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INFLUENCE OF ENVIRONMENTAL CHANGES ON THE RESOURCE USE AND ABUNDANCE OF BLACK SKIMMERS

BIANCA PINTO VIEIRA
B.Sc., Lic.Sc.
biancabioufsc@gmail.com

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Abstract

Understanding what environmental factors influence species' responses is crucial for adequate conservation management and prediction of responses to climate change. My study focused on a widespread aquatic migratory bird in Brazil; the Black Skimmer (*Rynchops niger*). Throughout the thesis I investigated the reliability of using photographs, citizen data, and visual observation to assess biological data such as moult score, occurrence, and identification of sexes. I also used stable isotopes and counts to assess changes in Black Skimmer's resource use and abundance according to ENSO. I found photographs can be used to score moult in primary feathers, and that sexes in this species can be identified by visual observation from skins and photographs with Black Skimmer males being significantly larger than females. Using citizen photographs from nature enthusiasts web platforms, I found Black Skimmers moult during austral spring to summer in Brazil. Individuals select areas mostly in southern and southeastern Brazil to perform moult. Both sub-species (Amazonian and South American Black Skimmers) and sexes in Brazil selected estuaries while moulting yet coastal built-up areas could also be used. The South American Black Skimmers also selected more dunes and less mudflats than the Amazonian ones. There were differences in timing or duration of moult between sub-species or sexes with males taking more time and starting to moult earlier than females. I found Black Skimmers changed resource and had a higher diet input from estuarine habitats during the El Niño. Not only the foraging use during moult changed but also the abundance. The number of individuals overstaging (staying longer at the non-breeding site during the breeding season) at the study site was higher during the El Niño and lower during the La Niña than in regular years. Abundance was higher during eastern and northern winds but negatively affected by an interaction of temperature and ENSO. This study provided affordable non-invasive methods to studies in ornithology, fulfilled gaps in Black Skimmer's life-history annual cycle, and was one of the first studies addressing how ENSO affects aquatic species in the South American Atlantic coast. Lessons learned from this study might underpin more effective conservation plans.

Keywords: non-invasive methods, moult, non-breeding season, aquatic bird species, climate change, El Niño Southern Oscillation, Neotropical zone

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Preface

Scientific efforts to understand species' ecological responses to environmental changes are still concentrated in the Northern Hemisphere while most of biodiversity is in the Southern Hemisphere. South America and especially Brazil, for example, hold most of the world's biodiversity and water resources however few studies have assessed the effects of environmental changes in this area. Most of this bias is related to access to logistic constraints and difficulties to cover a huge territory. When I planned this study, my motivation was to fill a gap in knowledge about a South American aquatic bird species, understanding how extreme environmental changes affect species' resource use and abundance. Through the process, I also wanted to provide tools that could be widely used despite researcher's access to funds. The thesis goes from a wide geographical context to a local one that could allow a better understanding of the big picture.

My motivation to fill gaps in the current knowledge about Black Skimmers (*Rynchops niger* Linnaeus, 1758) in a non-breeding site and its responses to environmental changes while moulting. The Black Skimmer is a migratory aquatic predator with a charismatic appeal, widespread distribution from North to South America, and clearly represents the gap in knowledge between North and South Hemispheres as seen in throughout the chapters in this study. In terms of environment, my study used the El Niño Southern Oscillation (ENSO) to assess Black Skimmers' response to extreme climate changes. The theoretical framework I followed considers environmental extreme oscillations as natural experiments. Although climate change by current common sense is an anthropogenic phenomenon, other significant climate changes occur in diverse time-scales from millennials to decades. ENSO is a phenomenon resulted from solar forcing that changes the sea surface temperature in the Pacific and affects temperature, winds, and precipitation in the entire world through teleconnections. The environmental oscillations are natural though extreme events and their effects have been considered experimental cases to assess the ecological responses to future anthropogenic climate change and underpin conservation plans.

This thesis investigates if large-scale climatic oscillations in the Pacific can affect estuarine predators such as the Black Skimmer in the Southern Atlantic coast. I followed a step by step process (1) understanding the context of ecological responses to an environmental change phenomenon, (2) reconstructing the study species' life-history annual cycle, (3) assessing the feasibility of affordable non-invasive methods to evaluate ecological data, and (4) analysing how ENSO affects the resource use and abundance of the study species. In Chapter 1, I review mechanisms of the ENSO acting on South American climate and how anomalies affect marine ecosystems, especially seabirds. Considering what is known about the ecological effects of ENSO on the aquatic wildlife, in Chapter 2 I chose an aquatic migratory bird species that is likely to be affected by ENSO but lacks investigation, the Black Skimmer (*Rynchops niger*). The Chapter 2 presents a review of the natural history aspects of Black Skimmers that underpin this thesis and why this species can be used to study the ecological effects of environmental changes such as the ENSO. Most of available knowledge about this species comes from North America and the sub-species there differs in behaviour and ecological needs from the two sub-species in South America. Thus, I traced comparisons between the three sub-species and pointed the relevance of using Black Skimmers as an umbrella species and bioindicator of environmental changes. For the gaps in the Black Skimmer's natural history, the Chapter 3 and 4 focused on testing reliability of using affordable non-invasive techniques for ecological purposes.

The Chapter 3 assesses the repeatability of photographic moult scoring and compares its performance in typically used moult models to data acquired from the same and other species using traditional methods. The Chapter 4 focused on assessing the reliability of visually identifying sexes without having to measure the individuals, by observing museum specimens with known sex and by using photographs taken by nature enthusiasts. In Chapter 5, I used photographs and citizen science to test whether Black Skimmers have specific moulting areas within their coastal non-breeding range. In this chapter, I also tested whether timing and duration of the moult were the same between sub-species and between sexes, and if habitat selection differed between the two sub-species and sexes.

Chapters 1 to 5 built a strong background on how Black Skimmers select resources in the non-breeding sites while performing energetic-demanding activities, such as moult. Chapter 5 demonstrated that both sub-species select estuaries in southern Brazil, thus I concentrated at a non-breeding area in southern Brazil for sampling feathers and studying the effects of ENSO in the next chapters. Chapters 6 and 7 investigated the effects of ENSO on the resource use and abundance of Black Skimmers at non-breeding sites in the Island of Santa Catarina in southern Brazil. I chose to focus on non-breeding sites because it was the topic with less available information yet corresponding to half of the individuals' life-cycle (Chapter 2). While breeding is an energetically-demanding phase focused on recruitment, the non-breeding phase focus on individuals' survival. Resource use is well understood in breeding sites but poorly addressed in non-breeding sites. While Chapter 6 focuses on the foraging needs during the non-breeding season when highest expected abundance at the Island of Santa Catarina, the Chapter 7 focuses on environmental conditions affecting abundance and overstaging. Chapter 6 estimated the contribution of different habitats to the assimilated diet of moulting Black Skimmers, and compared the foraging niche of Black Skimmers in response to ENSO. Chapter 7 tested whether timing of abundance of South American Black Skimmers at the non-breeding Island of Santa Catarina is affected by ENSO.

Finally, Chapter 8 addressed the limitations of data and methods, and interesting aspects to be considered in future researches. This thesis has not only provided affordable non-invasive methods to studies in ornithology, and fulfilled gaps in Black Skimmer's life-history annual cycle, but was also one of the first studies directly addressing how ENSO affects aquatic species in the South Atlantic. The lessons learned from this study might underpin more effective conservation plans, especially those focused on wetlands, coastal zones, and aquatic birds.

Victory is reserved for those who
are willing to pay its price.
– Sun Tzu

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Many people and institutions also contributed to this project with suggestions, unpublished information, access to collections, fieldwork, or data analysis. Not everything was used in this thesis but all the information helped me somehow. My memory will not help remembering all the names but if you think ‘yes, I helped her with that once’, my thanks to you too!

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Declaration

I, Bianca Pinto Vieira, declare that the work described in this thesis has been designed and conducted independently by myself under the supervision of Dr Ruedi G. Nager and Prof Robert W. Furness, and has not been submitted for any other degree.

This study was funded by the CAPES Foundation through the Science without Borders Program – Full Doctorate fellowship (BEX 11868-3/9). The stable isotope analysis was also sponsored by the Natural Environment Research Council through the Life Sciences Mass Spectrometry Facility (EK274-10/16).

Chapters were written in manuscript style for publication in different journals however here they have the same style, graphs and tables implemented in the text, British English as the standard language, singular person, and references cited and listed in the same format together in the end. These changes were implemented according to the rules for submitting the thesis at the University of Glasgow. Chapter 3 is published in Ibis Journal and benefited with suggestions from reviewers and editors. All co-authors have seen the manuscript and agreed on its content and submission.

The data used in this thesis were collected by myself except where specifically acknowledged. Data at the Island of Santa Catarina from 2011 to 2012 were collected during an independent research project designed and conducted by myself. Field data at the Island of Santa Catarina from February to July 2015, from February to November 2016, and from February to March 2017 were collected by volunteers Carlos Vieira and Iohranna Müller, and by students Cecilia Pereira, Maria Luiza Ramos, Ana Carolina Schmitz, and Kelvis Fischer during their undergraduate projects at the Federal University of Santa Catarina which were designed and fully supervised by myself.

The researcher Angelo Scherer provided raw data of Black Skimmers' moult at Lagoa do Peixe in southern Brazil for comparisons with data collected by myself at the Island of Santa Catarina. Paulo Antas and Lisa Davenport provided biometric measurements of Black Skimmers in Pantanal and Peru respectively. All their information was already published so the raw data provided by them were properly referenced to their respective publications.

The Wikiaves database (www.wikiaves.com) held photographs of Black Skimmers and other bird species taken by many nature enthusiasts all over Brazil. The authorship of their images is maintained and no images from this source were published in this study. The data obtained from photographs are certified as of free use for scientific purposes by Wikiaves and all photographers agreed with this condition when subscribing to the database. Data from GBIF (www.gbif.org), Xeno-canto (www.xeno-canto.org), and e-Bird (www.e-bird.org) follow the same free-use rules when for scientific purposes. All databases are properly acknowledged when used.

The stable isotope laboratory analysis in Chapter 6 was carried out at the NERC Life Sciences Mass Spectrometry Facility in East Kilbride with the help and supervision of Rona McGill. The Information Centre of Hydrometeorology and Environmental Resources of Santa Catarina (EPAGRI/CIRAM) provided the environmental data for the Chapter 7.

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Licenses

This study was carried out according to permits necessary to research wildlife in the Brazilian territory (SISBIO 36617-1, SISBIO 36617-2, SISBIO 36617-3, SISBIO 36617-4, IBAMA 125050, IBAMA 133364) considering specific licenses to use different methods of capture, ringing and tagging birds (CEMAVE/SNA 3869-1, CEMAVE/SNA 3869-2, CEMAVE/SNA 3869-3, CEMAVE/SNA 3869-4) as well as to export biological samples from Brazil to be analysed in the facilities of the University of Glasgow and the NERC Life Sciences Mass Spectrometry Facility (IBAMA 125050, IBAMA 133364, MAPA 012/2014, MAPA 012/2016, TARP(S) 2014/74, TARP(S) 2014/240, TARP(S) 2016/08, TARP(S) 2016/16). All samples that were not used in this research were incinerated or repatriated to Brazil and deposited at UNISUL.

Chapter 1: Lessons from 40 years of studies on ecological responses to the El Niño Southern Oscillation in South America

The El Niño Southern Oscillation

The El Niño Southern Oscillation (ENSO) is one of the most famous climatic oscillations affecting the weather conditions at different areas in both hemispheres through its teleconnections. ENSO results from solar forcing and is formed by a warm (El Niño) and a cold (La Niña) phase (Haigh 1996, Meehl 2008, Novello et al. 2016). The El Niño phase is characterised by the warming of sea surface temperature (SST) in the eastern tropical Pacific resulting in repositioning of the Walker cell closer to the South American coast (Haigh 1996, Trenberth 1997, Meehl 2008, Novello et al. 2016). The opposite trend with cooling of eastern tropical Pacific is called La Niña. Both phases have teleconnections which are cascade interplay of the Walker cell and oceanic thermoclines with other atmospheric cells and marine currents around the world (Haigh 1996, Trenberth 1997, Meehl 2008, Glantz 2015). The ENSO can be measured by different indexes and the most popular one is the Oceanic Niño Index – ONI (Huang et al. 2015). The ONI is a primary measure for monthly mean of ERSST.v4 which covers SST anomalies in the region 5ºN-5ºS and 120ºW-170ºW with a threshold of ± 0.5ºC (Huang et al. 2015). The ONI considers a period as regular if > -0.5 and < 0.5. Events higher than 0.5 are considered El Niño and intensity is measured as a weak event when over 0.5, moderate when over 1, strong when over 1.5, and very strong when over 2 (Huang et al. 2015). Events lower than -0.5 are considered La Niña and intensity is measured as a weak event when lower than -0.5, moderate when lower -1, strong when lower -1.5, and very strong when lower -2 (Huang et al. 2015). An ENSO event is differed from possible intra-seasonal variations in the tropical ocean when ONI is > 0.5 or < -0.5 for at least five months (Trenberth 1997). Although irregular, since 1950 the ONI has detected warm episodes every three to five years (Figure 1.1). Additionally, very strong peaks of warmer phases were observed every 10 to 20 years from 1970 onwards (Figure 1.1). The ENSO can result in periods of extreme droughts and rainfall leading to changes in ecosystem status (Cashin et al. 2017).

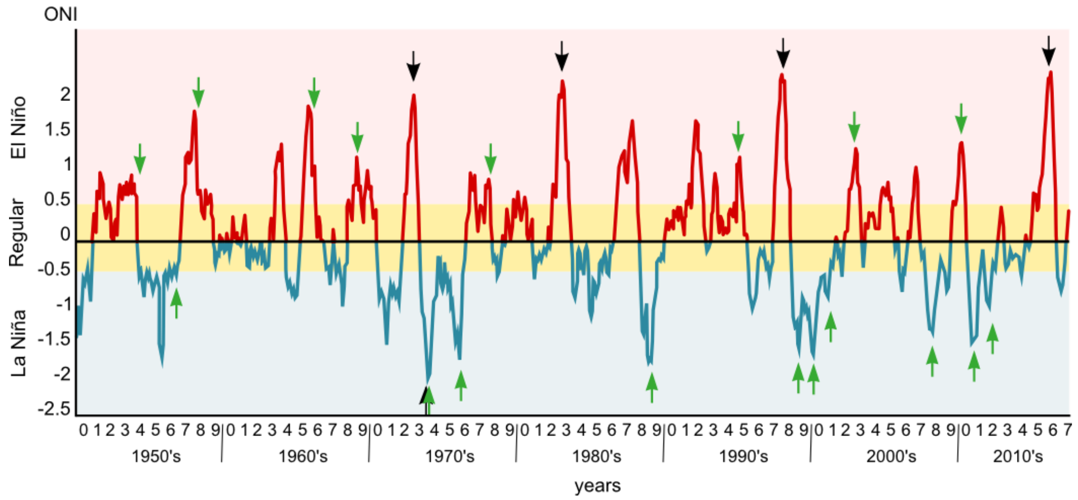

Figure 1.1: The Oceanic Niño Index from 1950 to 2017 reveals four very strong (black arrows) warm episodes (El Niño, red shadow) in 1972/73, 1982/83, 1997/98 and 2015/16, and one very strong (black arrow) cold episode in 1973/74 (La Niña, blue shadow). Modoki years are identified according to the El Niño Modoki Index and highlighted with green arrows. Data source: NOAA’s Climate Prediction Centre for ONI and Japan Agency for Marine-Earth Science and Technology for MEI. Author: BPV 2017.

Climate change is considered a well-established topic in biology with 100-years rich literature and applications from science to politics. In contrast, the ecological effects of ENSO are a relatively recent topic. Since Grinnell (1917), Andrewartha & Birch (1954) and MacArthur (1972), studies addressing the effects of climate on the distribution and resource use of species are escalating, and especially considering the anthropogenic climate change (ACC) predicted by Sawyer (1972). On the other hand, non-systematic observations on the ecological effects of ENSO started with Murphy (1939) and Cowles (1977), and it was only during the 1982/83 El Niño that researchers (e.g. Barber & Chavez 1983, Duffy 1983, Schreiber & Schreiber 1984a, 1984b, Wallace & Temple 1988, Anderson 1989) started to focus on its ecological consequences on the South American marine wildlife. These will be addressed in this chapter.

Similarities between conventional ENSO and ACC include an increase in SST and air temperature that generates alterations in precipitation, salinity, pH, and winds. Furthermore, ACC models detected have linked increases in global evapotranspiration to higher air temperatures (Miralles et al. 2003) which also happens during ENSO (Haigh 1996, Trenberth 1997, Meehl 2008). Habitat-forming species, such as corals, sea grass, mangroves, and salt marsh grasses, are particularly susceptible to changes in temperature, precipitation, pH, and salinity, and therefore both ENSO and ACC can strongly affect the survival of these, as well as other species that exclusively depend on them (Glynn 1988, Williamson et al. 2000, Barlow & Peres 2004, Harley et al. 2006, Kelmo & Attrill 2013, Glynn et al. 2014, Vinueza et al. 2014). The difference in timing and intensity between ACC and ENSO is considered by some researchers as a limitation of using ENSO as a current experiment to reflect future constant conditions expected from ACC (Corti et al. 1999, Pounds et al. 1999, Parmesan 2006). Indeed, ENSO's chaotic behaviour makes it difficult to predict the onset of events (Glantz 2015). However, even with its unpredictability, forecasts became quite accurate to short term predictions, and even a very strong warm phase predicted for 2014 (Ludescher et al. 2013) taken as a forecast failure (Glantz 2015) did not fail completely because a very strong El Niño arrived in 2015/2016 (Figure 1.1).

This suggests that understanding the ecological effects of ENSO provides access to the ecological response to ACC. Models developed to predict the future frequency and intensity of ENSO are not consistent in terms of details but all of them seem to predict a higher occurrence of events and an increase in intensity (Timmermann et al. 1999, Easterling et al. 2000, Collins et al. 2010, Cai et al. 2014). In addition, two new ENSO phases – El Niño Modoki and La Niña Modoki – have also been identified (Figure 1.1, Ashok et al. 2007, Yeh et al. 2009, Li et al. 2010). El Niño typically initiates with warming in the eastern tropical Pacific (Trenberth 1997), however during an El Niño Modoki event the maximum temperatures were instead located in central tropical Pacific and trapped by cooling areas at the eastern and western sides (Figure 1.2, Ashok et al. 2007, Yeh et al. 2009). This new phase results in maximum SST persisting in central Pacific instead of reaching the South American coast during the warm phase, thus modifying climate teleconnections (Ashok et al. 2007, Yeh et al. 2009).

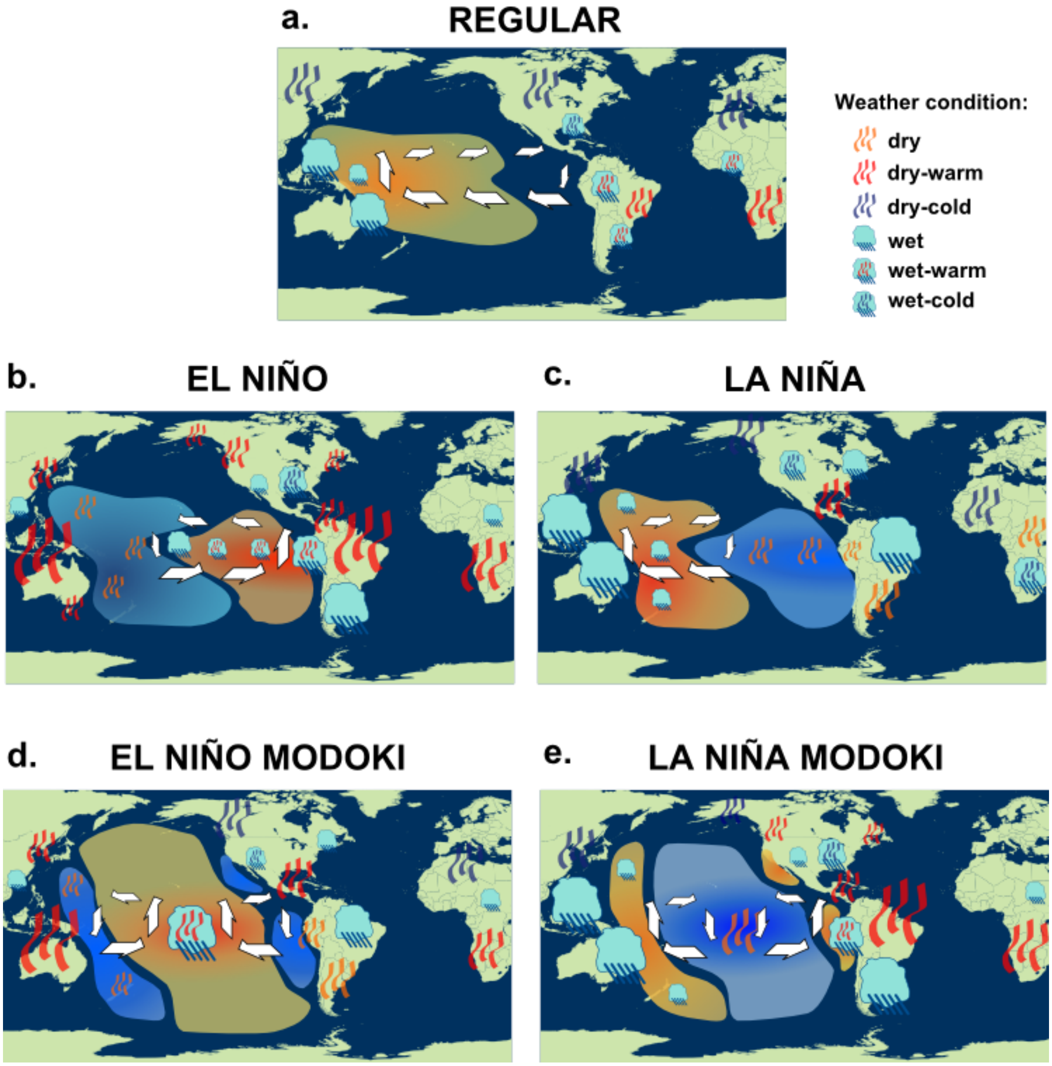

Figure 1.2: Theoretical framework of conditions for precipitation and temperature considering sea surface temperature (redder colours – warmer waters, bluer colours – cooler waters) in the tropical Pacific during regular periods (a) followed by conventional El Niño/La Niña (b, c) and El Niño/La Niña Modoki oscillations (d, e) between December and February. a. Regular condition has warm surface water and air pushed to the west by prevailing winds in the Walker cell (bigger white arrows). Consequences are drier and cooler weather in most Northern Hemisphere, precipitation along the Equator with higher volumes in Oceania and Asia, and dry-warm weather in parts of South America and Africa. b. Conventional El Niño has warmer waters in South America and cooler ones in the western Pacific caused by prevailing western winds. Drier and warmer weather occurs in both hemispheres while higher precipitation is observed mainly in South America. c. The opposite occurs during La Niña although a dry-warm front remains in the Caribbean. d. The El Niño Modoki has the anomalous warm waters in central Pacific trapped between cooler waters to the east and west. e. The opposite occurs during La Niña Modoki. Author: BPV 2017; based on information from Ashok et al. (2007).

The ENSO Modoki is detected by the Modoki El Niño Index (MEI) which has similar interpretation to ONI (Figures 1.1) but with oscillations significant if > 0.7 to El Niño Modoki or < -0.7 to La Niña Modoki (Diaz et al. 2001, Ashok et al. 2007, Li et al. 2010). To capture the different warming pattern, the MEI considers a tripolar nature for the ENSO Modoki including functions already used to detect oscillations in different areas of the Pacific Ocean (Ashok et al. 2007). An analogy could be the conventional ENSO phases as +/– and –/+ for El Niño and La Niña, while Modoki are +/–/+ and –/+/–, respectively. In the western part of the Pacific, ecological consequences may be as expected for a + or – phase, but the eastern Pacific will not respond to an opposite – or + phase during this same time. In a Modoki phase, both western and eastern Pacific will respond to a similar climatic condition (Ashok et al. 2007).

The frequency of climate oscillations also leads to uncertainties about direct links between or within conventional and Modoki phases (Ashok et al. 2007, Yeh et al. 2009). For instance, La Niña Modoki could follow a conventional El Niño, which seems the situation between 1972/73 and 1975/76 events (Figure 1.1); or occur in sequence with El Niño Modoki; i.e. the El Niño Modoki in 2009/10 and the La Niña Modoki in 2011/12 (Figure 1.1).

ENSO can generate very strong effects on aquatic and terrestrial trophic chains (Barber & Chavez 1983, Glynn 1988, Jaksic 2001, 2004), and consequently there is an economic and conservation opportunity in understanding ENSO’s effects on ecosystems, species, and populations. For example, Holmgren & Scheffer (2001) reinforce the potential of using wetter and drier conditions created by the ENSO to recover woodlands while Chavez et al. (2003) point out how fisheries could benefit from changing target species according to abundance peaks caused by climatic oscillations. In addition, Humphries et al. (2017) suggests seabirds in New Zealand could be used as 14-months earlier forecast to El Niño events. However, the potential of using the current knowledge on ENSO’s effects in ecosystems depends on reviewing how these interrelations work at different scales and across species. In this General Introduction, I review mechanisms of the El Niño Southern Oscillation acting on South American climate and how anomalies affect marine ecosystems, especially seabirds. My theoretical framework for this thesis is based on climatic cells and ecosystems working as interconnected gears. The application of this framework on ENSO's ecological effects have potential not only to be applied in biodiversity management and conservation but also as socio-political tools to enhance economic productivity and create a monitoring networking on global hazards.

Ecological effects on the South American marine wildlife

In regular conditions (not affected by ENSO), the South American Pacific coast has warm surface water with air pushed to the west by prevailing winds while the Atlantic coast has scarce winds pushed to the east along the Equator (Sutton et al. 2000). Southern polar winds hit both Pacific and Atlantic coasts although reaching farther north in the Pacific (Grimm 2000, Acha et al. 2014). Most marine wildlife in this region associates with the Humboldt, Cape Horn, and Patagonian sea currents up to the Equator in the Pacific and to the Atlantic Upwelling Zone in Brazil (Acha et al. 2014).

During conventional El Niño and La Niña Modoki, the South American Monsoon System weakens because of the eastward shift of prevailing winds and extreme dry conditions hitting ecosystems from 10°N to 20°S (Grimm 2000, 2003, Sutton et al. 2000, Grimm & Zilli 2009, Novello et al. 2016). The central Pacific coast has increased rainfall in Peru, Bolivia, and northern and central Chile flanked by dry weather in the northern Amazonia basin, the Andean plateau, and southern Chile (Trenberth 1997, Fittkau et al. 2012). From 20ºS southward, the Andean low-level jet increases and joins intense Atlantic coastal winds leading to a Summer Monsoon (Grimm 2000, 2003, Sutton et al. 2000, Marengo & Soares 2004, Grimm & Zilli 2009). The southeastern coastal winds also take the Patagonian sea current further north along the Atlantic coast and increased upwelling results in greater primary productivity in the South Atlantic (Acha et al. 2014). The Brazilian Atlantic coast is also affected by the increase in precipitation at the same time the ENSO events occur in the Pacific because of the faster responses in atmospheric teleconnections (Grimm 2000, 2003, Sutton et al. 2000, Grimm & Zilli 2009). The increase in precipitation affects the river discharges and freshwater outflow up to 130 km offshore in Lagoa dos Patos (Ciotti et al. 1995). An El Niño event, is also immediately associated with cooler SSTs in the South Atlantic; followed by warm SST anomalies after 1.5-2 years (Meredith et al. 2008).

Along the Pacific coast, El Niño pushes the thermocline down and the Humboldt current further south, warming Colombian, Ecuadorian, Peruvian, and northern Chilean waters (Trenberth 1997). Many marine predators, such as seabirds and marine mammals, alter their foraging strategies by extending their trips and diving deeper to catch prey (Limberger et al. 1983, Culik et al. 2000, Bost et al. 2015). During the ENSO's conditions, species remaining in exceptional warm waters of low salinity and low productivity near the Equator such as the Galápagos Islands, the Central-east Pacific coast, and the Central-west Atlantic coast struggle with depleted food resources (Cowles et al. 1977, Barber & Chavez 1983, Duffy 1983, Schreiber & Schreiber 1984a, 1984b, Trillmich & Limberger 1985, Duffy & Merlen 1986, Hays 1986, Glynn 1988, Guerra et al. 1988, Wallace & Temple 1988, Anderson 1989, Massey et al. 1992).

The extreme high or low precipitation during ENSO events also affects river discharges (Figure 1.3). Between 65 and 90% of anomalous flow discharges in South America from La Plata (Argentina/Uruguay) to Magdalena (Colombia) and Paranaíba (Brazil) rivers occur during the ENSO (Aceituno 1988, Restrepo & Kjerfve 2000, Foley et al. 2002, Sahu et al. 2014). Extreme rainfall causes higher discharge in rivers with runoff to estuaries and coastal waters altering salinity, productivity, and thus the fish assemblage in these habitats (Figure 1.3, Garcia et al. 2001, 2003, 2004, Foley et al. 2002, Sahu et al. 2014). In contrast, droughts reduce seasonal inundation of floodplains and allow marine waters to enter rivers thus reducing local freshwater habitats (Figure 1.3, Garcia et al. 2001, Foley et al. 2002). For example, Garcia et al. (2003) found that the abundance of fish in estuaries during the El Niño phase in southern Brazil was five times lower than expected, although species richness was higher. The mixture of waters induced exclusively freshwater fish to appear in the estuary in greater numbers while estuarine-dependent species were forced out and expanded through the marine areas (Garcia et al. 2001, 2003). The changes also prevented larval estuarine-dependent fish, such as mullets (*Mugil* spp.) and Brazilian Silversides (*Atherinella brasiliensis*), settling into the estuary to continue their development (Garcia et al. 2001, 2003). Finally, rainfall and river discharge can also affect certain species of water bird in a positive feedback by providing more available habitat to forage and breed (Vilina & Cofre 2000, Schlatter et al. 2002, Vilina et al. 2002).

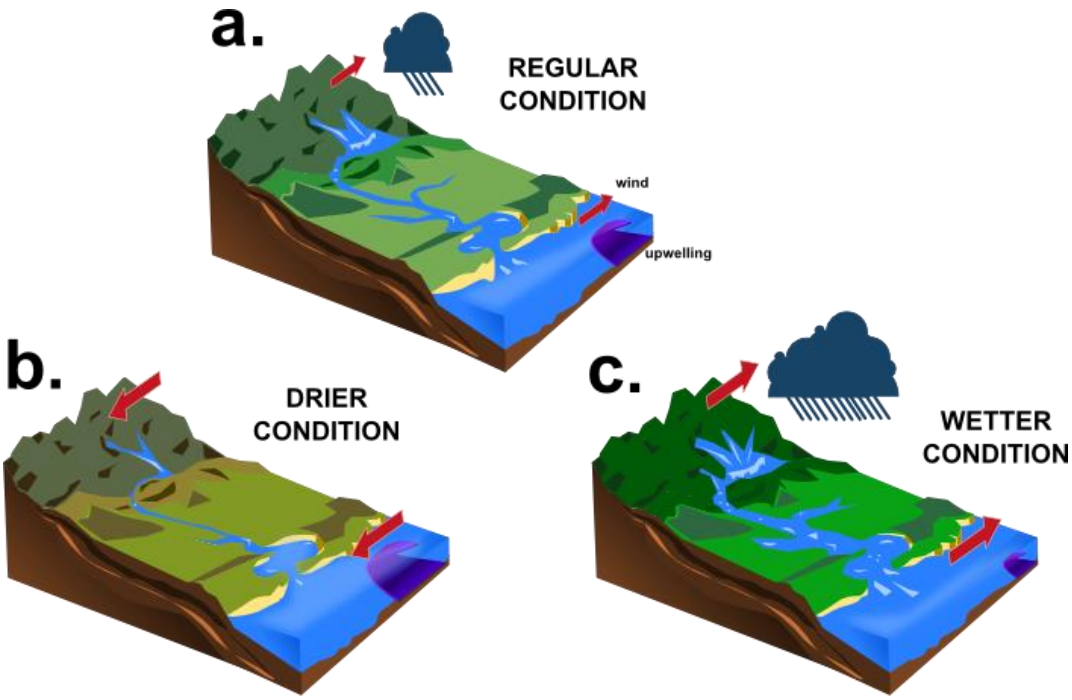

Figure 1.3: Regular and extreme conditions of river discharge affected by the El Niño Southern Oscillation. a. Regular condition has river discharge regulated by rainfall, evapotranspiration, and winds. b. Extreme drier conditions have less precipitation thus reduced river discharge (constrained river and less light-blue marks). Cold currents are closer to the coast causing stronger upwelling and saline intrusion (whitish shapes) into estuaries and rivers. Vegetation defoliates leading to less terrestrial primary productivity (lighter green) and emission of CO_2 however phytoplankton and algae are benefited at sea increasing marine primary productivity. c. Wetter condition have enhanced rainfall therefore increased river discharge (larger river and more light-blue marks). Warm winds take the cooler waters deeper and farther from the coast. Salinity is reduced at estuaries and neighbour coastal zone. Vegetation enhances terrestrial primary productivity (darker green) and creates a CO_2 sink while marine primary productivity is reduced with phytoplankton and algae depleted by low salinity and warmer waters. Author: BPV 2017.

