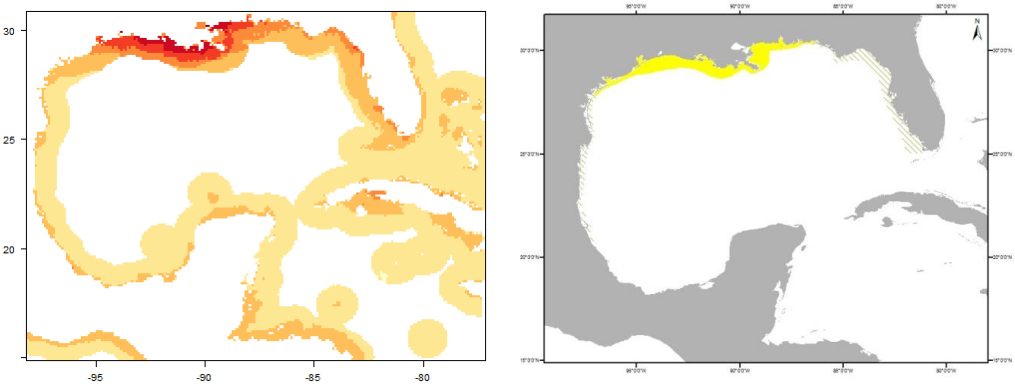


Figure 6.9. Annual 95% kernel density estimates for locations of brown pelicans originally captured at breeding colonies in the eastern (blue), central (orange), and western (green) regions. Areas shared by one or more regions are shaded in purple, and areas shared by all regions are shaded in red (detail in inset).

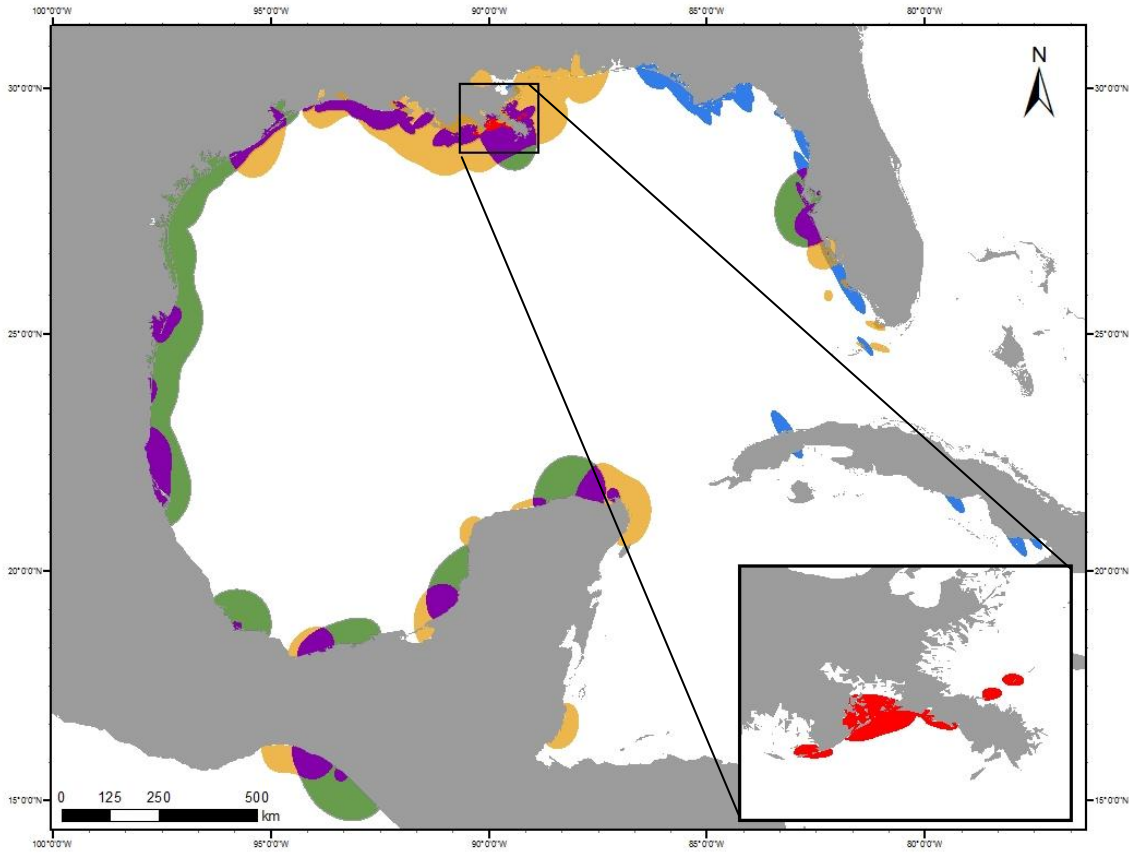


Figure 6.10. Overlap between preferred brown pelican habitat and surface pollution concentrations. Darker colors indicate higher degrees of overlap.

