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GROUND-NESTING BIRDS IN A CHANGING CLIMATE: CASE STUDIES OF PROXIMATE BEHAVIORAL MECHANISMS USED BY SKIMMERS AND TERNS TO ADDRESS SEASONAL VARIATION IN RESOURCES

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GROUND-NESTING BIRDS IN A CHANGING CLIMATE: CASE STUDIES OF PROXIMATE BEHAVIORAL MECHANISMS USED BY SKIMMERS AND TERNS TO ADDRESS SEASONAL VARIATION IN RESOURCES

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BY THE COMMITTEE CONSISTING OF

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ABSTRACT

Understanding how species will adapt to anthropogenic climate change is one of the greatest challenges for ecologists and evolutionary biologists. For organisms with low dispersal abilities, rapid adaptation will often be critical for survival. Some species, primarily microorganisms and invertebrates with short generation times, might be able to adapt to changing environmental conditions or evolve in response to climate change. For species with longer generation times, the unusual rate and extent of anthropogenic alterations of the environment may exceed the capacity of mechanisms that populations have evolved to deal with environmental change. It has been posited that behavioral plasticity can reduce exposure to selective pressures and shield population from climate extremes. For this dissertation, I focus upon behavioral mechanisms that are used by individuals and populations to mitigate selective influences upon reproduction. Specifically, the chapters in this dissertation focus on dietary plasticity, alteration in parental reproductive strategies, and seasonal alteration in migration strategies. Combined, the three chapters provide support that phenotypic plasticity in behavior can be an important mechanism used address varying selective pressures in changing environments for longer lived species such as the Black Skimmer and Gull-billed Tern. For dietary generalists, having a degree of opportunism is valuable in changing climates where food resources are vulnerable to changing climactic conditions. Having the ability to alter parental investment, in the form of nest attendance and offspring provisioning can influence offspring survival by accelerating the advancement of offspring to the next developmental stage. And by adjusting migration strategies, individuals can control

investment in time and energy allocation which thereby influences both reproduction and individual survival.

INTRODUCTION

Coastal ecosystems are some of the most productive and most complex ecosystems in the world as they form a dynamic interface between terrestrial, marine, and freshwater systems (Deegan *et al*. 2007). Understanding avian responses to changes within these ecosystems is critical as both the systems themselves and the species that use them are anticipated to be greatly impacted by global climate change, urban development, and synergistic interactions between the two (Gannes 2001, Palestis 2014).

Ground-nesting bird species in the coastal zone are especially vulnerable because aspects of climate change influence populations on multiple levels (individual to population scale) and throughout different stages of the annual cycle. Climate driven impacts have already been documented in marine, terrestrial, and freshwater environments, e.g., changes in range, abundance, density, phenology, and migration patterns (Hughes 2000, Walther *et al*. 2002). Sea level rise (SLR) is already influencing nesting grounds for islandic nesting species (Church *et al*. 2001) and increased sea surface temperatures (SST) and ocean acidification have the potential to radically change coastal and aquatic food webs. There is concern that increased air and water temperatures in oceanic and freshwater systems could shift marine food webs from a high productivity assemblage to a low productivity community lacking in energetically important food resources for birds and other aquatic life that could greatly impact populations that are dependent upon particular prey species (Veit *et al*. 1997).

Understanding how species will adapt to anthropogenic climate change is one of the greatest challenges for ecologists and evolutionary biologists (Visser 2008). For organisms with low dispersal abilities, rapid adaptation will often be critical for survival.

Some species, primarily microorganisms and invertebrates with short generation times, might be able to adapt to changing environmental conditions or evolve in response to climate change. But for species with longer generation times, the unusual rate and extent of anthropogenic alterations of the environment may exceed the capacity of developmental, genetic, and demographic mechanisms that populations have evolved to deal with environmental change. It has been posited that behavioral plasticity can reduce exposure to selective pressures and shield population from climate extremes (Huey *et al*. 2012, Muňoz 2022) termed the Bogert effect but this has so far only been applied to invertebrate and lizard species.

Within the context of life history theory, there is a vast amount of research that has been conducted on life history traits, strategies, evolution, and selective pressures (Stearns 1976, 1977; Bell 1980; Charlesworth 1980; Warner 1984; Reznick 1985, Partridge and Harvey 1985,1988; Bell and Koufopanou 1986). Environmental pressures can vary across latitudes and within locations such that it creates variation in life history strategies used to mitigate impacts to survival and reproductive success (Stearns 1989, Bright Ross *et al*. 2020. Individuals must negotiate tradeoffs between how much time or energy they should invest in reproduction and how much goes to self-maintenance and survival (Martin 1987). These tradeoffs pertain to behavior and physiology that ultimately determine an organism’s overall life-history strategy (Rickleffs 1969, Burger 1982, Sargeant *et al*. 1984, Amat and Masero 2004, Lima 2008, 2009). This variation can reflect either phenotypic plasticity or genetic differentiation among populations in response to local adaptation to environmental conditions (Bradshaw and Holzapfel 2006, Charmantier *et al*. 2008), and there is evidence to suggest that phenotypic plasticity can lead to adaptive genetic changes creating a circular relationship between the environment and genetic components (Lundblad and Conway 2019).

The diversity of bird species within the Order Charadriiformes (shorebirds, waterbirds, and some seabirds) provides an opportunity to better understand how ground nesting species respond to seasonal environmental variation. These species are a dominant component of coastal habitats, and they represent important energy and nutrient transport linkages within estuaries and among coastal beaches, marsh, and upland habitats (Erwin et al. 2003). Many are already in decline with expected increases in vulnerability owing to SLR predictions and continued loss of coastal nesting habitat to urban development. It is estimated that 70% of the world’s human population will live within 10 miles of the coast by 2050 (Schlacher et al. 2008). This continued urban pressure combined with global climate change will continue to change the coastal environment. What will happen to coastal dependent species remains uncertain but indications suggest there will be important shifts in species ranges and population declines for species dependent upon the coastal zone (Veit *et al*. 1997).

There are over 350 Charadriid species that are globally distributed and highly diverse in life history strategies, morphology, behavior, and ecology (Clements 2000; Smith and Clark 2012). Most of the species within this order are distributed along coasts or freshwater, inland waterways. A smaller number have an annual cycle strategy that includes breeding in freshwater or terrestrial systems and spending the non-breeding season along the coast or at sea (Davenport *et al*. 2016). All species within this Order have some form of k-selected life history strategy that includes a longer lifespan and delayed sexual development (Schreiber and Burger 2002). Foraging strategies for this order are also quite varied with a continuum of generalist-specialist strategies. Many species have unique foraging constraints that prevent them from responding rapidly to changes in the prey base leaving them even more vulnerable to changes within the food web (Gremillet and Boulinier 2009). Migration strategies in the Charadriiformes range from partial migration to long-distance migration, although for many species these strategies are relatively unknown (Chapman *et al*. 2011). Migratory patterns are not uniform between species, populations, or individuals, and there is an impressive variation in the type of migratory behaviors that occur in the Charadriid order including the most famous circumpolar migration of the Arctic Tern (*Sterna paradisea*) from breeding grounds in Alaska to wintering grounds in Antarctica (Alerstam 1990; Egevang *et al*. 2009).

For this dissertation, I focus upon behavioral mechanisms, or tradeoffs that are used by individuals and populations to mitigate selective influences upon reproduction. Specifically, the chapters focus on dietary plasticity, alteration in parental reproductive strategies, and alteration in migration strategies to examine behavioral mechanisms that longer lived species may use to mitigate seasonal variation. Chapter 1 is entitled, "Dietary Plasticity Mitigates Impacts to Reproduction for the Gull-billed Tern *Gelochelidon nilotica* in Coastal Southern California During Abnormally Warm Sea Surface Temperature Events". Dietary plasticity has long been an important focus of avian research to understand how seabirds may alter their foraging strategies to address seasonal variation in resources and potential impacts upon reproductive success. This research focus has become increasingly important with heightened awareness of global climate change's impacts upon both avian reproductive activities and shifting prey resource dynamics (Piat et al. 2020). For this chapter I focused research upon three goals: 1) monitoring Gull-billed Tern diet variation during the breeding season using analyses of regurgitated pellets, 2) monitoring an important food source for the Gull-billed Tern that is typically ubiquitous but has declined in density over time at the study location, and 3) ascertain if there is a discernable relationship between declining seasonal resources and annual Gull-billed Tern reproductive success. I hypothesize that: (1) annual variation in Pacific sand crab (*Emerita analoga*) density will be reflected in the tern diet and (2) *Emerita analoga* availability will drive Gull-billed Tern annual reproductive success.

Chapter two of this dissertation is entitled, “Selective pressures influence a grow fast, fly young strategy for Black Skimmers nesting in the Peruvian Amazon”. For this chapter, I compared ‘pace-of-life’ parameters across the Black Skimmer breeding range to test whether inter-population variation adheres to typical latitudinal patterns observed in other species. Variation in biotic and abiotic stressors (e.g., predation, food limitation, extreme temperatures, drought, competition, growth in stressful conditions) can create challenges that influence how organisms resolve tradeoffs during different periods in the annual cycle (Boonstra 2013; Wingfield 2013; Ferguson et al. 2018). As a general means of comparing life histories, species, populations, or individuals can be aligned along a 'fast-slow' pace-of-life continuum depending upon how they resolve fundamental life-history tradeoffs (Ricklefs 1997, Ricklefs and Wikelski 2002). The Pace of Life Syndrome (POLS) provides a framework for understanding how life-history traits and suites of behavioral and physiological traits coevolve in response to environmental conditions (Reale et al., 2010, Møller and Garamszegi 2012, Niemelä et al. 2013, Londono et al. 2015, Pap et al. 2015, Mathot and Frankenhuis 2018, Sol et al. 2018). In general, in temperate populations, where pronounced seasonality may limit the number and duration of reproductive opportunities, we expect faster POLS; whereas a slower POLS is typical of tropical populations that are free from some of the time constraints that affect temperate organisms (Ricklefs and Wikelski 2002, Wikelski et al. 2003, Wiersma et al. 2007). New life history data of a tropical-nesting Black Skimmer population in Manu National Park, Peru is compared with data collected from the literature that describes Black Skimmer populations in North America and to a lesser extent from South America to examine skimmer life-history traits under the POLS framework. Research from the Praia de Totelão in the Brazilian Pantanal documented growth rates for Black Skimmers that were about 30% lower than rates reported in previous studies from Virginia, USA (Erwin 1977, Gordon et al. 2002). This comparison supports the hypothesis that tropical taxa grow more slowly than taxa from temperate regions (Schuchmann et al. 2022) and leads to the prediction that the tropical Manu population will also have a slower pace of life with more extended incubation periods and lower chick growth rates compared to North American populations. However, the increased daily likelihood of nest failure and the high availability of food associated with the Manu River could select for smaller clutch sizes, reduced incubation periods, and accelerated chick growth, which represents a fast pace of life strategy.

Finally, Chapter three entitled, “The “how” of migration: Proximate behavioral mechanisms that the Black Skimmer *Rynchops niger* uses to adjust migration strategies”, focuses upon migration strategies for a coastal nesting species closely tied to the coastal estuarine environment. Current migration research has begun to focus on how trade-offs and accompanying effects may vary with endogenous factors such as sex, body size, age, and sexual maturity (Dolbeer 1982, Hedenström 2007, Catry et al. 2005, Sergio et al. 2014). In cases of migratory behavior these tradeoffs may also incorporate exogenous factors such as weather, topography, habitat quality, and connectivity of stopover locations along the migration route (Liechti 2006, La Sorte et al. 2013, Kelly et al. 2016, Xu et al. 2019, Chen et al. 2020). We know, more or less, that migration arose in response to seasonal changes in the geographic distributions of resources (Rappole 2013) but the proximate mechanisms, or how birds alter or adjust these migration events, is still being realized (Schmaljohann 2017). Individuals can adjust migration strategies through any of several mechanisms, i.e., increasing average distance covered non-stop during the migration period, altering stopover behaviors, and taking advantage of wind effects and other weather variables. In this study we employ a GPS tracking system to generate the first detailed account of an Atlantic coast Black Skimmer migration and comparison of proximate behaviors among individuals. We first examine directness of migration route, migration speed and distance, active flight speed comparisons, and stopover duration to determine what mechanisms Black Skimmer uses to adjust migration strategies. Next, using finer-scale information provided by GPS telemetry, we focus upon answering three questions: 1) is differential migration an important influence on Black Skimmer migration strategies, 2) does the Black Skimmer use wind effects to alter autumn and spring migration strategies, and 3) what type of energy allocation strategy is used by skimmers during migration?

Combined, the three dissertation chapters provide support that phenotypic plasticity in behavior can be an important mechanism to address varying selective pressures in changing environments for longer lived species such as the Black Skimmer and Gull-billed Tern. For dietary generalists, having a degree of opportunism is valuable in changing climates where food resources are vulnerable to changing climactic conditions. Having the ability to alter parental investment, in the form of nest attendance and offspring provisioning can influence offspring survival by accelerating the advancement of offspring to the next developmental stage. And by adjusting migration strategies, individuals can control investment in time and energy allocation which thereby influences both reproduction and individual survival.

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CHAPTER 1: DIETARY PLASTICITY MITIGATES IMPACTS TO REPRODUCTION FOR THE GULL-BILLED TERN GELOCHELIDON NILOTICA IN COASTAL SOUTHERN CALIFORNIA DURING ABNORMALLY WARM SEA SURFACE TEMPERATURE EVENTS

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ABSTRACT

Large scale oceanic processes can have profound consequences for marine and coastal food webs. Mortality and reproductive related impacts to seabirds have been documented for decades, and current research suggests that dietary flexibility may be a key component by which birds can mitigate environmental variation. Our motivation for this research was to better understand how a dietary generalist in the coastal environment responds to changes in prey food availability. The Gull-billed Tern *Gelochelidon nilotica* is a coastal nesting species that has an opportunistic generalist diet. For this research, we monitored both tern diet and density of a main prey resource to examine how responsive these terns are to seasonal variation in prey resources. Our results documented that the loss of a ubiquitous prey resource did not appear to influence tern annual reproductive success even though, in some years, *Emerita analoga* comprised greater than 70% of Gull-billed Tern diet. During breeding season with warmer than average sea surface

temperatures, the Gull-billed Tern switched to a more terrestrial diet and focused aquatic foraging activities upon crustacean species that are more tolerant of warmer water temperatures. Dietary plasticity can be beneficial to mitigate variation in prey resource availability upon reproductive success, and the ability to respond rapidly to changes in resources may play an important role in how coastal species can acclimate or adapt to changes in the prey base.

INTRODUCTION

Dietary plasticity has long been an important focus of avian research in an attempt to understand how species may alter their foraging strategies to address seasonal change. This research focus has become increasingly important with heightened awareness of global climate change impacts upon both avian reproductive activities and shifting prey resource dynamics (Piatt *et al*. 2007). Considerable scientific effort has been expended to understand how seabirds respond to shifting prey resource distributions and its effect upon reproductive activities (reviewed by Einoder 2009). Seabirds are considered good sentinels to note changing prey resources because their diet choices typically reflect the occurrence of prey within foraging ranges making them sensitive to environmental change. Foraging parameters (e.g., foraging effort, success, and efficiency) have been documented to co-vary with environmental aspects, and links between seabird population pathology and global climate change have been documented (reviewed by Piatt *et al*. 2020, Parsons *et al*. 2008, Harding *et al*. 2006, see also Gremillet and Charmantier 2010).

Generalist predator foraging strategies can be difficult to understand given that these generalists feed on a variety of prey species at differing trophic levels. For some species, dietary flexibility may extend to prey within a particular taxon such as fish

(Hamer *et al*. 2007), while for other species, dietary flexibility may extend to a range of prey taxa (Schwemmer and Garthe 2007). Prey or diet switching has been observed in many species including gulls (Annett and Pierotti 1989; Schwemmer and Garthe 2007) and penguins (Booth *et al*. 2018 and references within). This diet switching allows for a flexible foraging strategy which provides organisms with a way in which to mitigate seasonal changes in prey resources through changes in foraging behavior.

From 2013 to 2016, the eastern Pacific Ocean experienced the largest marine heat wave on record with above normal seas surface temperatures (SST) due to a combination of the ‘Blob’, a persistent high-pressure system in the northeastern part of the Pacific Ocean (Di Lorenzo and Mantua 2016; Bond *et al*. 2015; Thompson *et al*. 2019), and a strong El Niňo Southern Oscillation (ENSO). The Blob extended as far south as Baja California by late 2013, and it was responsible for fisheries collapses and massive seabird die-offs (Bond *et al*. 2015; Piatt *et al*. 2020). In late 2014, conditions in Southern California waters were further compromised by the start of an ENSO that produced anomalous warm SST through 2016 (Cavole *et al*. 2016). These combined events had many impacts to marine ecosystems of the Northeast Pacific (Lonhart *et al*. 2019; Cavanaugh *et al*. 2019; Arafeh-Dalmeo *et al*. 2019; Rogers-Bennett and Catton 2019; Piatt *et al*. 2020) affecting higher trophic levels. Seabird declines in reproductive success (Ainley *et al*. 1995), range-wide shifts in seabird distribution, and high mortality (Velarde *et al*. 2015; Cavole *et al*. 2016; Piat *et al*. 2020) are documented regularly with strong ENSO events.