How a population responds to ENSO varies spatially (Romero & Wikelski 2001). For example, resident iguanas on each island of the Galápagos are differently affected by changes in wind, temperature, and precipitation during El Niño (Romero

& Wikelski 2001). The high precipitation in most places washes terrestrial nutrients away to the sea reducing food supply to iguanas and negatively affecting the population (Romero & Wikelski 2001). However, when runoff washes nutrients that are trapped and concentrated in bays algae production is enhanced and the resident iguana population is stable (Romero & Wikelski 2001). In a large-scale perspective, oscillations in South America affect not only resident wildlife but also transcontinental migrants. Migratory birds in the southern Pacific and continental areas are affected at both breeding and non-breeding sites. In general, abundance and breeding success were typically reduced during drier and warmer conditions (Duffy & Merlen 1986, Guerra et al. 1988, Schreiber & Schreiber 1984, Hays 1986, Wilson 1991, Massey et al. 1992, Boersma 1998, Butler et al. 2008, Calvert et al. 2009, Wolfe & Ralph 2009, Simeone et al. 2002, Shaman & Lipsitch 2013, Paxton et al. 2014).

Some terrestrial bird species respond to wetter conditions with enriched assemblages, higher abundance of individuals, and successful breeding with longer breeding period and more broods, but under the same conditions marine and estuarine birds suffer nest losses from flooding and show altered migration routes and stopover sites (Hays 1986, Jaksic & Lazo 1999, Sillet et al. 2000, Grant et al. 2000, Wolfe & Ralph 2009, Shaman & Lipsitch 2013, Paxton et al. 2014). Species differ in their ability to cope with the strong environmental pressures during ENSO events. Highly mobile species may look for other places to breed, forage or spend the non-breeding period (Barber & Chavez 1983, Glynn 1988, Culik et al. 2000, Garcia et al. 2001, 2003, Simeone et al. 2002, Bost et al. 2015). This movement to other areas also leads to more vagrants being found. An alternative strategy is to change physiological needs, for example, Jumbo Squids (*Dosidicus gigas*) born during the El Niño trade gigantism and high fecundity near the coast for accelerated reproduction at small sizes offshore (Hoving et al. 2013). Also, Humboldt Penguins (*Spheniscus humboldti*), which usually breed all year and only stop to moult in January and February change to two marked breeding seasons; one in the austral autumn and another in the austral spring (Simeone et al. 2002).

Among the ecological consequences of the ENSO in South America, the best recorded example are the effects on populations of Peruvian Anchoveta (*Engraulis* *ringens*) and South American Pilchard (*Sardinops sagax*). These species of fish forage typically on large zooplankton and warmer waters associated with ENSO are linked to lower phytoplankton availability and selection of smaller zooplankton (Barber & Chavez 1983, Chavez et al. 2003). Anchovies are affected in their larval stage by low phytoplankton abundance, such that El Niño cause local populations to decrease (Bakun & Broad 2003, Chavez et al. 2003), occupy deeper waters or move to cooler waters in southern Chile (Santander & Zuzunaga 1984). On the other hand, sardines cope better with small zooplankton and have a high mobility capacity so their survival rate is lower than in regular circumstances but still higher than the anchovies' survival rate under ENSO conditions (Arntz et al. 1991, Bakun & Broad 2003). However, these fish stocks not only experience pressures from low food supply but also from increasing predation. Refugia in bodies of cooler waters at shore (Santander & Zuzunaga 1984, Arntz et al. 1991) can increase predation risk from seabirds and marine mammals (Limberger et al. 1983, Culik et al. 2000, Bost et al. 2015). Marine mammals feeding almost only on anchovies, such as the South American Fur Seals (*Arctocephalus australis*) or on fish and squid such as Galapagos Fur Seals (*Arctocephalus galapagoensis*) and California Sea Lions (*Zalophus californianus*) have a lower reproductive success during the El Niño with females having lower body mass and adults spending more time at sea looking for food (Limberger et al. 1983, Glynn 1988).

As the climatic oscillations are first perceived at the Pacific Ocean, seabirds in this area are emblematic models to understand the effects of ENSO on the ecosystem status (Table 1.1). How these species cope with ENSO events depends on their breeding sites, location, mobility, and diet specialisation. Specialised predators, such as Guanay Cormorants (*Phalacrocorax bougainvillii*) on anchovies, Blue-footed Boobies (*Sula nebouxii*) on sardines, and Humboldt Penguins (*Spheniscus humboldti*) on anchovies and sardines, consume the few fish that are available and, with no alternative preys, are negatively affected when these stocks are depleted (Boersma 1976, 1978, Anderson 1989, Arntz et al. 1991, Culik et al. 2000, Simeone et al. 2002, Jaksic 2004). All species that specialise on fish are affected by ENSO conditions, although seabirds that also feed on fishery discards, such as gulls, are more able to mitigate these effects (Jaksic 2004).

Table 1.1: Ecological effects of the El Niño Southern Oscillation's distinct phases described in literature on body condition, breeding, foraging strategy, local demography, movement, and survival of seabirds in South America. Period is considered according to the El Niño Oscillation Index and the El Niño Modoki Index.

Species	**Location**	**Perceived change**	**Period**	**Literature**
White-tufted Grebe (*Rollandia rolland*)	Port San Antonio, Chile.	Breeding increases due to flooding with more available aquatic habitat during El Niño. Lag response in local demography with more individuals in the next year after rainfall.	1992-93 (Strong El Niño), 1994-95 (Moderate El Niño Modoki), 1995-1996 (Weak La Niña), 1997-98 (Very Strong El Niño), 1998 (Strong La Niña Modoki)	Vilina & Cofre 2000
Pied-billed Grebe (*Podilymbus podiceps*)	Port San Antonio, Chile.	Breeding increases due to flooding with more available aquatic habitat during El Niño. Lag response in local demography with more individuals in the next year after rainfall.	1992-93 (Strong El Niño), 1994-95 (Moderate El Niño Modoki), 1995-1996 (Weak La Niña), 1997-98 (Very Strong El Niño), 1998 (Strong La Niña Modoki)	Vilina & Cofre 2000
Great Grebe (*Podiceps major*)	Port San Antonio, Chile.	Breeding increases due to flooding with more available aquatic habitat during El Niño. Lag response in local demography with more individuals in the next year after rainfall.	1992-93 (Strong El Niño), 1994-95 (Moderate El Niño Modoki), 1995-1996 (Weak La Niña), 1997-98 (Very Strong El Niño), 1998 (Strong La Niña Modoki)	Vilina & Cofre 2000
Silvery Grebe (*Podiceps occipitalis*)	Port San Antonio, Chile.	Breeding increases due to flooding with more available aquatic habitat during El Niño. Lag response in local demography with more individuals in the next year after rainfall.	1992-93 (Strong El Niño), 1994-95 (Moderate El Niño Modoki), 1995-1996 (Weak La Niña), 1997-98 (Very Strong El Niño), 1998 (Strong La Niña Modoki)	Vilina & Cofre 2000
American Flamingo (*Phoenicopterus ruber*)	Galapagos Is., Ecuador.	Disappeared. Flooding, warmer waters, and storms reduced food plants and invertebrates in salt ponds.	1982-83 (Very Strong El Niño)	Valle & Coulter 1987
Humboldt Penguin (*Spheniscus humboldti*)	Central and northern Chile; Peruvian coast.	Loss of body mass. Nest flooding and desertion, and reduced number of breeding pairs. Only half of expected adults and juveniles moulting. Deeper foraging dives and longer travels. Decrease in local demography by dispersal and mortality. Migration from Peru southward to southern Peru and northern Chile, and from central Chile southward to southern Chile. Die-offs at the Peruvian coast.	1982-83 (Very Strong El Niño), 1997-1998 (Very Strong El Niño)	Hays 1986, Anderson 1989, Culik et al. 2000, Simeone et al. 2002
Galapagos Penguin (*Spheniscus mendiculus*)	Western Galapagos and Galapagos Is., Ecuador.	No reproduction and decrease in local demography by dispersal and mortality during both phases. Gain of body mass during La Niña but loss during El Niño.	1970-71 (Strong La Niña), 1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Boersma 1976, 1998, Anderson 1989
Magellanic Penguin (*Spheniscus magellanicus*)	Argentina; Rio Grande do Sul, Brazil.	Nest flooding with heavy rains but low related nest desertion. Die-offs (mainly juveniles) in Brazil.	1984, 85, 89 (La Niña Modoki El Niño), 2006 (Weak La Niña Modoki), 2007 (Weak El Niño), 2008 (Moderate La Niña Modoki)	Yorio & Boersma 1994, Mäder et al. 2010
Waved Albatross (*Phoebastria irrorata*)	Galapagos Is., Ecuador.	No breeding. Vagrancy closer to the coast.	1925 (Weak El Niño), 1982-83 (Very Strong El Niño)	Murphy 1936, Rechten 1986,

Species	Location	Perceived change	Period	Literature
				Anderson 1989
Macronectes sp.	Peru.	Migration southward to southern Peru and northern Chile.	1925 (Weak El Niño)	Murphy 1936
Cape Petrel (*Daption capense*)	Peru.	Migration southward to southern Peru and northern Chile.	1925 (Weak El Niño)	Murphy 1936
Galapagos Petrel (*Pterodroma phaeopygia*)	Galapagos Is., Ecuador.	Increase in local demography but retarded chick growth rates.	1983 (Very Strong El Niño)	Duffy & Merlen 1986, Cruz & Cruz 1990
Phoenix Petrel (*Pterodroma alba*)	Christmas Is., Ecuador.	Courting but not nesting. Decrease in local demography by dispersal and mortality during El Niño but increase during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b
Parkinson's Petrel (*Procellaria parkinsoni*)	Ecuador.	Vagrancy closer to the coast.	2016 (Weak La Niña)	Reyes et al. 2017
Procellaria sp.	Peru.	Migration southward to southern Peru and northern Chile.	1925 (Weak El Niño)	Murphy 1936
Cory's Shearwater (*Calonectris diomedea*)	Atlantic and Mediterranean Sea.	Lower survival off sea likely due to Hurricane season in the Atlantic. Reduced first-reproduction during La Niña due to mortality and dispersal at the Atlantic the year before (lag response to El Niño). Increased reproduction in the Mediterranean during El Niño.	1988-89 (Strong La Niña Modoki), 1994-95 (Moderate El Niño Modoki), 1995-1996 (Weak La Niña), 1997-98 (Very Strong El Niño), 1998 (Strong La Niña Modoki), 2000 (Strong La Niña Modoki), 2002 (Moderate El Niño Modoki), 2004-05 (Weak El Niño), 2006 (Weak La Niña Modoki), 2007 (Weak El Niño), 2008 (Moderate La Niña Modoki)	Brichetti et al. 2000, Genovart et al. 2013
Wedge-tailed Shearwater (*Ardenna pacifica*)	Christmas Is., Ecuador.	Decrease in population by dispersal and mortality during both phases. High breeding success during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b
Sooty Shearwater (*Ardenna grisea*)	Peruvian coast; Gulf of Guayaquil and Galapagos Is., Ecuador.	Increase in local demography in the Peruvian coast before El Niño. Vagrancy in Galapagos and die-offs in the Ecuadorian coast during El Niño.	1919 (Strong El Niño), 1982-83 (Very Strong El Niño), 2014 (Before Very Strong El Niño)	Murphy 1936, Aid et al. 1985, Curry & Stoleson 1988, Humphries et al. 2017
Christmas Shearwater (*Puffinus nativitatis*)	Christmas Is., Ecuador.	Courting but not nesting. Decrease in local demography by dispersal and mortality.	1982-83 (Very Strong El Niño)	Schreiber & Schreiber 1984a, 1984b
Audubon's Shearwater (*Puffinus lherminieri*)	Christmas and Galapagos Is., Ecuador.	No reproduction during both phases. Typical flock-feeders grouped in smaller flocks or alone during El Niño. Decrease in local demography by dispersal and mortality during El Niño but increase during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b, Duffy & Merlen 1986
Elliot's Storm-petrel (*Oceanites gracilis*)	Galapagos Is., Ecuador.	No changes.	1983 (Weak La Niña)	Duffy & Merlen 1986
Polynesian Storm-petrel (*Nesofregetta fuliginosa*)	Christmas Is., Ecuador.	Failing reproduction during both phases. Decrease in local demography by dispersal and mortality during El Niño but increase during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b
Leach's Storm-petrel (*Oceanodroma leucorhoa*)	Eastern Pacific.	Decrease by dispersal and mortality during El Niño but increase during La Niña.	1984-86 (Moderate La Niña), 1987-88 (Strong El Niño)	Ribic et al. 1992

Species	Location	Perceived change	Period	Literature
Band-rumped Storm-petrel (*Oceanodroma castro*)	Galapagos Is., Ecuador.	Increase in local population.	1983 (Very Strong El Niño)	Duffy & Merlen 1986
Wedge-rumped Storm-petrel (*Oceanodroma tethys*)	Genovesa and Galapagos Is., Ecuador; eastern Pacific.	Decrease in local demography at Genovesa Is. but increase at Galapagos Is. during El Niño. Also, increase in local demography at the eastern Pacific during La Niña.	1982-83 (Very Strong El Niño),	Duffy & Merlen 1986, Anderson 1989, Ribic et al. 1992
Black Storm-petrel (*Oceanodroma melania*)	Gulf of Guayaquil, Ecuador.	Arrived at the site in substantial numbers.	1925 (Weak El Niño)	Murphy 1936
Markham's Storm-petrel (*Oceanodroma markhami*)	Gulf of Guayaquil, Ecuador.	Left the site in substantial numbers.	1925 (Weak El Niño)	Murphy 1936
Red-billed Tropicbird (*Phaethon aethereus*)	Peruvian coast; Gulf of Guayaquil, Ecuador.	Vagrancy closer to the coast. Migration southward to southern Peru and northern Chile.	1925 (Weak El Niño)	Murphy 1936
Red-tailed Tropicbird (*Phaethon rubricauda*)	Christmas Is., Ecuador.	Disrupted reproductive cycle during El Niño. Increase in breeding pairs and breeding success during La Niña partly also because El Niño changed vegetation making more habitat available.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña), 1989-92 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b, Clark et al. 1990
Lesser Frigatebird (*Fregata ariel*)	Christmas Is., Ecuador.	Increase in local demography but low breeding success (less than 10%) during El Niño. Local demography recovered during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b
Magnificent Frigatebird (*Fregata magnificens*)	Peru; Gulf of Guayaquil, Ecuador.	Earlier courtship in Ecuador. Migration southward to southern Peru and northern Chile.	1925 (Weak El Niño), 1997 (Very Strong El Niño)	Murphy 1936, Haase 1997
Great Frigatebird (*Fregata minor*)	Christmas Is., Ecuador.	Nest desertion. Switched from eating marine fish and squid to large numbers of Tilapia (*Sarotherodon mossambicus*). Decrease in local demography by dispersal due to disappearance of small fish and squid.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b, Anderson 1989
Masked Booby (*Sula dactylatra*)	Christmas, Española and Galapagos Is., Ecuador; Peru.	Loss of body mass. No breeding in Christmas Is. but no changes in Española Is. during El Niño. Decrease in local demography by dispersal and mortality in both phases. Migration southward to southern Peru and northern Chile.	1925 (Weak El Niño), 1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Murphy 1936, Schreiber & Schreiber 1984a, 1984b, Duffy & Merlen 1986, Anderson 1989
Blue-footed Booby (*Sula nebouxii*)	San Cristobal and Española Is., Ecuador.	No breeding during El Niño. Increase in local demography in Española but decrease in San Cristobal Is. during El Niño.	1982-83 (Very Strong El Niño)	Anderson 1989
Peruvian Booby (*Sula variegata*)	Christmas Is., Ecuador; Peruvian coast.	Nest desertion and breeding failure. Grouping of individuals in the Peruvian coast before dispersing to other areas. Decrease in overall demography by dispersal and mortality. Migration southward to southern Peru and northern Chile, and northward to Ecuador, Colombia, and Panama.	1982-83 (Very Strong El Niño), 1997 (Very Strong El Niño), 2014 (Before Very Strong El Niño)	Duffy 1983, Aid et al. 1985, Valle & Coulter 1987, Anderson 1989, Arntz et al. 1991, Haase 1997, Humphries et al. 2015
Brown Booby (*Sula leucogaster*)	Christmas Is., Ecuador.	No breeding in both phases. Decrease in local demography by dispersal and mortality during La	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b

Species	Location	Perceived change	Period	Literature
		Niña but no changes during El Niño.		
Red-footed Booby (*Sula sula*)	Christmas and Española Is., Ecuador.	No changes in breeding at Española Is. Low breeding success (less than 10%) in Christmas Is. during El Niño. Local demography recovered during La Niña. No changes in local demography during La Niña when compared to regular years.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b, Anderson 1989
Flightless Cormorant (*Phalacrocorax harrisi*)	Eastern Pacific.	Failure in breeding.	1982-83 (Very Strong El Niño)	Anderson 1989
Guanay Cormorant (*Phalacrocorax bougainvillii*)	Gulf of Guayaquil and Christmas Is., Ecuador; Peruvian coast.	Nest desertion. Decrease in local demography by dispersal and mortality. Migration southward to southern Peru and northern Chile, and northward to Ecuador, Colombia, and Panama. Die-off in the Ecuadorian coast.	1982-83 (Very Strong El Niño)	Murphy 1936, Duffy 1983, Valle & Coulter 1987, Anderson 1989, Arntz et al. 1991, Haase 1997
Peruvian Pelican (*Pelecanus thagus*)	Peruvian coast; Christmas and Galapagos Is., Ecuador.	Nest desertion. Decrease in local demography by dispersal and mortality. Migration southward to southern Peru and northern Chile, and northward to Ecuador, Colombia, and Panama.	1982-83 (Very Strong El Niño)	Duffy 1983, Duffy & Merlen 1986, Valle & Coulter 1987, Anderson 1989, Arntz et al. 1991
Red-necked Phalaropes (*Phalaropus lobatus*)	Talara, Zorritos and Point Pariñas, Peru; central eastern Pacific; United Kingdom.	Decrease in local demography by dispersal and mortality. Vagrancy closer to the coast.	1925 (Weak El Niño), 1972-73 (Very Strong El Niño), 1982-83 (Very Strong El Niño)	Murphy 1936, Nisbet & Veit 2015
Gray-hooded Gull (*Chroicocephalus cirrocephalus*)	Gulf of Guayaquil, Ecuador.	Low breeding success.	1997 (Very Strong El Niño)	Haase 1997
Gray Gull (*Leucophaeus modestus*)	between Paquica and Antofagasta, Chile.	No change in weight but decrease in lipid storages during El Niño. The opposite during La Niña. Delayed or supressed gonads during both phases. Delayed and shorter moult during El Niño. Earlier and longer moult during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Guerra et al. 1988
Laughing Gull (*Leucophaeus atricilla*)	Peru; Galapagos Is., Ecuador.	Vagrancy in Chile and Galapagos.	1925 (Weak El Niño), 1982-83 (Very Strong El Niño)	Murphy 1936, Curry & Stoleson 1988
Brown Noddy (*Anous stolidus*)	Christmas and Galapagos Is., Ecuador.	Low breeding success (less than 10%). Typical flock-feeders grouped in smaller flocks or alone during El Niño. No changes in local demography during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Duffy & Merlen 1986, Schreiber & Schreiber 1984a, 1984b
Black Noddy (*Anous minutus*)	Christmas Is., Ecuador.	Nests washed out of trees during El Niño and very few nesting during La Niña. No changes in local demography during El Niño but fewer individuals than expected during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b
Blue-gray Noddy (*Anous cerulea*)	Christmas Is., Ecuador.	Low breeding success (less than 10%) during El Niño. Higher breeding success during La Niña. No changes in local demography during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b
White Tern (*Gygis alba*)	Christmas Is., Ecuador.	Low breeding success (less than 10%) during El Niño. Higher breeding success during La Niña.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña)	Schreiber & Schreiber 1984a, 1984b

Species	Location	Perceived change	Period	Literature
Sooty Tern (*Onychoprion fuscatus*)	Christmas Is., Ecuador; eastern Pacific.	Failing reproduction during both phases. Decrease in local demography by dispersal and mortality during La Niña but increase during El Niño.	1982-83 (Very Strong El Niño), 1983-84 (Weak La Niña), 1984-86 (Moderate La Niña), 1987-88 (Strong El Niño)	Schreiber & Schreiber 1984a, 1984b, Ribic et al. 1992
Gray-backed Tern (*Onychoprion lunatus*)	Christmas Is., Ecuador.	No changes.	1982-83 (Very Strong El Niño)	Schreiber & Schreiber 1984a, 1984b
Gull-billed Tern (*Gelochelidon nilotica*)	Ecuador.	High breeding success.	1997 (Very Strong El Niño)	Haase 1997
Inca Tern (*Larosterna inca*)	Peruvian coast; Colombia.	Increase in local demography in Peru. Migrated northward to Colombia.	1982-83 (Very Strong El Niño), 1997 (Very Strong El Niño), 2014 (Before Very Strong El Niño)	Aid et al. 1985, Haase 1997, Humphries et al. 2015
Black Tern (*Chlidonias niger*)	Galapagos Is., Ecuador.	Vagrancy in Galapagos.	1982-83 (Very Strong El Niño)	Curry & Stoleson 1988
Common Tern (*Sterna hirundo*)	Argentina/Germany.	Stayed closer to the coast due to increased river runoff. Return rates of juveniles were higher during La Niña. Premature timing of migration in juveniles during El Niño.	1994-95 (Moderate El Niño Modoki), 1995-1996 (Weak La Niña), 1997-98 (Very Strong El Niño), 1998 (Strong La Niña Modoki), 2000 (Strong La Niña Modoki)	Favero & Becker 2006
South American Tern (*Sterna hirundinacea*)	Ecuador.	Vagrancy in Ecuador.	1997 (Very Strong El Niño)	Haase 1997
Royal Tern (*Thalasseus maximus*)	Peru.	Vagrancy in Chile.	1925 (Weak El Niño)	Murphy 1936
Great Crested Tern (*Thalasseus bergii*)	Christmas Is., Ecuador.	No changes.	1982-83 (Very Strong El Niño)	Schreiber & Schreiber 1984a, 1984b

Some species of seabird, such as frigatebirds (*Fregata* spp.), boobies (*Sula* spp.) and some terns (Sternidae), appear to be highly affected by El Niño conditions and do not recover during the subsequent La Niña phase (Table 1.1). Perceived changes impacting these species are suppressed gonads in adults, loss of body mass, changes in timing of breeding, nests being washed out, nest desertion, lower chick rearing, and decreased chick survival and adult abundance (Table 1.1). Other species such as the Red-tailed Tropicbird (*Phaethon rubricauda*) are affected by lack of food supply during the breeding season but benefit in the following year when food supplies are back to normal, furthermore increased rainfall during previous El Niño resulted in more suitable nesting sites (Table 1.1). Similarly, the increase of marine fish resources during La Niña conditions allows populations of Red-footed Boobies (*Sula sula*), Lesser Frigatebirds (*Fregata ariel*), Wedge-tailed Shearwaters (*Ardenna pacifica*) and some terns to increase breeding performance, compared to regular years (Table 1.1).

Few species in South America were identified to benefit from changes in rainfall conditions during the El Niño phase. However, the Gull-billed Tern (*Gelochelidon nilotica*) breeding in Ecuador may benefit from an increase in fish diversity in estuaries, if freshwater fish are pushed out to sea and marine fish seek coastal refugia, and grebes may benefit from larger body waters in coastal wetlands by providing safer breeding habitats (Table 1.1). In contrast, scarcity of food resources during El Niño conditions has been linked to altered species' foraging strategies and habitat selection. For example, typical flock-feeders grouped in smaller flocks or were seen alone, such as the Brown Noddy (*Anous stolidus*) and the Audubon's Shearwater (*Puffinus lherminieri*) (Table 1.1). Similarly, Great Frigatebird (*Fregata minor*) switched from eating marine fish and squid to large numbers of Mozambique Tilapia (*Sarotherodon mossambicus*) (Schreiber & Schreiber 1984b). The numbers of vagrants and die-offs also increased significantly during ENSO (Table 1.1). Resilience of populations and the speed of recovery indicate however that dispersal and recruitment are stronger drivers of population decrease than mortality in these areas. As long-lived species, seabirds typically prioritise individual adult survival rather than individual breeding attempts.

Migratory birds have staging sites where they stay for long non-breeding periods resting and accumulating energy to come back to breeding sites (Skagen & Knopf 1994); but may also have stopover sites where they stop for short periods to refuel during the migratory journey (Skagen & Knopf 1994). Marine and estuarine bird species show altered migration routes and stopover sites during the ENSO, and although most reports consider negative effects of ENSO on migratory seabirds in the South American Pacific Ocean, it is possible that species may respond differently in other regions. Common Terns (*Sterna hirundo*) in Argentina and Gull-billed Terns (*Gelochelidon nilotica*) in Ecuador stayed closer to the coast during years of increased river runoff, benefiting from high food availability (Haase 1997, Favero & Becker 2006). Food availability in migratory stopover and staging sites affects the timing of return migration in Common Tern sub-adults, but not adults, thus indicating differential affects according to life-stage (Favero & Becker 2006). On the other hand, Magellanic Penguins (*Spheniscus magellanicus*) had higher nest flooding during La Niña Modoki events but breeding success was not affected (Yorio & Boersma 1994) as happened to other *Spheniscus* spp. at the Pacific coast (Table 1.1).

Nonetheless, massive die-offs of juveniles during El Niño and La Niña Modoki events (Mäder et al. 2010) seem to follow the same patterns of its congeners in the Pacific (Table 1.1). Moreover, the Atlantic Ocean has more hurricane activities during ENSO (Goldenberg et al. 2001, Pezza et al. 2005) which leads to high Cory's Shearwater (*Calonectris diomedea*) mortality in the Atlantic during the non-breeding season thus lower first-year recruitment in the following year at the Mediterranean Sea (Brichetti et al. 2000, Genovart et al. 2013).

Despite an increase in the number of studies examining the ecological effects of ENSO, most studies are based on the Pacific Ocean and Northern Hemisphere. Moreover, only 20% of the studies on South American seabirds (Table 1.1) have examined more than two ENSO events, and only 15% of studies have assessed the effects of ENSO in the South American Atlantic Ocean. Furthermore, these studies are limited to three species; Common Tern, Magellanic Penguin, and Cory's Shearwater, and results for the Magellanic Penguin come from assumptions rather direct analysis (Table 1.1). Therefore, more studies in the South American Atlantic are necessary to understand how generalised ENSO's ecological effects are on seabirds and the associated trophic chain.

Remarks and future directions

ENSO affects marine species in South America mostly by increasing rainfall and changing water temperature and salinity. The main consequences in the Pacific populations are depletion of food resources and decrease of suitable available nesting habitats. However, some species benefit from improved foraging or nesting conditions. The Atlantic populations are largely understudied, and other effects such as increase in hurricane frequency may also affect seabird populations in this area. Long-lived seabird species seem to respond to ENSO by constraining, delaying, or skipping reproduction; changing habitat use due to lack of their normal prey resources; and prioritising adult survival by moving to farther areas and deserting breeding attempts. In general, species capable to move to farther sites look for alternative areas during both breeding and non-breeding seasons. Alternative strategies include adjusting breeding cycles (e.g. *Spheniscus humboldti*) or supressing moult (e.g. *Leucophaeus modestus* and others in Table 1.1). Despite adaptations, the number of seabird wrecks along both Pacific and Atlantic South America coastlines are higher during the ENSO than in regular years (Murphy 1936, Anderson 1989, Mäder et al. 2010).

Despite the knowledge acquired in over 40 years of research on the effects of ENSO, ecological changes on the Atlantic coast are still largely unknown. Methods that can underpin studies on ecological effects of ENSO include not only long-term monitoring but also use of big data and citizen science. Other possible approaches are the analysis of marine sediments and fossils, stable isotopes from different tissues, and analysis of changes in river deposits (Glynn 1988). The climatic oscillations affect habitats in a cascade of events that might influence the biology of seabirds which are already recognised bioindicators of marine biodiversity and productivity (Furness & Camphuysen 1997).

Some seabird species can be used as bio-monitors of how ENSO has impacted ecosystem status because they respond to this oscillation with dramatic changes in breeding success, foraging patterns and population abundance (Table 1.1 Humphries et al. 2015, 2017). Humphries et al. (2017) noticed Sooty Shearwaters (*Ardenna grisea*) in New Zealand respond to climate oscillations in the South Pacific Convergence Zone by decreasing breeding success one year prior to the ENSO formation. It is possible these features can turn seabird into indicators for forecast tools that could predict the impact of ENSO events thus creating a network to monitor global hazards. Although forecasting ENSO's onset is still to be debated, the sequence of events once it is triggered are certain and its teleconnections and the different timing of response between species would also allow to establish a network of warnings (Glantz 2015). Climate and biotic teleconnections are of key interest to manage risks in a changing world. Applications of such bio-indicator species are especially valuable to management of endangered species and exploitation of marine resources. The ENSO has wide-ranging consequences and is therefore an important topic of study for managing current and future ecological responses to environmental changes. However, this also implies a shift from being passive and simply observing changes in species populations to having proactive action plans designing flexible management policies and reinforcing multiple target species for conservation and economical exploitation according to the most suitable timing (Bakun & Broad 2003).

Chapter 2: The Black Skimmer as a study species

Abstract

The Black Skimmer (*Rynchops niger*) is a coastal migratory bird with three sub-species based on distinctive morphometric, plumage, and breeding distribution. In this chapter, I conducted an extensive review of the Black Skimmer's natural history. I used 41,247 records collated from databases and literature to establish the distribution and location of breeding colonies for each sub-species. I also collected dates and life-history events described in 145 papers and books to describe the annual-cycle of the three sub-species. The North American sub-species (*R. n. niger*) has white underwing, is significantly smaller than the other sub-species and seems to be restricted to North America and the Caribbean. The other two sub-species occur in South America. The Amazonian sub-species (*R. n. cinerascens*) has well delimited dark grey underwings, while the South American sub-species (*R. n. intercedens*) has white or not delimited light grey underwings. The North American sub-species breeds, migrates, and stages along the coast with few records inland. The South American and Amazonian sub-species breed inland, and migrate to stage mostly at the coast. Black Skimmers have site selection affected by the presence of species, such as terns and plovers, as well as the availability of sandbanks with high granulometry (fine sand) and the distance to calm shallow waters. The Black Skimmer occupies coastal and freshwater habitats that are highly affected by climate change, especially environmental oscillations such as the El Niño Southern Oscillation (ENSO). Black Skimmers' breeding, migrating, foraging, and moult depends on temperature, precipitation, and winds, which are abiotic variables highly affected by ENSO. As Black Skimmers are widespread and usually associated with other species such as terns and gulls, their conservation is directly related to the conservation of other species which turns Black Skimmers into suitable umbrella indicator species.