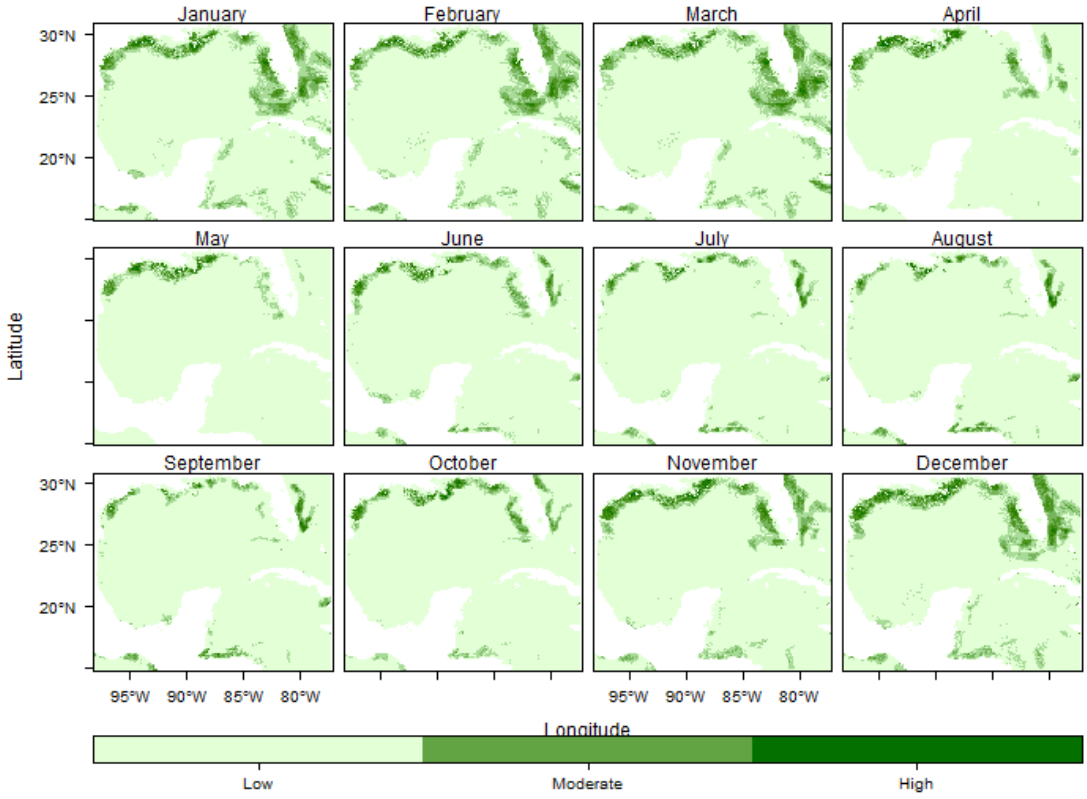
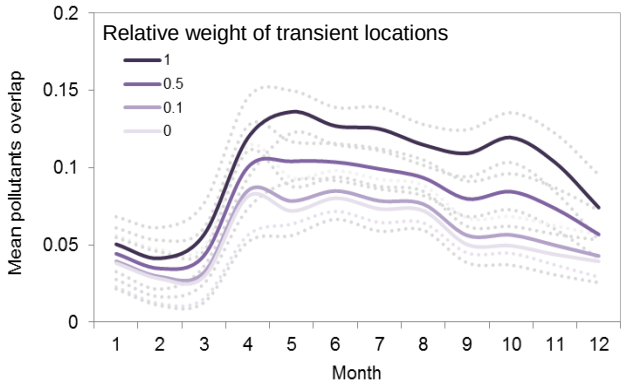