These above-normal SST events provided a unique opportunity to study the foraging ecology of a dietary generalist, the Gull-billed Tern *Gelochelidon nilotica* as one of the main prey resources for the Gull-billed Tern in southern California is Pacific sand crabs *Emerita analoga*, hereafter referenced as *Emerita* or Pacific sand crab, that was greatly impacted by both anthropogenic activities of beach nourishment and the effects of the ENSO-Blob above average SST (Wooldridge *et al*. 2016, Cavole *et al*. 2016).

The Gull-billed Tern ranges along both the Atlantic and Pacific Coasts of North America and is well known for its generalist diet foraging on a range of ephemerally abundant aquatic and terrestrial prey items across trophic levels in estuarine ecosystems of Europe, Africa, North America, and Australia (Bogliani *et al*. 1990; Sánchez *et al*. 1993; Sánchez *et al*. 2004; Dies *et al*. 2005; Molina *et al*. 2014; Goodenough 2014). It is not well understood how changes in prey resources might influence Gull-billed Tern reproduction as this particular species can alternate to other food resources when primary prey are not available (Bogliani *et al*. 1990; Dies *et al*. 2005). The Gull-billed Tern may be able to mitigate seasonal variation using flexible foraging strategies, e.g., diet and habitat switching such that there is not a detectable influence of diet variation upon reproductive activities. The alternative outcome of prey resource variation is that major changes in the prey base, e.g., loss of a ubiquitous food resource could negatively influence tern reproductive activities such as altering clutch size and the number of offspring produced.

To better understand the relationship between seasonal variation in food resources and influences upon reproductive activities of this estuarine generalist, we focused research upon three goals: monitoring variation in Gull-billed Tern diet during the breeding season using analyses of regurgitated pellets, monitoring *Emerita* density at six beaches within the tern’s foraging range and evaluating the relationship between seasonality of food resources and Gull-billed Tern reproductive success based upon the number of offspring produced. We hypothesize that: (1) annual variation in *Emerita* density will be reflected in the tern diet and (2) *Emerita* availability will drive Gull-billed Tern annual reproductive success. These comparisons contribute to the knowledge base of foraging ecology and will increase our understanding of the impacts of seasonal diet variation on reproductive success for coastal foraging and nesting species like the Gull-billed Tern.

METHODS

Study location

Research was conducted in the coastal estuarine ecosystems of South San Diego Bay and the Tijuana River Estuary in southern California (Fig. 1-1). The site is highly fragmented and comprised of multiple habitats including intertidal areas, sandy beaches, coastal strand, dune and transition habitats, invasive *Carpobrotus* sp.-dominated dunes, coastal marsh, and coastal sage scrub uplands interspersed among highly urbanized areas. The Gull-billed Tern nests in only one location in coastal southern California - at the South San Diego Bay National Wildlife Refuge, (32°35’56.81” N, 117°6’11.32” W, Fig. 1-1), herein referred to as the Refuge. The majority of tern foraging occurs within the Refuge, to the west and northwest along the Silver Strand peninsula, and south along the coast from the Refuge to the US-Mexico border that includes the Tijuana River National Estuarine Research Reserve and Border Field State Park (Goodenough 2014).

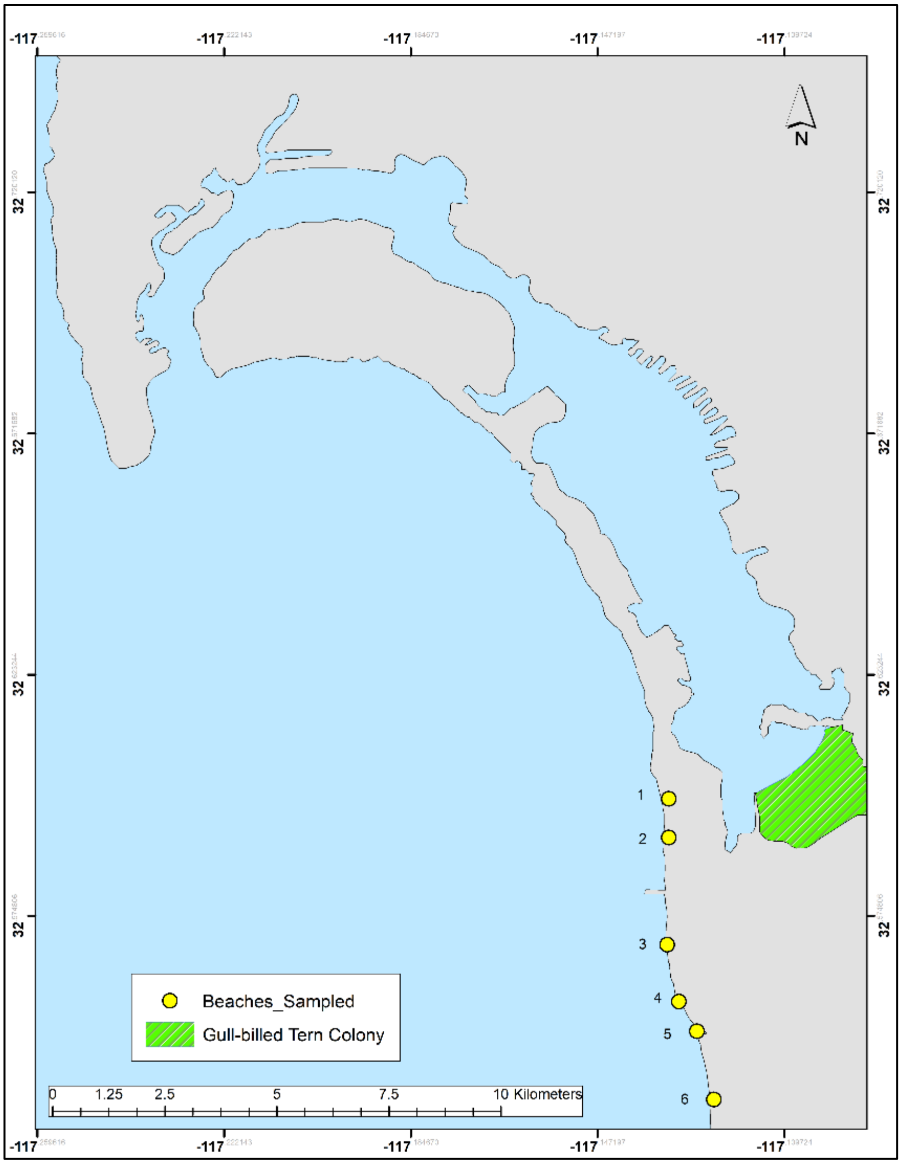

Figure 1-1: A map of the study area that encompasses the San Diego Bay National Wildlife Refuge, USN Silver Strand Training Complex, Imperial Beach, and Tijuana River National Estuarine Research Reserve south to the US-Mexico border. The green hatch marking indicates the South San Diego Bay National Wildlife Refuge where the Gull-billed Tern (*Gelochelidon nilotica*) breeding colony is located. Beach sampling locations for Pacific sand crab (*Emerita analoga*) are indicated with yellow circles and are listed from north to south: 1-Silver Strand Training Complex North (SSTC-N), 2-Silver Strand Training Complex South (SSTC-S), 3-Seacoast Drive- Imperial Beach, 4-North of the Tijuana River Mouth, 5-South of Tijuana River Mouth, 6-Border Field State Park.

We chose regurgitated pellet analyses to monitor tern diet as it is an inexpensive and non-invasive method to quantify diet. For certain avian species, i.e., owls, some seabirds and some waterbirds, prey items that are not completely digested are regurgitated in the form of pellets. These pellets can reveal diet composition, and this type of diet analysis has been previously employed as a method to monitor diet for terns and their allies (Duffy and Jackson 1986; Rosenberg and Cooper 1990; Bugoni and Vooren 2004; Mariano-Jelicich and Favero 2006; Favero and Becker 2007).

Pellets were collected within the Gull-billed Tern breeding colony in the San Diego Bay National Wildlife Refuge, California, USA from May through August over seven nesting seasons from 2012 through 2019 during weekly monitoring surveys, except for 2013 as colony dynamics were disrupted by an acanthocephalan-related mass mortality event (Patton *et al*. 2017). The pellets were dried at room temperature, dissected, and sorted under a dissecting scope to the lowest possible taxa depending on the extent of diagnostic features of the food items that were available for identification. Species of insects, fish, lizards, and chicks of birds were grouped together for analysis due to the degree of digestion in the pellets and/or small sample size. We quantified prey items within the pellets as frequency of occurrence (percentage of sample/all samples) as suggested by Duffy and Jackson (1986). Frequency of occurrence data were categorized by taxa and further grouped into aquatic versus terrestrial prey sources.

Previous telemetry research on the Gull-billed Tern home range in San Diego, California was used to select *Emerita* sampling locations, as the majority of foraging by the tern occurs within 10 km of the nesting colony located at the San Diego Bay National

Wildlife Refuge (Goodenough 2014). Six Pacific sand crab sampling locations were selected: four locations along the barrier beach of the Tijuana River estuary (Border Field State Park, North and South of the Tijuana River mouth, and Seacoast), and two along the coastal beaches of South San Diego Bay (SSTC-S and SSTC-N) located 1.5km west of the Gull-billed Tern breeding colony (see Table 1-1, Fig.1-1). All sampling locations were within 7 km of the breeding colony to ensure that the terns would use the resource if available during the breeding season.

Table 1-1: Location of beaches sampled for Pacific sand crab (*Emerita analoga*) density and distance to the Gull-billed Tern (*Gelochelidon nilotica*) breeding colony at the South San Diego Bay National Wildlife Refuge, San Diego, California, USA, 2013-2017.

ID	**Location Sampled**	**Latitude**	**Longitude**	**Distance from breeding colony (km)**
1- SSTC-N	west of Refuge	32.599933	-117.133348	2.25
2- SSTC-S	north of jetty, Imperial Beach	32.589477	-117.132766	2.75
3- Seacoast	Seacoast Drive, Imperial Beach	32.566203	-117.132959	4.0
4- North River	north of Tijuana River Mouth	32.554045	-117.127805	5.0
5- South River	south of Tijuana River Mouth	32.549328	-117.126059	5.5
6- Border Field	Border Field State Park	32.535982	-117.124007	6.2

San crab density sampling was conducted annually in June at lowest tide to coincide with peak energetic demands of nesting terns. At each beach location, we laid out a 800m transect in the intertidal zone of the beach parallel to the surf line. We collected sand crab samples every 200m along the transect with a 20cm diameter core. We took nine cores at each sampling location and documented the quantity and size of sand crab within each core.

For the statistical analyses, we compared seasonal diet information within Gull-billed Tern regurgitant pellets to assess tern diet variation, changing resource base e.g., aquatic base versus terrestrial, and the influence of prey resource variation upon the number of chicks raised to fledge and annual mean clutch. We used multiple Analysis of Variance (ANOVAs) to compare 1) annual variation in prey taxa across seven breeding seasons, 2) to compare variation in changing resource base, e.g., aquatic versus terrestrial base, and 3) to compare annual variation in *Emerita* density at six sampled beaches within San Diego County, California across five breeding seasons 2013 to 2017 to use as a proxy for *Emerita* availability within the tern home range. We did not use data from 2013 as there was a mass Gull-billed Tern colony die-off (Patton et al. 2017).

Reproductive data from the Inventory and Monitoring Program at San Diego Bay National Wildlife Refuge was used to calculate mean clutch size and the number of chicks produced, represented as fledgling-breeding pair ratios for the Gull-billed Tern breeding colony from 2012 through 2019. We used fledgling-breeding pair ratio as a proxy metric for seasonal reproductive success. Fledgling-breeding pair ratios were calculated by summing the number of fledglings produced for the season and dividing by the total number of breeding pairs for the season.

RESULTS

We collected 1103 pellets during the 2012, 2014- 2019 breeding seasons from May through August at the San Diego Bay National Wildlife Refuge, California, USA (Fig.1-1). Five taxa were identified within the Gull-billed Tern pellets, although only four taxa were consistently observed in the diet for all seasons sampled. Crab species included Pacific sand crab (*Emerita analoga*), Mexican fiddler crab (*Leptuca crenulata*), striped shorecrab (*Pachygrapsus crassipes*), and tuna crab (*Pleuroncodes planipes*). Lizard taxa included western fence lizard (*Sceloporus occidentalis*) and side-blotched lizard (*Uta stansburiana*). Insects included sphinx moth (*Hiles lineata*), tiger beetle (*Cincindela* sp.), and brine fly (Family Ephydridae). Avian prey items were present in the form of unfledged chicks including California Least Tern (*Sternula antillarum browni*), Western Snowy Plover (*Charadrius nivosus nivosus*), Horned Lark (*Eremophila alpestris*), Killdeer (*Charadrius vociferis*), and Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*). Fish were present for only one year and in small quantities and consisted of California killifish (*Fundulus parvipinnis*), and long-jawed mudsuckers (*Gillichthys mirabilis*) (Fig.1-2).

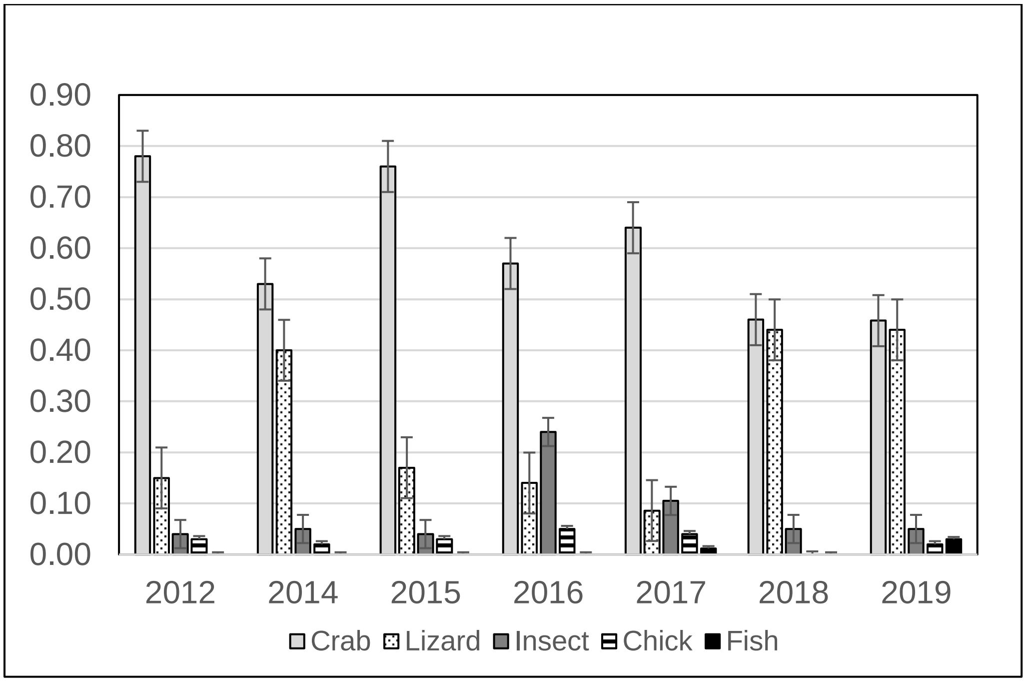

Figure 1-2: Frequency of occurrence of prey taxa in Gull-billed Tern (*Gelochelidon nilotica*) regurgitant pellets from 2012 through 2019. Prey taxa varied across breeding seasons ($F_{4,20} = 52.88$, $P < 0.01$). Crab taxa were dominant in all years (range 46-78%), followed by lizards (9-44%), insects (4-24%), avian species (0-5%), and fish (0-5%).

Prey taxa varied significantly across breeding seasons ($F_{4,20} = 52.88$, $P < 0.01$, Fig. 1-2). In all years, crab taxa were dominant prey species ranging from 79% (2012) to a low of 46% (2018 and 2019). Lizard contributions to diet ranged from a low of 9% (2017) to a high of 44% (2018-2019). Insect taxa were also variable ranging from a low of 4% (2015) to a high of 24% (2016). Avian contributions were low in all years with 0-5% abundance within the tern pellets. Fish species were only documented in 2017 and 2019 (1-3%; Fig. 1-2).

When comparing crab taxa, *Emerita* (sand crab) was at high frequency of abundance in 2012 (76%) that declined to just 5% in 2019 (Fig. 1-3). In contrast *Leptuca crenulata* (Mexican fiddler crab) increased in frequency from 2% (2012) to a high of 40-42% (2018-2019). *Pachygrapsis crassipes* (shore crab) remained in low abundance in all years (1-3%). The most striking change in diet was the inclusion of a novel prey item *Pleuroncodes planipes* (tuna crab) in the tern diet for the 2015 and 2016 breeding seasons. Southern range species such as *Pleuroncodes* are documented to shift distributions northward in ENSO influenced years (Stewart *et al*. 1984).