Keywords: Black Skimmer, natural history, annual cycle, resource use.

The Black Skimmer

The Black Skimmer (*Rynchops niger* Linnaeus, 1758) has a knife-like black and orange bill, and lower mandible extending beyond the upper mandible (Murphy 1936, Zusi 1962, 1996, Gochfeld & Burger 1994). It is also unique among birds with slit pupil shape and five times more rods than cones, which sacrifices the colour range to increase ability to see in low light (Zusi & Bridge 1981, Rojas et al. 1997). These adaptations are related to nocturnal foraging habits, in which individuals soar and skim the water surface with the bill to catch fish prey (Murphy 1936, Zusi 1962, Clayton et al. 1979, Burger & Gochfeld 1990, Malmström & Kröger 2006). Wetmore (1944) distinguished three sub-species (*niger*, *intercedens*, and *cinerascens*) based on distinctive morphometrics, plumage, and breeding distribution. The North American sub-species (*R. n. niger*) has white underwing, is significantly smaller than the other sub-species and seems to be restricted to North America and the Caribbean (Wetmore 1944). The other two sub-species occur in South America. The Amazonian sub-species (*R. n. cinerascens*) has well delimited dark grey underwings, while the South American sub-species (*R. n. intercedens*) has white or not delimited light grey underwings (Wetmore 1944).

Adult skimmers have black and white countershading plumage which is typical of aquatic predators such as sharks, dolphins, and penguins. Gochfeld & Burger (1994) classified five stages of Black Skimmer plumage from natal to definitive alternate plumage. These plumages can be also grouped into two age stages: juveniles and adults. Juveniles from 1-month and up to 1-year old have a distinctive spotted or brownish dorsal plumage (Burger & Gochfeld 1990). When reaching 2-years old, they acquire the adult basic plumage and later in the breeding season the alternate plumage (Murphy 1936, Burger & Gochfeld 1990). The basic plumage is distinguished from the alternate plumage by a white nuchal collar (Murphy 1936, Burger & Gochfeld 1990).

The natural history and ecology of Black Skimmers from North America is well established. In comparison, the sub-species in South America, known to differ in many aspects such as breeding (Zusi 1996) and moulting (Vieira et al. 2017), still have fewer studies published (Appendix 2.1) and almost no reviews about their distinct ecology and life-history. Moreover, as noticed from Chapter 1, there are no studies testing ecological effects of environmental changes on Black Skimmers in South America. Here, I present a review of the natural history aspects of Black Skimmers that underpin this thesis and why this species might be suitable to study the ecological effects of environmental oscillations in the Atlantic coast. This study fills some gaps in the Black Skimmer’s natural history, especially about the occurrence of individuals, location of breeding sites, and timing of the annual cycle.

Methods

The Black Skimmer is known to occur in the New World from 45ºN in Canada to 43ºS in Chile and Argentina (Zusi 1996). To update the Black Skimmer’s occurrence and location of breeding sites, I reviewed a total of 115,990 records from North, Central and South Americas available in literature or uploaded on web databases. Records covered a period from January 1700 to December 2016. The web databases considered were www.wikiaves.com, www.xeno-canto.org, and www.GBIF.org. Data from www.eBird.org is already included in the GBIF website. Literature review considered approximately 145 papers and books found through Web of Knowledge, Google Scholar, the Periódicos CAPES, and the SORA databases (Appendix 2.1). Searches used the terms “Black Skimmer” or “*rayador*” or “*talha-mar*” or “*corta-água*” or “*Rynchops niger*” or “*Rynchops nigra*” and were not case sensitive.

For this study, the occurrence in one locality was counted only when sub-species and coordinates were available and considered accurate. Data were double checked to avoid duplicates, errors, and inaccuracies. When sub-species was not already designated but images showing the underwing and location were available, the sub-species was identified following Wetmore (1944). After checking data for sub-species, duplicates, errors, and inaccuracies, I selected a total of 41,247 from the 115,990 records. The selected data covered 37,465 records for the North American sub-species, 2,274 records for the Amazonian sub-species, and 1,508 records for the South American sub-species (Figure 2.1).

Based on the timing and events described in the reviewed literature between 1866 and 2017 (Appendix 2.1), I reconstructed a generalised life-history annual cycle for each Black Skimmer sub-species (Figure 2.2). Major events were considered as breeding, migrating, and staging with the non-breeding season covering migrating and staging. The minor events were considered as moulting during the non-breeding season; and laying, incubating, hatching, raising young, and fledglings leaving the colony during the breeding season (Figure 2.2). For each event, I considered the average month cited in the literature according to species and major or minor events.

Occurrence

There are some overlapping areas of distribution between sub-species (Figure 2.1). The North American and the Amazonian sub-species can both be seen around Panamá, Colombia, and Venezuela (Figure 2.1). The Amazonian and South American sub-species can be found in the whole South America (Figure 2.1) however there are more records of South American individuals in Pantanal and the Atlantic coast (Figure 2.1) than in the Amazon, the Caribbean, and the Pacific Coasts where the Amazonian sub-species prevails (Figure 2.1).

Venezuela has the southernmost record of a North American Black Skimmer’s breeding colony (Figure 2.1, Appendix 2.2). While the North American sub-species breeds on sand beaches and sandbanks across coastal North America and the Caribbean, the Amazonian and South American sub-species breed on river sandbanks inland South America (Figure 2.1). Overlap between colonies is not common. However, Antas et al. (2016) captured an Amazonian individual in a colony of South American Black Skimmers at Pantanal in Brazil. Also, a South American individual ringed in an Amazonian colony was found non-breeding at Florianopolis in southern Brazil in 2016 and 2017 (Bianca Vieira pers. obs.).

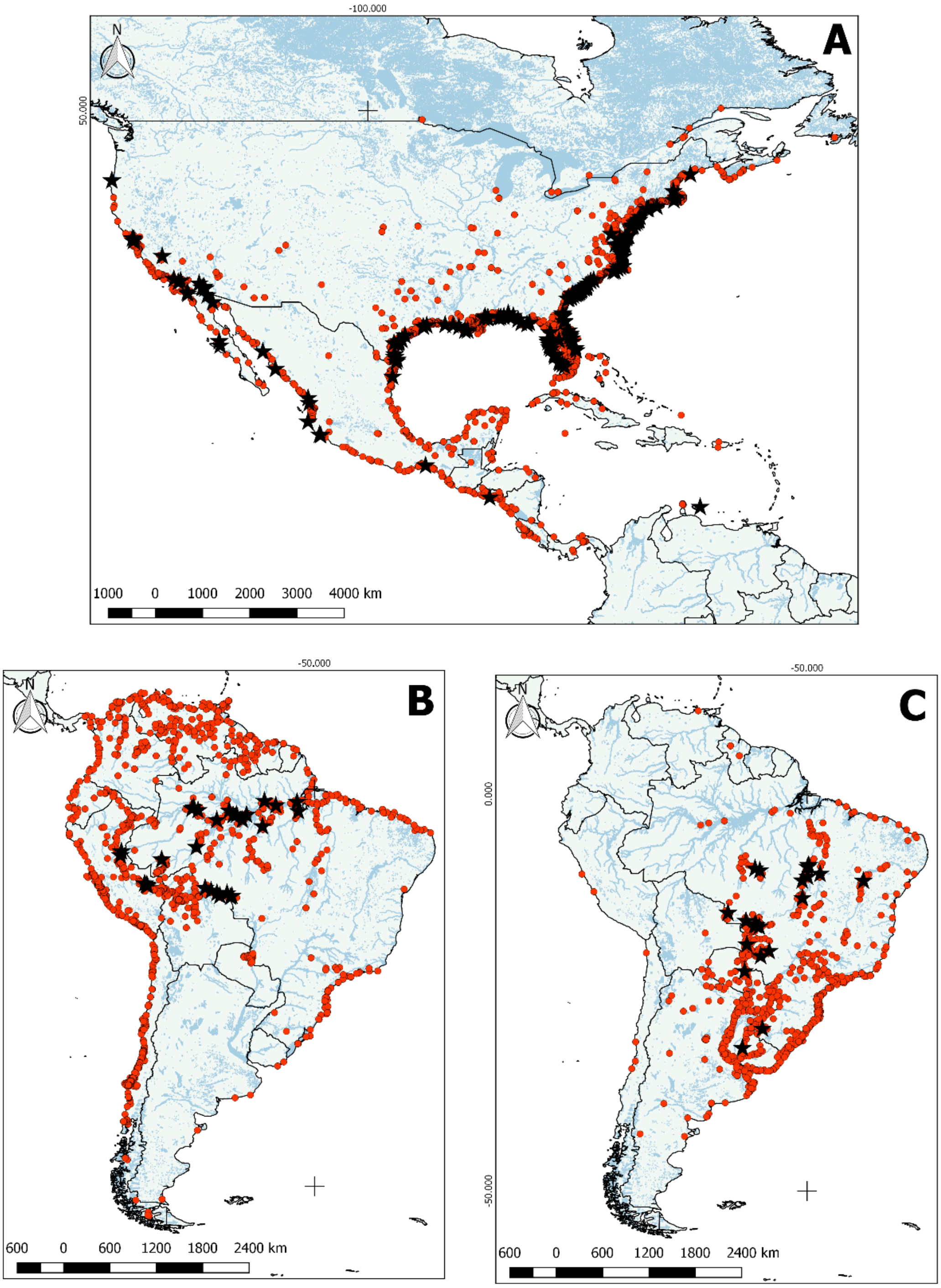

Figure 2.1: Occurrence (red points) of the North American (A), the Amazonian (B), and the South American (C) Black Skimmer sub-species recorded in literature and web databases from 1700 to 2016. Black stars are breeding colonies. The list of colonies is presented in the Appendix 2.2.

During an expedition in the Amazonian colonies at the Xingu River in Brazil in September 2015, I found mixed groups of South American and Amazonian Black Skimmers although they did not inter-bred during the observations. While Aluisio

Ramos (*in litt.* 2016) found a South American individual in an Amazonian colony north at the Guapore River (Brazil/Bolivia), João Ribeiro (*in litt.* 2016) found a full colony of Amazonian individuals in the southern Guapore River (Brazil/Bolivia) near colonies of the South American sub-species. These observations point to the possibility of sub-species breeding at the same site yet there is no confirmation for inter-breeding. An alternative explanation is that individuals were just crossing the area during their movements from or to their actual breeding sites.

There are no overall population estimates for the species. Gochfeld & Burger (1994) listed around 93,000 North American Black Skimmer breeding pairs across the USA. Mellink et al. (2007) counted around 1,000 breeding pairs in Western Mexico. Blanco et al. (2008) estimates the South American sub-species population ranges from 25,000 to 100,000 individuals. Antas et al. (2016) estimates 20,000 South American Black Skimmer individuals in Pantanal during the breeding season. Branco & Fracasso (2005) estimated up to 5,000 individuals along the Santa Catarina coast in southern Brazil during the non-breeding season. Vooren & Chiaradria (1990) counted 600 individuals in 60 km of the Cassino Beach in Rio Grande do Sul in southern Brazil during the non-breeding season. Barbieri (2007) counted around 2,640 individuals at Ilha Comprida and Olmos & Silva (2001) up to 450 individuals Santos; both sites in São Paulo in southeastern Brazil during the non-breeding season. Estades & Vukasovic (2013) counted almost 4,000 Amazonian Black Skimmers in Central Chile while González et al. (2011) found around 2,000 individuals in the estuary of Itata River during the non-breeding season. The population at Mar Chiquita in Argentina is estimated in 12,000 individuals (Silva-Rodrigues et al. 2005) with both Amazonian and South American individuals (Mariano-Jelicich & Madrid 2014). Alfaro & Clara (2007) counted 350 Black Skimmers non-breeding in Rocha Lagoon in Uruguay. Antas et al (2016) estimated a population up to 35,000 individuals possibly of both sub-species in Paraguay based on data from Hayes (1996).

Aspects of the life-history annual cycle

All Black Skimmer sub-species are migratory but the North American sub-species has some resident populations bordering the Caribbean Sea. The North American sub-species seems to breed, migrate, and stage entirely along the coast (Burger & Gochfeld 1990, Gochfeld & Burger 1994) with few records inland (Figure 2.1). The South American and Amazonian sub-species breed inland, and migrate to stage mostly at the coast (Murphy 1936, Zusi 1996).

Burger & Gochfeld (1990), Gochfeld & Burger (1994) and Antas et al. (2016) reported Black Skimmer's fidelity to breeding sites when successfully breeding in previous years. All sub-species lay 2 to 4 eggs but more frequently 3 eggs (Burger & Gochfeld 1990, Groom 1992, Zusi 1996, Antas et al. 2016). Up to 60% of chicks in the colonies seem to survive to fledgling stage and leave the colony in successful seasons (Burger & Gochfeld 1990, Groom 1992, Zusi 1996, Antas et al. 2016). Courtship and preparation of nests in colonies take less than 15 days, laying eggs take up to 6 days when laying 4 eggs, incubation varies from 20 to 25 days and rising young can take up to 30 days (Burger & Gochfeld 1990, Groom 1992, Zusi 1996, Antas et al. 2016). The species has shared parental care from incubation to feeding and protecting chicks (Burger & Gochfeld 1990, Zusi 1996, Antas et al. 2016). Black Skimmers keep a minimum nearest neighbour distance of 100 cm (Gochfeld & Burger 1994). In the USA, the species' foraging range during the breeding season varies from 5 to 8 km from the colonies (Tomkins 1951, Gochfeld & Burger 1994). Tracking data from Davenport et al. (2016) suggests that Amazonian Black Skimmers in Peru have a rough foraging range up 15 km from colonies. No data were found for the South American Black Skimmer in terms of foraging trips. All sub-species feed chicks with fish but Amazonian Black Skimmers in Suriname and South American ones in Pantanal also feed chicks with insects (Burger & Gochfeld 1990, Antas et al. 2016).

There is some evidence that Black Skimmers stay in the same roosting area while moulting (Gochfeld & Burger 1994, Davenport et al. 2016). Gazzaniga (1996) found that 55% to 100% of Black Skimmers marked were seen again after the first year and showed a between-year site fidelity at non-breeding sites in the USA. This percentage would drop to 22% in the second year (Gazzaniga 1996) however it does not exactly mean birds lost fidelity to sites because they could have just lost the rings. Gazzaniga (1996) also reports the percentage of times an individual was seem at the same area from the first to the last observation in the season varied from 52.2% to 83.5%. Four birds marked or tracked by Davenport et al. (2016) in 2012 and 2014 in Peru have been seen at the same moulting sites in Chile until 2017, while a male marked in the Brazilian Amazon in 2012 has been recorded non-breeding at the Island of Santa Catarina in southern Brazil annually since 2014 (Roberto Saavedra & Bianca Vieira unp. data). The timing of major events in Black Skimmer’s life-history varies between colonies according to distribution and there is some evidence for a latitudinal effect (Burger & Gochfeld 1990, Antas et al. 2016).

In contrast to the Northern Hemisphere, breeding in South America occurs in the dry season when low waters in Pantanal and Amazonia expose more river sandbanks and trap fish prey in ponds (Nunes & Tomas 2008, Antas et al. 2016). Black Skimmers rest and breed in open areas with sandy substrate and some surrounding vegetative cover (Erwin 1977, Gochfeld & Burger 1994, Zarza et al. 2013, Antas et al. 2016). Nesting on dry sandbars has implications on the thermoregulation of eggs so skimmers breed near water sources to not only forage more efficiently but also to wet their feet and bring water to the eggs (Grant & Paganelli 1984).

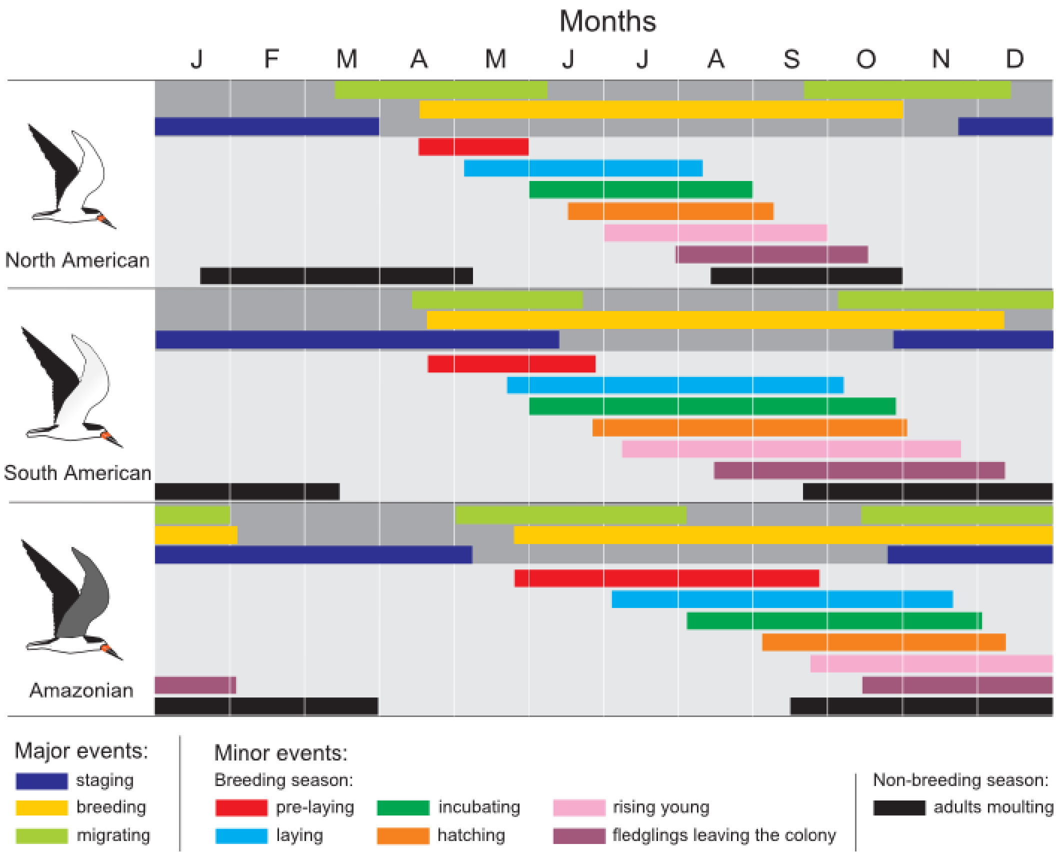

Figure 2.2: Generalised life-history annual-cycle of North American, South American, and Amazonian Black Skimmer sub-species based on mean dates of major and minor events described in the literature (Appendix 2.1).

Events take the same period for individuals of all sub-species. The overlap between breeding, migratory and non-breeding events in Figure 2.2 are related to differences in timing of events between colonies (Burger & Gochfeld 1990, Antas et al. 2016). In addition, an individual can move up to 700 km per day during migration (Davenport et al. 2016), meaning that in a same month an individual could be at the breeding and non-breeding site. Compared to other breeding minor events, adults are likely to have longer movements from pre-laying to incubation periods and when fledglings are leaving the colony (Davenport et al. 2016). During the non-breeding season, birds in moult are likely to be more grouped at specific moulting sites (see Chapter 5) than while migrating, and possibly have reduced movements to save energy while replacing feathers (Pyle 2008, Howell 2010).

Black Skimmers establish colonies based on the previous presence and concentration of tern colonies (Murphy 1936, Erwin 1977, Krannitiz 1989, Gochfeld & Burger 1994, Efe et al. 2001). Colonies at the same area have synchronous timing

(Gochfeld 1979, Gochfeld & Burger 1994) and can be mono-specific (Oberholser 1938) or more frequently multi-specific (Murphy 1936, Preston 1962, Buckley et al. 1978, Erwin 1979, Clapp et al. 1983, Kale & Maehr 1989, Krannitiz 1989, Burger & Gochfeld 1990, Groom 1992, Gochfeld & Burger 1994, Zusi 1996, Vooren 1998, Efe et al. 2001, Zarza et al. 2013). Mixed flocks occur in both breeding and nonbreeding sites (Vooren & Chiaradia 1990, Chiaradia 1991, Vooren 1998, Vieira 2014). As Black Skimmers are usually associated with other species, their conservation is directly related to the conservation of others which highlights the Black Skimmer as a useful umbrella indicator species.

Although usually breeding in mixed colonies, the Black Skimmer's timing of migration is independent from other species in the mixed colony. The three sub-species also seem to select different migratory routes and destinations between them. The North American Black Skimmers migrate mostly from north to south with possible movements between islands in the Caribbean (Clapp et al. 1983, Gochfeld & Burger 1994, Zusi 1996). Unlike the other sub-species, inland migration in the North American sub-species is unusual (Figure 2.1, Gochfeld & Burger 1994). In South America, Davenport et al. (2016) tracked Amazonian individuals breeding at the Peruvian Amazon crossing the Andes and using stopover sites along the Pacific coast before reaching their non-breeding site in southern Chile where they staged the whole non-breeding season. Indeed, if we observe the records for the Amazonian sub-species, there are likely several Andean crossings in Venezuela, Colombia, Ecuador, Peru, and in Bolivia to Chile (Figure 2.1).

Mainly in the Brazilian territory, both Black Skimmer sub-species seem to rely on great water masses such as the Amazon, the Tocantins, the Guapore, the Tiete, and the Paraguay rivers (Bianca Vieira unp. data). Individuals ringed in the Amazon and Pantanal have been reported in southern Brazil and Argentina in the non-breeding season (Nunes & Tomas 2008, Antas et al. 2016, Bianca Bernardon *in litt.* 2016, Bianca Vieira pers. obs.). Mariano-Jelicich & Madrid (2014) also found a genetic migratory connectivity between individuals from the Amazon, Pantanal, and Argentina.

In the southeastern and southern Brazilian non-breeding sites, Branco & Fracasso (2005), Barbieri (2007) and Vieira (2014) found lower numbers of Black Skimmers during austral winter and spring yet there were always overstaging birds (individuals that spend the breeding season in the non-breeding site). Around 600 individuals from an estimated peak abundance of 1,200 Black Skimmers overstaged at the Island of Santa Catarina in southern Brazil between 2011 and 2012 (Vieira 2014). Most of them were juveniles or adults in non-breeding plumage (Vieira 2014). Gochfeld & Burger (1994) also reported 1-year-old birds do not return to breeding colonies and that it is common to observe them overstaging in the USA. North American individuals that skip breeding usually also skip moulting of primaries and do not change from basic to alternate plumage (Gochfeld & Burger 1994). However, there are no data about individuals skipping moult in South America.

The moult cycle of North American Black Skimmers occurs with some primaries being renewed from January to May and the rest together with the body feathers from August to October (Figure 2.2, Gochfeld & Burger 1994, Pyle 2008). Gochfeld & Burger (1994) described breeding as being four to six weeks earlier in warmer Gulf States and the same for moulting. Post-breeding moulting in North American sub-species may occur after breeding and before migration but continues at the non-breeding site up to final migration season (Figure 2.2, Gochfeld & Burger 1994). The South American and Amazonian sub-species on the other hand have a complete sequential moult of primaries which starts after arriving to the non-breeding site and finishes before leaving to the breeding sites (Chapter 5, Scherer et al. 2013, Vieira et al. 2017). It is possible these differences in moulting strategies between sub-species are related to higher nutritional value of prey available at the coast, especially estuarine areas where fish species are rich in sulphur-containing amino-acids that are essential to the development of feathers (Lindström et al. 1993, Weinstein et al. 2000). Breeding, migration and staging at coastal areas may allow North American sub-species to start moulting before migration and stop the process until reaching more productive non-breeding sites. Amazonian and South American sub-species spend only the non-breeding season at coastal and estuarine areas so moulting is concentrated in the non-breeding season. Moreover, moult in Black Skimmers seems to be related to temperature and while North American sub-species' moult occurs during boreal autumn to spring (Pyle 2008), the South American and

Amazonian sub-species' moult occurs during austral spring to autumn (Chapter 5, Scherer et al. 2013, Vieira et al. 2017).

Resource use

Black Skimmers have two main components affecting nesting site selection. The first component is behavioural and related to the previous presence of other sand-nesting species, such as terns and plovers (Murphy 1936, Erwin 1979, Grant & Paganelli 1984, Krannitiz 1989, Gochfeld & Burger 1994, Efe et al. 2001). The second component is abiotic and related to availability of sandbanks with high granulometry (fine sand) and short distance from calm shallow waters (Erwin 1977, Burger & Gochfeld 1990, Zarza et al. 2013). In South America, permanent dry coastal sandbanks are not usual however river sandbanks are very common in large rivers during the dry season. Therefore, precipitation also affects availability of nesting sites for Black Skimmers in South America (Nunes & Tomas 2008, Antas et al. 2016). During the rainy season in South America, river sandbanks disappear, waters become more agitated, and Black Skimmers migrate to the coast (Zusi 1996, Antas et al. 2016). While precipitation also plays a significant role in Black Skimmers' migratory behaviour in South America, temperature is the major weather variable affecting the North American sub-species (Burger & Gochfeld 1990). Breeding in North America occurs with higher temperatures during boreal spring and summer and migration to southern areas starts as temperature decreases (Burger & Gochfeld 1990). However, Black Skimmers in the Equatorial Zone where temperatures are constantly warm seem to be resident (Gochfeld & Burger 1994, Zusi 1996). Environmental variables affecting migratory routes have not been studied yet great rivers and predominant winds seem to be important in selection of routes and stopover sites (Bianca P. Vieira unp. data). Black Skimmers have a high flight capacity reaching 70 km/day during breeding and staging seasons, but 500 km/day during migration (Trevor Hardaker *in litt.* 2013, Davenport et al. 2016).

Most staging sites selected by all sub-species are coastal and related to rivers, estuaries, bays, lagoons, salt marsh pools, creeks, and ditches (Murphy 1936, Zusi 1962, Erwin 1977, Black & Harris 1983, Gochfeld & Burger 1994, Zusi 1996).

Skimmers forage mainly on surface fish and crustaceans (Stone 1921, Davis 1951, Leavitt 1957, Zusi 1959, Potter 1982, Black & Harris 1983, Gochfeld & Burger 1994, Neves & Vooren 2006, Mariano-Jelicich et al. 2007). While foraging mostly at dawn, dusk and night, Black Skimmers select these habitats because of smooth shallow waters where it is easier to spot and trap the prey under low wind conditions (Tomkins 1951, Zusi 1962, Erwin 1977, Black & Harris 1983). Open waters are used with less frequency (Erwin 1977, Mariano-Jelicich et al. 2007).

McNeil et al. (1995) explained nocturnal activities are selected because favoured prey fish feed more frequently on invertebrates near water surface at night than during the day. On the other hand, Rojas et al (1997) showed that at night winds are reduced and water surface is smoother. Diurnal feeding seems to be more related to low tides when fish prey might get trapped at pools in mudflats (Tomkins 1951, Burger 1982). Charles Darwin was the first to notice that Black Skimmers locate prey by tactile feeding while skimming the water with the lower mandible (Murphy 1936). Skimmers are agile, but often forage with motionless wings to soar near the water (Murphy 1936, Tomkins 1951, Zusi 1962, Rojas et al. 1997). Zusi (1962) estimated a flight speed from 16 to 38 km/h while skimming. The flight speed should rise if they are not foraging and benefit from wind influence as in migratory movements or long-distance prey search.

Mariano-Jelicich et al. (2007) noticed diet segregation between the sexes in Black Skimmers at Mar Chiquita in Argentina. Black Skimmers are sexually size-dimorphic with males being larger than females (details in Chapter 4). Thus, males need more energy intake and capturing larger prey would be energetically more efficient – provided a sufficient abundance of large prey – than searching for more smaller prey. Mariano-Jelicich et al. (2008) also verified divergence between trophic level of food acquired by Black Skimmers according to sex, with males feeding on higher trophic level than females. This trophic difference is likely related to fish size than spatial segregation because both males and females forage together in small groups in the same habitats and at the same time (Murphy 1936, Gochfeld & Burger 1994).

The Black Skimmer in a changing world

The Black Skimmer is distributed in the New World with resource use differing according to breeding, migrating and non-breeding seasons as well as sub-species. The Black Skimmer already faces threats in this changing world. Censuses estimated that the population in North America is decreasing because of habitat loss, with sandbank habitat flooded by rising water levels due to global warming, and a variety of human activities, from recreation to dredging (Zusi 1996, BirdLife 2014). Persistent colonies usually are large and not significantly disturbed, while colonies that move site each year are small and usually fail because of intense disturbance and predation (Erwin et al. 1981, Burger 1982, Safina & Burger 1983, Gochfeld & Burger 1994, Burger et al. 2010). Since the 1930s in North America, Black Skimmers are adapting to habitat loss by selecting nesting sites in dredge deposition islands, dead vegetation in salt marshes, and flat rooftops (Tomkins 1933, Greene & Kale 1976, Parnell & Soots 1980, Gochfeld & Burger 1994, FFWCC 2011). Most breeding sites in South America are isolated from anthropogenic influence (Zusi 1996, Vooren 1998, Antas et al. 2016) and there are no records of Black Skimmers using nesting sites associated to anthropogenic structures (e.g. houses and buildings) or human disturbance (e.g. boat and walking recreation). However, they use dredge deposition islands to roost on the coast and do not seem to be disturbed by the presence of houses (Pereira 2016). Nonetheless, the presence of intense human activities in the South American non-breeding sites, mainly recreational, forces Black Skimmers to leave areas despite available prey or roosting sites (Vooren & Chiaradia 1990, Chiaradia 1991, Vooren 1998, Vieira 2015).

The Black Skimmer occupies coastal and freshwater habitats that are highly affected by climate changes, especially environmental oscillations such as the El Niño Southern Oscillation – ENSO (Chapter 1). Moreover, Black Skimmers' successful breeding, migrating, foraging, and moulting depend on temperature, precipitation and winds which are abiotic variables highly affected by ENSO (Chapter 1). The only studies addressing the effects of ENSO on Black Skimmers are for the North American Black Skimmer sub-species in Mexico. Carmona et al. (1995) and Mellink (2003) found individuals had improved breeding performance and more individuals were found in resting areas near the breeding sites along the coast during the El Niño. However, as in other widespread species, responses might differ according to populations (Chapter 1). Although Carmona et al. (1995) and Mellink (2003) focused on breeding sites, the species’ responses to environmental changes might also diverge in other life-history events such as migration and moulting.

South America represents an important tropical zone for biodiversity conservation. The South Atlantic coast in South America is intensively used by Black Skimmers (Figures 2 and 3) and high abundances have been recorded along the estuaries between São Francisco do Sul in Brazil and La Plata River in Argentina (Vooren & Chiaradia 1990, Branco & Fracasso 2005, Barbieri 2007, Scherer et al. 2013, Mariano-Jelicich & Madrid 2014). The productivity in the southern and southeastern Brazilian Atlantic coast is related to the Atlantic upwelling and the Temperate estuarine zones (Acha et al. 2004). These zones are formed by the South Atlantic Central Waters (SACW), which includes resurgences and mixtures of waters from La Plata River and Lagoa dos Patos, the warm Brazilian Current, and the cold Subantarctic Current from the Patagonian Shelf (Odebrecht & Castello 2000). This thesis investigates if large-scale climatic oscillations in the Pacific can affect estuarine predators such as the Black Skimmer in the Southern Atlantic coast.

Chapter 3: Using field photography to study avian moult

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Abstract

Methods to obtain moult data from wild birds have not changed much over the last century and most studies still depend on checking museum specimens or capturing birds. Here I assess the applicability of systematic field photography for detecting and scoring moult in adult Black Skimmers (*Rynchops niger*) from southern Brazil. Moult data extracted from photographs have a high within- (R_{GLMM} = 0.98) and between-observer repeatability (R_{GLMM} = 0.97), and show very good fit to current Underhill-Zucchini moult models (R^2 = 0.75). Photography offers the advantages of being less invasive, requiring less equipment and human effort, being feasible in areas where captures may not be possible, and causing less disturbance, so enhancing the number of sampled individuals.

Keywords: Black Skimmers, feathers, non-invasive moult assessment, Underhill-Zucchini moult model.