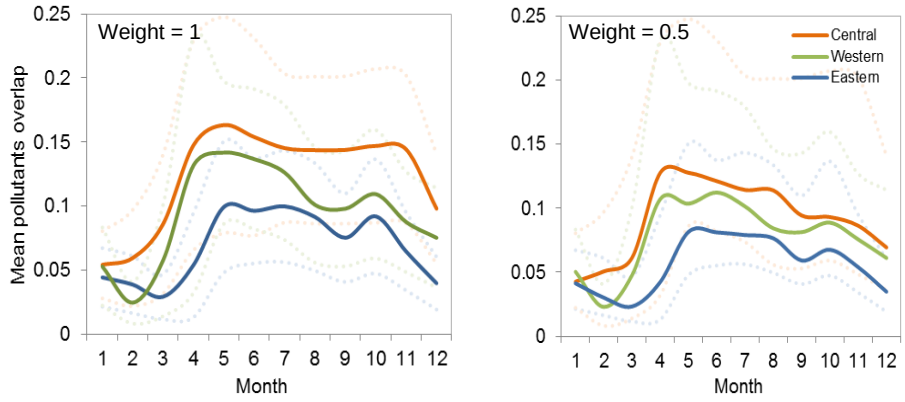
Figure 6.11. Overlap between year-round brown pelican locations (weighted by movement state) and surface pollutant concentrations for (a) all individuals, all weights, (b) individuals separated by breeding region and weighted by 1 and 0.5, and (c) individuals separated by sex and weighted by 1 and 0.5, Gulf of Mexico, 2013-2016. Dotted lines represent 95% confidence intervals of monthly mean values.

(a)

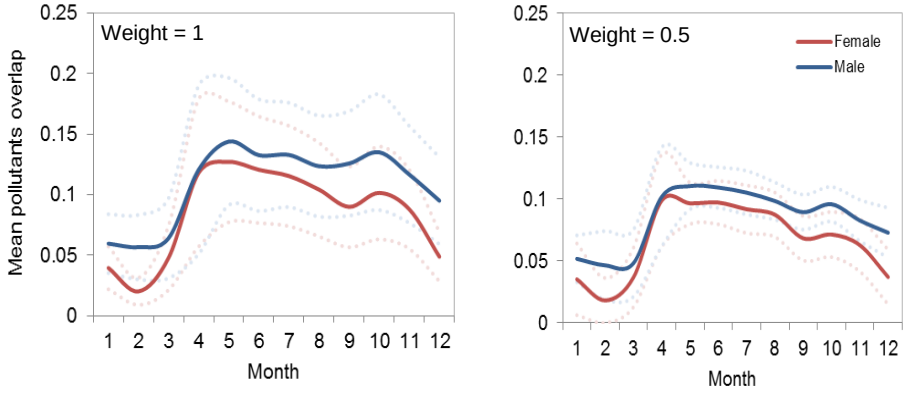


(b)

.



(c)



CHAPTER SEVEN

CONCLUSIONS

This dissertation includes several interconnected studies exploring the ecological factors that govern brown pelican habitat use and reproduction in the Gulf of Mexico. By using a variety of novel metrics including energy provisioning rates, feather corticosterone, and individual GPS tracking, I have attempted to fill gaps in understanding of brown pelican biology in this region and explore techniques for measuring the species' response to changes in environmental conditions.

Significant findings

Measuring the effects of transmitters on individuals is an important but overlooked initial step in collecting and interpreting tracking data (Hebblewhite and Haydon 2010, Vandenabeele *et al.* 2011). In Chapter Two, I demonstrated the feasibility of using individual GPS tracking technology on brown pelicans. I observed only short-term behavioral adjustments in the hours following capture and tagging; within a few days of capture, individuals carrying GPS transmitters displayed normal behavioral patterns. Tracked pelicans captured at nests continued nesting at the same sites and raised chicks with success rates comparable to those of untagged individuals.

Our understanding of density-dependent effects on seabird populations (Ashmole 1963) is confined primarily to temperate seabirds during the breeding period (*e.g.*, Wakefield *et al.* 2013). In Chapter Three, I quantified movement patterns of adults from

colonies of varying sizes and demonstrated a strong linear relationship between the number of nesting pairs of brown pelicans at breeding colonies and the distance traveled by adults during breeding-season foraging movements as well as post-breeding migration. These differences did not appear to affect chick condition, indicating that adults that travelled further to forage were still able to meet the energetic needs of nestlings. Colony size has rarely been explored as a possible driver of partial migration patterns in seabirds, and this chapter demonstrates its potential effects.