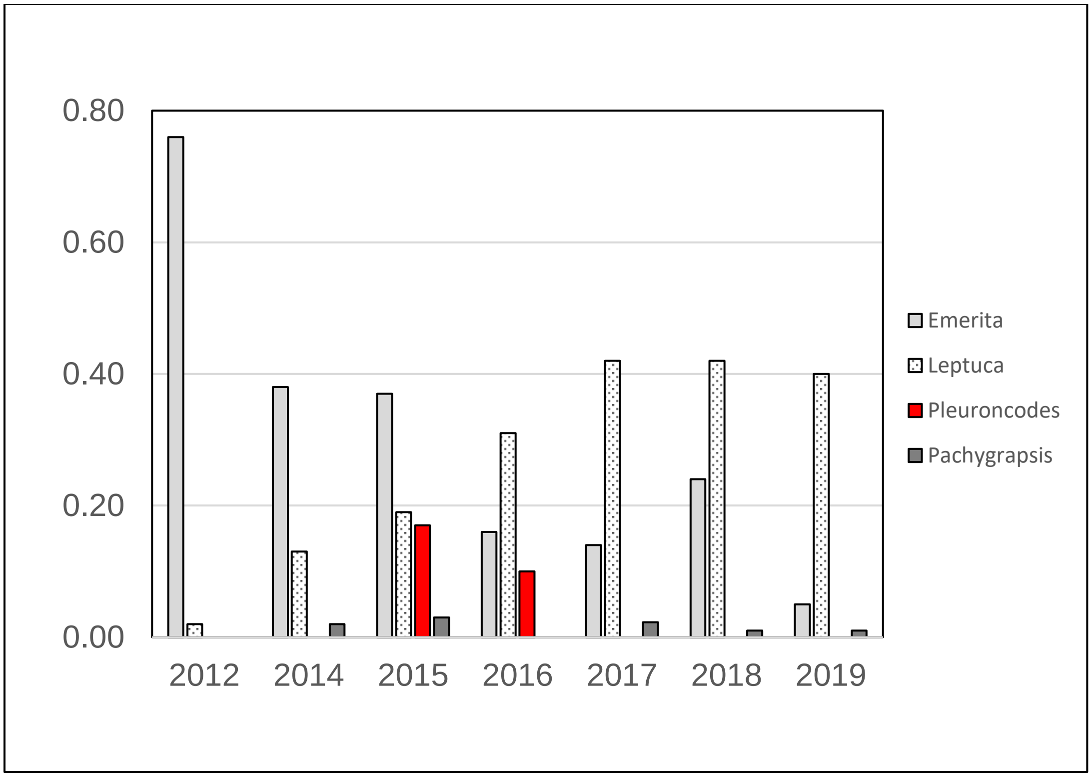

Figure 1-3: Crab species observed in the Gull-billed Tern diet, 2012-2019. There was an overall decline in Pacific sand crab *Emerita analoga* abundance in tern diet (78-5%) overlayed by an increase in Mexican fiddler crabs *Leptuca crenulata* (2-40%). Of note is the inclusion of *Pleuroncodes* sp., a southern ranging species in the Gull-billed Tern diet during the ENSO-influenced seasons of 2015-2016.

To understand if the prey base changed significantly among seasons, we binned the pellet frequency of abundance data into aquatic versus terrestrial sources. Prey sources were predominantly aquatic (53% to 78%; Fig. 1-4) although significant changes in prey base occurred across seasons ($F_{1,10} = 4.964$; $P < 0.001$). Crustaceans were a major component of the Gull-billed Tern diet in all years (range 53-78%). The increase or maintenance of aquatic resources in the years after the Gull-billed Tern die-off in 2013 appears to be due to increases in the consumption of other crab species which may be more temperature tolerant (i.e., increased proportions of fiddler crab, shoreline crab, and tuna crab, Fig. 1-4).

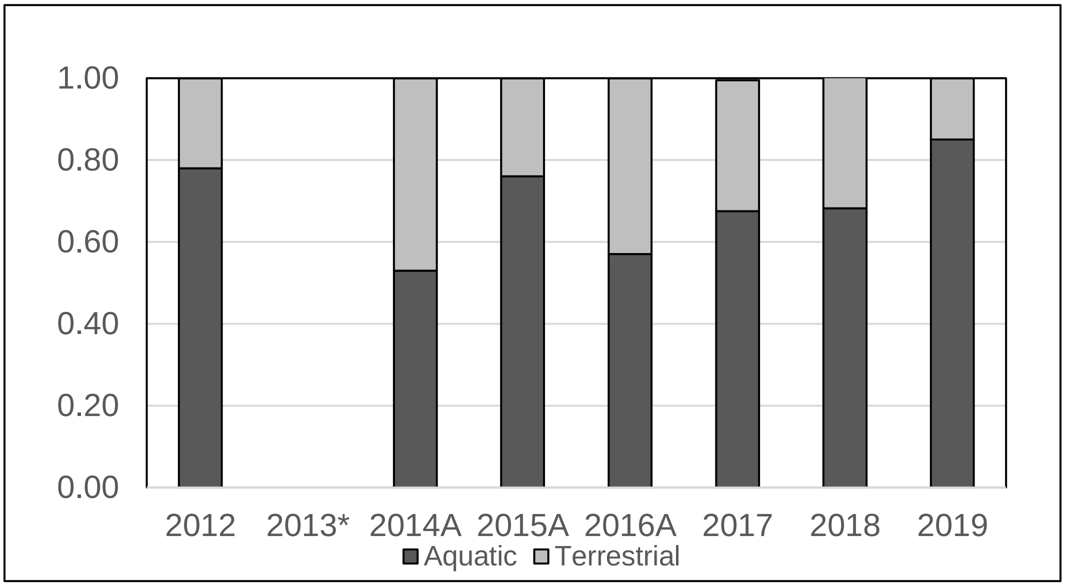

Figure 1-4: Gull-billed Tern frequency of abundance data from regurgitated tern pellets were binned into aquatic or terrestrial base. Aquatic resources were most dominant (range 53-85%) compared to terrestrial resources (15-47%). A= ENSO present. *Indicates that no diet information was used for analyses due to colony mortality (Patton et al. 2017).

The Gull-billed Tern had a mean fledgling-to-breeding pair ratio of 0.68 for the duration of the study (Table 1-2). Fledgling-breeding pair ratios were lower during the Blob-ENSO period but started to recover in 2017 after SST began to return to normal temperatures.

Table 1-2: Annual fledge to breeding pair ratios and mean clutch size for the Gull-billed Tern colony in San Diego, California for 2012-2019.

Year	No. Breeding Pairs	FL:PR ratio*	Mean Clutch Size
2012	62	0.61	2.28
2013	65[a]	0.02[a]	[a]
2014	10	0.70	1.50
2015	23	0.57	1.76
2016	35	0.49	1.95
2017	35	1.29	2.39
2018	38	0.71	1.78
2019	32	0.41	2.38

*FL:PR is the calculated fledgling to breeding pair ratio that is considered a metric of annual reproductive success. [a]In 2013, an Acanthocephaliasis outbreak occurred in the Gull-billed Tern breeding colony killing over 87% of the San Diego breeding population (Patton *et al*. 2017).

We regressed *Emerita* frequency in pellets with tern productivity and found no significant relationship between frequency of abundance of *Emerita* in the tern diet with fledgling to breeding pair ratios (Pearson Correlation = -0.002). Annual mean clutch size was used as a secondary metric of reproductive activity. Gull-billed Tern mean clutch size varied from a low of 1.50 eggs per clutch (2014) to a high of 2.39 eggs per clutch (2017) and differences were detected for the study period (t = 2187.7, df = 6, $P < 0.01$).

To assess sand crab density at beaches within the Gull-billed Tern home range, six beaches in south San Diego County, California were sampled for five breeding seasons (Table 1-1). We documented the overall highest density of sand crab across all six beaches in 2013, while the lowest density occurred in 2017. Sand crab density was highest at the South Tijuana River (S River), North Tijuana River (N River), and Border Field State Park (Border Field) sampling locations (Fig.1-5). Between 2013 and 2014, we documented a 57-96% decline in Emerita densities at five of the six beaches. Silver Strand Training Complex-South (SSTC-S) was the only beach to show an increase in *Emerita* abundance in 2013-14 (191%), although a strong decline was observed the following season at SSTC-S in 2014-15 (79%) with a continued decline through 2017 and an overall decline in sand crab density at all beaches across the five seasons sampled (Fig. 1-5). Beaches sampled in 2017 had the lowest density of *Emerita*. As sand crab density declined on the sampled beaches, abundance within the Gull-billed Tern diet also declined (Figs. 1-2,1-5).

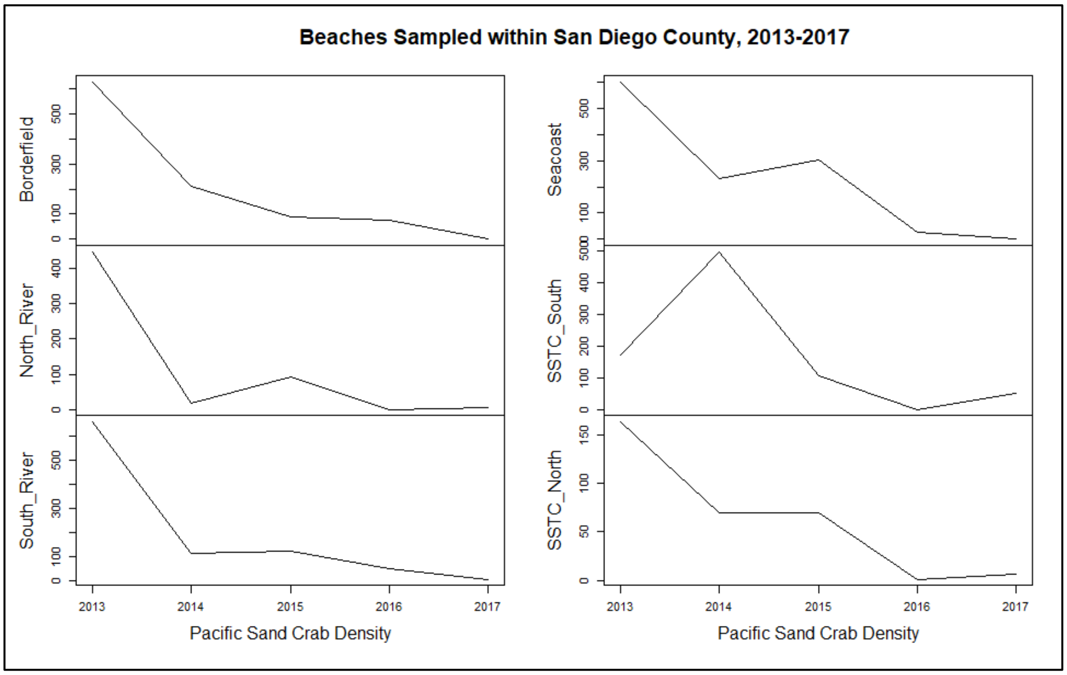

Figure 1-5: Observed decline in Pacific sand crab (*Emerita analoga*) densities at six beaches in South San Diego County, 2013-2017. Sample collection of sand crabs began in 2013 after Gull-billed Tern colony mortality. Six beach sampling locations included Silver Strand Training Complex North (SSTC-N), Silver Strand Training Complex South (SSTC-S), Seacoast Drive- Imperial Beach, North of the Tijuana River Mouth, South of Tijuana River Mouth, and Border Field State Park. Our study documented a strong decline in Pacific sand crab density at all six beaches over the five-year period monitored (-95.7%).

DISCUSSION

The effects of ENSO upon terrestrial and coastal species, are complex and not straightforward, i.e., secondary and tertiary primary productivity and predator-prey interactions (Holmgren *et al*. 2001, Goldenberg *et al*. 2017). The intent of our research was to better understand how a dietary generalist dependent upon coastal resources could weather significant variation in prey resource abundance during extended anomalous warm water periods. We hypothesized that annual variation in Pacific sand crab *Emerita analoga* density would be reflected in the Gull-billed Tern diet and that sand crab availability would drive tern annual reproductive success. While declines in sand crab density were observed in the Gull-billed Tern diet, no single species was identified as an important influence upon fledgling-breeding pair ratios, and hence reproductive success.

The Gull-billed Tern diet is a combination of aquatic and terrestrial prey that appears to alternate with seasonal availability of these resources. Prior to 2013, the Gull-billed Tern diet was dominated by Pacific sand crab [60-76% of diet, (Goodenough 2014)]. This sand crab can be super-abundant, reaching tens of thousands per square meter and comprise over 80-90% of intertidal invertebrate biomass on beaches in southern California that is an important prey contribution to coastal nesting birds such as the Gull-billed Tern and migrating shorebirds (Dugan *et al*. 1991, 1994, 2003). Warmer "Blob"-related SST at the end of 2013 may have precipitated a collapse of Emerita that resulted in lower densities in 2014. The combined influences of the 'Blob' and the ENSO from late 2013 through 2016 had strong negative impacts on sand crab population densities and recruitment along southern San Diego Beaches that was also observed in other studies occurring during the same period as our research (Wooldridge *et al*. 2016).

During the warmer than average years of 2014-2016, aquatic prey in the Gull-billed Tern diet declined while terrestrial prey increased (e.g., lizards, flying insects, and avian species) in the Gull-billed Tern diet. We also documented a switch from sand crabs to temporarily more abundant crustaceans (e.g., *Pleuroncodes planipes*) and a switch to crustaceans more resistant to warm water temperature effects (e.g., increased proportions of Mexican fiddler crabs *Leptuca crenulata*) which highlights the high degree of dietary plasticity evident in the Gull-billed Tern.

Dietary flexibility is beneficial in terms of mitigating variation in prey availability as what we observed with the Gull-billed Tern population in California, USA but it is a double-edged sword. The ability to diet and habitat switch has been suggested as an important factor in the stability of Black-headed Gull *Larus ridibundus* populations in the German Black Sea (Schwemmer and Garthe 2007). The upland, coastal estuarine, and ocean beach systems of San Diego may provide numerous opportunities for the tern to forage for aquatic and terrestrial prey and having access to these variable foraging habitats may allow the Gull-billed Tern a higher level of dietary plasticity in San Diego, which in turn influences the tern's ability to compensate for seasonality of prey resources. A higher degree of foraging success can then result in higher rates of reproductive success. Hence, a highly malleable foraging ecology could translate to a strong capability to withstand variation in prey resources associated with widescale oceanic events such as the 'Blob" and ENSO.

In contrast, there is evidence that being an opportunist can positively influence disease infection rates thereby impacting populations negatively through potential disease outbreaks (Hoodless *et al*. 2002, Morgan *et al*. 2007, Hoch *et al*. 2010, Byers *et al*. 2015, Patton *et al*. 2017, Daversa *et al*. 2018, Byers 2021). Frequent visits to parasite-infected areas over time can lead to exacerbated disease and parasite infections (Smith 2007). Sand crabs such as *Emerita analoga* are a known intermediate host of *Profilicollis altmanti* (Order Ancanthocephala), and both *Profilicollis altmani and P. kenti* have been responsible for mass mortalities of seaducks and sea otters that consume large quantities of crabs (Kreuder *et al*. 2003). The 2013 Gull-billed Tern colony mortality was a result of such parasite infection resulting in the loss of greater than 85% of the breeding population due to acanthocephaliasis (Patton *et al*. 2017). Increased SST in San Diego during 'the Blob' event in early 2013 may have resulted in a stress-induced decline in immunity for *Emerita* that resulted in increased parasite infection rates for the Gull-billed Tern later in May during the breeding season.

Annual Gull-billed Tern fledgling-breeding pair ratios and mean clutch size were lower during our study than in non-ENSO years and there was significant variation in clutch size means across years. The variation we observed in clutch size and fledgling-breeding pair ratios may have been due more to nesting inexperience of returning first time breeders than food resource influences (Klomp 1970, Pianka and Parker 1975, Crawford 1977) as productivity in later breeding seasons was similar to those observed prior to the ENSO-Blob event. Greater than 72% of the Gull-billed Tern breeding population returning to breed during 2014-2016 were young birds returning to nest for the first time (Patton unpub data). What is also of note is that sand crab densities have still not recovered to pre-ENSO years suggesting there may be additional influences upon *Emerita analoga* recruitment to southern California beaches that have not yet been identified.

Dietary generalists like the Gull-billed Tern may be able to detect key structural changes in coastal estuarine food webs under heavy influence of climate change. Hence, it is critical to continue to monitor Gull-billed Tern diet long term to understand the impacts of a changing climate. Diet research in Europe has documented significant variation in Gull-billed Tern chick growth rates when varying food resources, revealing that chicks fed only an invertebrate diet grew slower and fledged later than the chicks fed a vertebrate diet (Albano *et al*. 2011). Short term adjustments in diet influenced by ENSO induced changes may not have an appreciable impact upon lifetime reproductive success for species that can mitigate such variation as in what we observed with the Gull-billed Tern. But in years where important prey resources may be limited or impacted by large scale oceanic processes such as ENSO, a diet shift towards prey that is not as energetically beneficial for offspring could affect lifetime fitness depending upon the time scale of variation (Navarro-Lopez *et al*. 2014). Unfortunately, both environmental and anthropogenic stressors in concert with climate change are leading to changes in foraging strategies of marine and coastal species highlighting a critical need to continue diet research focused upon the relationship between foraging plasticity, tradeoffs, and the synergistic influences of global climate change upon important stages of the avian annual lifecycle.