Introduction

Moult in birds is an evolutionary strategy of feather renewal that influences flight efficiency, thermoregulation, and seasonal appearance, and therefore has fitness consequences at key stages in birds' lifecycles, such as breeding and migration (Newton 2009). Assessing the moult process can provide better understanding of individuals' choice and use of resources and thus also of breeding, migratory and foraging strategies (Newton 2009). Methods to obtain moult data from wild birds did not change much in the last century and largely depend on scoring feathers or verifying the presence/absence of moult of museum specimens and/or captured birds (e.g. Newton 1966, Underhill & Zucchini 1988, Newton & Rothery 2009, Scherer et al. 2013, Morrison et al. 2015). However, such data may also be acquired with other techniques such as photography, a method that has been used to study moult in marine mammals (McConkey et al. 2002) and waders (Conklin & Battley 2011, 2012).

Other studies used opportunistically taken photographs of birds in moult to complement information based on conventional methods (Snyder et al. 1987, Ryan 2013, Zuberogoitia et al. 2016). Keijl (2011) suggested that photography would be a promising way to study moult in pelagic seabirds that are difficult to catch. Bugoni et al. (2015) studied seabird moult by catching birds at sea, and they also presented photographs to show whether feathers were moulted or not. González-Solís *et al.* (2011) used photographs from websites to confirm the moulting patterns described in the literature to determine what feathers to use for stable isotope analysis. However, few studies have yet used photography as a systematic method to study moult nor compared its performance with other methods. I took photographs of Black Skimmers (*Rynchops niger*) from southern Brazil during the moulting period and scored their moult from the photographs. Here I assess the repeatability of photographic moult scoring and compare its performance in typically used moult models to data acquired from the same and other species using traditional methods. This study thus explores the value of systematic use of photography as a method to study moult in birds by researchers.

Methods

I studied Black Skimmers on the Island of Santa Catarina in southern Brazil during the moulting period. From October 2015 to April 2016, photographs of flocks were taken with a Canon© EOS Rebel T1i SLR camera using fast shutter speed (≥1/4000 s) and a 75-300mm lens during two sessions each month in the estuary of Ponta das Canas (27°24’26”S, 48°25’41”W). Each session lasted two hours and involved walking systematically along two parallel 650 m long-line transects 100 m apart from each other, covering all habitats suitable for Black Skimmers. Limiting each session to two hours was intended to minimize the chances that individuals were photographed more than once during the same session. I took 2,054 photographs with most of photographs containing one bird, yet photographs could contain up to 130 individuals with open wings while flying, landing, taking off or stretching (Figure 3.1A-D). Whenever possible I viewed the upper-wings of birds, although under-wings were also suitable (Figure 3.1B).

The 2,054 photographs contained a total of 2,278 skimmers and I could record a moult score for 1,418 individuals, representing 62% of all birds detected. I used the traditional scoring system allocating a score between 0 and 5 for each of the ten primary feathers (Figure 3.1E, Newton 1966, Underhill & Zucchini 1988). Moult differs from incidental feather replacement by having the same pattern on both wings (Pyle 2008). Because moult pattern is similar for both wings (Pyle 2008) the score was given to the more visible wing. Old feathers scored as 0 were recognised by full length, dull colour and at least some wear (Figure 3.1E). Feathers missing or in small pin stage were scored as 1 while feathers in large pin or brush stage grown up to a third of their full length when compared to old feathers were scored as 2. Feather brushes grown half of their full length were scored as 3. Feathers grown to half to three-quarters of their full length were scored as 4, and feathers grown more than three-quarters of their full length with bright colour and no wear were scored as 5 (Figure 3.1E). The moult scores of all individual primaries of one wing were summed and then divided by the maximum score possible (= 50). The resulting moult index ranged between 0 and 1 and was used as response variable in the moult model.

Figure 3.1: Black Skimmers flying with fully open wings (A, B) provide a good view of moulting patterns. Birds landing or taking off (C), or even flying at various angles (D) can also allow for moult-scoring of primaries. (E) Detail of a Black Skimmer’s right wing and the moult scoring system used in this study. Primaries are identified from inner (P1) to the outermost feather (P10 in this species). Double-counting the primaries from inner to outermost feather and vice-versa with special attention to gaps between feathers is recommended because pins can be hidden. Old feathers have a dull colour, with some wear and often lighter edges such as P4 to P10 shown in (E); thus, these seven feathers were scored as 0. New feathers are brighter, darker and have no wear, such as P1 shown in (E); thus, these were scored as 5. P2 shown in (E) is half-grown compared with old feathers and was scored as 3, whereas P3 shown in (E) is less than a third of the full length of old feathers and thus was scored as 2. Note that primaries with scores of 2 or 3 (P2 and P3 in this

example) are partially visible, whereas feathers with score 1 are barely visible, but the gap of a missing feather can be detected. Thus, the moult score of the right wing of the individual shown in (E) is 10. This sum is then divided by the maximum possible score (= 50) to result in the moult index of 0.2 (= 10/50) used in the analysis. Photos by BPV 2016.

To test within- and between-observer repeatability of moult scoring I re-sampled 20 randomly selected photographs containing on average 4.5 individuals per photograph that could be scored, yielding a total of 91 moult indices. For the within-observer repeatability I performed a second scoring around five months after the first scoring by the same person without checking any information relating to those photos. To assess the between-observer repeatability the same 20 photographs were also scored by three additional people that had no previous information on any of the photographs. Each of the within- and the between-observer repeatability was tested using a general linear mixed model (R_{GLMM}) with original scale, 100 bootstraps and 100 permutations using the *rptR* package (Nakagawa & Schielzeth 2010) in R 3.2.4 (R Core Development Team 2016). As moult indices were not normally distributed I used a logarithmic transformation and applied a Bland-Altman plot of estimates against each other using the *MethComp* package in R 3.2.4 (Carstensen et al. 2013). A Bland-Altman plot is a graphical method to compare two measurement techniques, whereby the differences between the two techniques are plots against the averages of the two techniques. An ideal within- or between-observer repeatability is expected to present a mean difference of zero and all estimates within the limits of agreement (Bland & Altman 1999). From the moult indices derived from the photographs I estimated the duration and timing of moult by plotting the moult index (response variable) against date and applying the Underhill-Zucchini (UZ) model that uses a likelihood approach to estimate timing and duration of moult in a population assuming independent observations (Underhill & Zucchini 1988). The UZ model considers data has less variability in the beginning and end of moult thus violating homoscedasticity that would be required in linear models (Underhill & Zucchini 1988). The UZ model was implemented in the package *moult 2.0* (Erni et al. 2013). Date was considered the number of days from 30 September (1 October = day 1) when the photograph was taken. I specified type 3 data considering only individuals in moult, therefore excluding individuals scored as 0 and 1 (Underhill et al. 1990), so that 519 moult indices were considered in this analysis.

I compared my photographic moult indices with conventionally derived indices from captures from other studies. The comparison between the methods was based on standard error values from the UZ models and the R^2-values of the estimated moult trajectories. The model explains variation in the moult index in relation to date, but additional variation may occur due to individual differences in moult dynamics, for example due to age, sex, or body condition. Assuming different populations have a similar composition, any differences in the accuracy of scoring between methods could introduce additional variation. Thus, if the R^2-value from the photographic moult scoring falls within the range of models using conventional data, it is unlikely that the photographic method has introduced additional variation. I compared my photographic moult indices with capture data for the same species in Scherer et al. (2013). Raw data were obtained from the authors for 58 Black Skimmers mist-netted at Lagoa do Peixe (31º21'18"S, 51º03'03"W) in southern Brazil during the non-breeding seasons between October 2010 and April 2012. I also compared the R^2-value of my data set to those from other studies that analysed temporal variation in moult using the same scoring principle although unfortunately few studies published the performance of their data (Underhill & Zucchini 1988, Newton & Rothery 2009).

Results

The within-observer repeatability showed photography allows for consistent scoring of primary moult (R_{GLMM} = 0.983 ± 0.015 (SE), 95% confidence interval = 0.903 – 0.995, P = 0.01). The mean difference between the two repeated moult indices by the same observer was -0.02, limits of agreement: -0.20, 0.17 (Figure 3.2A). The between-observer repeatability was also high (R_{GLMM} = 0.969 ± 0.062, 95% confidence interval = 0.939 – 0.986, P = 0.01) with a mean difference between the four observers' indices of -0.009, limits of agreement: -0.012, 0.006 (Figure 3.2B). The number of moult indices out of the limits of agreement was higher for the between- than for the within-observer repeatability (Figure 3.2).

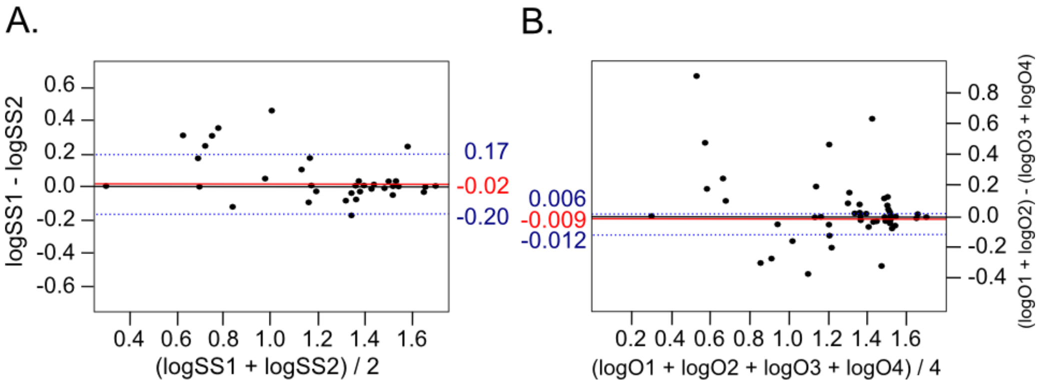

Figure 3.2: Bland-Altman plots of within- (A) and between-observer repeatability (B) of the photographic moult index. Horizontal solid and dotted lines are the mean difference and limits of agreement, respectively. The within- (mean = -0.02, limits of agreement = -0.20, 0.17) and the between-observer differences (mean = -0.009, limits of agreement = -0.012, 0.006) are based on logarithmically transformed data.

The photographic moult indices provided a larger sample size and showed a better fit to the UZ model than the data collected from the nearby Black Skimmer population scored conventionally in the hand. The UZ models applied to data from Scherer *et al*. (2013) provided estimates of timing and duration of moult with large standard errors (duration = 270.2 ± 182 days; mean start date = 5 ± 92.2). My estimates for duration and mean start date of moult based on the UZ model (Figure 3.3) had narrower standard errors and fell within the band of estimates derived from the conventionally collected data by Scherer *et al*. (2013): duration = 194.2 ± 6.5 days, mean start date = 28 ± 4.5. Comparing across the few studies that reported a fit of the model relating moult index to date, the R^2-value of my photographic study is within the range found in studies using birds in the hand (Table 3.1).

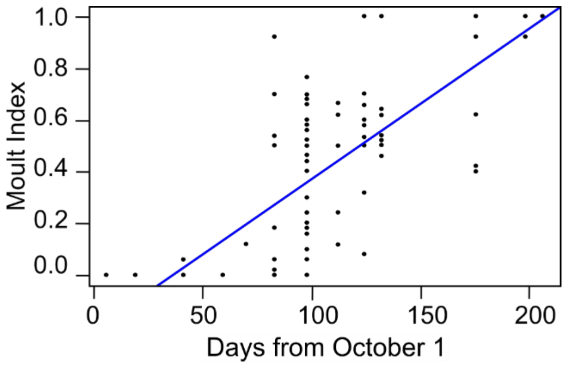

Figure 3.3: Photographic moult index in relation to date (day 1 is October 1) based on photographs of moulting Black Skimmers with open wings. The line represents the estimated

moult trajectory beginning at the mean start date based on Type 3 data (Underhill & Zucchini 1988).

Table 3.1: R^2-values related to studies using photography (this study) and examining individuals in the hand (Underhill & Zucchini 1988, Newton & Rothery 2009 and Scherer et al. 2013) to score moult in birds. Sampling size refers to the total number of moult scores analysed. Type data refers to classification in Underhill et al. (1990) in which type 2 requires moult scores of all sampled individuals; type 3 only includes individuals in moult; and type 5 uses scores of the population pre-moulting and in moult.

	species	**sample size**	**type data**	***R*²-value**
This study	Black Skimmer (*Rynchops niger*)	519	3	0.755
Scherer et al. (2013)[1]	Black Skimmer (*Rynchops niger*)	53	3	0.246
Underhill & Zucchini (1988)	Sanderling (*Calidris alba*)	164	3	0.847
Newton & Rothery (2009)	European Goldfinch (*Carduelis carduelis*)	108	5	0.966

[1] R^2-value calculated from raw data provided by the authors.

Discussion

Here I evaluated the suitability of photography to assess moult in birds by determining within- and between-observer repeatability. The repeatability was high in both cases. The mean difference being almost zero, with most differences between the measurements within estimated narrow limits of agreement, suggests that moult of primary feathers can be consistently scored by the same or different observers using photography. However, as in any other scoring method depending on human observations, variability in results exists and might be related to the observer's experience in detecting feathers moulting in a certain species. A further strength of the photographic approach is that it can provide a permanent archive available for future research uses.

I found that photography is a convenient method to study moult reliably and remotely, and yields results that are comparable in accuracy to results from studies handling birds. Data based on photographs allowed us to determine the timing and duration of Black Skimmers' primary moult in southern Brazil. The species starts moulting primary feathers in October and their complete moult takes around 194 days from austral spring to summer.

Advantages of systematic photography include its feasibility in areas and situations where birds in flight can be readily photographed but their capture might be difficult, for instance due to intense human disturbance, type of landscape, and license restrictions on capturing birds. Although these factors can make captures more difficult, they do not affect photography to a similar extent. There are, however, some limitations in systematic photography. Although the method works for flight feathers, recording moult of body feathers is much more difficult because those feathers are normally hidden (but see Conklin & Battley 2011). Photographs do not normally allow individual recognition as capturing and marking individuals does, unless the study species was already marked in another season or has distinct natural markers such as specific bill or iris patterns. Photography cannot be applied to all birds and conditions since data depend on a clear view of at least one open wing. Nonetheless, systematic photography can be adapted, for example using bait and playback to attract and photograph birds in certain positions. Photography may reduce disturbance to birds, thus enhancing sample sizes that can be obtained. This method also needs less equipment and less fieldwork effort compared to catching birds.

Considering the studies that made R^2-values available, photographic data yielded a similarly good fit as conventional studies, suggesting that the photographic method has not introduced significant additional variation to the intra-individual variation present in such data sets. However, further evaluations of the photographic method on other species and populations would be desirable.

Conventional moult scoring of birds in the hand (Scherer et al. 2013) and my photographic results indicated Black Skimmers in southern Brazil began their primary moult in October and that primary moult lasted from austral spring to summer. The results indicate a consistent pattern for the species in southern Brazil which is clearly distinct from the timing of moult observed in North America where moult occurs during boreal autumn to spring (Pyle 2008).

Snyder et al. (1987), Conklin & Battley (2011, 2012) and Keijl (2011) advocate the use of photographs to assess moult scores and I show the potential value of systematic photography for the study of moult. I believe this method could also be extended to assess moult centres in secondaries, as well as the timing and duration of moult in secondaries, tertials, and rectrices. This approach also provides a relatively low-cost method for studying geographic variation in moult patterns across different populations. Moreover, photographs can benefit from associations with the citizen science movement to cover wider geographic areas. The photographic method can also be carried out in association with other imaging techniques such as thermal imaging cameras to monitor stress levels under challenging conditions (Jerem et al. 2015).

Chapter 4: Visual observation to identify sexes in adult Black Skimmers

Abstract

Identifying sexes in birds from visual observations is a very useful and inexpensive method. Although sexual dichromatism and ornaments are more easily perceived by observers, sexual size dimorphism can be used to identify sexes in some bird species. This study assessed the applicability of visual observation to identify sexes in adult Black Skimmers (*Rynchops niger*) based on overall sexual size dimorphism. Black Skimmers have no sexual dichromatism however males are larger in size and weight than females. The study focused on two sub-species: Amazonian (*R. n. cinerascens*) and South American (*R. n. intercedens*) Black Skimmers. Sex identified by visual observation was consistent with the sex identified from museum specimens based on body size measurements and sex identified at specimen preparation ($R_{GLMM} = 0.996 \pm 0.004$). The identification of sexes from photographs based on visual observation of size had a very high within- ($R_{GLMM} = 0.995 \pm 0.001$) and between- ($R_{GLMM} = 0.984 \pm 0.002$) observer repeatability. Low cost non-invasive methods for identifying sex by visual observation might help providing enhanced use of data from photographic datasets, citizen science projects, and surveys using direct observation or images.

Keywords: non-invasive sex assessment, sexual dimorphism, *Rynchops niger*.

Introduction

The ability to identify sexes of animals is essential in many biological studies. Sexual dichromatism and ornaments in birds are easily perceived by observers and so can provide an appropriate tool for sex determination. However, many species show little or no sexual dimorphism in colour or ornamentation. In these cases, sex can be determined with confidence by molecular analysis from blood or other tissues (Griffiths et al. 1998, Fridolfsson & Ellegren 1999). However, this requires catching the bird, sampling of tissues as well as molecular-genetics laboratory facilities, and hence information on sex might only be available for a sub-set of the data.

Sexual size dimorphism is a feasible mean of identifying sex by visual comparison in many monochromatic species such as raptors and some seabirds (Schreiber & Burger 2001, Redman et al. 2002, Ropert-Coudert et al. 2005, Serrano-Meneses & Székely 2006). Sexual size dimorphism has been associated with different foraging strategies and parental care roles between sexes during breeding (Selander 1966, Fairbairn & Shine 1993, Lewis et al. 2002, Elliott et al. 2010). Discriminant analysis on biometrics is often used to assign the sex of size-dimorphic species (Genovart et al. 2003, Dechaume-Moncharmont et al. 2011). It needs, however, handling of individuals to obtain the biometrics, something that is not always possible. Alternatively, sex may also be identified non-invasively by observing sex-specific behaviours such as egg laying, vocalization, nest attendance, and by perceived sexual size dimorphism (Redman et al. 2002; Zavalaga et al. 2009; Rishworth et al. 2014).

Black Skimmers (*Rynchops niger* Linnaeus, 1758) were thought to be monomorphic with no significant visual characteristics to identify sexes (Zusi 1996). However, many studies have reported significant differences between body size measurements of male and female Black Skimmers. The males are heavier than females by 23 days old (Shew & Collins 1990). Furthermore, head length, bill length, bill depth at base, wing length, and body mass are all between 9 to 35% larger in adult males, compared to adult females, with very little or no overlap between the sexes (Burger & Gochfeld 1990, Quinn 1990, Mariano-Jelicich et al. 2007, Scherer et al. 2013). Because sexual size differences are significant, I hypothesise that an individual’s sex can be visually perceived without the need for measurements of captured birds in the hand. Here, I assessed the reliability of visually identifying sex in the South American (*Rynchops niger intercedens*) and Amazonian Black Skimmer (*R. n. cinerascens*) sub-species.

Methods

I first compiled the measurements for body mass, culmen length, lower bill, head + bill length, bill depth at base, tarsus length, and wing chord (Figure 4.1) that are available in the literature according to sex and sub-species (Table 4.1). I considered additional measurements of specimens from the Rio de Janeiro National Museum and the British Natural History Museum. The measurements taken from specimens in these two museums were: wing chord, head + bill length, culmen length, bill depth at base, and lower bill. Wing chord is represented by the maximum wing chord from the junction of the metacarpus with the radial bone to the external tip of primary feather P8, the longest primary feather in a closed wing in the Black Skimmer (Figure 4.1). Head + bill length is measured from the occipital bone to the external tip of the lower mandible or lower bill (Figure 4.1). Culmen length is considered the distance between the base of the nasal bone to the external tip of the upper mandible or upper bill (Figure 4.1). Bill depth at base is considered the distance from the base of the nasal bone down to the post-articular process in the lower mandible (Figure 4.1). The lower bill is considered from the post-articular process to the external tip of the lower mandible. And, the tarsus length is represented by the maximum length from the medial condyle in the tibiotarsus (heel) to the trochlea for Mt III in the tarsometatarsus.

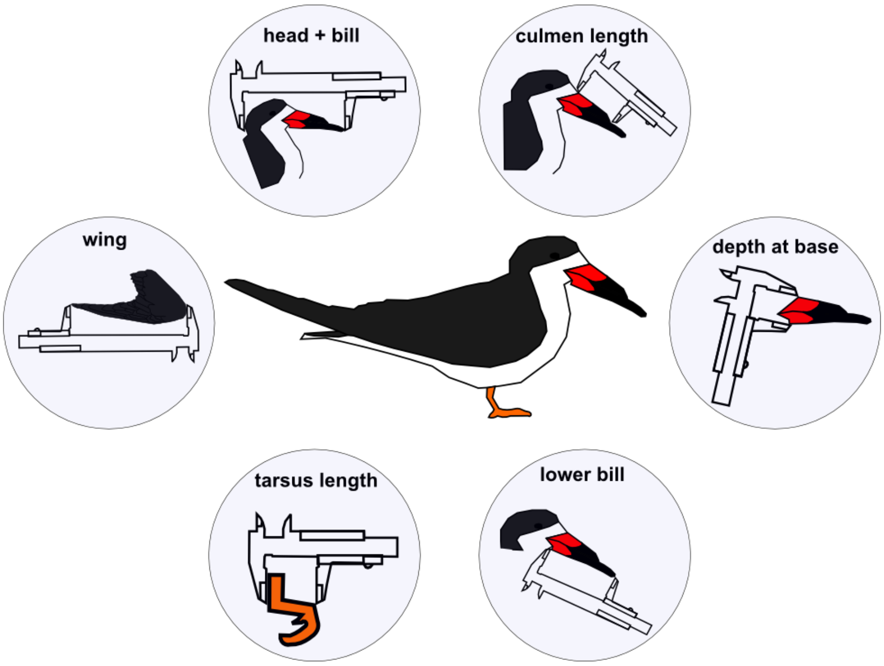

Figure 4.1: The biometric measurements taken from Black Skimmer specimens from museums. Author: BPV 2016.

I checked the reliability of visually identifying sex without having to measure the bird by using data from 46 specimens of the South American (*Rynchops niger intercedens*) and the Amazonian (*R. n. cinerascens*) sub-species held at the British Natural History Museum. I first assigned the sex to each specimen visually, and blind to the information on the labels, based on perceived size. Individuals were checked separately to avoid bias from comparison of sizes between them.

The measurements were used to classify individuals and compare results from visual identification, measurements, and labels. I tested collinearity between the biometric measurements using a Spearman test in the package *corrplot* (Wei & Simko 2016) in R 3.2.4 (R Core Development Team 2016) and considering a variable collinear when $r > 0.5$ (Booth et al. 1994). The only variables that did not correlate in both sub-species were head + bill length and depth at base (Amazonian: $r = 0.39$; South American: $r = 0.37$). Therefore, I used these biometric measurements to determine a discriminant function for each sub-species. For the two variables (bill depth at base and head + bill length), I tested the multivariate normality with a Henze-Zirkler's test (Amazonian: HZ = 0.65, $P = 0.11$; South American: HZ = 0.52, $P = 0.24$) and the homoscedasticity with a box's M test (Amazonian: $\chi^2_3 = 5.49$, $P =$

0.13; South American: $\chi^2_3 = 3.37$, $P = 0.33$) using packages *MVN 4.0.2* and *biotools 3.1*, respectively (Korkmaz et al. 2014, Silva et al. 2017). I ran the linear discriminant analysis using the package *MASS 7.3-45* (Venables & Ripley 2002) with a jackknife cross-validation as suggested in Dechaume-Moncharmont et al. (2011). The discriminant power of the linear discriminant function was assessed with a Wilks' Lambda test using package *rrcov* (Todorov & Filzmoser 2009) which varies from 0 to 1 with lower values indicating higher discriminant power. I used a *t-test* to verify differences between sub-species based on the pooled mean and standard deviation.

Finally, I checked the label for information on sex. Although most naturalists will have confirmed the sex by checking the specimens' gonads at time of collection, others did not check it. The method of sexing had not been recorded, and thus, relying only on labels could potentially be misleading in a few specimens (Mark Adams, pers. comm.).

To determine the concordance between the three assessment methods of sex identification (labels, biometric measurements, and visual determination), I later used the Bray-Curtis dissimilarity index which varies from 0 to 1 with maximum value meaning full similarity (Bray and Curtis 1957). The repeatability of binomial data (sex) between the three methods was tested with an additive generalized linear mixed-effects model (GLMM) with binomial error structure, logit link function, 1,000 bootstraps, and 1,000 permutations using the *rptR 0.9.2* package (Stoffel *et al.* 2017) in R 3.2.4 (R Core Development Team 2016).

After verifying feasibility of identifying sexes by perceived differences in body size, I also tested the within- and between-observer repeatability for identifying size differences from photographs. Sex of individuals from images was assessed independently by three observers, two times and six months apart, in a randomly selected subsample of 100 images from the Wikiaves web dataset containing a total of 165 individuals. Observers were instructed to give attention to overall size and bill, especially head + bill length and bill depth at the base which were the traits used by the discriminant functions to differ sexes in both sub-species. The individuals detected in the images were from the South American and the Amazonian sub-species. I did not run separate tests for each sub-species because differences between adult males and adult females were significant for both sub-species with very similar measurements within males and within females (Table 4.1 and see Results). Repeatability were calculated as described above.

Table 4.1: Biometric measurements (mean ± standard deviation) for adult South American and Amazonian Black Skimmer sub-species available in literature or verified at museums. All linear measurements in mm; body mass in grams. Pooled mean represents the pooled mean and pooled standard deviation. BNHM: specimens from the British Natural History Museum; RJNM: specimens from the Rio de Janeiro National Museum.

Sub-species	Sex	Character (Mean ± SD)							Source
		Wing	**Tarsus length**	**Depth at base**	**Head + bill length**	**Lower bill**	**Culmen length**	**Mass**	
South American	Male	403 (*n* = 6)	35 (*n* = 6)	-	-	-	79 (*n* = 6)	-	Murphy (1936)
		395 ± 45.3 (*n* = 6)	34.3 ± 23.1 (*n* = 6)	-	-	-	79.7 ± 23.2 (*n* = 6)	-	Wetmore (1944)
		413.1 ± 13.4 (*n* = 16)	41.9 ± 1.8 (*n* = 16)	-	144.6 ± 4.1 (*n* = 16)	111 ± 6.6 (*n* = 16)	-	362.7 ± 26.7 (*n* = 16)	Antas et al. (2016)
		-	-	31.1 ± 1.9 (*n* = 14)	151 ± 12.1 (*n* = 14)	103 ± 10.8 (*n* = 14)	85 ± 5.0 (*n* = 14)	-	BNHM
		394.3 ± 14.9 (*n* = 9)	30.0 ± 3.1 (*n* = 9)	30.3 ± 3.0 (*n* = 8)	154.6 ± 4.2 (*n* = 9)	101.5 ± 12.9 (*n* = 8)	78 ± 4.5 (*n* = 9)	280 (*n* = 1)	RJNM
	Pooled mean	404 ± 16.1	36.6 ± 4.9	30.8 ± 2.4	149.2 ± 7	106.1 ± 7.2	81.2 ± 6.8	357.8 ± 28.6	
	Female	354 ± 32.6 (*n* = 7)	29.7 ± 23.0 (*n* = 8)	-	-	-	61.1 ± 32.8 (*n* = 8)	-	Wetmore (1944)
		369.1 ± 7.6 (*n* = 24)	36.8 ± 2.1 (*n* = 24)	-	117.5 ± 4.2 (*n* = 24)	84.7 ± 6.3 (*n* = 24)	-	238.7 ± 26.7 (*n* = 24)	Antas et al. (2016)
		-	-	24.6 ± 1.2 (*n* = 9)	120 ± 10.4 (*n* = 9)	78.2 ± 7.7 (*n* = 9)	66.6 ± 4.6 (*n* = 9)	-	BNHM
		368 ± 16.1 (*n* = 5)	28.9 ± 2.6 (*n* = 5)	26.1 ± 2.4 (*n* = 6)	148.8 ± 24.6 (*n* = 6)	90 ± 15.5 (*n* = 6)	71.5 ± 7.2 (*n* = 6)	-	RJNM
	Pooled mean	366 ± 13.2	34.2 ± 6.4	25.2 ± 1.8	122.9 ± 8.4	84.0 ± 7.9	65.9 ± 15.1	238.7 ± 26.7	
	Difference between pooled means (%)	9.4	6.7	18.2	17.6	20.8	18.8	33.3	
Amazonian	Male	409.7 ± 14.7 (*n* = 5)	35.5 ± 3.2 (*n* = 5)	-	-	-	83.5 ± 10.0 (*n* = 5)	-	Murphy (1936)
		392 ± 34.2 (*n* = 19)	34.8 ± 8.8 (*n* = 19)	-	-	-	86.6 ± 17.6 (*n* = 19)	-	Wetmore (1944)
		-	-	32.6 ± 3.4 (*n* = 13)	155 ± 16.8 (*n* = 13)	107 ± 15.9 (*n* = 13)	90.2 ± 12.0 (*n* = 13)	-	BNHM
		403 (*n* = 1)	34 (*n* = 1)	31 (*n* = 1)	193 (*n* = 1)	122 (*n* = 1)	88 (*n* = 1)	-	RJNM
		421.8 ± 22.9 (*n* = 4)	35.9 ± 1.7 (*n* = 4)	-	-	-	83.5 ± 5.4 (*n* = 4)	365.7 ± 10.4 (*n* = 3)	Davenport et al. (2016)
	Pooled mean	399.5 ± 21.7	35 ± 6.8	32.5 ± 3.7	157.7 ± 18.3	108.1 ± 17.3	97 ± 13.3	365.7 ± 10.4	
	Female	370 (*n* = 1)	31 (*n* = 1)	-	-	-	66 (*n* = 1)	-	Murphy (1936)
		353.7 ± 36.0 (*n* = 10)	30 ± 1.9 (*n* = 10)	-	-	-	64 ± 13.0 (*n* = 10)	-	Wetmore (1944)
		-	-	24.1 ± 1.5 (*n* = 11)	121 ± 18.8 (*n* = 11)	78.8 ± 16.0 (*n* = 11)	66.9 ± 9.1 (*n* = 11)	-	BNHM
		376.5 ± 21.9 (*n* = 2)	30 ± 2.8 (*n* = 2)	28 ± 7 (*n* = 2)	164.5 ± 38.8 (*n* = 2)	101 ± 26.8 (*n* = 2)	75 ± 16.9 (*n* = 2)	-	RJNM
		375.5 ± 14.4 (*n* = 4)	32.4 ± 2.4 (*n* = 4)	-	215.4 (*n* = 1)	83.2 (*n* = 1)	65.6 ± 3.4 (*n* = 4)	228.5 ± 21.2 (*n* = 2)	Davenport et al. (2016)
	Pooled mean	362.5 ± 27.8	30.6 ± 1.9	24.7 ± 2.2	134 ± 20.6	82.3 ± 17	66.2 ± 9.4	228.5 ± 21.2	
	Difference between pooled means (%)	9.3	12.6	24	15.1	23.9	31.7	37.5	

Results

The pooled mean and standard deviation for all measurements in Table 4.1 between Amazonian and South American Black Skimmer males ($t_{1,6}$ = -0.05, P = 0.92) and between Amazonian and South American Black Skimmer females ($t_{1,6}$ = 0.01, P = 0.97) were similar and were not significantly different. Head + bill length and bill depth at base were 15.1% and 24% greater in males in the Amazonian sub-species, and 17.6% and 18.2% in the South American sub-species (Table 4.1). The linear discriminant function analysis of head + bill length and bill depth at base was accurate to identify sexes in both Amazonian and South American Black Skimmers (Figure 4.2); the jackknife cross-validation predicted sexes with 98% and 96% of accuracy. The discriminant function of 0.02 * (head + bill length) + 0.34 * (depth at base) – 12.05 predicted the sex of 95% of the Amazonian males and 100% of the Amazonian females with a very low Wilks' Lambda of 0.02 (χ^2_2 = 30.38, P < 0.001). The discriminant function of 0.05 * (head + bill length) + 0.44 * (depth at base) – 18.71 predicted the sex of 92% of the South American males and 100% of the South American females also with a very low Wilks' Lambda of 0.01 (χ^2_2 = 35.81, P < 0.001).