Snapshot measures of nestling health (Benson *et al.* 2003) offer a means of monitoring seabird reproductive output with limited resources. In Chapter Four, I compared the utility of two measures of nestling health, body condition index and feather corticosterone (Will *et al.* 2014), for predicting survival between different scales (individual, within-colony, between colony) and time periods (pre- and post-fledging). I demonstrated that, while both metrics were good predictors of individual nestling survival, feather corticosterone out-performed body condition index at broader scales and across larger time windows. Feather corticosterone provides an integrated measure of developmental stress and has significant potential to predict colony-wide nestling survival even after fledging.

Delivery of energy to seabird nestlings, which is a limiting factor in reproductive output, involves a complex set of interacting parameters (Jodice *et al.* 2006). In Chapter Five, I assessed the comparative roles of each of the three major components of energy delivery to pelican nestlings—feeding frequency, meal mass, and energy density—in driving nestling survival. I found that feeding frequency was the most important metric,

and that energy density varied little between prey species and was not a major component of variation in energy delivery rates. Biomass delivery was strongly related to reproductive output at the colony level, and prey delivery rates increased in the presence of small schooling fish including menhaden, thread herring, and anchovy (order Clupeiformes). These findings represent a departure from previous studies of seabirds at northern latitudes, which have found that differences in quality between prey species can drive variation in seabird reproductive success (Österblom *et al.* 2008).

Finally, in Chapter Six, I analyzed both habitat associations and surface pollutant exposure risk of brown pelicans tracked throughout the Gulf of Mexico during the annual cycle. I found strong associations with both net primary productivity (positive) and sea surface salinity (negative), which fluctuated during the year but were robust to different phenological stages and movement types. I observed the lowest availability of preferred habitat, as well as the highest probability of exposure to surface pollutants, during the early part of the breeding season and continuing throughout the breeding period. An additional spike in exposure risk occurred post-breeding, during a period that corresponds to molt in this species. Areas of suitable habitat were used by pelicans from a range of colonies, and breeders from different regions often occurred in the same locations during non-breeding.

Management implications

Damage from contamination events is often assessed as adult mortality alone (*e.g.*, Haney *et al.* 2014) or adult mortality plus direct loss of reproductive output

resulting from adult mortality (*e.g.*, *Deepwater Horizon* Natural Resource Damage Assessment Trustees 2016). My work demonstrates several other pathways by which damages to brown pelican populations could be incurred, which might be included in future efforts to better estimate and include the impact of sublethal and indirect population-level effects of acute or chronic environmental stressors.

Adult movement patterns and exposure: In Chapter Three, I describe the influence of colony size on adult movements both during and after breeding, and in Chapter Six I describe habitat factors driving the movements of pelicans outside the breeding season. Together, these chapters demonstrate that adult pelicans present in a given region may not be breeding locally. Particularly during the non-breeding season, breeders originating from colonies throughout the northern Gulf often occupy the same areas of suitable habitat. My results indicate that the process of determining the affected population for a contamination event should consider 1) the time of year and phase of the annual cycle during which the event occurs; 2) the location of the event in relation to both breeding colonies and preferred at-sea habitat, 3) the sizes of breeding colonies throughout the local area, and 4) other regions from which affected individuals might originate. Colonies outside the affected area, particularly very large colonies, should be monitored in subsequent years to assess the effects of potential breeding adult exposure.

Nestling development and survival: In Chapter Four, I demonstrate that elevated nestling stress during early development can cause increases in both pre- and post-fledging mortality. Contaminants in the environment can increase nestling stress directly, through exposure to substances either beached or transferred on adult plumage,

or indirectly, through decreases in feeding rates due to prey depletion or changes in adult condition. Either pathway would alter developmental conditions and could cause long-term effects on nestling survival and fitness. Measuring stress levels in nestlings has a great deal of potential for both long-term monitoring of baseline conditions and quantification of the effects of environmental disturbances or fluctuations. The fact that data collection and storage can be accomplished using minimal personnel and resources makes this a particularly promising tool for developing long-term data banks and detecting population-level change.

Prey resources: In Chapters Three and Four, I describe the dependence of nestling survival on the presence of sufficient prey biomass, particularly of small schooling fish. While effects on fish communities can be quantified following environmental perturbations, the repercussions of these effects on top predator populations are more difficult to measure. This study provides a basis for predicting the effects of prey depletion on reproductive success in brown pelicans, and thus estimating the cascading impact of population declines at lower trophic levels. Such effects could be included in future damage assessments, and rehabilitation of prey populations might be considered as a potential mitigation tool given its direct and quantifiable effects on reproductive output, stress, and, potentially, long-term survival and fitness of individuals.

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