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Research" (Fair *et al*. 2010). Gull-billed Tern diet sample collection occurred under US. Fish and Wildlife Service Migratory Bird Scientific Collection Permit MB36050A-0, a U.S. Fish and Wildlife Service San Diego Bay National Wildlife Refuge Complex Special Use Permit 81680-10002, and a California Scientific Collection Permit SC-6884. We would like to thank the U.S. Fish and Wildlife Service-San Diego Bay National Wildlife Refuge and California Department of Parks and Recreation for access to the Gull-billed Tern breeding colony and and assistance with fieldwork within state protected beaches. This project would have not been possible without the participation of numerous individuals assisting with Gull-billed Tern pellet collection and *Emerita analoga* sampling in south San Diego County: Lea Squires, Elizabeth Copper, Dalia Ruiz, Matt Sadowski, Robby Mraz, Sherry Lankston, Janne Torres, the US Fish and Wildlife Service Youth Conservation Corps (YCC), and volunteer students from MexCal at the Universidad Autónoma de Baja California, México. We would also like to thank current anonymous reviewers and Drs. Eli Bridge, Jeffrey Kelly, Lawrence Wieder, Rebecca Loraamm, and Torbjørn Haugassen for reviews of this manuscript.

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CHAPTER 2: SELECTIVE PRESSURES INFLUENCE A GROW FAST, FLY YOUNG STRATEGY FOR BLACK SKIMMERS RYNCHOPS NIGER NESTING IN THE PERUVIAN AMAZON

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ABSTRACT

Although selective factors are similar for populations across latitudes, the intensity and variation of these selective factors could drive variation in life history traits creating a gradient of population responses. Using data from an inland population of Black Skimmers on the Manu River in South America, we compared ‘pace-of-life’ parameters across the species range to test whether inter-population variation adhered to typical latitudinal patterns observed in other species. We found that mean clutch size, daily nest survival rate, hatching success, and incubation period did not vary across latitude. Manu chick growth rates were comparable to more northern populations; whereas provisioning was increased and time to fledging was decreased. We conclude that the Manu skimmers fall on the fast end of the pace-of-life spectrum versus the predicted slower pace of life that characterizes many other tropical species/populations. High food availability coupled with a tenuous nesting situation appeared to select for individuals that exploit abundant food resources and maximize chick growth rates, such that a reduced growth period limits exposure to floods and predators. The result is a pace of life that mimics that of many

northern bird populations, wherein food is seasonally abundant but only for a short period of time.

INTRODUCTION

Virtually all organisms must negotiate tradeoffs between how much time or energy they should invest in reproduction and how much goes to self-maintenance and survival (Stearns 1992). These tradeoffs pertain to behavior and physiology that ultimately determines an organism's overall life-history strategy (Martin 1987, 1996, Stearns 1989, 1992, Ricklefs 1997, Ricklefs and Wikelski 2002, Martin *et al*. 2006, Jetz et al. 2008). As a general means of comparing life histories, species, populations, or individuals can be aligned along a 'fast-slow' pace-of-life continuum depending upon how they resolve fundamental life-history tradeoffs (Ricklefs 1997, Ricklefs and Wikelski 2002). Organisms that prioritize reproduction over survival are considered to have a fast pace of life; whereas organisms that prioritize survival over reproduction have a slow pace of life.

The Pace of Life Syndrome (POLS) provides a framework for understanding how life-history traits and suites of behavioral and physiological traits coevolve in response to environmental conditions, and it posits that these traits should vary predictably across or within taxa under clearly defined circumstances (Reale *et al*., 2010, Møller and Garamszegi 2012, Niemelä *et al*. 2013, Londono *et al*. 2015, Pap *et al*. 2015, Mathot and Frankenhuis 2018, Sol *et al*. 2018). Populations with a 'slow' POLS should exhibit lower growth rates, delayed reproduction, longer lifespan, lower basal metabolic rates, and strong immune responses. Also, members of 'slow' populations are expected to avoid risky situations relative to 'fast' populations (Stamps 2007). In general, in temperate populations, where pronounced seasonality may limit the number and duration of reproductive opportunities, we expect faster POLS; whereas a slower POLS is typical of tropical populations that are free from some of the time constraints that affect temperate organisms (Ricklefs and Wikelski 2002, Wikelski *et al*. 2003, Wiersma *et al*. 2007). However, the underlying linkages between life-history, physiology, and behavior are not well understood and support for POLS has been ambiguous with examples of species and populations that do not fit the expected geographical POLS pattern (Royauté *et al*. 2018).

Variation in biotic and abiotic stressors (e.g., predation, food limitation, extreme temperatures, drought, competition, growth in stressful conditions) can create challenges that influence how organisms resolve tradeoffs during different periods in the annual cycle (Boonstra, 2013; Wingfield, 2013; Ferguson *et al*., 2018). Further, threat predictability can influence tradeoffs involved in mitigating threats. For example, nest site selection can change dramatically under varying scenarios of nest predation (Hunter *et al*. 2016). Similarly, environmental perturbations on tradeoffs can lead to variation in dietary choices and parental care strategies (Trakima *et al*. 2019) which may explain why some organisms do not fit within the expected POLS patterns. Complex systems of selective influences can therefore influence a nuanced relationship between life history, physiological, and behavioral traits.

For this research, we focus upon comparative studies of a bird species that nests across the Americas, with the aim of revealing potential links among environmental stressors, life-history trait variation, physiology, and behavior. The Black Skimmer (*Rynchops niger*) is a colonial nesting seabird whose breeding range spans the Americas from 40˚N to 38˚S. In North America, the Black Skimmer is predominantly a coastal species for the entirety of the annual cycle, whereas skimmers in South America nest inland in freshwater river and lake systems before migrating to coastal areas for the non-breeding season (Davenport *et al*. 2016, Gochfeld *et al*. 2020). The Black Skimmer has a unique style of foraging, whereby it ‘skims’ across the water surface collecting fish near the water’s surface (Zusi 1962, Blake 1985). Food availability for skimmer populations can vary greatly between marine and freshwater-based resources (Erwin 1977, Gordon *et al*. 2000). Hence, food availability, or lack thereof, likely influences several aspects of life history for the Black Skimmer (i.e., survival, reproductive success).

The Black Skimmer experiences a similar suite of threats to reproductive success across its breeding range (i.e., nest predation, flooding, and/or thermoregulatory threat). However, the intensity and timing of threats vary within and among populations. Nest predation is a common influence on life-history strategies of birds, although southern latitude populations are at higher risk of nest predation (reviewed by Lima 2009). Moreover, there may be an increased threat of predation for skimmers nesting in the Amazon Rainforest due to the proximity of nesting beaches to the surrounding forest and a relatively large suite of avian and terrestrial predators in the tropics as compared to temperate breeding locations (Groom 1992).

Flooding is also a common selective force for ground-nesting species that use coastal and riverine systems (Bailey et al. 2017, Maslo *et al*. 2016, van der Pol *et al*. 2010). Similar to predation threat, there is significant geographical variation in the type and intensity of flooding events. Coastal-nesting Black Skimmers are vulnerable to perigean spring tides (the highest tides of the year) that occur during the full and new moon. These events are lunar cycle related and most ground-nesting species respond by renesting either in a similar location or farther from the water's edge (O'Connell and Beck 2002, Brooks *et al*. 2014). In contrast, riverine systems are often more complicated and can have both annual cyclic flooding and unpredictable precipitation-influenced pulse flooding events (Gould 2003).

These threats combined with varying food conditions could influence variation in life-history traits associated with behavioral (parental effort during nesting and offspring care) and physiological traits (clutch size, chick growth rates). Our research combines new life history data of a tropical-nesting Black Skimmer population in Manu National Park, Peru, with data collected from the literature that describes Black Skimmer populations in North America and to a lesser extent from South America to examine skimmer life-history traits under the POLS framework (Table 1). Research from the Praia de Totelão in the Brazilian Pantanal documented growth rates for Black Skimmers that were about 30% lower than rates reported in previous studies from Virginia, USA. This comparison supports the hypothesis that tropical taxa grow more slowly than taxa from temperate regions (Schuchmann et al. 2022) and leads to the prediction that the tropical Manu population will also have a slower pace of life with more extended incubation periods and lower chick growth rates compared to North American populations. However, the increased daily likelihood of nest failure and the high availability of food associated with the Manu River could select for smaller clutch sizes, reduced incubation periods, and accelerated chick growth, which represents a fast pace of life strategy. Our research contributes to the POLS paradigm by investigating intra-specific latitudinal clines in life-history traits and offers a closer look at how selective influences may interact to produce behavioral-based tradeoffs in reproductive strategies.

METHODS

Study location

We monitored Black Skimmer nesting phenology within Manu National Park, Peru (11˚ 51' S 71˚19' W) for two breeding seasons in 2017 and 2018 (Fig. 2-1). The study site was a 47-km long stretch of the Manu River with associated beaches and oxbow lakes. In addition to the Black Skimmer, other waterbirds such as Large-billed Tern *Phaetusa simplex* and the Yellow-billed Tern *Sternula supercilliaris* nest on Manu River beaches created during the dry season when river water levels drop to expose sand along the inside banks of meander loops (Robinson and Terborgh 1997, Groom 1992, Davenport *et al*. 2016). The Manu River is located close to the Andes Mountain Range and is considered a white-water river due to high levels of suspended sediments and organic material from headwaters in the Andes. These inputs provide a source of nutrients which sustains high aquatic productivity (Fittkau et al. 1975; Osorio *et al*. 2011).

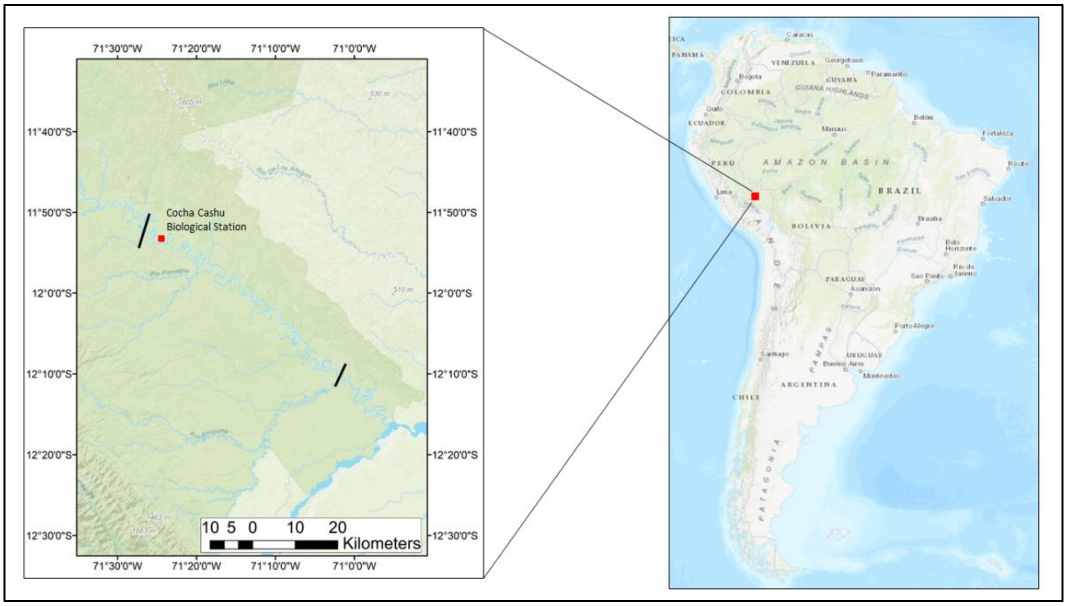

Figure 2-1: A Map of the location of Cocha Cashu Biological Station in Manu National Park, Peru. Red square denotes the Cocha Cashu Biological Station. Black bars denote the 47km stretch of the Manu Rio where fieldwork was completed in 2017-2018.

Field data collection

We conducted searches within the study site by boat from 01 July through 01 September 2017 and from July 17 through 30 September 2018. Nesting activity was detected by looking for skimmer presence and behaviors associated with nesting (i.e., courtship, nest scraping, egg incubation postures, or anti-predator displays). For all nests located, we noted the GPS location and the perpendicular distances of the nest from the water's edge and the forest edge. Nests were then monitored until they were depredated, hatched, or persisted through 28 days (Gochfeld et al. 2020). We considered a nest successful if one or more chicks hatched from the nest. We conducted twice-weekly visits to collect morphometric data on growing chicks and to document chick maturation to flight. Chicks were measured for wing chord (mm) and mass (g) and then banded with a combination of color bands to identify chicks uniquely. During successive checks, we remeasured wing chord, mass, and the growth of primary flight feathers (P7 through P10) and retrices (R1 through R6).

Forty Black Skimmer nests were selected (n = 20 each season) for detailed focal observation. We used a combination of video cameras and direct observation over the course of nest incubation and chick rearing to document nesting behavior (e.g. incubation bouts and chick provisioning) as well as depredation and other causes of nest failure. Nests were monitored until they hatched, failed, or reached 28 days. Chicks were monitored by camera until they were either depredated or they achieved 12 days of age. Once chicks became more mobile (typically 7-12 days), chick provisioning observations were conducted entirely from a boat at a mean distance of 100 meters with an 80mm spotting scope. For video observations we used E7000 action cameras (Akaso, China) coupled with a PowerCore 10000 portable charger (Anker Ltd, Japan) to collect continuous video with a 110° field of view for 6- to 8-hour bouts. Cameras were housed in a camouflaged waterproof case and set 2-5 meters from the nest.

We calculated daily nest survival rate (DSR) and hatch success following the Mayfield Method (Mayfield 1961, 1975). These calculations relied on three assumptions about daily nest survival data that were based on previous research by Erwin (1977, 1977b), Gordon (2000), and Dinsmore et al. 2008). First, we assumed that eggs were laid at one-day intervals, except in cases where age was confirmed by documentation of actual egg laying. Second, information from observations of clutch completion and the presence of chicks in the nest was used to estimate the timing of hatch. We assumed that one chick hatches per day (Gochfeld et al. 2020). Lastly, we assumed the incubation period for Manu skimmers lasts 23 days (Gochfeld et al. 2020). DSR calculations based on the Mayfield Method (Mayfield 1961, 1975) allowed for comparisons among Black Skimmer populations across North and South America (Custer and Mitchell 1987, Krannitz 1989, Owen and Pierce 2013), Specifically, DSR was calculated as:

$$DSR= (E/NF)/E$$

Where E = the sum of exposure days for all nest monitored, and NF= number of nests failed. Annual hatching success was calculated by summing the number of nests that successfully hatched at least one egg and dividing this sum by the total number of nests monitored.

Mean clutch size, incubation bout, total incubation period, and chick provisioning rates (±SD) were calculated for each year of the study, and differences between years were tested using a 2-tailed t-test ($p \leq 0.05$). All incubation bouts (nest relief) data were extracted from video cameras that were monitoring focal nests (see above).

Chick provisioning rates are a common metric used in seabird studies to quantify food availability (Sutherland et al. 2004). We used a combination of video and direct monitoring to collect information on provisioning episodes. Provisioning rates for each nest were calculated by summing the number of fish provisioned and dividing by number of offspring and further dividing by total amount of time monitored. Mean provisioning rate was then calculated per season and overall to obtain a mean provisioning rate for Manu nests monitored.

Chick growth rates were calculated using a logistic growth curve (Ricklefs 1967, 1973, 1976) which we compared to published Black Skimmer growth data (Erwin 1977, Erwin 1977b, Shew et al. 1994, Gordon et al. 2000, Shew and Collins 1990, Schuchmann et al. 2022). For the Manu data we calculated three measures: the growth rate constant, the inflection point, and the time in days to grow 90% of body mass. The Black Skimmer exhibits strong sexual dimorphism that is present in chicks as early as 12 days (Shew and Collins 1990). Hence, we calculated logistic growth curves separately for male and female chicks. Chicks were considered fledged when they were mature enough to complete sustained flight.

The growth rate constant (K) is proportional to the overall rate of nestling growth and allows direct comparisons regardless of adult body mass or asymptote of the growth curve and was calculated using the following formula (Ricklefs1967, 1973, 1976).

$$W(t) = \frac{A}{(1 + e^{K(t-t_1)})}$$

Where W(t) is body mass at age t, A= the asymptote. K= growth rate constant (days^{-1}), and t_1= age at inflection point. The inflection point was calculated as the asymptote divided by two (Ricklefs 1976). The third measure, (t_{10-90}) provides the time in days needed to grow 10 to 90% of body mass (Ricklefs 1967) and is expressed as

$$t_{10-90} = \frac{4.4}{K_G}$$

where K_G is the growth rate constant.

North and South American comparison data

We mined Black Skimmer data from the literature and compiled data on clutch size, total length of incubation period, chick provisioning rates, chick growth rates, and chick fledge rate (see Table 2-1). We completed a literature search using Web of Science (WoS) with keywords of Black Skimmer, *Rynchops niger*, *Rynchops niger cinerascens*, *Rynchops niger intercedens, Rynchops nigra,* daily nest survival, predation, flood, clutch size, growth rate, incubation period, fledgling rate. A total of 51 references were returned with 22 papers focused upon reproduction and foraging. In addition to the WoS results, we also searched the literature cited sections of published papers to attempt to include papers not incorporated into the WoS which resulted in the addition of four studies for a total of 26 publications. We did not use all publications found in our literature search as we required studies that included information on project sample size, means, and standard deviations to allow for weighted means calculation. We also selected studies that employed similar data collection methods. Not surprisingly, there were few studies which provided data for all parameters we wished to compare, and in some cases, we report data from the Manu population that have no testable comparison with published information. When possible, we calculated weighted means and 95% confidence intervals for nesting parameters to examine the significance of differences across populations. Means in the results are accompanied by 95% confidence intervals. See Table 2-1 summary for range of means information and literature sources used.