The Bray-Curtis dissimilarity index presented a full correspondence of 1 between visual determination, biometric measurements, and labels for both studied sub-species (Table 4.2). Similarly, the repeatability of sex identification between the different sexing methods was very high (R_{GLMM} = 0.996 ± 0.004, 95% confidence interval = 0.991 – 0.999, P < 0.001). In addition, the within- (R_{GLMM} = 0.995 ± 0.001, 95% confidence interval = 0.993 – 0.998, P < 0.001) and the between-observer repeatability (R_{GLMM} = 0.984 ± 0.002, 95% confidence interval = 0.981 – 0.994, P < 0.001) of perceiving size differences from photographs were very high and, because larger birds are males, indicates that Black Skimmers can also potentially be reliably sexed from photographic observations.

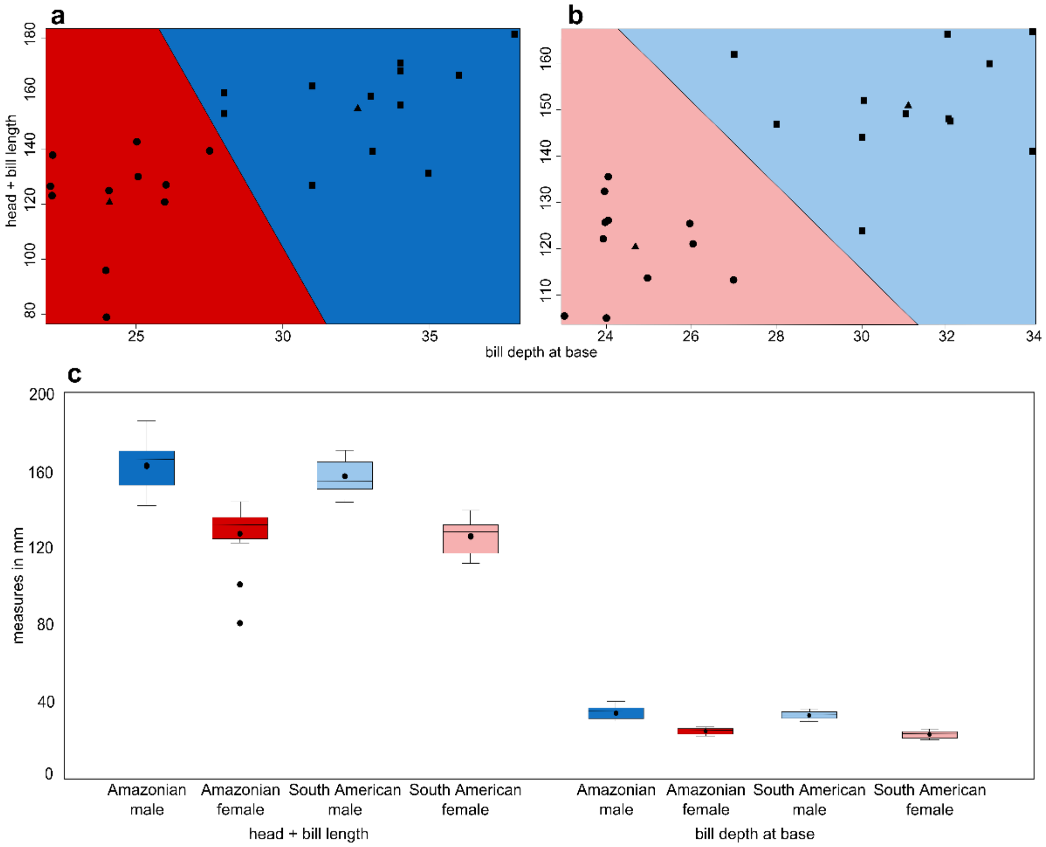

Figure 4.2: Groups of females (circle) and males (square) for Amazonian (a) and South American (b) Black Skimmer sub-species partitioned according to linear discriminant functions using head + bill length and bill depth at base and obtained measures in mm (c). The triangles represent the mean value for each group.

Table 4.2: Number of Black Skimmer specimens sexed per sub-species at the British Natural History Museum at Tring based on label information, visual determination, and biometric measurements. Discordance between methods indicates how many times one method disagreed with the other two.

	Label Information		**Visual Observation**		**Biometric Measurement**		**Discordance between methods**
	Female	**Male**	**Female**	**Male**	**Female**	**Male**	
South American Black Skimmers	11	12	11	12	11	12	0
Amazonian Black Skimmers	11	12	11	12	11	12	0

Discussion

Bird species without sexual dichromatism and ornaments may have differences in biometrics that still can result in distinctive visually perceived sexual size dimorphism. The repeatability between methods and between observers of visual identification of sexes in Black Skimmers was highly significant. Although I cannot be complete sure which sex each individual in photographs had, Black Skimmer males are significantly larger than females (Burger & Gochfeld 1990, Shew & Collins 1990, Quinn 1990, Mariano-Jelicich et al. 2007, Scherer et al. 2013, this study) with a mean difference between sexes of around 20%, which was big enough to reliably identify specimens from museums and individuals in images. Although the discriminant function had lower prediction to males when compared to females, the percentage of prediction were still high for both sub-species. Identifying sex from photographs might be easier for people not experienced with the species by looking for 'side on' photographs because of position of the bill yet overall size can be perceived at any position if other individuals are present in the photograph.

Sexual size dimorphism varies considerably among species. Some groups (e.g. gulls) have bigger males than females and others (e.g. skuas) the opposite (Fairbairn & Shine 1993, Serrano-Meneses & Székely 2006). Raptors such as Harpy Eagle (*Harpia harpyja*), Peregrine Falcon (*Falco peregrinus*), and Tiny Hawk (*Accipiter superciliosus*) were first identified as sexually monomorphic and nowadays the sexes are readily distinguished by size using direct observation (Ferguson-Lees & Christie 2001). Also, seabirds, such as King Penguin (*Aptenodytes patagonicus*), Herring Gulls (*Larus argentatus*), Great Frigatebird (*Fregata minor*), and Great Skua (*Stercorarius skua*) where the sexes differ by 2% to 24% in size had been reported to be assigned to sex with careful observation and experience (Burger & Gochfeld 1981, Hamer & Furness 1991, Fairbairn & Shine 1993, Serrano-Meneses & Székely 2006). It is possible that observer's experience may cause variability in results. The observer's experience with sexually monochromatic species such as the Black Skimmer may make a difference when identifying more cryptic characteristics. Observers not familiar with the species may find it difficult to visually discriminate sexes, however observing mainly the head + bill length and bill depth at base makes the identification easier. In the field, comparisons between males and females are facilitated by their gregarious behaviour, and sex identification is also because other individuals can be used as a scale.

Burger & Gochfeld (1981), for example, were comfortable assigning sexes to Herring Gulls visually by comparing the members of a pair or adjacent birds for unpaired birds, but they did not test the reliability of their sex identification. Moreover, Burger (1981) also visually assigned sexes to North American Black Skimmer (*Rynchops niger niger*) although she did not present a formal test of reliability of such method. Hamer & Furness (1991) reported that there was good agreement between sexing of Great Skuas by visual observation of the two members of breeding pairs and results from a discriminant analysis from their biometrics, with about 90% of visual assignments in accordance with the discriminant analysis. However, the discriminant analysis itself was not 100% effective because of some overlap in measurements between the sexes. The visual observation of Black Skimmers in the present study had highest agreement possible with the discriminant analysis. The discriminant analysis also had very low Wilk's lambda using head + bill length and depth at base to determine the sexes of both sub-species. Other studies had created discriminant functions to the North American Black Skimmer sub-species (Quinn 1990) and non-breeding populations of mixed sub-species in Argentina (Mariano-Jelicich et al. 2007) and southern Brazil (Scherer et al. 2013). However, accuracy and variables used varied between studies and none considered the Amazonian and South American Black Skimmers separately.

Visual observation to identify sexes in Black Skimmers is reliable and their flock behaviour when resting may improve the observer's ability to identify sexes. Flock behaviour is selected in nature because it confuses predators and diffuses individuality (Landeau & Terborgh 1986). Therefore, it may also confuse human observers. Taking photographs may help breaking the sensation of uniformity in the flock. And, as previously mentioned, a careful observation comparing individuals within the flock can make visually identifying sexes easier. With proper training on recognising the key differences between the sexes, i.e. head + bill length and bill depth at the base, it appears possible to visually assign the sex of Black Skimmers. This low cost and non-invasive method using visual observation for identifying sex may help providing more detailed use of data from photographic datasets, citizen science projects, and surveys using images or direct observation.

Chapter 5: Large-scale habitat selection by Black Skimmers moulting in Brazil

Abstract

Migratory species access different habitats during each part of the year, and energetically expensive activities, such as breeding and moult, require access to reliable high-quality resources. Habitat selection during moult depends on the individual's ability to recognise suitable sites, and can vary according to age, sex, populations, and sub-species. In this study, I used citizen photographs taken throughout Brazil to assess the spatio-temporal patterns of moult in the Black Skimmer, and to test whether the species selects specific resources when moulting according to sex and sub-species. I found Black Skimmers selected productive estuaries in southern latitudes during moult. They also selected mudflats and coastal urbanised areas. However, the South American sub-species selected less mudflats and more dunes than the Amazonian sub-species. Moult in both sub-species differed from conspecifics in North America by taking around six months to complete the process during austral spring and summer. There were significant differences between sexes and sub-species with males taking longer and starting moult earlier than females. Also, Amazonian individuals took longer and started moult earlier than South American ones. Using citizen science as a cheap non-invasive method is an innovative large-scale approach that can increase research in this area, hopefully improving the decision-making process for the conservation of habitats, resources, and species.

Keywords: moult, intraspecific variation, ecological use, migratory birds, Neotropical zone, South Atlantic coast.

Introduction

Habitat selection is considered fundamental to understand how species perceive the supplies distributed in the landscape they inhabit in space and time. Species select habitats based not only on perceived resource availability but also on safety from predators and other disturbances (Lindström et al. 1993, Kjellén 1994, Swaddle et al. 1996, Barta et al. 2008, Stephens et al. 2015). As some species have a high mobility between habitats of different quality that can affect individual fitness, they show adaptive habitat selection (Boulinier & Lemel 1996). Some species have strategies such as using different high-quality habitats to improve breeding and maintain fitness according to energetic needs (Boulinier & Lemel 1996, Espie et al. 2000, Daunt et al. 2007). A successful partitioning depends on experience to find such places, local conditions of resource availability, and local mortality risks (Boulinier & Lemel 1996, Espie et al. 2000, Daunt et al. 2007). Migratory birds show such habitat partitioning across an annual cycle. The habitat selection during breeding needs to support certain energetically consuming activities, such as egg production and chick rearing, whilst under relatively restricted foraging ranges. When conditions at the breeding site seasonally change, migratory species move sometimes very long distances to other sites that have resources to support performing other activities with high energetic intakes, such as moult.

Moult is one of the activities of birds that can be described through photography (Conklin & Battley 2012, Vieira et al. 2017). Feathers are essential for thermoregulation, movement and communication, and their constant use and exposure results in degradation, mostly within a year, in small and medium-sized species (Bergman 1982, Butler & Johnson 2004). Because feathers are inert tissues they lack the capability of self-repair, and therefore need replacing through the process of moult. Replacing feathers is highly demanding in energy and proteins, specifically in sulphur-containing amino-acids, and it also causes loss of insulation, reduced flight capacity, and increased predation risk. Therefore, species usually avoid overlapping moult with other key events in birds’ annual cycles such as breeding and migration (Lindström et al. 1993, Kjellén 1994, Swaddle et al. 1996, Barta et al. 2008, Newton 2009).

The individual risk during moult is reduced by strategies such as all primaries are shedding together, in sequence or stepwise, and through adequate habitat and resources selection (Pyle 2008). Moult strategies must balance loss of thermal insulation, decreased flight efficiency, and high metabolic and nutritional demands of developing new feathers, with food quality and availability, competition for resources, and exposure to predators (Lindström et al. 1993, Kjellén 1994, Swaddle et al. 1996, Barta et al. 2008). In general, migratory birds are likely to use highly productive habitats that are safe from predators during moult to acquire the necessary energy to moult (Leu & Thompson 2002, Rohwer et al. 2005).

When and where to moult might depend on individual's experience selecting resources, variation in size between sexes, distribution, and reproductive behaviour. In some species, males may need to arrive earlier in colonies, and establish territories to attract females on their arrival (Kokko 1999, Kokko et al. 2006). This could mean that males conduct a faster or earlier moult than females (Barta et al. 2008). Foraging ability and prey needs can vary in sexually size-dimorphic species. For example, Black Skimmer males are 20% larger than females and forage on larger prey (Chapter 4, Mariano-Jelicich et al. 2008), possibly affecting moult strategy according to sex. Variation occurs also between populations and sub-species, particularly for species with widespread distribution that select different resources for each season (Catry et al. 2013, Remisiewicz et al. 2014, Jukema et al. 2015). However, it is difficult to address moult in widespread species unless many research groups are collaborating or museum specimens from many different sites are available in large numbers.

Acquiring large-scale datasets to understand the habitat selection across a species range during energetically demanding activities has always been a challenge. Firstly, understanding the ecological interactions and decision making of an individual depends on knowing a species' complete annual cycle (Marra et al. 2015), especially critical stages to individual survival and population persistence. However, ecological studies largely focus on breeding and little is discussed about other energetically demanding stages, such as moult (Marra et al. 2015). Online public engagement and citizen science are occupying an important space in long-term monitoring, providing an affordable non-invasive method to assess distribution data.

Although citizen data does not provide details that could be used to assess individual decision making the same way tracking devices do, the development of cost-effective cameras and social platforms offers an opportunity to integrate millions of people and wildlife projects, resulting in large-scale data sets focusing on certain species and geographic areas (Bonney et al. 2009, Silvertown 2009, Sullivan et al. 2009, Dickinson et al. 2010, Newman et al. 2012).

Photography has been used repeatedly to monitor populations and develop species distribution models (Bonney et al. 2009, Sullivan et al. 2009, Dickinson et al. 2010, Newman et al. 2010, 2012, Lees & Martin 2014, Leighton et al. 2016). Examples of monitoring include census surveys (Huffeldt & Merkel 2013), reproductive success (Merkel et al. 2016), acute stress (Jerem et al. 2015), diet (Gaglio et al. 2016), and the progression of moult (Vieira et al. 2017). The availability of low cost professional cameras has boosted the use of online datasets displaying wildlife images, such as eBird, Wikiaves and Google Images helping scientists. Photographs can provide external characteristics of individuals and additional information from the photographer may complement datasets obtained on the web platforms, such as location, date of record, and method used to spot the birds such as point counts, playbacks, or in most cases opportunistic encountering (Sullivan et al. 2009).

Addressing habitat selection during moult and comparing differences between sub-species and sexes, especially in long distance migratory birds, is fundamental to fill major gaps in understanding a species' annual cycle to manage habitats that support vulnerable life stages (Marra et al. 2015). In this study, I used citizen photographs to assess the temporal patterns of moult for a widespread bird species and its large-scale habitat selection considering differences between sexes and sub-species. The study species, the Black Skimmer (*Rynchops niger*), has two sub-species occurring in Brazil – the South American (*R. n. intercedens*) and the Amazonian (*R. n. cinerascens*); and they spend most of the non-breeding period in coastal zones where they also moult (Murphy 1936, Burger & Gochfeld 1990, Zusi 1996, Pyle 2008). Scoring moult from photographs has been assessed for this species and provides a reliable measure for the moult of primary feathers (Vieira et al. 2017). Thus, I tested whether (1) timing and duration of the moult are the same for the two sub-species and the two sexes; (2) Black Skimmers have specific moulting areas within their coastal non-breeding range; and (3) habitat selection during moult differs between the two sub-species and sexes. This study provides insights into habitat requirements for a stage of the annual cycle that has been little explored in this respect.

Methods

Moult data

Images of Black Skimmers were opportunistically taken throughout Brazil by many nature enthusiasts between March 2005 and April 2016 (Figure 5.1) and deposited on www.wikiaves.com. The Wikiaves is a collaborative platform where users can upload photographs of species mentioning identification, location (coordinates or municipality), date, camera status, and any comments the enthusiasts may want to add about the record. The platform also has experienced ornithologists and birdwatchers as moderators ensuring quality of what is published. Moreover, the platform allows other users to question identification by checking photographs and discussing with the Wikiaves' community, thereby enhancing quality control. In April 2016, the Wikiaves database contained 2,060 photographs of Black Skimmers (Table 5.1). On 294 of these photographs, birds had their primaries sufficiently visible so that the sub-species and their primary moult could be scored for 1,961 individuals (Table 5.1). We chose to score primaries because they are important flight feathers and therefore habitat conditions need to be favourable during this period (Newton 1966).

To identify the sub-species only images of wings seen from underneath were included (see section below). The Amazonian sub-species (*R. n. cinerascens*) has well delimited dark grey underwings while the South American sub-species (*R. n. intercedens*) has white or not delimited light grey underwings (Wetmore 1944). Birds moulting primaries could be distinguished from those having accidentally lost some feathers by checking for missing feathers in the equivalent position in both wings, as primary moult is expected to be symmetric (Pyle 2008). The score was based on the traditional six-point scoring system from 0 to 5 for each primary feather following its development and with a cumulative score for all primary feathers (Newton 1966). Black Skimmers have ten primaries so the cumulative score can range from 0 if moult had not yet started (pre-moult) to 50 if primary moult was complete (post-moult). This score was then converted into a Moult Index, ranging from 0 to 1, by dividing the cumulative score by 50, the maximum possible score for this species (Chapter 2, Vieira et al. 2017).

Table 5.1: Number of analysed photographs of Black Skimmers from the Wikiaves database and number of individuals scored and in moult for the Amazonian and the South American Black Skimmer sub-species in Brazil. A bird in pre-moult has not yet started moult and has browner and more worn feathers than freshly moulted feathers thus receiving a score of 0 (Vieira et al. 2017). A post-moult bird has completed moult and can be identified based on the colour tone and condition of the freshly grown feathers and receives a score of 50 (Vieira et al. 2017).

	Amazonian	**South American**	**TOTAL**
Total of photographs accessed	446	1,614	2,060
Total of individuals detected	3,735	15,108	18,843
Total of photographs with individuals scored (pre, in and post moult)	60	234	294
Total of individuals scored (pre, in and post moult)	246	1,715	1,961
Total of individuals in pre-moult	36	281	317
Total of individuals in moult	167	917	1,084
Total of individuals in post-moult	43	517	560
Total of male adults in pre-moult	17	171	188
Total of male adults in moult	78	487	565
Total of male adults in post-moult	24	279	303
Total of female adults in pre-moult	16	87	103
Total of female adults in moult	85	389	474
Total of female adults in post-moult	19	224	243
Total of juveniles in pre-moult	3	23	26
Total of juveniles in moult	4	41	45
Total of juveniles in post-moult	0	14	14

I extracted coordinates and date of record for each image where primary moult could be scored for at least one individual visible on the image. For each scored individual, I also identified sub-species and sex (see section below). In the very few cases ($n = 5$) the habitat presented in the image did not match the habitat expected for the designated coordinates, I corrected these coordinates by asking the image's author for extra details thus reducing possible bias in the habitat selection function analysis.

Sub-species, age, and sex of individuals

Sub-species were distinguished by the colour of the underwing. The age of each bird included in the analyses was determined by plumage. Individuals from 1-month and up to 1-year old have a distinctive spotted or brownish dorsal plumage and birds with such plumage were classified as juveniles (Burger & Gochfeld 1990). Individuals were classified as sub-adults and adults if they were in basic or alternate black dorsal plumage (Murphy 1936, Burger & Gochfeld 1990). I only included birds in adult plumage in the analysis because of the small number of juveniles recorded (Table 5.1). All juveniles were excluded from the dataset to avoid any bias. The sexes differ in body size already in chicks from day 23 (Shew & Collins 1990). I identified sexes in adults according to overall size and bill shape (see Chapter 3). Overall, males have a more robust bill and larger body size than females (Chapter 3, Vieira 2016).

Spatial data

Maps for Brazilian land cover, continental water masses, and sea surface were downloaded from www.diva-gis.com. All layers were expressed as raster files with pixel resolution of 1 km² and georeferenced to geographic coordinate system GCS WGS84. As moulting birds were mainly located along the coastline that runs north-south, latitude can be considered as a proxy for large-scale geographical distribution of moulting sites along the Brazilian coastline.

Black Skimmers breed inland on freshwater sandbanks, and migrate to the coast during the non-breeding season (Murphy 1936, Zusi 1996). The Brazilian coastline is composed of coastal marshes, rocky coasts, dunes and beaches, salty lagoons, bays, estuaries, mangroves and everglades, mudflats, costal vegetation, and built-up areas (MMA 2010). Although rocky coasts and coastal vegetation are available, there are no published records of Black Skimmers occupying them. My aim is to assess habitat selection within Black Skimmers' moulting habitats, thus I excluded rocky coasts and coastal vegetation from the model. Salty lagoons, mangroves and everglades are associated with estuaries (MMA 2010) and the 1-km² resolution does not always allow to distinguish between them. Thus, I considered these habitats as one class called 'estuary'. In Brazil, coastal marshes occur in dunes which are also integrated to fine sand beaches therefore band in maps for these habitats are the same and I considered them as one class called 'dunes'. Mudflats are usually associated with estuaries, mangrove areas and everglades (Dyer et al. 2000), however they can also be associated with lagoons and bays (Kirby 2000) thus I kept 'mudflats' as a separate class (Table 5.2).

In addition to choosing specific habitats, I also hypothesise that moulting Black Skimmers will avoid 'built-up' urbanised areas that could have higher human disturbance thus making individuals expend energy in unnecessary flights and defensive behaviours (Molina 2000, Burger et al. 2010, Vieira 2015). I also hypothesise skimmers will look for specific coastal habitats with high fish productivity thus I used data of chlorophyll concentration as a proxy for fish productivity (Downing et al. 1990). Chlorophyll concentration values (mg/m³) were based on a composite map from Aqua MODIS with a fixed smoothing parameter of 9 km using data from 2005 to 2016 provided by OBPG (2017).

Statistical analyses

Statistical analyses were performed in the software R 3.2.4 (R Core Development Team 2016). I estimated the duration and timing of moult for each sub-species and sex with the Moult Index as a response variable using the *moult* 2.0 package (Erni et al. 2013). The package is based on Underhill-Zucchini models (Underhill & Zucchini 1988) and uses the maximum-likelihood approach to determine the average date when the moult period started, the duration of moult period, and the related standard errors (Erni et al. 2013). I considered scores for all adults from pre-moult to post-moult, thus using Type 2 data (Underhill & Zucchini 1988). Dates were expressed as days since 31 August (1 September = day 1).

I tested the differences in the mean start date and duration of moult between the sexes, sub-species, and the interaction between these two factors using a 2x2 factorial design analysis of variance (2x2 ANOVA) (Rankin 2012). For this 2x2 ANOVA test I considered the mean value, the standard deviation, and the sample size (Rankin 2012) for Amazonian male, Amazonian female, South American male, and South American female. The 2x2 ANOVA assumes variances between groups are similar which is true within but not between sub-species; yet if differences between sub-species are large, not meeting this assumption is of little concern (Rankin 2012). To account for variance between sub-species, I also assessed the differences in the mean start date and duration of moult for South American males vs. Amazonian males, and South American females vs. Amazonian females using a *t-test* with unequal variance. If results from the 2x2 ANOVA and *t-tests* were similar, then violation of the equal variance assumption has no consequences in this study.

I used the number of Black Skimmers moulting per location as the response variable to estimate the kernel interpolation with quadratic function using discrete bands of 95%, 75% and 50% confidence intervals, a fixed smoothing parameter of 70 km, a grid size of 500 m, and the geographic coordinate system GCS WGS84 in QGIS 2.14.1. The measure of 70 km is based on the rounded average for daily local movement distance of Black Skimmers tracked during a non-breeding season in South America (Davenport et al. 2016). The 70 km was constrained to the coastline because there were no detected efforts at sea.

I selected the number of clusters of adult Black Skimmers in moult (n = 267 clusters) to run the resource selection function. Each cluster represented the number of photographs taken at a certain time and place. I used the number of clusters instead of detected individuals to avoid pseudo-replication. I constrained the dataset to individuals detected in moult only to avoid false positive moulting sites because using the period of moult and including pre- and post-moult data, for example, could bias results due to transiting individuals (Chapter 2, Davenport et al. 2016) that left the breeding colony at various times (Chapter 2, Antas et al. 2016). The clusters inside the 70-km wide buffer area contained 96% (n = 1,039) of all Black Skimmer individuals identified from the photographs as being in moult.

To examine whether Black Skimmers in Brazil appear to select moulting sites that have specific characteristics, I used a resource selection function (RSF) model to compare sites with actively moulting birds to those without (*ResourceSelection* package in R 3.2.4; Lele et al. 2016). The RSF model was constructed with quasi-binomial error distribution, maximum likelihood estimates and nonparametric bootstrap standard errors. The used/available values were extracted inside the 70 km-wide band in the terrestrial coastline. The clusters' coordinates were considered as used points (assigned as 1). I randomly selected 2,670 points (10 points per cluster) inside the buffer as available points (assigned as 0). The used/available points were considered the response variable in the RSF. The nearest distance from each point to habitat classes of estuaries, dunes, mudflats, and built-up areas were considered covariates. I extracted values between points and the habitat covariates (Table 5.2) using the nearest neighbour join function in QGIS 2.14.1 with a reference unit of 1 km and a repetition for the factors (sex and sub-species) to similar coordinates to a precision of 0.01 decimals thus accounting for the proportion of factors in the availability points across the buffer. Chlorophyll values were directly extracted to each used and available point, and added as a covariate. Because birds can fly up to 70 km per day during the non-breeding season (Davenport 2016), we assume that each record represents habitats that Black Skimmers favour or specialise on during moult.

Because the used/available response variable does not account for abundance, I added the number of Black Skimmers in moult per location as a covariate measure of abundance. The Wikiaves database had Black Skimmers recorded throughout Brazil yet there was a higher concentration of images at the coastline (Figure 5.1). Photographs in the Wikiaves database were not systematic therefore this *ad hoc* monitoring is opportunistic. Because sites with opportunistic records could have differed in sampling effort of observers, I added the number of records of Roadside Hawks (*Rupornis magnirostris*) from the same coordinates and month that Black Skimmers were detected in moult as a covariate to account for spatial variation in observer's effort. Number of records of the Roadside Hawk were also extracted for the availability points. The species chosen to correct for effort must follow few criteria such as occupying the same habitat as the target species and being a common and frequent species easy to identify that would not lead observers to a certain place as would happen with rare and vagrant species. The Roadside Hawk was chosen for several reasons; (1) it is the most-recorded species with a similar distribution to Black Skimmer on the Wikiaves database (Figure 5.1C); (2) it is abundant but solitary thus not biasing the correction with possible differences in flock size; (3) it is widespread except in dense forested areas which Black Skimmer does not occupy either; (4) it is not a perceived predator of Black Skimmers therefore there is no interaction between these species; and (5) it is easily detected and identified by key features such as yellow cere, tight rufous banding from the breast to the vent, and orange marks in the underwing while flying. I expect the *ad hoc* monitoring of Black Skimmers approach will not be biased if the abundance of Black Skimmers and of Roadside Hawks does not interact in the model.

The RSF considered use/availability as the response variable; and habitat (distances from estuaries, dunes, mudflats, and urban areas), productivity (chlorophyll), location (latitude in decimals), individuals (sex, sub-species, and abundance), and effort as explanatory variables. Sex and sub-species were added to the resource selection function model as factors (Table 5.2). Covariates were tested for multi-collinearity with a pairwise Spearman correlation test considering two variables collinear if $r > 0.5$ (Booth et al. 1994). No pair of covariates presented collinearity (all $r \leq 0.34$). I selected the RSF model based on a forward stepwise approach, analysing first interactions, and adding other covariates in sequence (Appendix 5.1). I chose the RSF that best explained the variation in the data based on highest log-likelihood and lowest Bayesian Information Criteria – BIC (Lele et al. 2016).

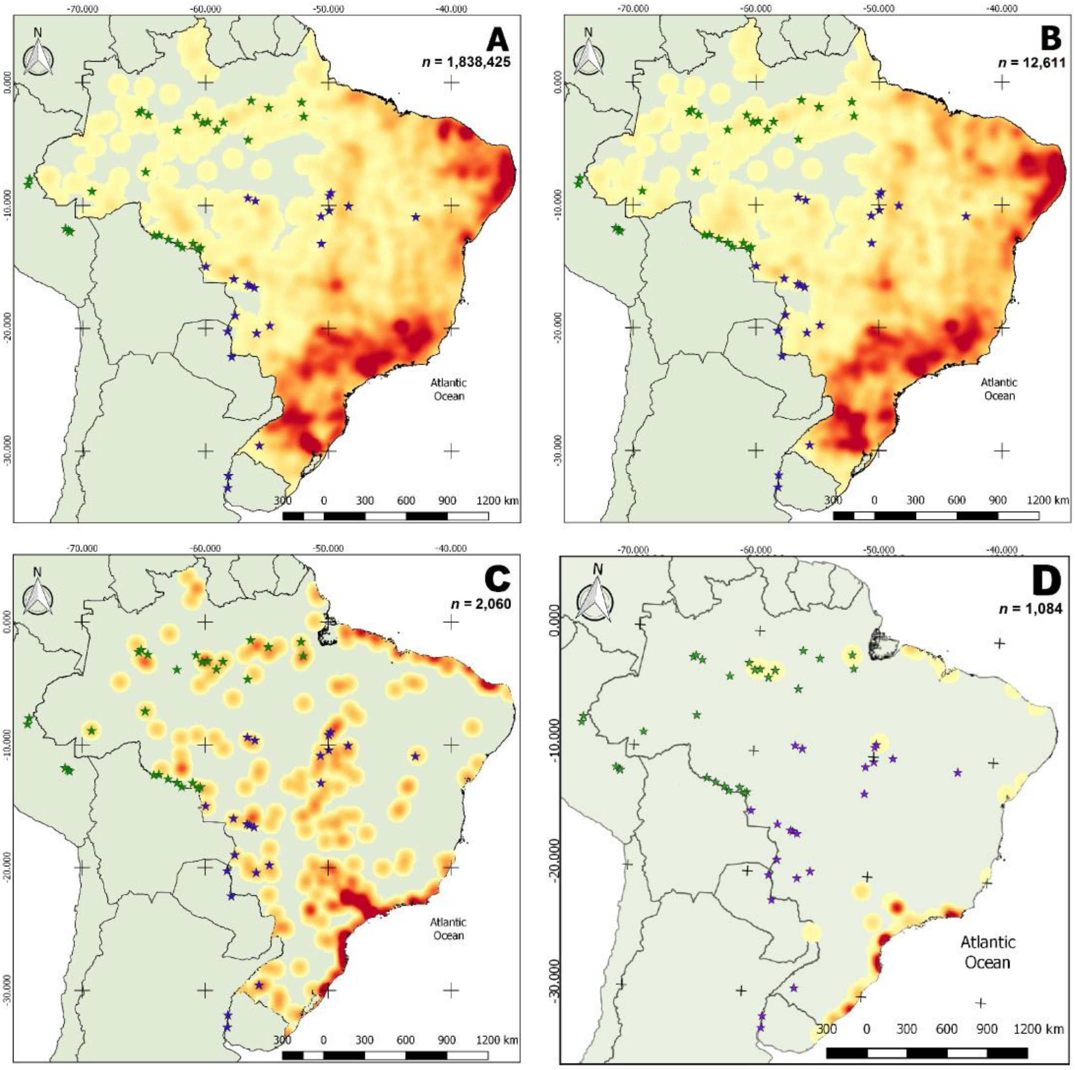

Figure 5.1: Concentration of photographs for all bird species in Brazil on the Wikiaves database representing the total coverage of observers (A), for the Roadside Hawk that was used to correct for observer effort (B), and for Black Skimmers from March 2005 to April 2016 (C). A total of 1,084 Black Skimmer individuals were scored in moult in the photographs (D). Kernel interpolation estimates represented in discrete bands of 50% (yellow), 75% (orange) and 95% (red) of concentration of records. Stars represent known breeding colonies of the Amazonian (green) and the South American (purple) Black Skimmer sub-species (Appendix 2.2).

Table 5.2: Effects by group and respective notation used for modelling the resource selection function of adult Black Skimmers moulting in Brazil.

Class	Effect	Notation	Description
Habitat	Estuaries	dstE	Distance (km) from the location of a moulting Black Skimmer to the nearest estuary or mangrove area.
	Mudflat	dstM	Distance (km) from the location of a moulting Black Skimmer to the nearest mudflat.
	Dunes	dstD	Distance (km) from the location of a moulting Black Skimmer to the nearest dune or beach.
	Urban area	dstU	Distance (km) from the location of a moulting Black Skimmer to the nearest urban area.
Productivity	Chlorophyll	chl	Chlorophyll concentration (mg/m^3).
Location	Latitude	lat	Latitude in decimals related to the location where the moulting Black Skimmer was recorded. Lower values represent southern latitudes. Greater values represent northern latitudes.
Individuals	Sub-species	ssp	Factor: Amazonian (*Rynchops niger cinerascens*) or South American (*R. n. intercedens*) Black Skimmer sub-species.
	Sex	sex	Factor: male or female.
	Abundance	abund	Number of Black Skimmer in moult counted in photographs
Effort	Effort	eff	Effort in number of photographs of the Roadside Hawk (*Rupornis magnirostris*) recorded in the same month as Black Skimmers.

Results

Timing and duration of moult

The differences in the mean start date and duration of moult using the 2x2 factorial ANOVA varied significantly between males and females within and between the two sub-species (Figure 5.2, Table 5.3). The South American males started moulting (day 19.91, SE = 6.37, n = 937) later than Amazonian males (day -34.31, SE = 38.52, n = 119; t_{1054} = -15.32, P < 0.001). The South American males (203 days, SE = 8.76, n = 937) also took less time moulting than Amazonian males (293.1 days, SE = 46.27, n = 119; t_{1054} = 21.19, P < 0.001).

The South American females (day 32.92, SE = 5.06, n = 700) also moult later than Amazonian females (day 13.29, SE = 40.70, n = 120; t_{818} = -5.27, P < 0.001) although differences are not as pronounced as between males. The duration of moult, however, did not differ between South American (189 days, SE = 7.54, n = 700) and Amazonian females (182.6 days, SE = 40.15, n = 120; t_{818} = -1.74, P = 0.082).

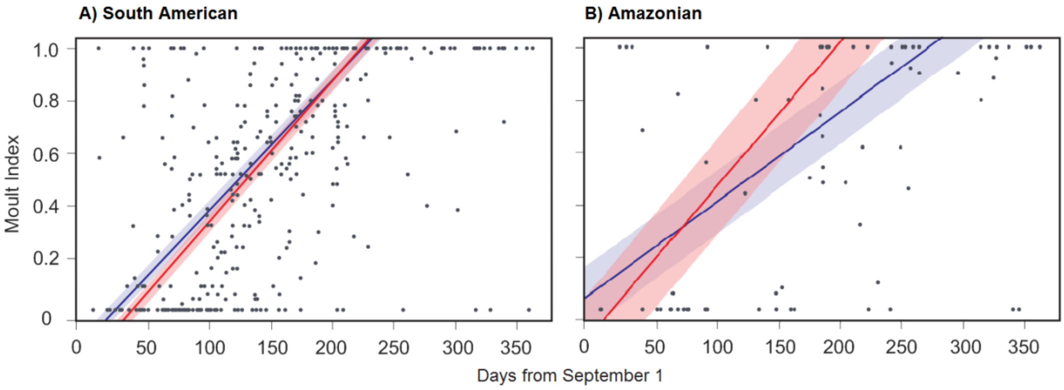

Figure 5.2: Moult Index of adult South American (A) and Amazonian (B) Black Skimmers in relation to date (day 1 = 1 September). The lines represent estimated moult trajectories and shadows represent the standard error of each trajectory for females (red) and males (blue). The R^2-value for the estimated moult trajectory in the South American Black Skimmer was 0.41, and 0.20 for the Amazonian Black Skimmer considering sexes pooled.

Table 5.3: Summary of 2x2 factorial design analysis of variance (ANOVA) considering differences in the mean start date and duration of moult in adult Black Skimmers according to sex and sub-species. DF is degrees of freedom; *P*-values were considered significant if ≤ 0.05 and are represented in bold.

Variable	*F*-value	DF	*P*-value
Mean start date			
Sex	835.27	1, 1872	**0.002**
Sub-species	1240.05	1, 1872	**< 0.001**
Sex * Sub-species	272.04	1, 1872	**< 0.001**
Duration			
Sex	2713.40	1, 1872	**< 0.001**
Sub-species	1226.38	1, 1872	**0.01**
Sex * Sub-species	1639.16	1, 1872	**0.006**

Habitat selection

As expected, abundance of individuals and effort were significantly different according to use/availability and concentrated in coastal areas (Figure 5.1, Table 5.4). However, the interaction between abundance and effort was not significant in the RSF, meaning there was no bias from effort in the RSF analysis (Table 5.4, Appendix 5.1). The RSF showed a significant effect of latitude with skimmers of both sub-species observed in moult mostly at southern latitudes (Table 5.4, Figure 5.3).

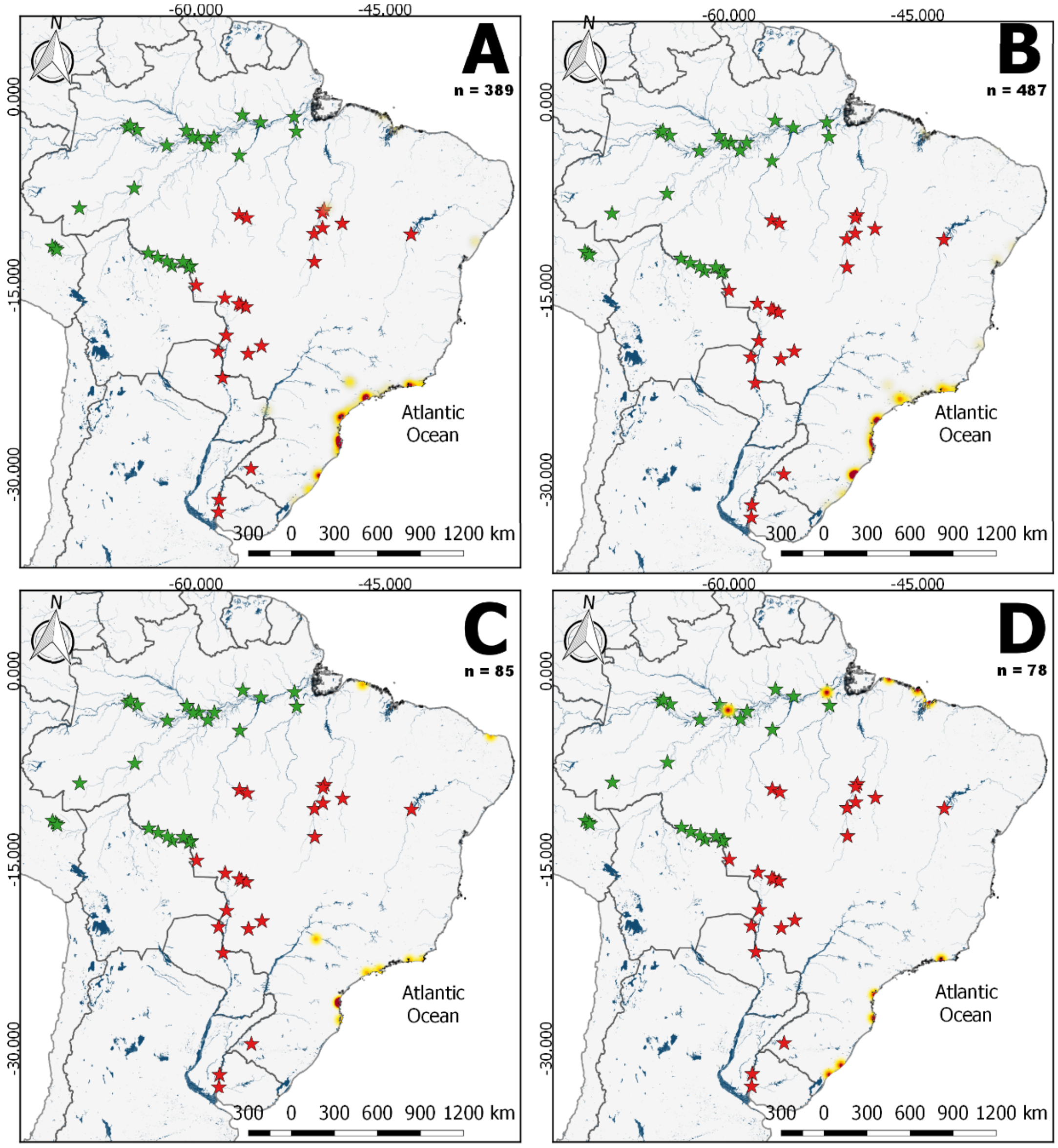

Figure 5.3: Distribution map of Black Skimmers moulting in Brazil. Details for South American female (A) and male (B), and Amazonian female (C) and male (D). Kernel interpolation estimates were represented in discrete bands of 50% (yellow), 75% (orange) and 95% (red) confidence intervals. Green stars represent known breeding colonies of the South American Black Skimmer while red starts represent known breeding colonies of the Amazonian sub-species (Appendix 2.2). Blue areas represent continental freshwater masses.

Although both sub-species occupy mostly the southern latitudes, the kernel interpolation suggests the concentration of individuals is slightly higher for South American individuals in southern Brazil (Figure 5.3). The kernel also suggests Amazonian individuals are relatively more likely to be found in moult in northern Brazil than the South American ones (Figure 5.3). Few Amazonian males in moult were found inland (Figure 5.3), however they were all already finishing moult (scores 45 to 49) which would explain a lower need of coastal resources. There was no significant effect of sex on the distribution of Black Skimmers between latitudes while moulting (Figure 5.3, Appendix 5.1). I found no difference in the associations with the different habitats between the sexes (Table 5.4).

Table 5.4: Summary of the population-level resource selection function model predicting habitat selection for Black Skimmers in moult as a function of individual, habitat, productivity, location, and effort across the Brazilian coastline. *P*-values were considered significant if ≤ 0.05 and are represented in bold. In terms of distance from habitats, negative estimates (β) indicate selection of a certain variable (shorter distance to the nearest habitat) while positive estimates indicate avoidance (greater distance to the nearest habitat). In terms of chlorophyll, positive estimates indicate selection (higher concentration of chlorophyll) and negative estimates indicate avoidance (lower concentration of chlorophyll). In terms of latitude, negative estimates indicate selection of southern latitudes (lower values closer to the South Pole) while positive estimates indicate northern latitudes (greater values closer to the Equator). Description of variables are available in Table 5.2. Notation: ssp = Black Skimmer sub-species; sex = sex of individuals; abund = abundance; dstE = distance from 'estuaries'; dstM = distance from 'mudflats'; dstD = distance from 'dunes'; dstU = distance from 'urban areas'; chl = amount of chlorophyll; lat = latitude in decimals; eff = effort.

Group	**Variable**	**β**	**SE**	***z*-value**	***P*-value**
Individuals	ssp (*intercedens*)	1.475	0.303	4.861	**< 0.0001**
	sex (male)	-0.302	0.229	-1.319	0.187
	abund	0.009	0.002	3.913	**< 0.0001**
Habitat	dstE	-0.116	0.014	-8.398	**< 0.0001**
	dstM	-0.023	0.004	-5.644	**< 0.0001**
	dstD	-0.005	0.004	-1.362	0.173
	dstU	-0.010	0.004	-2.490	**0.012**
	dstM * ssp (*intercedens*)	0.014	0.004	3.471	**0.0005**
	dstD * ssp (*intercedens*)	-0.010	0.004	-2.597	**0.009**
	dstU * sex (male)	0.011	0.007	1.704	0.088
Productivity	chl	0.004	0.001	6.340	**< 0.0001**
Location	lat	-0.145	0.014	3.471	**< 0.0001**
Effort	eff	0.012	0.001	8.255	**< 0.0001**

Among the habitat variables, occurrence of moulting Black Skimmer was positively related to chlorophyll (Table 5.4). Black Skimmers in moult of both sub-species were more likely to be present near estuaries (Table 5.4). Black Skimmers are also likely to be found near built-up areas (Table 5.4). The presence of Black Skimmers in moult near mudflats and dunes however differed between sub-species (Table 5.4). While the overall species selects mudflats, adding sub-species as an interaction indicates that South American Black Skimmers in moult are more likely to select dunes and less likely to select mudflats than Amazonian Black Skimmers (Table 5.4).

Discussion

I found both South American and Amazonian sub-species moulted from austral spring to austral summer. In both sub-species, males started earlier than females, although this difference was more pronounced in the Amazonian sub-species. Although I expected males would finish moulting earlier due to the species' territorial breeding behaviour with adult males establishing a nesting territory before females arrive (Burger & Gochfeld 1990), this behaviour does not explain the longer duration of moult for males. An alternative to early start and long duration of moult in males is their larger body size reflecting a higher energetic need. Males have longer primary feathers compared to females (Chapter 4). If moult results in a constant rate of growth of new feather then the longer feathers of males would require more time for growth.

Both sub-species and sexes selected mostly the same southern latitudes to moult. The resources selected by Black Skimmers in moult were positively related to chlorophyll concentration and negatively related to the distances to estuaries and built-up areas in both sub-species. Selection of mudflats and dunes differed between sub-species with South American Black Skimmers more likely to select dunes and less likely to select mudflats. Because birds can fly up to 70 km per day during the non-breeding season, the model assumed the records made with photographs reliably point sites that are at least near suitable habitats Black Skimmers specialise on during moult. Abundance of Black Skimmers and effort in this study were concentrated in coastal Brazil. However, abundance and effort did not interact meaning usefulness of the photographic datasets for large-scale analysis.

Although I could assess sub-species, age, and sex of Black Skimmers from photographs; the number of juveniles moulting detected was much lower than the number of adults for both sub-species. The differences could be related to an observer bias due to photographers focusing more on adults than juveniles or to a low juvenile survival rate as in gulls and terns (Sæther 1989, Spendelow et al. 2002, Stienen & Brenninkmeijer 2002, Keedwell 2003, Monticelli et al. 2008). I highlight observer's bias should be accounted for in future research focusing on species that have eye-catching features, such as ornamented birds, that are likely to be more photographed than cryptic individuals. The percentage of Black Skimmers scored per image (~30%) was lower than in Vieira et al. (2017) when photographs were deliberated taken to score moult. The lower percentage of birds scored occurs because citizens do not have the specific aim of photographing birds in the best positions to score feathers. However, percentage of scored individuals could increase in projects guiding citizens to take photographs in best positions to score moult and identify other characteristics such as sex and sub-species. This study shows the potential of citizen photographs, and indicates that it can be explored not only to confirm taxonomic identification and species distribution but also to assess subjects such as population structure, habitat selection, and detection of important conservation sites in a broader spatial and temporal perspective.

The temporal strategy of moult in both sub-species in Brazil was consistent with descriptions in Scherer et al. (2013) and Vieira et al. (2017) in southern Brazil. While the mean start day varied from day 19.91 ± 6.37 to day 32.92 ± 5.06 (day 1 = 1 September) according to sex, Scherer et al. (2013) provided a mean start day of 5 ± 92.2 (day 1 = 1 October) and Vieira et al. (2017) presented it as day 28 ± 4.5 (start day in 1 October) for the South American Black Skimmer. The one-month difference could be related to lower statistical power in the study by Scherer et al. (2013). An alternative explanation, is a variation between sites, because Scherer et al. (2013) and Vieira et al. (2017) studied Black Skimmers in the southern extremity of the moulting distribution found in this study.

South American and Amazonian sub-species have a distinct pattern of moult from the North American one. The North American Black Skimmer takes less time (150 days) to moult between boreal autumn to spring. North American Black Skimmers moulting primaries take a break with first P1 to P3 primaries being replaced in the breeding site and the other P4 to P10 primaries replaced later in the non-breeding site after post-breeding migration (Pyle 2008). The results in this study show the Amazonian and South American Black Skimmers on the other hand have a complete moult apparently with no interruption, that lasts around 200 days during the non-breeding season from austral spring to summer. The Black Skimmer spent a prolonged period replacing primary feathers as do other aquatic groups such as Procellariidae and Pelecaniformes (Edelstam 1984, Langston & Rohwer 1996, Pyle 2008). Black Skimmers in Brazil started moulting primary feathers soon after arriving to the non-breeding sites (see annual cycle in Chapter 2), which are mostly concentrated along the coastline. Skimmers also finished moulting primary feathers before migrating back to breeding colonies inland (see annual cycle in Chapter 2), thus separating moult from pre-migratory fattening and reproduction (Bonier et al. 2007, Cyr et al. 2008).

Black Skimmers appeared to select productive habitats mainly in specific coastal areas along the southern coast of Brazil. Contrary to prediction, Black Skimmers also selected built-up areas during the moulting season despite human presence potentially affecting individuals with unnecessary flights and defensive behaviours (Molina 2000, Burger et al. 2010, Vieira 2015). Black Skimmers also strongly selected estuaries while moulting. A study testing several types of beaches used by South American Black Skimmers in southern Brazil during the non-breeding season found the species selected sand habitats of higher granulometry, such as the ones associated to dunes and estuaries, over the ones of lower granulometry (Pereira 2016). Coastal habitats of higher granulometry include estuaries that accumulate runoff sediments and nutrients in sheltered waters promoting excellent fish nurseries and resulting in a productivity of small sized specimens listed as Black Skimmer's prey items such as juvenile mullets (*Mugil* spp.) and silversides (*Odontesthes argentinensis* and *Atherinella brasiliensis*) (Mariano-Jelicich et al. 2003, Naves & Vooren 2006). Migratory birds are expected to look for productive habitats due to their high energetic needs to breed, move between sites, and moult (Butler et al. 2001, Leu & Thompson 2002, Rohwer et al. 2005). Black Skimmers are likely to select southern latitudes in the South Atlantic and the southern and southeastern Brazilian Atlantic coast are known for the high productivity related to the Atlantic Upwelling and the Temperate Estuarine zones (Acha et al. 2004). Although chlorophyll is only a proxy for fish productivity (Downing et al. 1990), the areas selected by Black Skimmers are known for their productivity and coastal bird diversity (Butler et al. 2001, Acha et al. 2004).

The relationship between habitat selection and moult is little explored but has an immense potential as an indicator of environmental quality, food availability and thus correlated biodiversity (Leu & Thompson 2002). The presence of migratory birds is already an impact factor when evaluating priority areas for bird conservation purposes (David 1994, Butler et al. 2001, BirdLife 2015), and the high concentration of individuals moulting is an ecological indicator of environmental quality and resource availability (Leu & Thompson 2002). Knowledge of when and where species moult enhances the understanding of ecological processes and supports conservation and management activities. For instance, interpreting stable isotope ratios in feathers, a valuable method to study trophic relationships, environmental quality, and migration (Hobson 1999, 2005, Connolly et al. 2004), depends on the knowledge of time and location of moult. Moreover, considering global changes have interfered in how species respond to the environment, habitat selection during key activities is fundamental to identify areas that should be prioritised for conservation, restoration, and suitable habitats for species translocations thus encouraging responsible management actions (Stephens et al. 2015).

Chapter 6: The El Niño affects diet composition of Black Skimmers in the South Atlantic coast

Abstract

To implement conservation and management plans that consider a species' response to the environment, information on resource use and the plasticity of foraging strategies are required. Environmental oscillations such as the El Niño are reported to affect the diet of seabird species. In southern Brazil, the El Niño increases precipitation and pushes freshwater fish into estuarine areas, and estuarine fish into marine habitats. Black Skimmers (*Rynchops niger*) are coastal birds known to feed on estuarine and marine fish. This study estimated the contribution of different habitats to the assimilated diet of moulting Black Skimmers, and compared their resource use in response to the strong El Niño event that occurred in southern Brazil between April 2015 and May 2016. Prey from different habitats vary in δ^{15}N, δ^{34}S and δ^{13}C depending on origin if from marine or freshwater habitats with values increasing with salinity. I measured the isotopic signature of feathers for Black Skimmers in a non-breeding area at the Santa Catarina Island in the Brazilian South Atlantic coast. I used δ^{13}C and δ^{34}S as proxies of foraging habitat, δ^{15}N as a proxy for the trophic level of prey consumed. I expect that target fish species would change due to the environmental fluctuation, thus altering the dietary isotopic signature of Black Skimmers. The target prey type of Black Skimmers significantly changed during El Niño to a higher contribution of estuary and freshwater fish species, compared to regular years. This study demonstrates how large-scale climatic oscillations in the Pacific affect coastal predators through changes in target prey and foraging strategy.

Keywords: climate change, foraging habitat, stable isotopes, estuary, *Rynchops niger*, southern Brazil.

Introduction

An effective management of habitats and species for conservation purposes under scenarios of climate changes depends on the species' response to environmental drives. Environmental drivers of behavioural change include the El Niño Southern Oscillation (ENSO) which generates fluctuations at lower trophic levels through changes in temperature, precipitation, and winds (Furness & Camphuysen 1997, Ramirez-Bastida et al. 2008, Robinson et al. 2008) (Barber & Chavez 1983, Brichetti et al. 2000, Garcia et al. 2004, Bost et al. 2015). Marine predators, such as seabirds, are particularly vulnerable to changes in prey availability when performing energetically demanding activities, such as breeding and moult.

The ENSO changes sea surface temperature in the Pacific Ocean and affects climate cells all over the world (Trenberth 1997). In South America, ENSO causes extreme decreases and increases in precipitation levels depending on the region (Trenberth 1997). Many seabird species depend on aquatic ecosystems during the breeding and non-breeding seasons. Therefore, ENSO can impact these species; firstly, if they are specialist foragers depending on specific resources that are affected by climate oscillations, and secondly, if their annual movements rely on a complex range of habitats (Anderson 1989, Culik et al. 2000). Seabirds select breeding and moulting sites that provide reliable resources and safety from predators (Myers 1987, Parish 1987, Newton 2010, Rushing et al. 2016). Migratory birds move seasonally between sites to meet the energetic and nutritional needs of resource-demanding activities, such as breeding and moulting (Jenni & Kéry 2003, Daufresne et al. 2009, Sydeman et al. 2012, Stephens et al. 2016, Wauchope et al. 2017).

The effects of ENSO on the foraging strategies of different seabird species have been recognised as switches in target prey species and foraging site (Anderson 1989, Culik et al. 2000, Simeone et al. 2002). Prey species, such as fish, that originate from different foraging habitats vary in isotopic signature (Peterson & Fry 1987, Hobson 1999). The δ^{13}C signature is widely used to distinguish foraging habitat with greater enrichment within inshore, compared to offshore waters, while δ^{15}N is often used as a proxy for trophic level (Peterson & Fry 1987, Hobson & Clark 1992, Hobson 1999). To identify slight differences of estuarine areas from marine and freshwater signatures, δ^{34}S is the most reliable isotope ratio applied in ecological studies, becoming enriched along the freshwater-estuarine-marine gradient (Peterson & Fry 1987).

Black Skimmers (*Rynchops niger*) are migratory aquatic birds that are largely studied at their breeding colonies located along inland rivers in South America. For example, the El Niño is known to affect Black Skimmers in Mexico by increasing breeding success, and the abundance of individuals at sites nearby the colonies (Carmona et al. 1995, Mellink 2003). However, little is known about their resource use during the non-breeding period and how this changes in relation to environmental variation. In southern Brazil, Garcia et al. (2001, 2004) found the fish assemblage that are target by Black Skimmers in an estuarine area during the non-breeding season (Naves & Vooren 2006, Mariano-Jelicich et al. 2008) was altered by the El Niño. There was an increase in freshwater fish and depletion of estuarine species, mainly mullets (*Mugil* spp.) and silversides (*Odontesthes argentinensis* and *Atherinella brasiliensis*), due to higher precipitation increasing river discharge, and changing salinity and water transparency in the estuary. Consequently, I would expect Black Skimmers moulting in coastal habitats to change their diet composition during the El Niño.

When migratory birds, such as the Black Skimmer, forage in different habitats, the tissues growing at that period acquire the prey's isotopic signature, which is also going to vary according to its turn-over rate. As an inert tissue, feathers reflect the signature of prey consumed when grown during moult (Hobson, 1999). Black Skimmers moult at the Brazilian coast (Chapter 5) once a year during the non-breeding season, from October to March (Chapter 3, Chapter 5, Vieira et al. 2017).

If the target prey species change due to environmental oscillations because more freshwater fish is found in estuaries, the isotopic signature of the Black Skimmer is likely to reflect this. To control for signatures reflecting the movement of prey between habitats, as opposed to environmental changes, primary filters reflecting the aquatic habitat signature such as bivalves can be used as baseline. If the baseline between two regular years show no inter-annual variation but they vary with El Niño, then an El Niño effect on environment's isotopic signature is likely.

Changes in both source and consumer stable isotope ratios during El Niño could indicate a significant change in the foraging habitat and the consumer exploiting it. However, if changes occur in the source ratio but not the consumer (or vice-versa), it is likely the consumer's response is to change habitat and fit its foraging needs. Therefore, this study aimed to (1) estimate the contribution of different habitats to the assimilated diet of moulting Black Skimmers, and (2) compare the diet composition by Black Skimmers in response to the El Niño phenomenon. I hypothesise that the El Niño will affect Black Skimmer's diet composition by reducing the use of estuaries while foraging and making more use of alternative habitats, mainly freshwater. The variation in Black Skimmer's diet composition according to El Niño demonstrates how large-scale climatic oscillations in the Pacific affect coastal predators through changes in its foraging use also in other oceans.

Methods

Study area

The study area at the Island of Santa Catarina and the adjacent mainland in southern Brazil (27º 22'S to 27º 50'S and 48º 25'W to 48º 35'W) consists of a mosaic of potential foraging habitats including estuaries, freshwater, and shallow marine habitats (Figure 6.1) where Black Skimmers have been found foraging (Vieira 2014, Pereira 2016). These suitable habitats were classified into three groups. Estuaries were classified based on salinity tested at each site with a salt refractometer RTS-101-ATC Instrutherm® (precision ± 0.001%). Based on Levinton (1995), I classified the habitats as estuarine if salinity was between 1 and 35‰, as freshwater if salinity was lower than 1‰, and as shallow marine water if the salinity was over 35‰ and the beach area faced the Atlantic Ocean with no estuaries nearby.

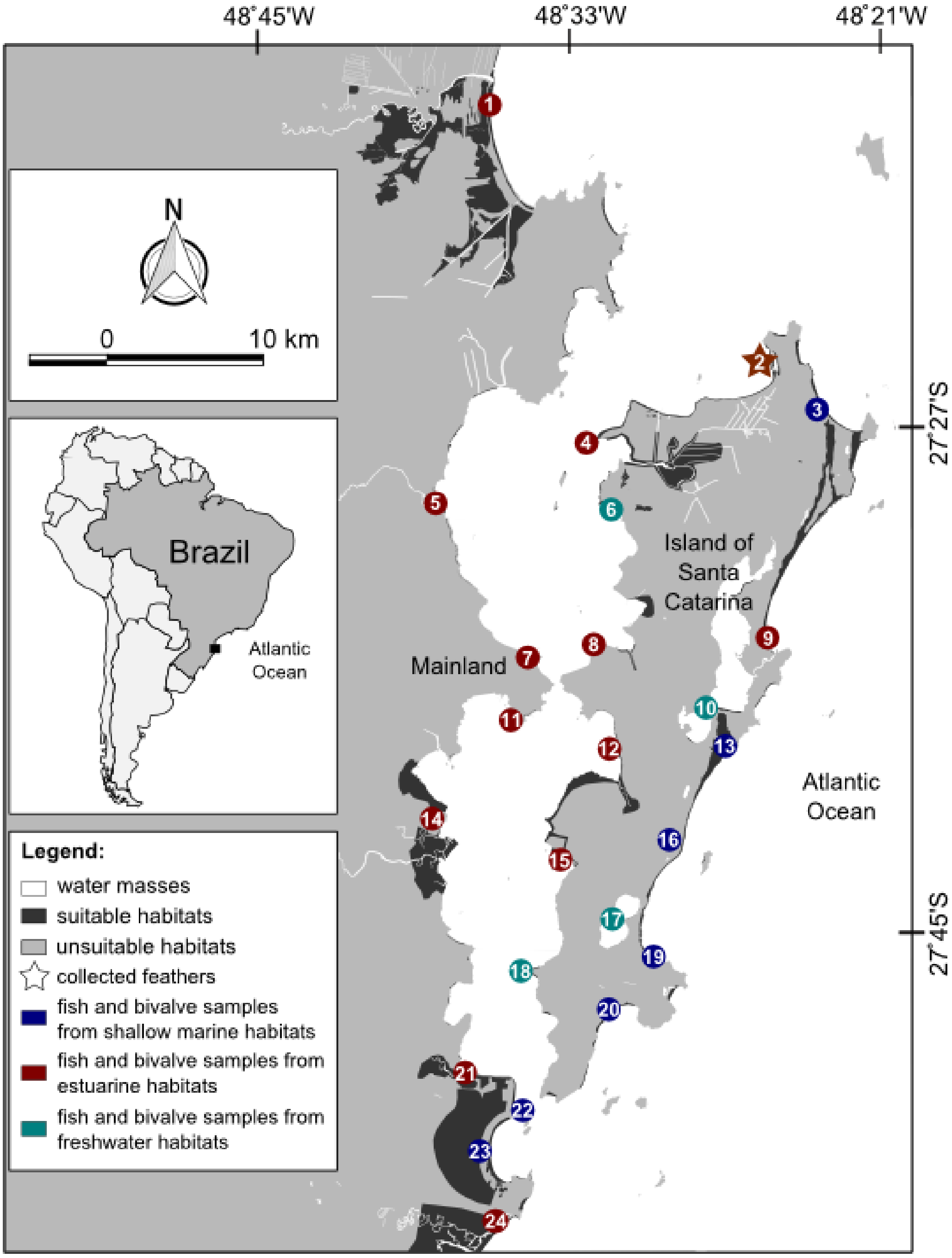

Figure 6.1: A total of 24 sites were sampled for Black Skimmer's fish prey covering suitable habitats which they may use as foraging area near the roosting site (star) where Black Skimmer's primary feathers were collected at the Island of Santa Catarina in southern Brazil. 1- Tijucas, 2- Ponta das Canas, 3- Ingleses, 4- Pontal do Jurerê, 5- Biguaçu, 6- Sambaqui, 7- Estreito, 8- Ponta do Coral, 9- Barra da Lagoa, 10- Lagoa da Conceição, 11- Coqueiros, 12- Pirajubaé, 13- Joaquina, 14- Barra do Aririú, 15- Tapera, 16- Campeche, 17- Lagoa do Peri, 18- Ribeirão da Ilha, 19- Armação, 20- Pântano do Sul, 21- Maciambu, 22- Papagaio, 23- Pinheira, 24- Guarda do Embaú.

Although Black Skimmers usually roost on estuarine mudflats during the moulting season (Murphy 1936), they can move up to 70 km per day (Davenport et al. 2016) covering different potential aquatic foraging habitats far from the roosting site. Black Skimmers have a complete moult mainly from October to March (Vieira et al. 2017) and stay in the approximate area during the whole period (Davenport et al. 2016). I collected moulted feathers at the Ponta das Canas (27º24'S, 48º25'W; star in Figure 6.1) and potential prey at 24 sites across the study area up 60 km from the roosting site (Figure 6.1). The coast to the north of the study area consisted of unsuitable habitats and therefore was not included.