RESULTS

Field data

We monitored a total of 93 nests across the 2017 and 2018 breeding seasons. Manu DSR was calculated as 0.967 in 2017 and 0.983 in 2018. Overall nest success was 38% in 2017 and 46% in 2018, with higher hatching success in 2018. River flooding accounted for 60.9% of skimmer nest loss during the 2017 season (Table 2-1), whereas nest predation was the leading cause of nest loss in 2018, causing 55.3% of nest failure followed by river flooding (41.2%). Combined, nest predation and river pulse flooding accounted for 96% of nest failure in both years.

River flooding in Manu was variable between the 2017 and 2018 breeding seasons. Six strong precipitation events occurred during the 2017 breeding season which led to high flood waters until 02 August when the river began to recede. During this time period, water levels rose an estimated 2-5m, inundating playas from the Pakitza Park ranger checkpoint upriver 15 kilometers to the Cocha Cashu Biological Station. All but two nests initiated in July 2017 were destroyed by river flooding. Renesting occurred starting 04 August 2017 and continued through October. The 2018 breeding season was characterized by low water levels but there was one significant flood that occurred in late May-early July which did not greatly influence skimmer breeding as pairs were only in the initial stages of nest site selection. The lack of strong flooding in July 2018 created an opportunity for skimmers to begin nesting up to two weeks earlier in late June. Consequently, two breeding pairs already had chicks prior to the beginning of nest monitoring on July18, 2018. The majority of successful nesting in 2018 occurred relatively early in the season (17 July through 30 September).

North and South American comparisons

Daily nest survival rates calculated for North America populations were quite variable ranging from 0.7 to 0.982 within and among locations with 95% confidence intervals overlapping with the Manu population (Table 2). Likewise, confidence intervals for nest success overlapped (Table 2), although the most influential factors for nest loss did vary. In Manu, the two main influences of nest failure were nest predation and river pulse flooding. Combined, they accounted for 96% of nest failure in Manu. For the North American populations nest predation, spring tide flooding, human disturbance, extreme weather events, and food limitation act to influence nest success (Burger 1982). O’Connell and Beck (2002) observed that reproductive success was influenced by documented and presumed gull predation (84.4%) and spring tide flooding (16.7%). Nest predation, spring tide flooding, and heterospecific competition were also documented as contributors to nesting failure for colonies in Louisiana (Owens and Pierce 2013). More recent studies include human disturbance as a factor of influencing reproductive success as poorly protected skimmer colonies in Mississippi had reduced nest survival compared to undisturbed colonies (Dinsmore *et al*. 2008). Spring or perigean tide overwash in North America destroyed nests early in the breeding season (O’Connell and Beck 2002). Throughout the remainder of nesting, nest predation was most influential, although Gordon et al. (2000) documented decreased DSR and clutch means occurred during seasonal food limitations. Predation was documented as the main agent of ness and chick loss in the Pantanal (Schuchmann et al. 2022).

TABLE 2-1: List of life history parameters, range of means, and literature sources for data comparisons of Black Skimmer populations in Manu National Park, North America, and the Brazilian Pantanal.

Parameter	**Manu Mean (SD), 95%CI**	**North American weighted mean, 95% CI**	**North America Data**	**Brazilian Pantanal Data**
Clutch size (egg per clutch)	3.1(0.72), [2.95,3.27]	3.29 (0.24), [2.82, 3.75]	Range 1.3- 3.70	not provided
Incubation bout (mins)	8.65 (2.05), [8.54,8.76]		25-57	20.6 (15.65)
Egg incubation period (days)	22.25 (2.4), [21.70,22.65]	23.3 (0.48), [22.36,24.27]	Range 20-24	
Daily nest survival rate (DSR)	0.967 (2017) 0.983 (2018)		0.7- 98.2, variable with location	
Hatch Success	38% (2017) 46% (2018)		36-88% variable	
Provisioning rate (fish/young/hour)	3.6 (1.6), [3.17,3.21]		0.12-1.5	
Fledge rate (days)	18 (2.3), [17.89,18.11]		28-31.5 days	27*
Growth rate constant (K)	0.19 (m), 0.31 (f)		0.22 (m), 0.19 (f)- VA, 0.18- VA, 0.28- CA	0.12*
Upper Asymptote	299g (m), 239g (f)		326g (m), 260g (f)- VA Erwin, 366g (m)-CA, 271g (f-CA)	
Inflection point (I) (days)	14 (f), 23 (m)		CA-11.73 (f), 4.25 (m), VA 15 (m&f)	
$t_{(10\text{-}90)}$ (days)	23.1 (m), 14 (f)		20 (m-VA), 23(f-VA), 15.7 (CA)	37.7

The mean clutch size for the Manu population was 3.1 ± 0.15 eggs per clutch and it was not remarkable compared to other populations. Clutch size for the Manu skimmers fell between that of populations in Texas (3.09 ± 0.18 eggs) and Virginia (3.18 ± 0.1 eggs) and was clearly lower than more northerly populations in New York (3.70 ± 0.12

eggs). The Manu mean incubation period was 22.25 ± 0.55 days which was not different than known estimated incubation rates of North American nesters. The incubation periods between the two seasons monitored in Manu differed (t = -2.2298, df = 34, *P* = 0.032), but both seasons were similar to incubation rates found in the southeastern United States (Quinn 1989). This was not surprising as incubation can be somewhat flexible in timing depending upon nest laying sequence and disturbance issues (Gochfeld *et al*. 2020). Incubation periods in North America varied from a high of 23.85 ± 2.8 in South Carolina (Brooks *et al*. 2014) to a minimum of 21 ± 1.58 in Texas (Quinn 1990).

To quantify chick provisioning and incubation behavior, we attempted to observe a total of 93 clutches for both the 2017-18 breeding seasons, but we only obtained data from 35 nests as many were lost to river flooding and nest predation. We collected a total of 209 hours of incubation monitoring for the 35 nests. Results of a 2-tailed t-test found no difference between years (t = 1.9359, df = 17.932, *P* = 0.0688); therefore, results were combined to obtain a mean incubation bout or switch rate of 7.3 ± 1.71 bouts per hour or a mean of 8.65 ± 2.05 minutes (Table 1). Comparison of incubation behavior with other populations was frustrated by a lack of studies that documented nest relief or incubation in North America. A small study from a population in North Carolina (Leslie 2005) and unpublished data from a population in San Diego, California (Goodenough unpub. data) suggests that nest switches are relatively infrequent in North American populations ranging from 24 to 57 minutes. A study from the Brazilian Pantanal (Schuchmann et al 2022) reported incubation bouts of 20.6 ± 5.65 min.

Chick provisioning rates varied widely across populations. Manu chick provisioning rates were at least twice that of northern populations, with a mean of 3.6

±1.36 fish/chick/hour compared to other population means of 0.12 to 1.5 fish/chick/hour (Table 2-1). A mean of 0.5 fish per chick per hour is considered the average provisioning rate for populations in New York (Burger and Gochfeld 1990), although rates can vary depending upon food resources. New York has observed 1.5 fish per chick per hour in seasons with extremely good fish availability (Burger 1996). A lower provisioning rate of 0.12 fish per chick per hour (Gordon et al. 2000) was observed in Virginia in a food limited environment, and this provisioning rate was associated with chick starvation and slow chick growth rates.

As one might expect based on provisioning rates, Manu chicks grew faster than skimmer chicks in more northerly populations. We measured a total of 93 Manu chicks that survived up to 10-20 days for the two seasons monitored. Only 18% survived to fledge (n= 17) which was higher than the 3% fledge rate documented for a nesting colony in the Pantanal of Brazil (Schuchmann et al. 2022). Mean daily wing chord growth was 7.07± 3.67 mm per day and mean daily increase in mass was 8.43 ± 5.0 grams. Manu chicks attained flight at 18 ± 2.3 days with two individuals observed flying at least one kilometer at 17 days of age. These observations were somewhat unexpected because the in other Black Skimmer populations fledglings fly at 28 to 31 days of age (Table 2-1).

For the Manu data we calculated three growth measures: the growth rate constant, the inflection point (I), and the $t_{(10-90)}$ or time to reach 90% of adult body mass. Mean growth rate constants (K) were variable across populations with Manu females having the highest growth rate constant (K= 0.31) compared to Manu males (K= 0.19). Manu females also reached inflection points in growth faster than Manu males, 14 days versus

23 days (Fig. 2-2). We expected growth rates to vary between males and females as sexual dimorphism begins to show at 12 days (Shew and Collins 1990).

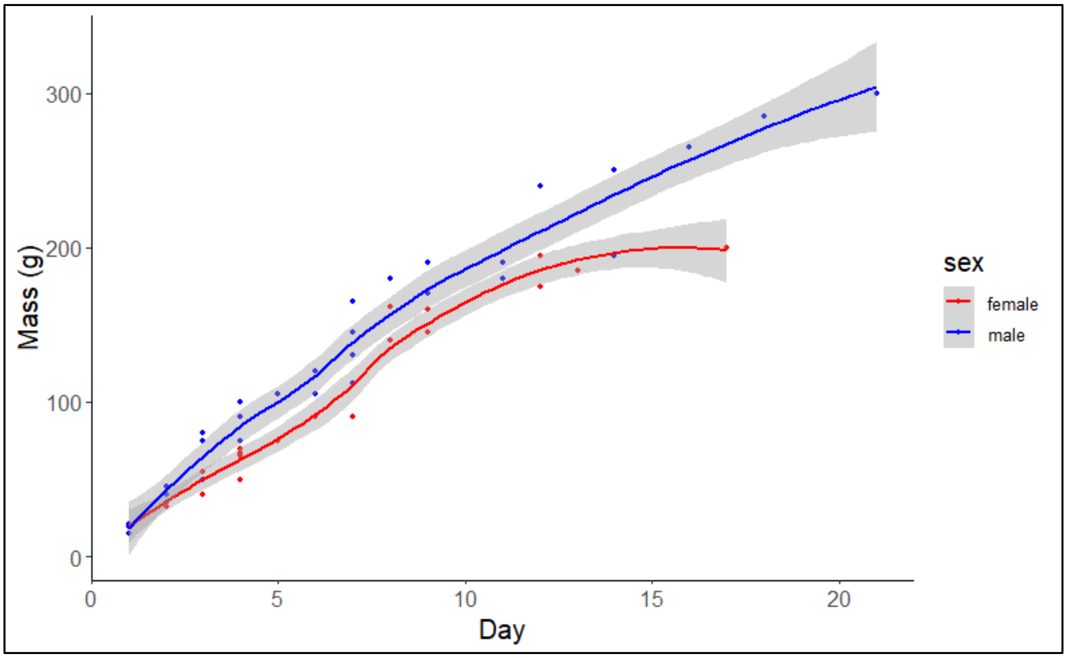

Figure 2-2: Logistic growth curves for the Manu Black Skimmer (*Rynchops niger*) chicks. Females grew faster (K= 0.31) and reached an inflection point of growth in 14 days compared to males who grew slower (K= 0.19) and reached an inflection point of growth in 23 days.

Similar chick growth results were found with the California study with females reaching inflection points faster than males (11.7 versus 14.3 days.) although no confidence intervals were provided to provide comparisons. A slightly different pattern was observed in Virginia (Erwin 1977) with males growing faster (K= 0.22) than females (K= 0.19). Even though the Manu chicks hatched at a smaller size than a published study in Virginia, 18g (Manu) versus 22g (Virginia). The Manu chicks were larger than those in Virginia by Day 3 and were on average 40 grams heavier by Day 11 (Fig. 2-3). The Pantanal study (Schuchmann et al 2022) had chicks hatching at 16.8 ± 1.6g, but further comparisons were not possible as only one chick survived beyond 5 days, although the authors provide a growth rate (K= 0.117) and a t $_{(10\text{-}90)}$ = 37.7 days for the single chick.

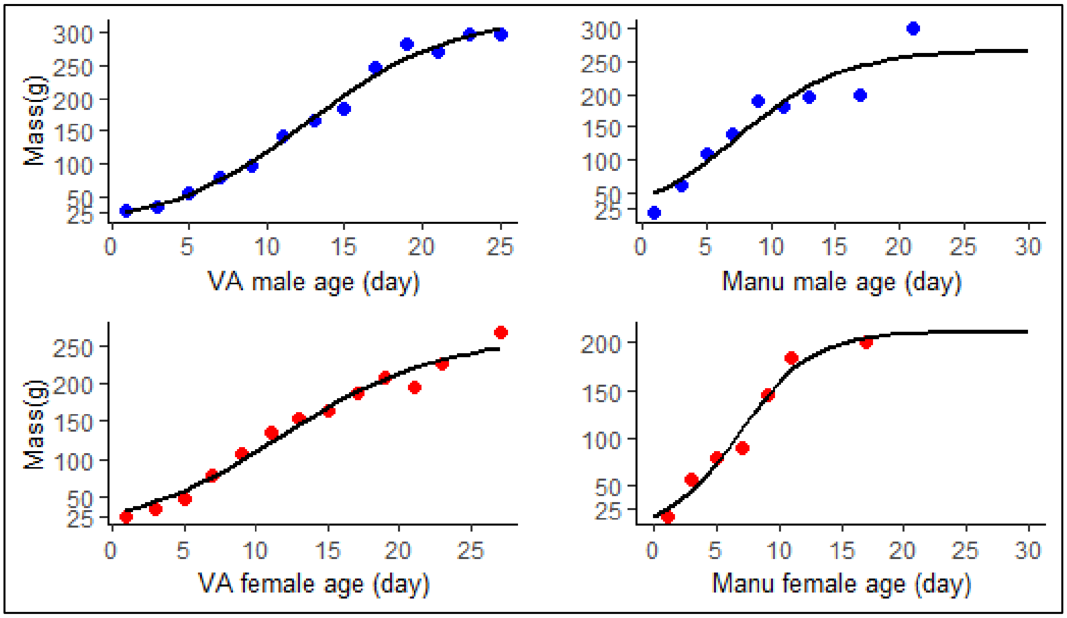

Figure 2-3: Logistic growth curves for two populations of the Black Skimmer (Rynchops niger). Figures on the left are growth curves from a Virginia population (Erwin 1977) for male chicks (upper left) and female chicks (lower left) while figures on the right are of Manu male (upper right) and female chicks (lower right). Blue circles= males, red circles= females. Manu female chicks had higher growth rate constant and reached inflection points (I) faster (K= 0.31, I=14 days) than Manu males (K= 0.19, I= 23 days) while the Virginia chicks sampled had slower but comparable growth rates to Manu males (VA males K= 0.22, VA females K= 0.19 with I= 17 days).

In regard to wingchord growth, only one study in California reported measures of Black Skimmer chicks (Schew and Collins 1990). There were considerable differences in wingchord between Manu and California. By Day 10, the Manu chicks had a mean wing chord of 101.6 mm which was double that of the Day 10 California chicks (wingchord = 50mm). The Manu chicks also matured at a faster rate, gaining flight capability as early as day 17 post hatching (mean 18 ± 2.3 days). Among North American populations, chicks did not fly until 28-31 days post hatching (Erwin 1977, Gochfeld and Burger 1990, Schew and Collins 1990, Gochfeld et al. 2020).

DISCUSSION

We compared life history traits across a latitudinal gradient for the Black Skimmer with the goal of examining trait variation within a POLS framework. We found no evidence of a latitudinal cline for most of the life history traits examined, and population comparisons were generally at odds with what is expected with POLS in relation to tropical vs temperate populations. We expected Manu skimmers to have smaller clutch size, higher nest failure, longer incubation periods, slower chick growth rates, and longer nestling periods compared to northern populations. There were no differences observed in clutch size, hatching success, or incubation period across populations, but there were marked differences in incubation bout or nest reliefs, chick provisioning rates, chick growth rates, and fledge period- parameters that can be highly influenced by adult behaviors. Manu chicks had growth rates higher but comparable to northern latitude populations and attained flight capability on average about 10 days earlier. Moreover, Manu provisioning rates were almost three times higher than those of northern populations.

The relatively high frequency of food provisioning, higher than expected chick growth rates and reduced nestling period in the Manu population indicates that these birds have altered parental investment in a manner that accelerates growth and development of their offspring. We argue that there is a tradeoff between nest success and food availability wherein tropical skimmers engage in riskier nesting behavior to exploit an abundant food resource. There are numerous examples of year to year variation in growth in the Charadriiformes (e.g., Lecroy and Collins 1972, Lecroy and Lecroy 1974, Langham and Hulsman 1986, Shew et al. 1994) providing evidence that growth patterns are not rigidly fixed and respond to environmental fluctuations (Shew et al. 1994). This finding is contrary to Ricklefs (1968, 1973), who suggests that avian growth rates are intrinsic and tend to be confined within narrow physiological limits that are imposed by body size and development. In theory, chick growth under the influence of predation threat without food limitation is expected to be high (Martin et al. 2011). Growth rates for Manu chicks were higher for females and comparable for males to North American populations but with differences in energy resource allocation to wing growth rather than daily mass gains. This pattern suggests that Manu skimmer chicks allocate resources to wing growth to gain flight capability in less than 20 days which is considerably faster than the mean of 28 days of North American populations (Gochfeld et al. 2020).