Feather samples

The isotopic signature of different body tissues provides a coarse description of the average dietary signature during formation (Hobson 1999). Black Skimmers have an annual complete moult during the non-breeding season (Vieira et al. 2017). Thus, the isotopic signature of full-grown feathers represents the resources consumed during the previous non-breeding season. I collected more than 300 moulted flight feathers from Ponta das Canas (27º24'S, 48º25'W; Figure 6.1) over three moulting seasons between 2014 and 2016. Feathers were identified as Black Skimmers' by comparing them with museum specimens, photographs of individuals with open wings and by direct observation of individuals losing feathers.

I selected 25 feathers for each study year that came from the same wing side and position (right wing, P8). This avoided potential pseudo-replication by sampling different feathers from the same individuals and standardised the type of feathers and the period in which they were grown (Figure 6.2). Feather position (right or left wing) was confirmed according to the orientation of the rachis' insertion in the wing when facing the superior vane of the feather. Moreover, Black Skimmer's primaries P10 to P8 are different from others by their long shape (> 25 cm), tapered tip, blackish colour and unique lighter (not white) marks skirting the larger vane parallel to the rachis. Feathers P1 to P7 are different from P8 to P10 because P1 to P4 are whitish and have a wider tip while P5 to P7 are blackish but with a whitish mark skirting the larger vane parallel to the rachis, and are shorter than 25 cm. Differences in size between P8, P9 and P10 are dependent on bird's size and thus I relied on the month when these feathers were moulted to distinguish between them (Figure 6.2). Feathers P8 are moulted between December and May, while P9 and P10 are moulted from January to July (Figure 6.2). To minimise overlap between P8 and P9-10 in the samples I therefore collected feathers in December only.

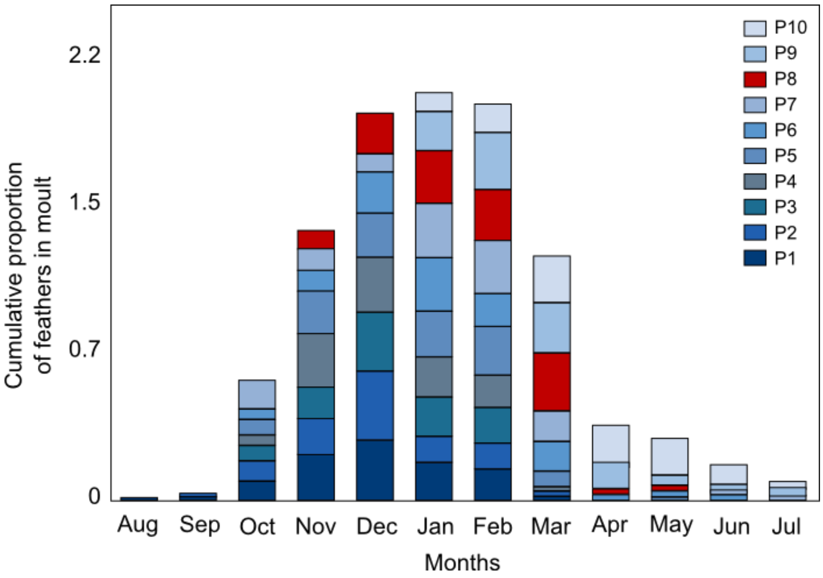

Figure 6.2: Cumulative proportion of Black Skimmers' primary feathers (from P1 to P10) in moult at Ponta das Canas in southern Brazil per month. The cumulative proportion per feather is expressed by the number of feathers in score 1 at a certain position P*i* in a month *j* divided by the sum of feathers in score 1 at a certain position P*i* in all months. Score 1 has a clear gap between neighbour feathers and suggests the feather was moulted within days. The score was obtained from photographs of 1,418 individuals with open wings in Vieira et al. (2017).

I assigned feathers to regular or El Niño conditions depending on the Oceanic Niño Index (ONI) available from the NOAA's Climate Prediction Centre on www.cpc.ncep.noaa.gov in that month. An El Niño event is considered when ONI > 0.5 for at least five months (Trenberth 1997). I collected feathers in 2014 and 2015 to represent feathers grown in two regular years; December 2013 and December 2014. Feathers collected in a third season (2016) represented feathers grown in December 2015, a very strong El Niño event that occurred from April 2015 to May 2016.

Feathers collected in the field were first cleaned by brushing mud from barbs. They were later cleaned of surface contaminants using a liquid detergent solution (1 *Ecover*™ detergent : 99 deionised water by volume) followed by a solution of 2 chloroform : 1 methanol (by volume). Feathers were air-dried after cleaning (Cherel et al. 2005). To control for potential variation in stable isotope ratios within individual feathers due to position and variation in melanin, I took only black barbs and at regular intervals from along the entire length of the feather (Hobson et al. 1994, Michalik et al. 2010, Grecian et al. 2015).

Fish prey and bivalves

Black Skimmers mostly forage on the same fish species during the entire non-breeding season (Naves & Vooren 2006, Mariano-Jelicich et al. 2008), so I collected samples of local fish prey across the 24 study sites (Figure 6.1) to represent the freshwater-estuarine-marine gradient. The isotopic turnover rate of fish muscles is on average 3 ± 3 months but varies according to species (Hobson & Clark 1992, Hesslein et al. 1993, Weidel et al. 2011). Prey were sampled between December and February for two regular years (2014/2015, 2016/2017), and the El Niño year (2015/2016). These years do not directly match with the feather samples and therefore we tested the isotopic baseline signature during regular years using resident primary consumers. Bivalves are filter feeding from the local waters thus reflecting local stable isotope ratios at a lower trophic level in the same habitats as Black Skimmers forage. I used bivalves as a year and habitat-specific proxy of stable isotope baseline signature for the studied foraging habitats.

In each of the 24 site a total of 10 fish prey were caught using casting nets and 5 bivalves were collected from each of the three habitats (freshwater, estuarine, and marine). However, no bivalves were found in freshwater. To catch fish throughout the water column that were representative of the Black Skimmers' usual prey size, I used a casting net with 8 mm mesh and 1.8 m diameter (Naves & Vooren 2006, Mariano-Jelicich et al. 2008). Each site was sampled for intervals of 3 hours, with 1-hour breaks between the casting of the net and bivalve collection, between 6:00 am and 5:00 pm. When 10 individuals of target fish species of appropriate size were collected, I moved to another site.

Because I wanted fish prey to reflect the isotope value of each habitat and species that occupy multiple habitats could interfere in the site's signature, I selected only species that exclusively live in the habitat I sampled, such as resident species and juvenile migratory fish born in that habitat. I focused on sampling mullets and silversides that the literature lists as important part of Black Skimmers' diet in southern Brazil and Argentina (Naves & Vooren 2006, Mariano-Jelicich et al. 2008). However, if mullets and silversides were not found at a site (such as in freshwater habitats), other fish listed as typical prey (Naves & Vooren 2006, Mariano-Jelicich et al. 2008) or with similar phenology occupying that habitat were collected. Silversides are estuarine resident species while mullets are coastal species that depend on estuaries to breed (Garcia et al. 2001). From the total of 720 fishes and 340 bivalves sampled, I randomly selected a sub-sample of 90 fish and 30 bivalve samples (10 fish per habitat and year, and 5 bivalves per habitat and year except freshwater that had no bivalves) to run for stable isotope analysis. The sub-samples were collected between 20 and 30 January 2015, between 1 and 10 February 2016, and between 25 January and 2 February 2017.

Fish were euthanised in a freezer and a 1 cm^3 piece of muscle was taken from each individual excluding bones, scales, and other organs. Muscle tissue samples were washed in deionised water twice and stored in glass vials in a freezer to avoid deterioration and possible changes in stable isotope signatures until lipid extraction. Bivalves were left in deionised water for 24h to clean sediments they ingested before capture that could affect isotopic signatures. They were then euthanised in a freezer. I extracted the muscles and stored them in glass vials in a freezer until lipid extraction.

Lipids are depleted in $\delta^{13}C$ in relation to the whole tissue or protein, and therefore variation in lipid content between samples can confound interpretation of diet (Becker et al. 2007, Post et al. 2007). Lipid extraction results in a small fractionation of $\delta^{15}N$ (Post et al. 2007) and it is possible it also affects $\delta^{34}S$. Therefore, I decided to test the isotopic differences between lipid and non-lipid extracted samples. I selected half of each sample and extracted lipids from one of the half of each individual fish and bivalve sample. Tissue samples were folded individually into glass fibre filter papers and lipids extracted using a Soxhlet apparatus containing a boiling solution of 2 volumes chloroform : 1 volume methanol (Cherel et al. 2005). The samples were then dried at 45ºC for 48h until weight was constant.

Stable isotope analysis

Feather, fish, and bivalve samples were individually homogenised and weighed (mass between 1.200 and 1.400 mg) into tin capsules. Capsules were combusted in a Elementar® Vario Pyro Cube producing N_2, CO_2 and SO_2 gases (with a 1st combustion tube filled with Tungsten Oxide at 1120ºC and 2nd reduction furnace, filled with copper wire at 850ºC), interfaced with a mass spectrometer Isoprime® VisION which measures the ratios of the different isotopes in the gases being released. Stable isotope ratios (δ) are presented as parts per thousand (‰) relative to international isotopic reference materials V-PDB (δ^{13}C), Air (δ^{15}N), and SO_2 (δ^{34}S) (Bond & Hobson 2012). The δ notation was expressed as:

$$\delta^{j/i}\mathrm{X}(‰) = \left[\left(\frac{\delta sample}{\delta standard}\right) - 1\right] * \ 1000$$

where $\delta^{j/i}$X = ^{15}N/^{14}N (δ^{15}N), ^{13}C/^{12}C (δ^{13}C) or ^{34}S/^{32}S (δ^{34}S) from samples and standards. Blind to sample type (feather, fish, or bivalve), four international standards (USGS40: glutamic acid; IAEA-S1, S2 and S3: silver sulphides) were measured in each analytical run and three internal laboratory standards (MSAG2, M2 and SAAG2) were analysed every 10 samples to correct for any instrument drift over the course of a 3-day run. MSAG2, M2 and SAAG2 are all soluble in water and easier to homogenise with dispensing into capsules using a syringe. They also have elemental concentrations, and the range of isotope ratios covers most samples (Higgs et al. 2016). MSAG2 is a methane-sulphonamide and gelatine mixture that corrects for linearity and drift (Werner & Brand 2001). M2 is methionine and gelatine mixture enhanced with ^{15}N-enriched alanine, and SAAG2 is a sulphanilamide and gelatine mixture enhanced with ^{13}C-enriched alanine. Precision of measurements was expressed as the standard deviation (± SD) of repeated analysis of the standard values (Appendix 6.1). The drift correction accounts for differences in the laboratory environment, such as temperature in the room, ash built-up in the combustion tube, and oscillations in the machine (Werner & Brand 2001). This correction compares values for each of the three laboratory standards across the whole of the analytical run (60-70 hours) and provides a correction metric to apply to the data for ^{13}C, ^{15}N and ^{34}S. The values were plotted and equation of best R^2-value were used to correct the dataset.

To account for effects of lipid extraction, I first used paired *t-tests* between the lipid and non-lipid extracted δ-values for fish (source) and bivalves (baseline). Bivalve samples differed between lipid and non-lipid extracted samples for δ^{13}C ($t_{39} = 3.78$, $P < 0.001$) and δ^{15}N ($t_{39} = 2.08$, $P = 0.04$) but not δ^{34}S ($t_{39} = -0.79$, $P = 0.43$). Fish samples differed between lipid and non-lipid extracted samples for δ^{13}C ($t_{109} = -2.13$, $P = 0.03$) and δ^{34}S ($t_{109} = -3.96$, $P = 0.001$), but not and δ^{15}N ($t_{109} = 0.63$, $P = 0.52$).

Despite variation between species and individuals, I would expect the amount of lipids to be higher in fish muscles (2 to 40% of dry weight according to Henderson et al. 1984, Venugopal & Shahidi 1996 and Nanton et al. 2001), compared to bivalve muscles (7 to 9% of dry weight according to Bruner et al. 1994). The ratio of the amount (mg) of carbon and nitrogen (C:N) can be used as a proxy to predict the percentage of lipids in animal samples (Post et al. 2007). Therefore, I used the C:N values before lipid extraction to assess the effects of lipid extraction on δ^{34}S and assumed it will also predict the percentage of lipids. I evaluated the normalisation using a regression between C:N and $\Delta\delta^{34}$S. $\Delta\delta^{34}$S was calculated as:

$$\Delta\delta^{34}S = \delta^{34}S_{le} - \delta^{34}S_{nle}$$

where $\delta^{34}S_{le}$ is the δ^{34}S value for the lipid-extracted fraction and $\delta^{34}S_{nle}$ is the δ^{34}S value for the non-lipid extracted fraction. I found the mean paired difference in δ^{34}S of bivalve samples before and after lipid extraction was -0.65 (SD = 1.52, $n = 30$), while δ^{13}C was 1.15 (SD = 0.03, $n = 30$), and δ^{15}N was 0.36 (SD = 0.24, $n = 30$).

The mean paired difference in δ^{34}S of fish samples before and after lipid extraction was -1.15 (SD = 1.28, n = 90), while δ^{13}C was -0.66 (SD = 2.25, n = 90), and δ^{15}N was 0.18 (SD = 1.14, n = 90). Only 0.3% and 2.5% of the variance in $\Delta\delta^{34}$S from bivalve and fish samples, respectively, was explained by the C:N ratio (Figure 6.3) suggesting a weak and statistically not significant effect of lipid concentration on the δ^{34}S estimate.

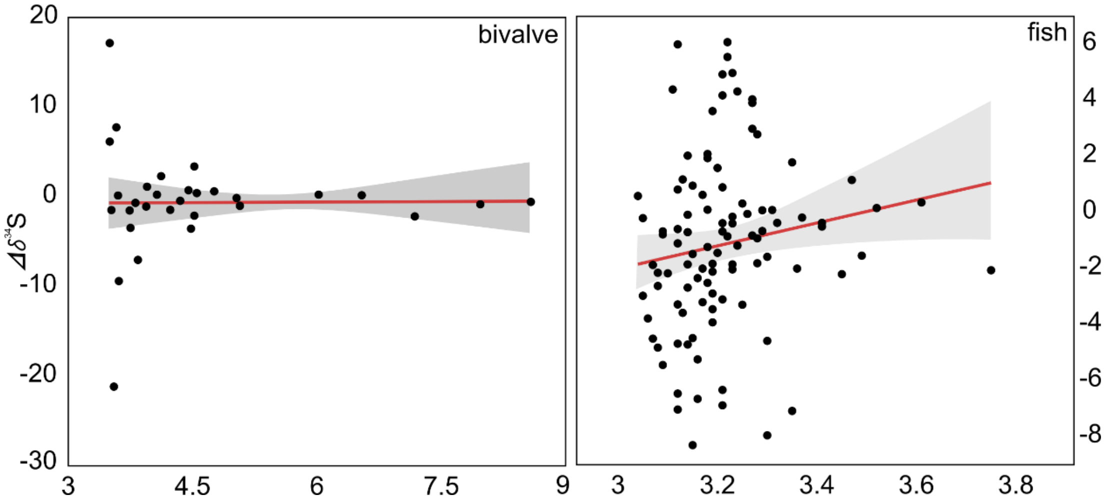

Figure 6.3: Linear relationship between C:N ratio and $\Delta\delta^{34}$S for tissues samples from bivalve ($y = 0.04x - 0.82$, $R^2 = 0.003$, $P = 0.95$) and fish ($y = 4.08x - 14.27$, $R^2 = 0.025$, $P = 0.09$) considering a 95% confidence interval.

I highlight this effect of lipid extraction on δ^{34}S estimates in fish muscles must be more extensively invesetigated. And as Post et al. (2007) considered δ^{15}N to be negatively impacted by lipid extraction and recommended the use of non-lipid extracted values, I also selected non-lipid extracted values for δ^{34}S to avoid possible bias. Thus, I used lipid extracted values for δ^{13}C and non-lipid extracted values for δ^{15}N and δ^{34}S when analysing the baseline (bivalve) and source (fish) data.

Statistical analysis

To account for possible inter-annual variation in data from regular years unrelated to ENSO, I first tested each dataset for normality using the Shapiro-Wilk test and considered them normally distributed if $P > 0.05$. Bivalve δ^{15}N had non-normal distribution ($P < 0.05$) so I adjusted it with a log transformation. I tested for inter-annual variation in the baseline using an analysis of variance (ANOVA). There was no inter-annual variation in the baseline (bivalves) stable isotope signature across the three years (ANOVA, δ^{13}C: $F_{1,29}$ = 0.09, P = 0.76; δ^{15}N: $F_{1,29}$ = 0.84, P = 0.36; δ^{34}S: $F_{1,29}$ = 2.44, P = 0.13). So, I excluded the possibility of inter-annual variability in the environment unrelated to ENSO affecting the data. Because there was no significant variation, I pooled regular years into one for fish and feathers.

To test for inter-annual variation in the fish prey, I first ran a principal component analysis (PCA) using δ^{13}C, δ^{14}N and δ^{34}S values for fish prey. The PC1 corresponded to 62% of the variance in δ^{13}C, δ^{14}N and δ^{34}S thus I selected it as the response variable. I used a generalised linear model (GLM) for the prey data to test the variance in PC1 (representing δ^{13}C, δ^{14}N and δ^{34}S) between habitats, years, and the interaction between them. Habitat (marine, estuarine, freshwater) and year (regular and El Niño) were added as factors.

The Bayesian Multi-Source Stable Isotope Mixing Models achieve higher resolution when combining prey with similar isotopic composition and similar ecological roles together in one group (Phillips et al. 2005). Fish prey (source) samples from regular years differed in δ^{34}S values between habitats (ANOVA: $F_{3,96}$ = 16.64, P < 0.001). And the post-hoc Tukey Honestly Significant Difference (HSD) pairwise variation was significant (P < 0.007) so I maintained the ‘estuarine’, ‘marine’ and ‘freshwater’ categories.

I tested the feathers’ stable isotope data for normality using a Shapiro-Wilk test to fit the assumption of variability associated with source being normally distributed in stable isotope mixing models (Parnell et al. 2010). I also assumed carbon, nitrogen and sulphur were equally assimilated by Black Skimmers within each P8 feather. I tested the differences on the stable isotope ratios of Black Skimmers’ feathers between years using a pairwise *t-test*. I used a Bayesian Multi-Source Stable Isotope Mixing Model (BSIMM) from the *MixSIAR* package (Stock & Semmens 2013) in R 3.4.0 (R Core Development Team 2017) to estimate the relative proportion of diet which Black Skimmers obtained from different habitats. The BSIMM was applied to the individual consumer (feather) isotopic values, and the mean and standard deviation of combined prey values according to freshwater, estuarine and marine habitats (Table 6.1). The model used a Markov Chain Monte

Carlo (MCMC) and the weights that made up dietary proportion were given a Dirichlet prior distribution (Parnell et al. 2010, Jackson et al. 2011). I used a sparse matrix of the BSIMM output in a permutational multivariate analysis of variance with 1000 permutations from the *vegan 2.4-3* package (Oksanen et al. 2017) to assess significance of changes in the dietary proportion between regular and El Niño years.

Table 6.1: Stable isotope mean values of marine, estuarine, and freshwater fish prey sources obtained during moulting seasons between 2014 and 2016, covering two regulars and one El Niño year. The values were used as reference in the Bayesian Multi-Source Stable Isotope Mixing Model. Mean and standard deviation (SD) values are in ‰. Fish samples from regular year 1 were collected in January 2014, from regular year 2 were collected in February 2017, and from El Niño in February 2016.

Year/Habitat	**Sample size**	**Mean δ^{13}C ± SD**	**Mean δ^{15}N ± SD**	**Mean δ^{34}S ± SD**
Regular year 1				
Estuarine prey	10	-16.12 ± 1.4	11.73 ± 2.06	11.95 ± 2.37
Marine prey	10	-17.37 ± 0.62	13.55 ± 0.85	17.6 ± 0.84
Freshwater prey	10	-24.96 ± 1.55	9.26 ± 1.03	11.07 ± 1.1
Regular year 2				
Estuarine prey	10	-18.04 ± 2.42	10.79 ± 2.08	12.65 ± 1.62
Marine prey	10	-17.86 ± 0.6	12.41 ± 1.32	15.55 ± 1.51
Freshwater	10	-24.59 ± 0.34	9.89 ± 2.13	11.19 ± 1.31
El Niño year				
Estuarine	10	-17.28 ± 1.35	12.66 ± 1.38	14.09 ± 1.95
Marine	10	-17.15 ± 0.56	12.26 ± 1.12	14.4 ± 1.88
Freshwater	10	-25.23 ± 0.72	7.85 ± 0.64	11.02 ± 0.37

The isotope discrimination factor (Δ) from fish-eating Black Skimmers was not available thus I followed an indirect approach. According to Caut et al. (2009), Δ^{13}C and Δ^{15}N from feathers are independent of diet and a constant discrimination factor could be applied across habitats. Thus, I used the constants for feathers of 2.16 ± 0.35‰ to δ^{13}C and 3.84 ± 0.26‰ to δ^{15}N (Caut et al. 2009). McCutchan et al. (2003) also found there is a correlation between Δ^{15}N and Δ^{34}S and so I expressed Δ^{34}S as a function of Δ^{15}N along the freshwater-marine gradient ($\Delta^{34}S = 1.1 * \Delta^{15}N - 1.6$) and obtained a value of 2.62‰.

Results

Inter-annual and spatial variation in baseline and prey

The stable isotope ratios of source (fish prey) varied between habitats but not between years, and there were no significant interactions between year and habitats (Table 6.2).

Table 6.2: Summary of generalised linear model predicting the variance of $\delta^{13}C$, $\delta^{14}N$ and $\delta^{34}S$ from fish samples represented by the factor 1 of a principal component analysis according to habitat and year. *P*-values were considered significant if ≤ 0.05 (bold); *n* = 90 samples.

Variable	**Estimate**	**SE**	$t_{2,118}$	***P*-value**
Habitat (freshwater)	-1.98	0.40	-4.97	**0.003**
Habitat (marine)	-0.71	0.38	-1.81	**0.05**
Year (regular)	-0.68	0.40	-1.71	0.09
Year (regular) * Habitat (freshwater)	0.42	0.49	0.84	0.40
Year (regular) * Habitat (marine)	0.91	0.56	1.60	0.11

Proportion of habitats on the Black Skimmer's diet

The estimated contribution of estuarine, marine, and freshwater species to the assimilated diet of Black Skimmers moulting in southern Brazil did not vary between the two regular years (Table 6.3, $\delta^{13}C$: $t_{1,49} = -0.96$, $P = 0.33$; $\delta^{15}N$: $t_{1,49} = -1.21$, $P = 0.31$; $\delta^{34}S$: $t_{1,49} = -1.94$, $P = 0.06$). However, the estimated contribution varied significantly between feathers collected during the first regular year of 2013 and the El Niño year of 2015 (Table 6.3, $\delta^{13}C$: $t_{1,49} = -8.05$, $P < 0.0001$; $\delta^{15}N$: $t_{1,49} = -2.81$, $P = 0.007$; $\delta^{34}S$: $t_{1,49} = -7.81$, $P < 0.0001$); and also between the second regular year of 2014 and the El Niño year of 2015 (Table 6.3, $\delta^{13}C$: $t_{1,49} = -8.1$, $P < 0.0001$; $\delta^{15}N$: $t_{1,49} = -4.61$, $P = 0.04$; $\delta^{34}S$: $t_{1,49} = -4.95$, $P = 0.01$). The contribution of prey species from estuaries to the assimilated diet was higher during the El Niño year (Figure 6.4), such that the marine habitat had a significantly lower contribution to the proportion of diet in the El Niño year than in the regular years (Figure 6.4).

Table 6.3: Stable isotope mean values of Black Skimmers during moulting seasons between 2014 and 2016, covering two regulars and one El Niño year. The values reflect the previous year. Mean and standard deviation (SD) values are in ‰.

Year of collection	**Year of signature**	**Sample size**	**Mean δ^{13}C ± SD**	**Mean δ^{15}N ± SD**	**Mean δ^{34}S ± SD**
2014	Regular year – 2013	25	-16.13 ± 0.6	15.89 ± 0.96	17.95 ± 1.18
2015	Regular year – 2014	25	-15.89 ± 0.94	16.15 ± 0.66	17.18 ± 1.13
2016	El Niño year – 2015	25	-17.96 ± 0.69	15.27 ± 0.25	15.90 ± 0.54

The proportion of diet assessed using a BSIMM indicated Black Skimmers assimilated 0.43 (95%-Bayesian credibility interval = 0.13, 0.55) of their diet from estuarine prey species, 0.54 (95%-Bayesian credibility interval = 0.42, 0.66) from marine prey species, and 0.03 (95%-Bayesian credibility interval = 0, 0.3) from freshwater prey species during regular years. The proportion changed during the El Niño year to 0.72 (95% Bayesian credibility interval = 0.3, 0.98) from estuarine prey species, 0.22 (95% Bayesian credibility interval = 0, 0.63) from marine prey, and 0.06 (95% Bayesian credibility interval = 0, 0.23) from freshwater prey species.

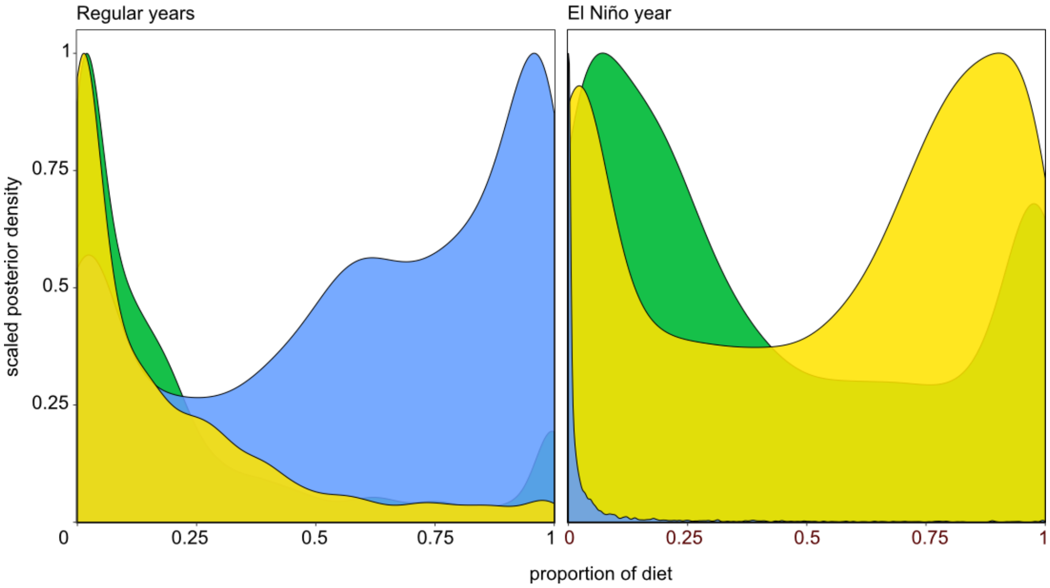

Figure 6.4: Estimated relative contributions of fish source assimilated by Black Skimmers at estuarine (yellow), marine (blue), and freshwater (green) habitats in southern Brazil during regular (left) and El Niño (right) years considering carbon, nitrogen, and sulphur.

Discussion

This study aimed to estimate the contribution of three different prey groups to the assimilated diet of Black Skimmers moulting in southern Brazil, and to examine diet composition in response to the El Niño environmental oscillation. There was a significant difference in the stable isotope signatures in fish sources between habitats but not between regular and El Niño years, indicating the trophic structure in each habitat did not significantly change between years. The stable isotope signature of feathers did not vary between regular years, however the differences between both regular years and the El Niño year were significant. Mariano-Jelicich et al. (2008) studied carbon and nitrogen stable isotope signatures from blood of Black Skimmers in Argentina and found higher contribution also of marine prey species. The mean value of δ^{15}N in the study by Mariano-Jelicich et al. (2008) (16.4 ± 0.2‰) was very similar to what I obtained during regular years (16.02 ± 0.11‰). However, the mean value of δ^{13}C obtained by Mariano-Jelicich et al. (2008) (-16.21 ± 0.14‰) differed from this study (-18.0 ± 0.3‰). This is likely to be related to the latitudinal gradient in δ^{13}C between our study site in southern Brazil, compared to theirs in northern Argentina.

Despite possible natural variation in the stable isotope ratios, the mean δ^{13}C, δ^{15}N and δ^{34}S signatures of the Black Skimmer feathers in this study declined from regular to El Niño years indicating a likely shift of diet composition. I highlight that the bivalve, fish, and feather samples do not exactly match in terms of time window, therefore they could reflect a variation in period, however variation is related to only weeks and is unlikely the whole ecosystem and food chain would respond to changes caused by the El Niño that quickly. The mixing-models indicated that the proportion of freshwater species increase in the diet of Black Skimmers during the El Niño. Furthermore, the δ^{15}N ratio indicated a potential change in trophic level with Black Skimmers feeding at a higher trophic level, or on prey from more complex food chains, during the regular years. In agreement with the mixing models, the δ^{34}S ratio indicated more freshwater and estuarine prey species, as opposed to marine species, in the diet of Black Skimmers during the El Niño. Thus, results indicate Black Skimmers changed their foraging target prey type during the very strong El Niño event of 2015/2016 in relation to the two regular years, foraging more on estuarine species in the El Niño year. I highlight however that feathers were collected at the roosting site, and not directly from the same marked individuals over the years, therefore the results reflect changes in diet composition by the local non-breeding population and not by individuals. Also, this study was based on comparing a single very strong El Niño year with two regular years so conclusions must be tentative until data from other El Niño events can be investigated to establish how consistent differences are between El Niño events.

As I expected, individuals were likely to change prey type while moulting by expanding niche width. The BSIMM indicated Black Skimmers foraged in both estuarine and marine areas during regular years which is supported by other findings in the South American Atlantic coast (e.g. Naves & Vooren 2006, Mariano-Jelicich et al. 2008). However, instead of including a significant amount of freshwater fish in the diet, Black Skimmers' diet increased in the proportion of estuarine fish. The Black Skimmer's moulting season during the El Niño in southern Brazil is affected by higher precipitation and temperature, stronger southern winds, and lower salinity in coastal areas (Grimm et al. 2000, Sutton et al. 2000, Grimm 2003). The study area has two bays (Figure 6.1) that are likely to trap the marine waters with lower salinity due to increased precipitation and river runoffs thus possibly creating an expanded estuarine condition during the El Niño. In Galápagos, Romero & Wikelski (2001) observed high precipitation washes terrestrial nutrients to bays where they are trapped and concentrated, enhancing algae production. The increase in estuarine habitat availability is likely to expand the distribution of estuarine fish such as silversides, and estuarine-dependent fish such as mullets (Garcia et al. 2001, 2004) which are Black Skimmer's main prey (Naves & Vooren 2006, Mariano-Jelicich et al. 2008). The amount of freshwater fish in the Black Skimmer's diet during the El Niño increased yet it was not significant in the proportion of diet, which suggests freshwater fish intrusion in estuaries (Garcia et al. 2001, 2004) did not induce a significant diet shift in the South American Black Skimmers.

Stapp et al. (1999) used stable isotope analysis to demonstrate that island terrestrial food webs on isolated arid areas in the Pacific differed between regular and El Niño years. They found seabirds' energetic input on food webs, as estimated from guano and carcasses of prey, were higher during El Niño years (Stapp et al. 1999).

The increase in guano and discarded food indirectly points to an increase in foraging activity. Seabirds such as penguins have demonstrated a shift in foraging sites during ENSO in the Pacific and Subantarctic Oceans (Culik et al. 2000, Simeone et al. 2002, Bost et al. 2015). Furthermore, Favero & Becker (2006) assumed runoff caused by increased rainfall attracted Common Terns (*Sterna hirundo*) to forage at the coast in the Atlantic. Species' response in each ocean and habitat are related to how the environmental oscillation affects prey's abundance and distribution, and predators' foraging plasticity to switch prey in extreme conditions.