The ‘fast’ strategy exhibited by the Manu skimmers is likely a result of the unique breeding environment that the Manu skimmers occupy. Manu National Park is located within the Amazon Rainforest and adjacent to the Andes Mountain range, and this area maintains a great diversity of nest predators. In addition, the Manu River is prone to river pulse flooding throughout the breeding season. Cold weather fronts from the Andean cordillera often result in large scale river flooding during the dry season in the Amazon Basin, especially in areas close to the mountain range. Skimmers nesting along the Manu are subject to unpredictable flooding events throughout the nesting season, and these floods can destroy the vast majority of active nests in a single event. Birds respond to the flash flooding by renesting but with smaller clutches and less attachment over time. During the transition between dry to wet seasons, the increasing number of precipitation events results in a relocation to areas outside of Manu National Park (Davenport et al.

2016). Therefore, there would be strong selective pressure to shorten the nesting and chick rearing periods through behavioral means.

Monitoring food provisioning of young in conjunction with their growth rates can provide insight into the selective influences that shape breeding behavior and life histories (Sutherland et al. 2004). The almost three-fold provisioning rates and accompanying chick growth rates among the Manu skimmers suggest that food is not a limiting resource for this population. Abundant food resources located close to chosen nest locations can result in parents needing less time for self-care and having more time and energy to participate in offspring care (Bost et al. 2009; Guse et al. 2009; Christensen-Dalsgaard et al. 2018). Contrarily, a limited food supply can severely limit parental care including behaviors that mitigate the impacts of predation (Ghalambor and Martin 2001, Martin et al. 2011).

Although we did not directly sample food resources available to the Black Skimmer, we feel confident that chick provisioning provided an adequate proxy for food availability for the Black Skimmer. The Manu River has high food availability due to nutrient inputs from headwaters in the Andes. Hence, skimmers have the nutritional resources necessary to support rapid chick growth via an increased provisioning rate. The combination of selective pressures for shortened nesting periods and abundant food resources is the best apparent explanation for rapid chick growth and early fledging in the Manu skimmer population. As a result, we see a pace of life on the Manu River that mimics that of many northern bird populations, wherein seasonally abundant food resources appear to select for abbreviated bouts of reproduction.

Several studies have linked predation risk to faster offspring development, shorter nesting periods, and attainment of flight at lower body mass (Martin and Li 1992, Martin 1995, Bosque and Bosque 1995, Martin 2002, Lima 2009, Martin et al. 2011). Responses to flood threats among ground nesting birds are variable, with some species renesting in areas farther away from the water's edge; whereas other species simply renest in the same conditions (Bailey et al. 2017). Responses to these different threats might be due to perception of the species studied as well as the predictability and intensity of the threat. Seaside Sparrows (*Ammodramus maritimus*) appear to respond to predictable predation threats by nesting at lower nest heights in years with higher predation risk. However, in years where the threat of flooding is prevalent, sparrows will place nests higher off the ground but only after nest failure from flooding (Hunter et al. 2017). Our data from the Manu River suggests that Black Skimmers may also be subject to alternating threats from floods and predators and understanding how species process these multiple-threat trade-offs could help shed light on conservation problems of the Black Skimmer in North America and other ground nesting species globally.

Growth rate plasticity in response to resource availability is a universal feature of animal life history (reviewed by Dmitriew 2011), however the long-term consequences associated with resource limitation, post-natal growth rates, and maturation to particular life stages are documented only for a few species. Faster post-natal growth and maturity could be disadvantageous because of alterations to offspring phenotype and quality (Arendt 1997, Martin et al. 2011); On the other hand, rapid development can be offset by compensatory growth during a juvenile period characterized by evening out maturation across different systems and/or delays in reaching the adult stage (Metcalfe and

Monaghan 2001). Growth rates are flexible and are usually regulated at optimal rather than maximal rates, such that the rate can be increased when selection pressures favor increased size at a particular age (Metcalfe and Monaghan 2001, Dmitriew 2011). Our understanding of the underlying causes of growth rate variation among species with diverse life histories remains a critical focus of research.

Lastly, we cannot determine whether the unique characteristics of the Manu skimmers are evolved life history traits or instances of phenotypic plasticity. Colonization of new habitats and even new hemispheres is sometimes associated with rapid behavioral changes that can only be attributable to phenotypic plasticity (i.e., Areta et al 2021). Differentiating between evolution and plasticity in life-history traits calls for more investigations of species with extensive breeding ranges that ideally span temperate and tropic latitudes. Unfortunately, there is considerable geographical bias with regard to documentation of fundamental life history traits--temperate bird studies outnumber those of tropical birds by a margin of greater than 100 to one (Stutchbury and Morton 2001). Hence, many questions about adaptation *vs*. phenotypic plasticity await a more complete scientific record regarding life histories in the tropics. Our study is one of several that demonstrate how in the tropics we often find environmental circumstances that lead to unexpected responses in life-history characteristics.

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CHAPTER 3: THE “HOW OF MIGRATION: PROXIMATE BEHAVIORAL MECHANISMS THE BLACK SKIMMER USES TO ADJUST MIGRATION STRATEGIES

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ABSTRACT

Numerous studies describe a seasonal influence upon avian migration whereby individual migrants advance their spring arrival by varied responses in speed and duration of migration. Individuals can optimize migration strategies through use of a number of proximate behavioral mechanisms. A GPS tracking system was used to generate data to examine directness of migration route, migration speed and distance, active flight speed, and stopover duration to determine proximate behavioral mechanisms that the Black Skimmer may use to optimize migration. Using finer-scale information provided by GPS telemetry, the study focused upon answering three questions: 1) is differential migration an important influence on Black Skimmer migration strategies, 2) does the Black Skimmer use wind assist to alter autumn and spring migration duration and speed, and 3) what type of energy acquisition strategy is used by skimmers during migration. Results of the study suggest the Black Skimmer uses an energy minimization strategy in the autumn with slower migration speed, flight speed, and extended use of stop over locations. During the spring, the Black Skimmer switches to a time minimization strategy with faster migration speed, faster flight speeds, and decreased duration of rest stops. While

there were no differences in distances traveled, there were sex-related differences in stop over dynamics. Wind speeds between active travel and stationary locations were similar suggesting individuals do not use headwinds or tailwinds to assist with active travel segments. Energy acquisition was a mixed strategy consisting of traditional stop over and fly-forage components.

INTRODUCTION

Migratory behavior and associated routes are often considered to be optimized in a manner that maximizes future survival and reproduction (Alerstam and Lindström 1998, Hedenström 2007, Alerstam 2011), yet the amazing diversity of migration strategies among species, populations, and individuals suggests that migratory behavior is shaped by a complex array of selective forces (Chapman *et al*. 2011, Vardanis *et al*. 2011). This observed variation has long been thought to result from different resolutions to trade-offs between time, energy and safety that minimize the cost of migration (Alerstam and Lindström 1990). Current migration research has begun to focus on how these trade-offs and accompanying effects may vary with endogenous factors such as sex, body size, age, and sexual maturity (Dolbeer 1982, Hedenström 2007, Catry *et al*. 2005, Sergio *et al*. 2014). In cases of migratory behavior these tradeoffs may also incorporate exogenous factors such as weather, topography, habitat quality, and proximity of stopover locations along the migration route (Liechti 2006, La Sorte *et al*. 2013, Kelly *et al*. 2016, Xu *et al*. 2019, Chen *et al*. 2020).

Presumably, migration is a response to seasonal changes in the geographic distributions of resources (Rappole 2013), but the proximate mechanisms that birds use to accomplish their migratory movements are still being realized (Schmaljohann 2017).

Individuals can adjust migration strategies through several mechanisms, i.e., increasing average distance covered non-stop during the migration period, altering stopover behaviors, and taking advantage of wind effects and other weather variables. This sort of behavioral plasticity likely helps balance migration speed and survival probability in accordance with environmental conditions (Alerstam and Lindström 1990, Hedenstrom 2008, Alerstam 2011, Schmaljohann 2018), but there are numerous examples of migratory behaviors that appear to contradict optimality models, such as the Greater Black-backed Gull *Larus marinus*, which has a slower spring migration speed compared to autumn movements (Bustnes *et al*. 2013), and the Icelandic Whimbrel *Numenius phaeopus*, which undertakes a risky continuous sea crossing rather than a conditionally safer overland migration route (Alves *et al*. 2016).

In cases where we know that individuals are capable of a variety of different migration strategies, we can view these individual differences as responses to extrinsic factors, and be concerned less with phylogenetic, physiological, and physical constraints that might limit the range of observed behaviors. The Black Skimmer *Rynchops niger* ranges across the Americas from latitudes 40˚N to 28˚S and has demonstrated diverse migration strategies having both resident and migratory populations in North America and near-continental wide migrations in South America (Davenport *et al*. 2016). Relatively little is known about Black Skimmer migration dynamics, yet this species is capable of extraordinary flight behaviors including traversing the Peruvian Andes at high altitudes (>4000 msl) to reach non-breeding grounds along the Pacific coasts of Peru, Bolivia, and Chile (Davenport *et al*. 2016).

Black Skimmer movement research in North America has largely focused upon reproductive success (Quinn 1990, Burger and Gochfeld 1994, Dinsmore *et al*. 2008, Owen and Pierce 2013), foraging dynamics (Arthur 1921, Zusi 1959, Erwin 1977, Black and Harris 1981, 1983, Blake 1985), and mark-recapture studies designed to understand apparent adult and juvenile survival and regional movements (Gillespie 1931, Sprandel *et al*. 1999, Snipes and Sanders 2011). In North American Atlantic populations, banded bird sightings have documented individuals migrating southward along the Atlantic coast rarely moving inland (Burger and Gochfeld 1994). Populations from Massachusetts south to North Carolina are migratory, whereas populations in Florida are year-round residents (Gochfeld *et al*. 2020). Pacific North American populations also perform a north-south migration along the coastline, with a mix of migratory and resident populations in California (Gazzaniga 1996).

In this study we employ a GPS tracking system to generate the first detailed account of Atlantic coast Black Skimmer migration that allows for comparison of in-route behaviors among individuals across autumn and spring migrations. We use these tracking data to quantify individual migrations in terms of distance, speed (both flight speed and overall migration speed), directness of the migration route, and stopover duration to identify proximate behavioral mechanisms that the Black Skimmer may use to adjust aspects of migration. From these assessments we sought to address the following topics and their associated questions and predictions.

1. Seasonal differences in migration speed and route. Numerous studies describe a difference between spring and fall migration wherein individual migrants advance their spring arrival via changes in the speed/duration of migration (La Sorte and

Fink 2017, Schmaljohann and Both 2017). These studies lead us to predict that for Black Skimmers, spring or pre-breeding migration speeds will be faster and routes traveled more direct than autumn or post-breeding activities.

2. Differential migration based on sex. Sexual size dimorphism is present in the Black Skimmer with males being 30% larger than females (Erwin 1977). Numerous studies have documented differential migration in sexual size dimorphic species ranging from differences in the distance traveled by the larger sex (Ketterson and Nolan 1983, Nebel *et al*. 2002) to sex-related differences in timing of departure (Baert *et al*. 2018). In fact, Cristol *et al*. (1999) suggested that differential migration exists in the majority of migrant species. Larger birds are expected to winter closer to the breeding grounds according to the body size hypothesis (Ketterson and Nolan 1983) because they are more capable of withstanding poor weather conditions. Alternatively, according to the social dominance hypothesis, differential migration may develop under body assortment across a habitat quality gradient (Gauthreaux 1982). Smaller sized individuals may be outcompeted for good wintering locations and be forced to travel farther to non-breeding locations. Here, we hypothesize that there will be sex-related variation in distances travelled to non-breeding grounds.

3. Flight behaviors that exploit wind effects. The degree to which skimmers exploit favorable winds during migration flights has not been previously investigated. Looking across related taxa we see that species which use dynamic gliding seem to prefer crosswinds or cross-tailwinds (Kempton *et al*. 2022) whereas non-pelagic birds may select for tailwinds (Liechti 2006). As the Black Skimmer has a wing profile more similar to pelagic seabirds with high aspect ratios and low wing loading (Withers and Timkin

1977), we predict here that the Black Skimmer will not necessarily use tailwinds to increase flight speeds as do shorebirds but will instead preferentially take advantage of crosswinds similar to pelagic seabirds.

4. General mode of Black Skimmer Migration. We sought to characterize the mode of Black Skimmer migration in terms of the birds' energy allocation strategy. In other words, do skimmers acquire resources during migration through traditional prolonged stopovers, do they forage periodically for short periods of time while migrating (i.e. a fly-forage strategy), or do they combine these behaviors? Birds that fly extensively while hunting for food, i.e., aerial insectivores, waterbirds, and some seabirds may have a fly-n-forage strategy or a combination of traditional stopover and fly-forage strategies (Strandberg and Alerstam 2007, Kempton *et al*. 2022, Amélineau *et al*. 2021, Rueda-Uribe *et al*. 2022). A fly-forage strategy combines foraging with covering migration distance and could influence migration activities by reducing the time individuals need to stop to replenish energy and therefore increase migration speeds (Hedenstrom and Alerstam 1997, Strandberg and Alerstam 2007, Nilsson *et al.* 2013, Rueda-Uribe *et al*. 2022). Fly-forage strategies can reduce fuel loads as there is continuous replacement of consumed energy, which is beneficial to species that need to maintain low wing loading. Moreover, Black Skimmers can extract food from a wide range of habitats, including shallow beaches, lakes, marsh edges, shallow mudflats, water impoundments, and rivers (Arthur 1921, Tomkins 1951, Zusi 1959, Erwin 1977, Black and Harris 1983, Gochfeld *et al*. 2020). Here, we hypothesize the Black Skimmer should have a migration route closely associated to potential forage locations and an energy allocation strategy whereby they use a fly-forage or mixed strategy which includes the ability to feed before and after daily flights or to take advantage of forage opportunities along the route (Nilsson *et al*. 2013).

METHODS

Study area

Our study population of Black Skimmers nests at Nickerson Beach Park (Fig. 1, 40.5894° N, 73.6036° W) located in Lido Beach on the barrier beach of Long Island, New York. Nickerson Beach hosts the largest of two Black Skimmer breeding colonies remaining in New York State where 350-400 breeding pairs of the Black Skimmer nest annually along with colonies of Common Terns *Sterna hirundo* and Least Terns *Sternula antillarum*.

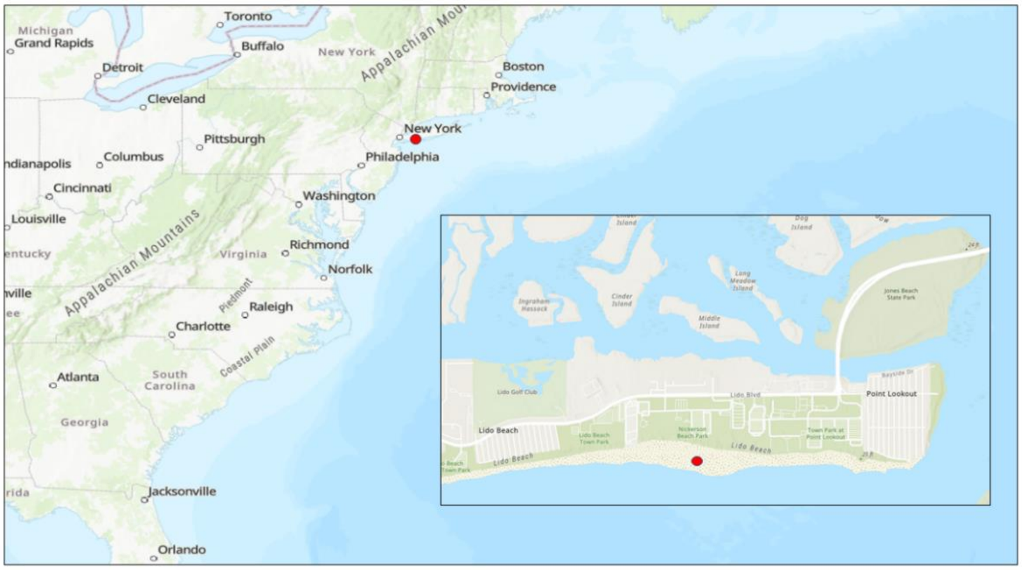

Figure 4: Location of the Nickerson Beach Black *Skimmer Rynchops* niger breeding colony at Lido Beach, New York (40.5894° N, 73.6036° W). The colony is located on the Long Island Barrier Island complex of New York, USA.

Black Skimmer adults were captured on nest using noose carpets during three breeding seasons from 2018 through 2021. To minimize disturbance to the colony, we targeted nests at the periphery of the nesting colony during capture events. Mean capture time was 13.6 minutes (range of 2-23 minutes). All field work occurred under USGS Federal Master Bander Permit 24164 and NYDEC Permit #100. See supplemental information for full capture methodology.

Migration Dynamics

A total of 48 Black Skimmers were captured. Each was processed through a series of morphometric measurements, and we collected feather, and blood samples for genetics and stable-isotope analyses. Skimmers were sexed using morphometric data with males being the larger size in all measurements including mass, wingchord, exposed culmen, total head, and tarsus (Erwin 1977). From the 48 birds captured, we selected 31 individuals for GPS datalogger deployment, 16 of which were males and 15 were females. The GPS dataloggers used for the project had remote data download capability and weighed 6.57-7.2 grams which is less than 3% of the smaller female body mass (Sterna, Ecotone Inc., Poland). GPS datalogger harnesses made from 9.5mm diameter Teflon ribbon (Bally Ribbon Mills Inc., Pennsylvania) were fitted to individual skimmers in a leg-loop harness configuration (Goodenough and Patton 2019). Once the harness was fitted to the bird, the bird was released back to the edge of the colony where it was previously captured.

Remote data retrieval occurred using a UHF radio base station that was set in the colony periphery within 200m of the nesting skimmers with dataloggers. The dataloggers were initially set to collect GPS locations and ground speed at 5-minute intervals throughout each 24-hour cycle. However, this collection cycle frequently drained the datalogger batteries, so we switched GPS data collection to 15-to-30-minute intervals after two weeks of 5-min data collection. In late August, we reprogramed the GPS loggers to collect 60-minute data prior to the onset of migration. Migration data was downloaded using the same base station the following May and June (2019, 2020, and 2021) when tracked individuals had returned to the breeding colony. All tracking data in this study are archived on Movebank.org (Movebank ID # 1429293947).

Migration and stopover dynamics

Migration routes for individuals were developed using the ‘move’ package in R (Kranstauber *et al*. 2020) and the ‘amt’ package (Signer *et al*. 2019). Start and end periods of migration were determined by visually examining the data and establishing when birds began moving southward and northward in a directed manner. Six parameters were calculated from the tracking data for analysis: straightness index, migration speed, migration distance, flight speeds during active travel, and stopover duration for both autumn and spring migration. Great circle distance was used as a measure of migration distance and was calculated using the package geosphere in R based upon breeding colony location and farthest latitude traveled to wintering ground for each individual (Hijmans 2019). We defined migration speed as the sum of the distance that each bird spent on migration divided by the sum of time it took to complete migration in days (Hedenström 2008, Sergio *et al*. 2014). We considered the start of autumn migration to begin when the bird left the breeding colony without returning to breeding areas and the end of autumn migration when birds arrived at the southernmost latitude in December. Similarly, spring migration began when birds started a northward movement without returning to non-breeding grounds. To compare seasonal flight speeds during active migration segments, we defined active tracks within the dataset as those having three or more consecutive locations with GPS tag speeds greater than 10m/sec and distances greater than 25km apart. Flight speeds were then compared between sexes and across seasons.

A route tortuosity index, hereafter referred to as SI, (Weimerskirch *et al*. 2002, Benhamou 2004, Wang *et al*. 2018) was developed to compare migration route tortuosity. SI was calculated as:

$$SI = \frac{great\ circle\ distance\ of\ migration}{sum\ of\ actual\ distance\ traveled}$$

Hence, individuals that move directly to wintering grounds without diversion will have a SI closest to one.

Migrating birds can have rest stops (<12 hours), stopover (>24 hours), and staging areas (weeks) along migration routes (per Warnock 2010). As such, we chose the smallest increment of time to summarize resting dynamics for the skimmer that includes rest stops, stopover, and staging. We summed the amount of time each individual spent on rest (hours) and compared time spent resting during migration across sex and seasons. We defined rest stops as locations where individuals stop but the rest duration is less than 24 hours. Stopover locations were identified as locations where individuals stayed for at least 24 hours and traveled less than a net squared distance of 100km per day (Warnock 2010, Rueda-Uribe *et al*. 2022). Staging locations were differentiated from stopovers by the use of a particular location for more than a week.

All statistical tests were run in R using package 'stat' (R Core 2021). We used paired t-tests to compare seasonal differences in migration speed, distances traveled, rest stops, and flight speeds among individuals. We used a general linear model (GLM) to compare differences in distances traveled by sexes. The model included sex as the independent variable, and the type of data (distances travelled, time period) as dependent variables, with bird ID as a random variable. We generated the model with the nlmr() function in the ‘lme4’ package (Bates *et al.* 2014) for Results were considered significant at $\alpha = 0.05$.

Wind dynamics

We accessed wind data associated with skimmer locations to address three questions. 1) Are wind speeds similar during the autumn and spring migration periods; 2) are individuals actively selecting for higher wind speeds during migratory flights; and 3) is there a set of preferred wind conditions associated with active travel? To address these questions, we narrowed our tracking data into subsets of bird locations where we could clearly determine that a particular bird was actively migrating (i.e., flying) or that a bird was clearly stationary. We selected criteria for active flight that included three or greater consecutive location points with GPS tag speeds with speeds greater than 10m/s, which is a typical ground speed for non-foraging flights of skimmers (Black 1985), and net distance displacement of greater than 100km for the flight to remove the possibility that these were foraging flights rather than active migration movements. Location data associated with stationary periods were characterized by location data with GPS tag speeds of zero and movements of less than 5 km between successive locations.

To examine whether skimmers were selecting for particular wind conditions when making migratory flights, we compared wind parameters associated with instances where the birds were clearly moving long distances to relevant reference data that sampled wind conditions within the same locations and time frames when birds were migrating. Finally, because Black Skimmer migration movements are mainly crepuscular or nocturnal, we considered only location data that occurred from two hours before sunset to two hours past sunrise.

To ensure that the reference data were relevant to the migration data we paired reference data with the movement data such that reference data came from the same time of day and time of year as the movement data. We derived the reference data in two ways. First, we used timestamps that were the same as the movement locations except that they were 24 hours earlier (i.e., on the previous day when the bird was not flying). It is possible that even with 24 hours of separation there could be autocorrelation between wind data from one day and the next. Hence, we generated another set of reference data based on the same time and day of year for each flight location, but we used the previous year.

For each of these points we assigned wind parameters from the North American Regional Reanalysis (NARR) data set. This data set provides interpolated weather data on a 32 km grid for all of North America, with weather values that are provided every three hours. We used wind data from NARR that are defined as vector components U and V, which represent the wind velocity west to east and south to north respectively. To assign wind values to each location on the migration track, we identified the NARR grid point nearest the bird's location and interpolated the U and V wind values for that grid point based on the NARR times immediately before and after the timestamp for the bird's location.

To compare actual flight data and reference data, we characterized wind conditions into one of four types. Winds below 3 m/s were labeled as calm. Winds greater than 3 m/s were divided into headwinds, crosswinds, and tailwinds based on the difference between the wind direction and the flight direction of the bird (based on its previous location in the tracking data time series). Headwinds were winds that differed from the flight direction by more than 120 degrees. Crosswinds differed from the flight direction by 60 to 120 degrees, and tailwinds differed by 60 degrees or less. We tested for evidence of selection for wind types by examining the frequencies of the wind types for flight data and for reference data and by applying Chi-square tests to these frequencies. We also generated a linear mixed model to test whether wind speed differed between instances when the birds were flying and reference data. The model included wind speed as the independent variable, and the type of data (actual flight, previous day, and previous year) as dependent variables, with bird ID as a random variable. We generated the model with the nlmr() function in the lme4 package (Bates *et al*. 2014) for R, and we tested for significance by applying an Type II Wald chi square tests to the model results via the Anova() function in the car package (Fox and Weisberg 2019).

Energy acquisition

We had two objectives for determining energy acquisition strategies of migrating skimmers. We first calculated the proportion of track locations that were located within 2km of a waterbody. We then used ArcGIS Pro 2.9 (ESRI.com) to map individual migration tracks and visually inspect the maps to look for possible instances of fly-forage behavior. Once we identified episodes of fly-forage behavior, we calculated the proportion of stopovers that appeared to be instances of fly-forage behavior. Our criteria for potential foraging episodes during migration included flight speeds of less than 10 m/s, net displacement distance of locations less than 25km (see Withers and Timko 1977, Blake 1985) that were either preceded or succeeded by a rest stop.

RESULTS

Of the 31 skimmers deployed with GPS dataloggers, 21 individuals returned to the Nickerson Beach colony the following breeding season post-deployment and provided partial and complete segments of migration. For instance, 16 skimmers with tags deployed in 2018 were downloaded in 2019, two skimmer tags deployed in 2019 were downloaded in 2020, and two individuals tagged in 2021 were downloaded in 2022. A total of 43,040 location points collected during the non-breeding period were successfully obtained from returning skimmers. Six additional skimmers with loggers were present in the breeding colony during the 2019-2022 breeding seasons. We managed to recapture three of the six individuals and remove GPS tags. Data downloads and resights suggest a minimum return rate of 86% of tracked individuals to Nickerson Beach Park the following breeding season.

Migration dynamics

Skimmers began autumn migration starting as early as mid-August through early October with the entirety of the breeding colony departing by 13-October for all years (Table 1). Spring migration began in early February and extended through 13-June annually. Strong fidelity to migratory routes was documented with all individuals using similar routes for both autumn and spring migration (Fig.2). Skimmer migration began 1-2 hours before sunset and extended 2 hours past sunrise, although the majority of movements were nocturnal 2000 to 0330 EST (82%) with a lesser percentage of travel (15%) occurring within 120 minutes of sunset and sunrise.

Table 2: Spatiotemporal aspects of autumn and spring migration, for 21 tracked Black Skimmers using GPS telemetry

	Autumn mean ± SD (range)	**Spring mean ± SD (range)**
Onset of migration	15-Sept (7-Aug to 13-Oct)	21-April (11-Feb to 30-May)
Arrival at wintering ground	5-Dec (3-Oct to 12-Jan)	
Return to breeding colony		28-May (21-May to 13-June)
Duration of migration (days)	75 ± 43	37 ± 35
Total migration distance (km)	3819 ± 309	2851 ± 285
Migration speed (km/day)	94 ± 65	248 ± 197
Direct Distance (km)	1637 ± 309	1574 ± 205

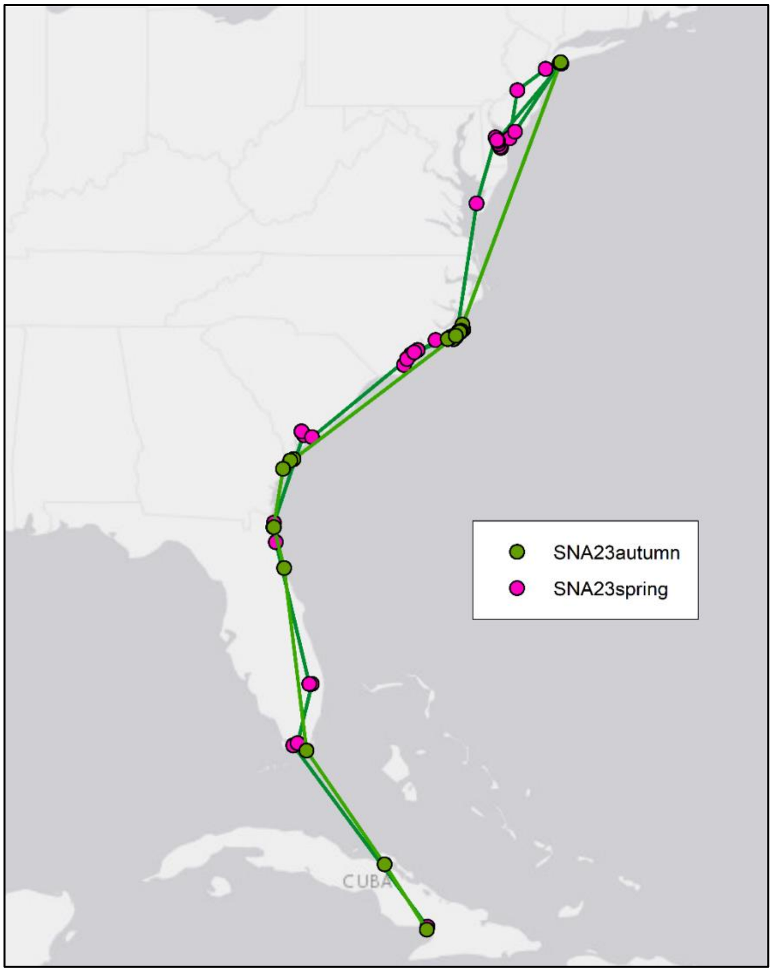

Figure 5: An example *migration* track of Black Skimmer (Rynchops niger) migration along the Atlantic coastline. Autumn routes (green) were similar to spring routes (pink). Individuals rarely ventured inland instead commuting within the coastal zone. Map created by Kate Goodenough 2022. See supplement 1 for tracks of all Black Skimmers.

Results of the tortuosity index (SI) were highly variable, ranging from 0.20 to 0.98. SI values differed between seasons (t = 2.057, df = 14, P < 0.001), with more direct migration routes in the spring, although there was no difference in SI between the sexes (t = -0.525, df = 17, P = 0.6065). Spring migration speeds were faster than autumn migration speeds (autumn mean = 94 ± 65 days. spring mean = 248 ±197 days, t = -2.9855, df= 14, P= 0.009). M There were differences in distances travelled by season (autumn mean = 1637 ± 309 km, spring mean = 1575 ± 285 km, t = -2.774, df = 16, *P* =

0.013) but not across sex (female mean = 1667 ± 314, male mean = 1500 ± 236 t = -0.229, df = 19, *P* = 0.8214). Spring rest duration (28.3 ± 27.8 days) was shorter compared to autumn rest duration (37 ± 38.7, t = 2.6656, df = 12, *P* = 0.021). Mean active flight speeds during autumn migration were 18.6 ± 6.6 m/sec and different compared to the spring mean flight speed of 23 ± 4.7 m/sec (t = -5.678, df = 16, *P* < 0.001).

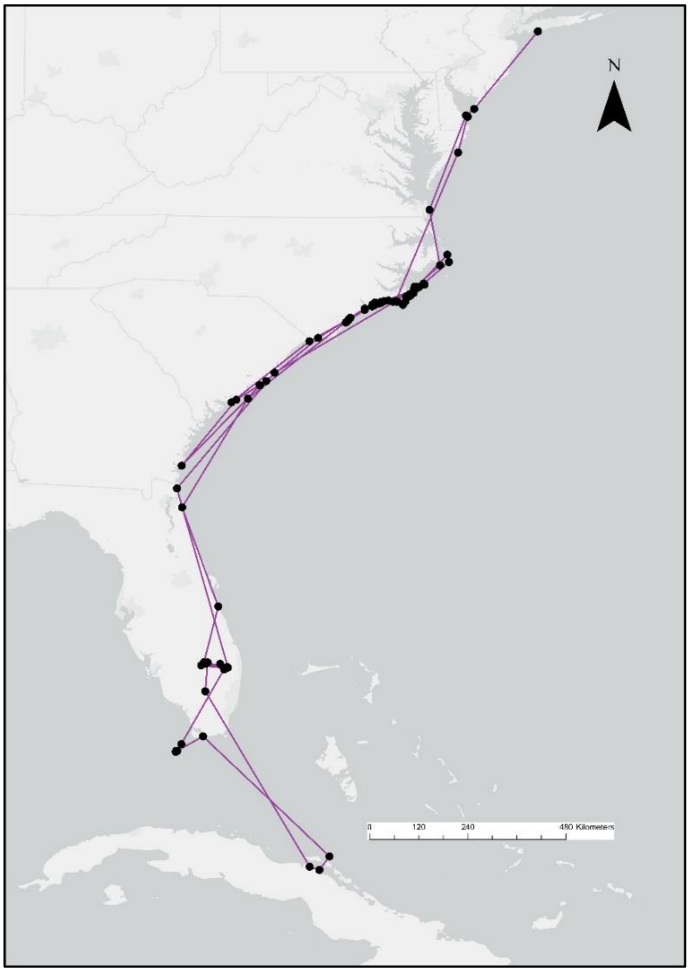

Figure 6: Black Skimmer (*Rynchops niger*) annual migration from the breeding location in New York to wintering locations in Florida and Cuba and back to New York in the spring. To reduce clutter in the figure, only one spring and autumn track is documented which is characteristic of skimmer migration along the Atlantic Coast of the United States. For maps of all tracks see Supplementary figure S1.

There was interesting variation in migration strategies when comparing the duration of migration. Some individuals migrated in the autumn quickly (8-22 days) compared to others that spent quite a bit of time at stopover locations in North Carolina (57 to 153 days). A similar pattern could be seen with individuals completing migration quickly (2-15 days) compared to individuals that migrated more slowly (22 to 104 days). This pattern occurred for both autumn and spring periods. This appears to be an individual trait as individuals who completed autumn migration quickly also migrated quickly during spring migration.

Tracked skimmers used a combination of rest stops (4-12hrs), stopovers (24-72 hours) and staging areas (two weeks or more). The type and duration of rest was a strong influence on migration speed and ranged from 0.3 days to 128 days depending upon the season. Females had a mean autumn stopover duration of 34 ± 25days compared to 11.5 ± 8.7 days in spring. Males had a mean autumn stopover duration of 51 ± 54 days and a mean spring stopover of 45 ±37 days. Rest areas of short duration were used more often in the spring and periods of foraging activity were identified just after arrival to the stop area. Also, there appeared to be two different sets of behaviors associated with individuals that leave the wintering grounds early (some as early as early February) and those that stay at the wintering grounds until late May.

An important staging area for autumn was a 293 km stretch of coastline in North Carolina from Cape Lookout National Seashore (34.6227° N, 76.5246° W) south to Fort Fisher State Recreation Area (33.9717° N, 77.9176° W, Fig. 4). Skimmers were frequently present in this location from late September through mid-November with tracked individuals spending an average of 40 days in this area (range of 19 to 85 days).

Movements consisted of short distances back and forth across the North Carolina coastline with no concentrated long-term roosting (greater than 3 days in a row) locations but several daily rest areas.

During spring migration, there was an increase in rest stops of short duration (hours versus days), fewer stopover locations, and fewer staging areas used. St Catherine Sound north to Tybee Island, Georgia was an important spring staging area with individuals arriving as early as mid-February to early May from wintering grounds and spending 4-6 weeks there (Fig. 4). Delaware Bay was also documented as an important spring staging area with all tracked individuals using the location for at least seven hours and 60% staying there for 7-21 days before heading northward to breeding grounds in New York. The southern portion of the Cape Fear River (Southport, Carolina and Cures Beaches, and Fort Fisher State Park), Cape Lookout National Seashore in North Carolina, and the Virginia Barrier Islands (Assawoman and Chincoteague Islands) were also used to a lesser degree with individuals staying only a few days before continuing northward. For skimmers that wintered in Cuba, important stopover locations in Florida included Loxahatchee National Wildlife Refuge, Everglades National Park, and the Florida Keys Island complex.

Of note, we documented an interesting use of Delaware Bay and the Virginia Barrier Islands in the spring. Four females arrived at the breeding colony in New York on 21-May 2019, spent 20-26 hours in the area before departing the breeding colony area. One female continued northeast and spent a week in the Hamptons before returning to the breeding colony by 02- June. Two returned to Delaware Bay for 14-18 days before returning to the breeding colony in early June. The fourth female traveled south to locations within and adjacent to Hog Bay, Virginia for 16 days before returning to the New York breeding colony.

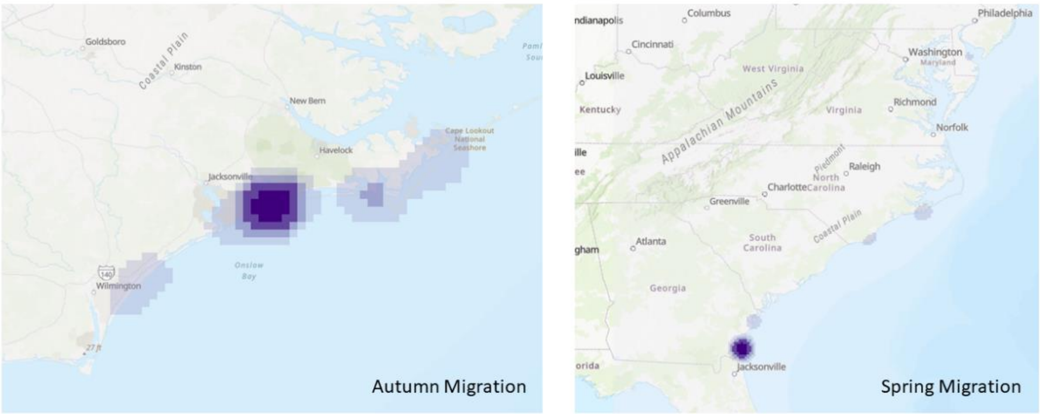

Figure 7: Density of stopover location duration for Black Skimmer Rynchops niger autumn and spring migration. For autumn, the North Carolina coast from Cape Lookout National Seashore south to Fort Fisher State Park was of highest density of use. For spring migration, St. Catherine sound north to Tybee Island in GA was used most followed by the Cape Fear River Ocean outlet in NC, Cape Lookout National Seashore in NC, and Delaware Bay in DE. Map created by Kate Goodenough.

Wind dynamics

We based our analysis of wind data on 93 locations from 14 birds, wherein it was clear that birds were migrating, as well as 93 matched locations from the previous day and an additional 93 locations from the previous year. There was limited evidence that the birds selected for particular wind conditions. Comparisons of wind conditions during flight were similar to the matched wind conditions from the previous day ($\chi^2 = 2.65$, df = 3, p = 0.44; table 2); however, this similarity may be due to autocorrelation across successive days. When wind conditions during flight were matched with data from the previous year, there was evidence of selection for calm conditions (χ^2 = 2.65, df = 3, p = 0.44; Table 2), as instances of calm winds were rare in the reference data (3 of 93). A linear mixed model applied to wind speed suggested that the mean wind speed for actual flight locations (6.61 m/s ± 0.66 95% CI) was lower than that from the previous-year reference data (7.39 ± 0.59 95% CI), but the p-value was just above the default significance value of 0.05 (Type II Wald (χ^2 = 5.63, df = 2, p = 0.060).

Table 3: Wind data type comparisons for Black Skimmer during active migration, and two reference data sets.

Data set	Calm	Tailwind	Crosswind	Headwind
Migration	15	35	24	19
Reference (previous day)	14	31	22	14
Reference (previous year)	3	46	24	20

Energy acquisition

A total of 128 instances of fly-forage behavior were documented with greater than 95% of skimmer rest stops adjacent to or within 2km of potential foraging grounds (Fig. 5).

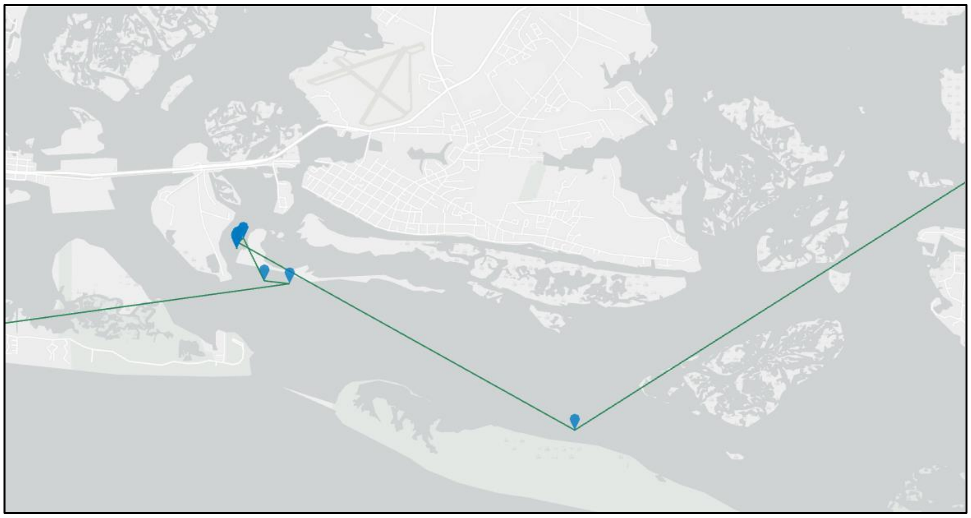

Figure 8: An example of fly-forage behavior that included alteration of flight path and a rest stop for Y_C48 during fall migration. The individual stopped near Morehead City, NC and rested for three hours before setting out to forage and then continue southward. Map created by Kate Goodenough. For more images of fly-forage behavior, see supplement 1.

DISCUSSION

Our detailed tracking data from 21 individual Black Skimmers allowed us to make several new inferences about migration in our study population. Generally, autumn migration was slower and more tortuous which implies a strategy that avoids intensive energy expenditure. Conversely, in the spring migration was faster and more direct which implies a time minimization strategy. However, it is important to point out that there was considerable individual variation in migration behaviors among the tracked birds. For example, some individuals completed migration in the autumn in as little as eight days in the fall and only three days in the spring whereas others took more than 90 days and 40 days for fall and spring migration respectively. Also, there appeared to be two different sets of behaviors associated with individuals that leave the wintering grounds early (some as early as early February) and those that stay at the wintering grounds until late May.

Reduced migration speed in autumn was due primarily to increased time spent at stopover locations, although flight speeds were also reduced. A third contributor was route tortuosity, with more direct routes in the spring. The more rapid spring migration aligns with the widely supported idea that individuals that can return to the breeding colony sooner gain an advantage in competing for favorable nesting locations (Parker and Courtney 1983).

We did not detect sex-related differences in migration speed or distance, but there were sex-related differences in stopover dynamics associated with spring migration. Males appear to start pre-breeding movements as early as February early but spend longer periods at stop over locations; whereas females leave wintering grounds later and use fewer stopovers. Interestingly, females appear to catch up with males such that they arrive together at the nesting colony within a 3-4 week period in late May to early June.

While skimmers are not considered a pelagic species, they have an ecomorphology similar to pelagic foragers, i.e., long and narrow winds with high aspect ratio (Pennycuick 2018). Pelagic seabirds are known to use crosswinds and cross-tailwinds for wind assist rather than tailwinds as what has been observed in non-pelagic birds (Conklin and Battley 2011, Deppe et al. 2015). We documented that the Black Skimmer is selecting for calm winds but our nomenclature may be misleading as our category for calm wind are wind speeds ranging from 0-3 m/s. We were very conservative with data selection criteria, and it may be worthwhile to add more instances of wind selection to better understand skimmer selection of wind types.

Last, energy accumulation is an important aspect of migration with a continuum of strategies that range from traditional stopover use to fly-forage strategies or combinations thereof (Hedenstrom and Alerstam 1997, Strandberg and Alerstam 2007, Schmaljohann and Booth 2017). The Black Skimmer appears to use a mixed strategy of both fly-forage and traditional stopover strategies. Greater than 95% of the rest stops made by tracked individuals during both autumn and spring migration were located at ocean inlets or within shallow embayment and coastal estuaries where skimmers can likely find both appropriate resting locations and prey.

However, traditional use of staging grounds was evident with the use of areas such as the Georgia Bight and Delaware Bay where some individuals stayed for several weeks. Individuals that wintered in Cuba were observed resting with several bouts of foraging in the Florida Key complex before attempting the Florida Straits crossing (150-220 km depending upon where individuals attempted to cross from Florida). With a mixed or fly-forage strategy, individuals may have some flexibility to adjust to unpredictable variation in food availability along the migration route. We also note that fly-forage behavior was especially evident during spring migration when individuals increased migration speed and generally decreased rest periods.

Black (1985) estimated that Black Skimmers must forage 4-8 hours per day to maintain a positive daily energy budget, which is dependent upon the density of available prey resources. Our data frequently indicated stopovers of approximately eight hours that suggest foraging bouts with a radius of 2.8 to 28km. The duration of these stopover events aligns with predicted needs for energy acquisition and assimilation (Withers and Timko 1977, Blake 1985), and we argue that they are indicative of fly-forage behavior.

This research was a first attempt to develop fine scale information on Black Skimmer migration along the Atlantic Flyway of North America. Our data provide clear evidence of sex-based differences in stopover behavior and suggest that there are variable mechanisms that skimmers employ to adjust their migration strategies such as altering flight speeds, taking advantage of particular wind types, and having variable energy acquisition strategies. Our research also revealed key stopover locations, which may contribute to conservation efforts that focus on full avian life cycles. Still, many aspects of Black Skimmer migration remain unknown.

There are several areas of skimmer research that merit more research that includes skimmer use of wind assistance and the influence of fly-forage behavior on stopover dynamics. While we were able to gather data on flight speeds and wind assistance, more information on skimmer responses to weather and other wind effects, (i.e., wind shear, ground effect, etc.) is needed to truly understand flight dynamics for this species. Selection for fly-forage locations is another area that would benefit from additional research. While we know that fly-forage behavior occurs, the selection process remains uncertain.

CHAPTER 3 ACKNOWLEDGEMENTS

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SUPPLEMENT 1

Black Skimmer Capture Protocol for Chapter 3

Our study population of Black Skimmers nests at Nickerson Beach Park (40.5894° N, 73.6036° W) located in Lido Beach on the barrier beach of Long Island, New York. Nickerson Beach hosts the largest of two Black Skimmer breeding colonies remaining in New York State where 350-400 breeding pairs of the Black Skimmer nest annually along with colonies of Common Terns *Sterna hirundo* and Least Terns *Sternula antillarum*. Capture occurred under USGS Federal Master Bander Permit 24164 and NYDEC Permit #100.

Black Skimmer adults were captured on nest using loop carpets made of monofilament line attached to three pieces of carpenter mesh measuring 5cm x 60cm (termed loop carpet) over three breeding seasons from 2018 through 2021. The loop carpets were laid out in a triangular format around the nest (Fig. S2). The carpet was then buried in the sand with only the loops exposed. Nests chosen for capture were those located at the periphery of the nesting colony to minimize disturbance to the colony. Once a bird was captured, a person walked to the trapped bird, removed the bird from the loop carpet. A second person would then move the carpet to another nest within the colony to continue capture of adults. Capture occurred between the hours of 0630- 1700 and was dependent upon sand temperatures. We halted capture activities when sand temperatures reached higher than 30˚ Celsius. Egg mortality occurs when eggs are left unattended in temperatures greater than 20˚C (Sutherland et al. 2003).

Figure S2: Loop carpet specially made to capture colonially nesting Black Skimmers *Rynchops niger*. The strips of loop carpet are arranged in a triangle shaped pattern to encircle the nest. This type of capture design allows for capture of individuals that may be nesting closely together or near vegetation. Once set, individuals return to the nest, walk over the loop carpet, and legs are snared in the loops.

Side notes on Black Skimmer flight dynamics

Skimmer morphology features high aspect ratio wings and low wing loading (Withers and Timko 1977, Blake 1983, 1985) and the Black Skimmer has been documented to use ground effect to aid in foraging strategies (Zusi 1962, Blake 1985, Pennycuick 2008). The term ground effect is an aeronautical term that refers to the reduced aerodynamic drag that flying objects, which include birds and bats, generate when they are in close proximity to a fixed surface such as the ground or water (Finn et al. 2012). The skimmer exploits ground effect when they forage, as it allows them to lower flight speeds and reduce energy devoted to flapping (Withers and Timko 1977, Blake 1983, 1985). Other species exploit the ground effect as well, but its role in migration of skimmers is unknown.

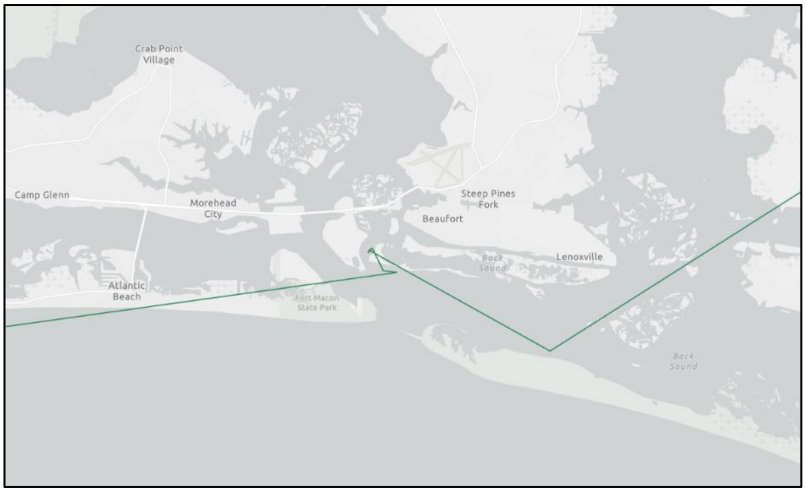

Figure S3: An example of fly-forage behavior for Y_C48 during autumn migration. The figure represents 60-minute data tracks from 9/30/2019 @ 1714 to 9/30/2019 @ 2316 at Morehead City, North Carolina (34.711467/-76.678517).

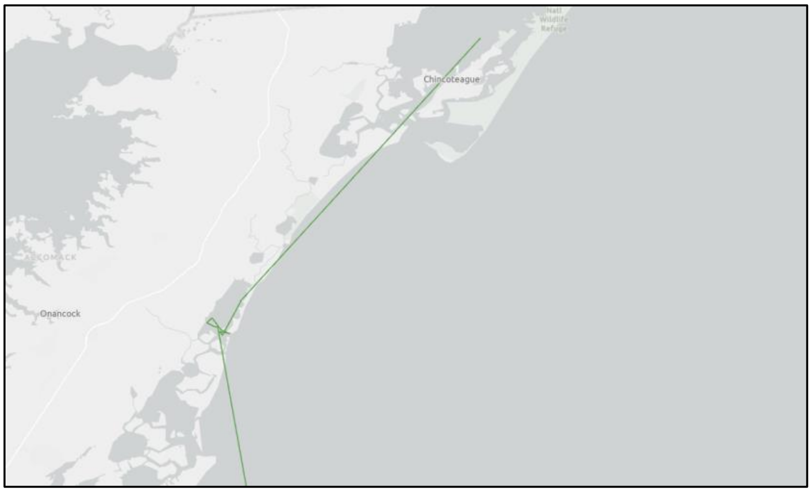

Figure S4: Fly-forage track for Y_C01 on 9/23/2018 @0915 to 9/23/2018 @1517. Y_C01 halted active movement in Metompkin Bay,Virginia to rest for three hours, forage for two hours and then return to active travel southward along the Atlantic coast.