Changes in prey availability due to environmental changes might impact the abundance of Black Skimmers at the moulting grounds. Although prey abundance cannot be detected in stable isotopes, the geographic conditions at the study area seem to favour the increase in numbers of estuarine and estuarine-dependent fish during the El Niño. Understanding factors influencing species' diet composition and foraging strategy is crucial for informed conservation management. A successful annual life-cycle, especially during moult, depends on reliable prey resources and the insights gained from this study showed a shift in diet composition as an ecological response of Black Skimmers to environmental changes.

Chapter 7: The El Niño increases number of overstaging Black Skimmers in southern Brazil

Abstract

The best-known natural climate oscillation resulting in critical deviations in temperature, precipitation and winds around the globe is the El Niño Southern Oscillation (ENSO). Ecological effects of ENSO have been studied well in the Pacific, but there are significant gaps in knowledge about how species are impacted by this climate oscillation in the Atlantic. In this study, I explore the ENSO effects on a South American Black Skimmer (*Rynchops niger intercedens*) local non-breeding population. I monitored the population and local weather in estuaries at the Island of Santa Catarina in southern Brazil from 2011 to 2017, and found ENSO affects Black Skimmer's abundance with an increase in the estimated abundance of overstaging individuals at the non-breeding site during the El Niño when compared to data from regular years. The number of birds during La Niña years however was lower yet not significantly different than regular years. The number of individuals was higher when winds were north and east, and negatively affected by an interaction between minimum air temperature and ENSO. This study corroborates that ENSO's teleconnections between climate across the globe affect coastal predators also at the South American South Atlantic coast.

Keywords: climate change, *Rynchops niger*, estuary, non-breeding site, Brazil, South Atlantic coast.

Introduction

The El Niño Southern Oscillation (ENSO) is known to highly impact the wildlife in the Pacific (Chapter 1). It also has links with anomalous climate patterns in the entire world through teleconnections (Trenberth 1997). ENSO's warm conventional phase "El Niño" starts in the eastern Pacific Ocean and is characterised by winds of lower intensity resulting in warm southward-flowing nutrient-poor surface waters off north-western South America (Trenberth 1997). The opposite pattern with cooler nutrient-rich upwelling waters reaching north-western South America is called La Niña (Trenberth 1997). Because ENSO causes extreme oscillations in temperature, precipitation, and winds around the globe, it is considered a unique natural experiment for understanding ecological responses to future anthropogenic climate change (Grimm et al. 2000, Sillett et al. 2000, Jaksic 2001, Grimm 2003, Robinson et al. 2014, Cai et al. 2014, Harrison et al. 2015).

Migratory seabirds in the southern Pacific and continental areas are affected in both breeding and non-breeding sites by ENSO. Most seabird species have low reproductive success, massive die-offs, changes in migratory pathways and stopover sites, and even timing of moult during the El Niño; but they also have better body condition and increase in breeding performance during the La Niña when compared to regular years (Schreiber & Schreiber 1984a, 1984b, Sillet et al. 2000, Jaksic 2001, Calvert et al. 2009, Paxton et al. 2014). Although most migratory seabird species along the Equator are negatively affected by the El Niño. Some species of seabird located at sites farther north from the Equator seem to benefit. For example, the Laysan Albatross (*Phoebastria immutabilis*) in Hawaii and terns (*Thalasseus maximus*, *T. elegans* and *Sternula antillarum*) in Mexico gain mass, increase breeding population, and have better breeding performance during the El Niño, and a poor body condition and low breeding success during the La Niña (Mellink 2003, Thorne et al. 2016). It has been hypothesised such inverted response to ENSO is related to stronger winds improving soaring and fish moving farther to higher latitudes due to changes in water temperature and salinity during the El Niño with opposite conditions during La Niña (Mellink 2003, Thorne et al. 2016).

Despite knowledge about ecological effects of ENSO having increased, and it is now well-known that ENSO affects the entire world through its teleconnections, most studies assessing impacts on wildlife are based on the Pacific and North Hemisphere. Few studies have directly assessed the effects of El Niño on seabirds along the South American Atlantic coast (e.g. Favero & Becker 2006). Most of ENSO's strongest impacts on marine predators are related to changes in food availability due to warming of waters, and increased river runoff causing changes in salinity of coastal waters (Foley et al. 2002, Sahu et al. 2014). However, unlike along the Pacific coast, the cold currents from the South Pole influence the South American Atlantic coast only up to 25ºS and warm waters dominate further south (Acha et al. 2004). The productivity along the South American Atlantic coast is related to other marine forces (Acha et al. 2004). For example, the productivity found at the southern and southeastern Brazilian coast is related to the Atlantic Upwelling Zone and the Temperate Estuarine Zone (Acha et al. 2004). Therefore, it is possible that ecological effects of ENSO on the Atlantic food webs, and especially on marine predators, could manifest in other ways, differing from the results seen in Pacific waters.

South American Black Skimmers (*Rynchops niger intercedens*) depend on both inland and coastal aquatic ecosystems. They spend the non-breeding period and moult along the coastline but breed on inland river sandbanks (Murphy 1936, Zusi 1996). It has been recorded that the North American Black Skimmer (*R. n. niger*) in Mexico improved breeding performance and more individuals were found in resting areas near the breeding sites along the coast during El Niño events (Carmona et al. 1995, Mellink 2003). However, in South America the species occupies different habitats which could lead to a different response. Black Skimmer's main prey in southern Brazil are mullets (*Mugil* spp.) and silversides (*Odontesthes argentinensis* and *Atherinella brasiliensis*) (Naves & Vooren 2006). Mullets and silversides are pushed away from estuaries in the El Niño phase in southern Brazil due to higher precipitation that causes river runoff and changes in salinity (Garcia et al. 2001). Changes are not restricted to fish assemblages since estuarine phytoplankton assemblages are also affected by ENSO with decrease in biomass and density (Sathicq et al. 2015) thus suggesting a bottom-up effect along the food chain (Jaksic 2001). Black Skimmers stage (*sensu* Skagen & Knopf 1994) in sites with warm temperatures, calm waters, and low wind speed (Murphy 1936, Burger & Gochfeld

1990) which are environmental variables directly affected by ENSO in the South Atlantic (Sutton et al. 2000, Grimm 2003, Grimm & Zilli 2009).

Because of this recognised effect of ENSO on phytoplankton (Sathicq et al. 2015), and silversides and mullets (Garcia et al. 2001, 2004) at the Atlantic Upwelling and the Temperate Estuarine zones, I expect Black Skimmer abundance at a non-breeding area in southern Brazil will respond to changes in fish assemblage by locally altering its timing of staging and decreasing its abundance. Here I tested if Black Skimmers have (1) timing of abundance in the non-breeding site affected by ENSO, and if so then (2) what are environmental variables affecting the species abundance at the study area. This study explores how large-scale climatic oscillations in the Pacific can affect estuarine predators such as the Black Skimmer on the Southern Atlantic coast. Implications of results not only help understanding predators' response to environmental extreme oscillations but also help underpin management actions on conservation of species facing future climate change.

Methods

Study site

The Black Skimmer is a migratory species using the South Atlantic coast during the non-breeding period with greatest abundances recorded between the estuaries of São Francisco do Sul (26º15'S and 48º42'W) in southern Brazil and La Plata River (34º55'S and 57º00'W) in Argentina (Vooren & Chiaradia 1990, Branco & Fracasso 2005, Scherer et al. 2013, Mariano-Jelicich et al. 2014, Chapter 5). My study sites were located at the Island of Santa Catarina (27º22'S to 27º50'S and 48º25'W to 48º35'W), a continental island of 424.4 km² in the Brazilian South Atlantic coast (Figure 7.1). The Island of Santa Catarina has two main bays with three sites sheltering the most extensive mudflats on the island. These three sites (Figure 7.1, Pirajubaé at 27º38'S, 48º31'W, Jurerê at 27º27'S, 48º31'W, and Ponta das Canas at 27º24'S, 48º25'W) are used by Black Skimmers as roosting areas during the non-breeding season (Rosário 2004, Branco & Fracasso 2005, Vieira 2014, Pereira 2016). All sites have estuarine bays with both suitable and unsuitable roosting habitats to

Black Skimmers. The suitable habitats include open fine-sand areas such as wetlands, mudflats, and beaches, while unsuitable habitats include places occupied by built-up areas and shrub or tree vegetation (Figure 7.1).

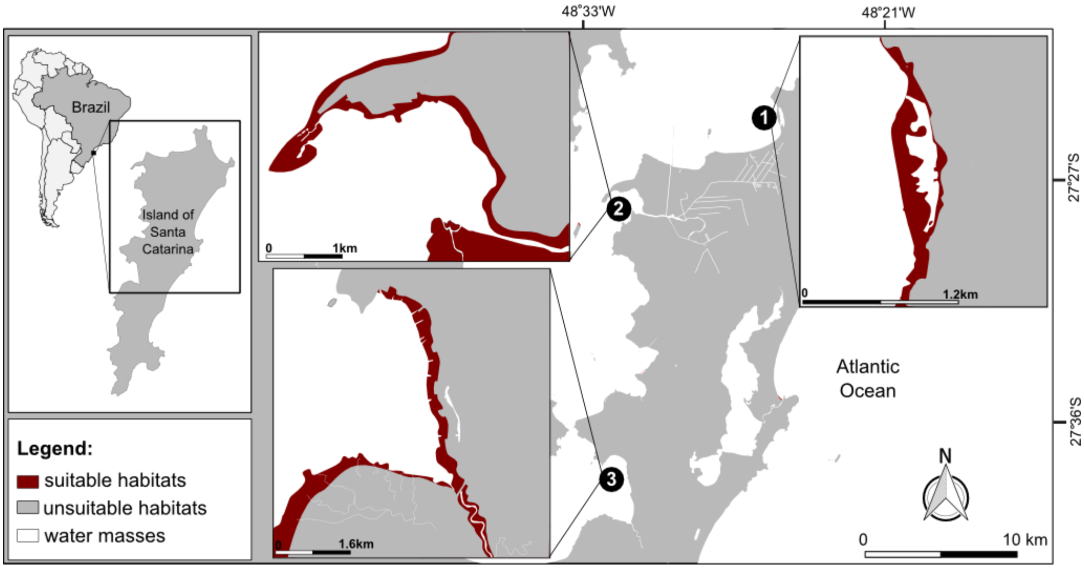

Figure 7.1: Study sites of Ponta das Canas (1), Pontal do Jurerê (2), and Pirajubaé (3) at the Island of Santa Catarina in southern Brazil. Black Skimmers forage in water masses (white) along suitable habitats (red) which they may use as roosting sites.

Bird counts

I performed distance sampling counts of Black Skimmers at the three sites twice every month from October 2011 to September 2012 and from December 2014 to April 2017. Black Skimmers are nocturnal foragers and spend most day-time resting in the same site (Murphy 1936, Burger & Gochfeld 1990, Zusi 1996, Rosário 2004); and a previous study showed tide has no significant effect on counts in these study sites because skimmer's local habitat changes from mudflats to beaches that can be all fully observed from the point counts (Vieira 2014). At each study site, I therefore performed a 1-hour distance sampling point-count during daylight hours. To estimate abundance using the distance sampling method, I measured the distance from individuals using a laser telemeter AF1000L Aofar® (maximum range 1 km and accuracy of ± 0.2%). I assumed no change in counts over the day.

The point counts were repeated twice every month from October 2011 to September 2012 and from December 2014 to April 2017. The repetition twice a month was used to account for migratory movements (flocks leaving or arriving at the study sites) and only the highest count was included in the analysis to avoid oscillations due to flocks arriving or leaving the area. Double counting within sites was minimised by applying the scan technique which consisted of counts starting at a certain position A and following one direction to left or right to count birds in a 360º round back to position A (Bibby et al. 1998). The double counting between sites was avoided by doing sites on the same day (Bibby et al. 1998). The monthly counts between 2011 and 2017 were performed by different observers and, to account for inter-observer variation, I took a three-step procedure in which (1) observers were trained in theory and practice by the most experienced researcher for one month until the new observers matched the counts by the most experienced observer before they carried out their own counts; (2) in the field new observers took 360º images of the area to be counted for the most experienced researcher to crosscheck the count with the photographs avoiding underestimations; and (3) only the highest estimate between the observers in the field and off site was considered, to reduce variability in counts (Cunningham et al. 1999). I assumed the 360º photographs included a significant part if not all individuals present in the area because 97% of Black Skimmers in the study area are visible while spending daytime resting, preening, thermoregulating or socially interacting at open habitats such as beaches and mudflats (Vieira 2014).

Environmental data

I determined whether ENSO effects in the Southern Atlantic coast were present on the counts of Black Skimmers by using the Oceanic Niño Index – ONI available from the NOAA’s Climate Prediction Centre on www.cpc.ncep.noaa.gov (Figure 7.2). The ONI is a primary measure for monthly mean of ERSST.v4 SST anomalies in the region 5ºN-5ºS and 120ºW-170ºW with a threshold of ± 0.5ºC (Huang et al. 2015). The ONI indicates El Niño as a weak event when over 0.5, moderate when over 1, and very strong when over 2 (Figure 7.2, Ashok et al. 2007). On the other hand, negative ONI values indicate a La Niña event as weak when between -0.5 and -

1, and moderate when lower than -1 (Figure 7.2, Ashok et al. 2007). Bird counts occurred during one very strong El Niño, and two moderate La Niña events (Figure 7.2). The three months of ONI = 0.6 between November 2014 and January 2015 (Figure 7.2) did not compose an El Niño event.

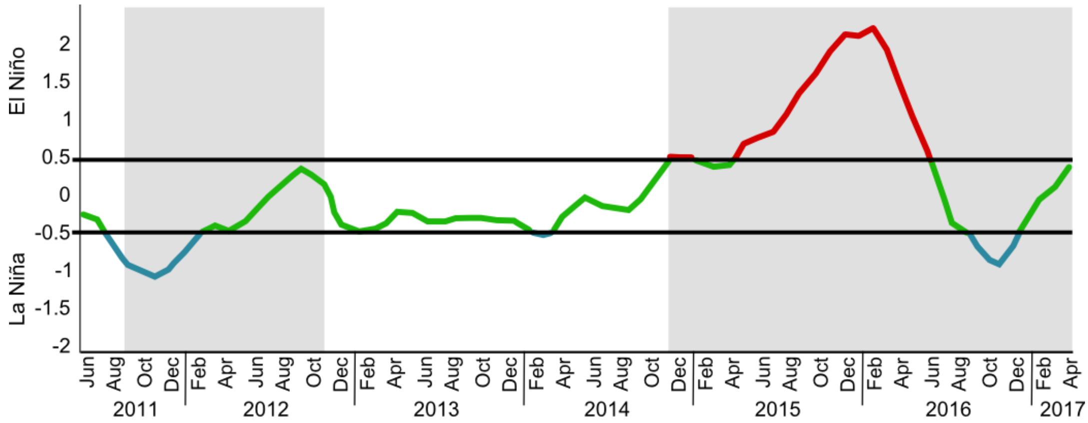

Figure 7.2: Seasonal fluctuation of the Oceanic Niño Index (ONI; full line) between 2011 and 2017. ONI indicates an oscillation if ≤ -0.5 or ≥ 0.5 (horizontal lines). Data used in this study comprises regular (green line), El Niño (red line), and La Niña (blue line) periods. Sampling occurred from October 2011 to September 2012 and from December 2014 to April 2017 (grey shadow).

ENSO affects the climate on the Atlantic coast in southern Brazil by raising the mean temperature and precipitation from July to November (Grimm et al. 2000, Grimm 2003) and keeping higher temperatures but low precipitation from November to February (Grimm 2003, Grimm & Zilli 2009). ENSO is also recognised to change wind speed, with higher frequency of more intense winds during an El Niño event (Sutton et al. 2000). Southern intense winds occur from December to February and northern intense winds dominate the rest of the months during ENSO events (Sutton et al. 2000).

Thus, I used monthly averages of data collected by three weather stations administrated by the Information Centre of Hydrometeorology and Environmental Resources of Santa Catarina (EPAGRI/CIRAM) from 2011 to 2017. The variables considered in this study were maximum air temperature (ºC), minimum air temperature (ºC), mean air temperature (ºC), precipitation index (accumulated precipitation of the month divided by the total of days of rain > 0.02mm/h in that month), mean humidity (%), wind speed (m/s), and wind direction (expressed as angles clockwise with 0º in North and 0º=360º). Because wind direction is a circular variable, I first transformed it into linear using a trigonometric approach with sine and cosine (Gill & Hangartner 2010).

I tested the weather variables cited above and oscillation index (ONI) for multicollinearity using a Spearman correlation and considered two variables collinear if $r > 0.4$, excluding the one with higher number of collinearities (Booth et al. 1994). I thus excluded humidity because of correlation with ONI, wind speed, and mean and maximum air temperature (r = 0.59, 0.57, -0.42, -0.48, respectively), maximum air temperature because of correlation also with mean and minimum air temperatures (r = 0.95 and 0.71, respectively), and mean air temperature because of correlation also with minimum air temperature ($r = 0.80$). The minimum air temperature was maintained and hereafter called temperature.

Statistical analysis

Abundance data were grouped in peak and non-peak seasons. The peak season occurred from November to April, Black Skimmer's non-breeding season when they are expected to be at the study sites in larger numbers (Rosário 2004, Branco & Fracasso 2005, Chapter 2). The non-peak season occurred from May to October when Black Skimmers were expected to have left the coastal study area to breed inland (Murphy 1936, Burger & Gochfeld 1990, Scherer et al. 2013, Antas et al. 2016, Chapter 2). Distance sampling abundance estimates were implemented using the package *Distance 0.9.6* (Miller 2016) in R 3.2.4 (R Core Development Team 2016). I estimated the abundance of Black Skimmers considering the performance of a hazard rate model for the detection function. The hazard rate model was chosen in a pre-analysis by fitting the detection probability against distance of recorded clusters of individuals (Thomas et al. 2010). The hazard rate model used a mark-recapture distance sampling (MRDS) engine accounting for any possible remaining inter-observer variability (Diefenbach et al. 2003, Thomas et al. 2010). A cosine adjustment term was fixed considering that the detection probability decreased with distance but increased again with long distances because of the distribution of mudflats and sandbanks occupied by Black Skimmers that are surrounded and isolated by deeper waters. Models assumed certainty of detection, counting, and measurement of distances (Thomas et al. 2010). I calculated the coefficient of variation (CV) for all estimators using the package *Distance 0.9.6*. The CV is considered a measure of relative precision for the comparison of parameter estimates and considered models' CV reasonable if < 0.4 (Marsden 1999, Hagen et al. 2016).

To assess changes in abundance due to ENSO accounting for possible inter-annual variation, I created an Index of Change (IC). I detected a change in Black Skimmer count related to ENSO events relative to the count in the same month in regular years as the baseline for the expected abundance. The Change Index is computed as:

$$IC = \frac{M_{iENSO}}{M_{iR}}$$

where M_{iENSO} = mean estimated abundance in Month *i* during ENSO events and M_{iR} = mean estimated abundance in Month *i* during regular years. To assess changes in timing of staging of Black Skimmers due to ENSO, I used the IC as the response variable in a generalised linear model (GLM, β) in R 3.2.4 with an interaction of ONI (continuous) and season (factor: peak and non-peak).

To explore what environmental variables affect the Black Skimmers abundance, I performed a GLM in R 3.2.4 with the IC as the response variable and weather (wind speed, wind direction, precipitation, temperature) as covariates. I also added interactions of wind speed, wind direction, precipitation, and temperature with ONI. To select only the relevant explanatory variables in the final model, I followed a univariate forward stepwise approach considering the smallest Akaike information criteria – AIC (Burnham & Anderson 2004).

Results

The estimated abundance of Black Skimmers had low CV values (Table 7.1). During the non-peak season, there are relatively more individuals during the El Niño and less during the La Niña, compared to regular years. In contrast, during the peak season there are relatively more individuals in the regular years than during either ENSO events (Table 7.1). In regular years, Black Skimmers are expected to arrive at the study area by November and start to leave in May (Figure 7.3). There are few individuals overstaging into the non-peak season and an additional influx of individuals in July (Figure 7.3). During the El Niño, the number of overstaging individuals and the input of individuals are higher (Table 7.1, Figure 7.3). The polynomial interpolation and the estimated abundance suggest the number of individuals is lower during La Niña than regular and El Niño years (Table 7.1, Figure 7.3).

Table 7.1: Local estimated abundance for Black Skimmers according to sex and age in estuaries at the Island of Santa Catarina in southern Brazil during regular, El Niño and La Niña years. SE is the standard error; CV is the coefficient of variation of model fit (in bold if significant); LCL and UCL are lower and upper 95%-confidence intervals of abundance estimates; DF is degrees of freedom.

Treatment	**Estimate**	**SE**	**CV**	**LCL**	**UCL**	**DF**
Non-peak season						
Regular	301.50	109.59	**0.36**	140.87	645.27	13.02
El Niño	542.83	278.77	**0.40**	182.90	1611.06	9.37
La Niña	119.86	37.89	**0.32**	52.63	272.98	4.46
Peak season						
Regular	456.91	122.10	**0.27**	262.84	794.28	17.49
El Niño	331.04	107.63	**0.33**	170.44	642.97	18.84
La Niña	284.26	102.55	**0.36**	131.48	614.55	10.86

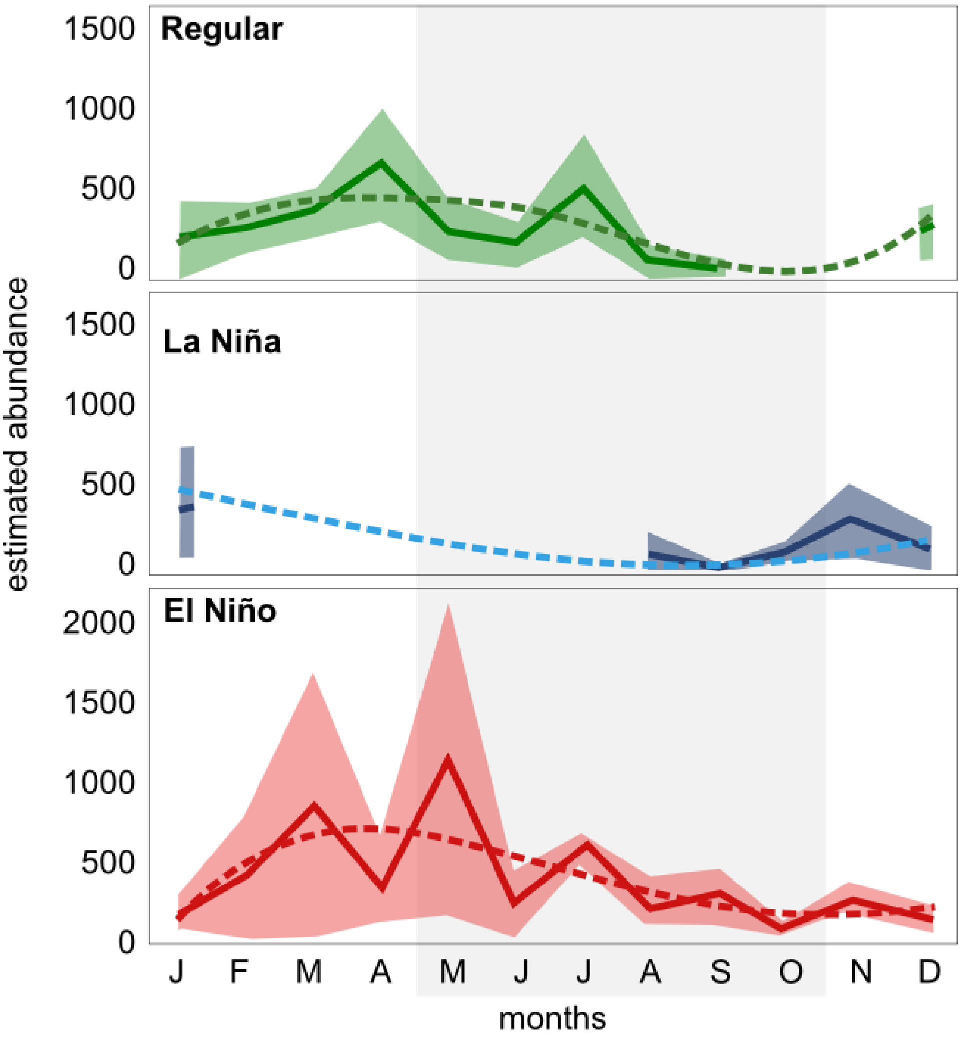

Figure 7.3: Estimated abundance of Black Skimmers per month at the Island of Santa Catarina in southern Brazil during regular, El Niño, and La Niña years. Coloured shadows represent standard errors. Grey shadow highlights the non-peak season (May to October) from the peak season (November to April). I fitted polynomial curves (dashed lines) to visualise overall trends (Regular: $y = 0.27x^4 - 3.86x^3 - 5.48x^2 + 164.81x + 79.95$, R^2-value = 0.43; El Niño: $y = -0.27x^4 + 11.17x^3 - 149.41x^2 + 715.62x - 417.82$, R^2-value = 0.48; La Niña: $y = 7.85x^2 - 119.87x + 564.29$, R^2-value = 0.75).

I found a significant effect of ENSO on the relative local abundance of Black Skimmers however with a different relationship with each season expressed by a significant interaction of ONI and season (Figure 7.4). The index of change increased with increasing ONI values during the non-peak season whereas there were no significant changes in the peak season (Figure 7.4). As expected, estimated abundance was higher in the peak season than in the non-peak season during regular years (Table 7.1). However, in the non-peak season the index of change during El Niño was higher than regular years (IC > 1, Figure 7.4) which means fewer individuals left the non-breeding area in El Niño conditions. On the other hand, La Niña had lower estimated abundances then in regular years (Table 7.1).

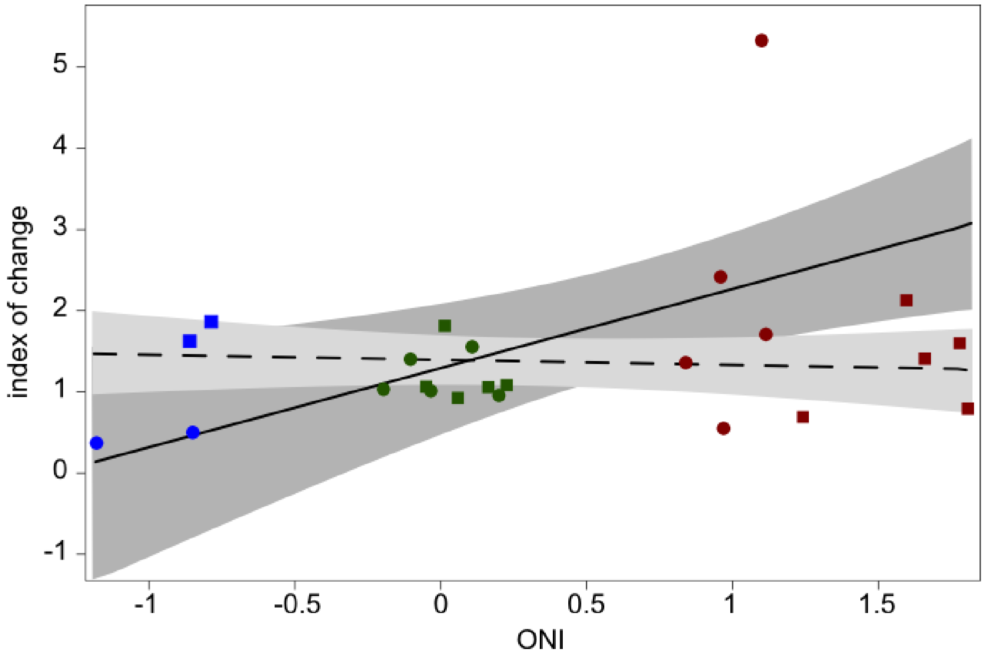

Figure 7.4: Generalised linear model of the index of change (*n* = 24) in the abundance of Black Skimmers in southern Brazil against ONI according to peak and non-peak seasons considering a 95%-confidence interval. Peak season (full line and squares): β = -0.08, SE = 0.16, $t_{2,9}$ = -0.51, *P* = 0.62. Non-peak season (dashed line and circles): β = 1.01, SE = 0.46, $t_{1,10}$ = 2.16, *P* = 0.05. ONI * season: β = -1.09, SE = 0.47, $t_{1,10}$ = -2.29, *P* = 0.03. Colours indicate El Niño (red), La Niña (blue) and regular (green) periods.

ENSO is known to significantly change the weather in southern Brazil, mainly by raising air temperature, precipitation, and wind speed and changing predominant wind direction (Grimm et al. 2000, Sutton et al. 2000, Grimm 2003), thus I tested how local weather affected the abundance of Black Skimmers in the study area. Considering the final selected model, Black Skimmer abundance was negatively affected by ONI and wind direction (Table 7.2). The abundance was higher with northern and eastern winds, and lower with southern winds (Table 7.2). The abundance of Black Skimmers was also negatively affected by an interaction of temperature and ONI (Table 7.2).

Table 7.2: Univariate forward stepwise generalised linear model selection and summary of the final model (bold) predicting the influence of environmental variables on the abundance of Black Skimmers at the Island of Santa Catarina in southern Brazil. The abundance is represented by the index of change – IC (*n* = 24). The model selection considered the smallest Akaike information criteria (AIC). I present the estimate (β), standard error (SE), *t*-value and *P*-value (bold if $P \leq 0.05$) for the last covariate added in the models.

Model	**AIC**	**DF**	**β**	**SE**	***t*-value**	***P*-value**
Univariate forward selection						
IC ~ precipitation	71.23	22	0.10	0.32	0.31	0.76
IC ~ wind speed	71.34	22	-0.01	0.23	-0.01	0.99
IC ~ temperature	71.04	22	-0.02	0.04	-0.52	0.61
IC ~ ONI	70.11	22	0.22	0.20	1.07	0.29
IC ~ wind direction	66.48	22	-0.01	0.01	-2.22	**0.03**
IC ~ precipitation * ONI	73.93	20	3.25	8.75	0.37	0.71
IC ~ wind speed * ONI	74.08	20	-0.04	0.32	-0.14	0.88
IC ~ wind direction * ONI	69.90	20	-0.01	0.01	-0.46	0.65
IC ~ temperature * ONI	67.36	20	-0.17	0.08	-2.11	**0.04**
IC ~ temperature * ONI + precipitation	68.36	19	-0.28	0.32	-0.89	0.38
IC ~ temperature * ONI + wind speed	68.52	19	-0.18	0.22	-0.82	0.42
IC ~ temperature * ONI + wind direction	**65.20**	**19**	**-0.02**	**0.01**	**-2.01**	**0.05**
Summary of the selected model above						
temperature	65.20	19	-0.03	0.08	-0.31	0.76
wind direction	65.20	19	-0.02	0.01	-2.01	**0.05**
ONI	65.20	19	3.76	1.51	2.50	**0.02**
temperature * ONI	65.20	19	-0.17	0.07	-2.22	**0.03**

Discussion

This study assessed if large-scale climatic oscillations in the Pacific could affect populations also in the South Atlantic coast such as the South American Black Skimmer. I found there was an increase in the estimated abundance of Black Skimmers during the non-peak season in an El Niño event but a decrease during La Niña when compared to data from the regular year. During the non-peak season, South American Black Skimmers normally leave the area to their inland breeding grounds. There is a pulse of individuals in July which is likely individuals from other sites passing by the study area during migration because they do not stay longer during the non-peak period. The number of individuals in the peak season however did not significantly change when comparing ENSO to regular events. Fluctuations in abundance were related to ONI, wind direction, and an interaction of minimum air temperature to ONI. During the South American Black Skimmer's non-peak season, the El Niño causes low austral winter temperatures (± 10ºC) to increase; and northern and eastern winds, which have less impact in the study area than southern winds, dominate (Grimm et al. 2000, Sutton et al. 2000, Grimm 2003) creating a climate similar to the one in the peak season of regular years when individuals are expected to concentrate in the study area.

I highlight the changes identified in this study concerning habitat selection reflect the selection of the study site and not a change in the overall population. Black Skimmers are migratory and the studied population likely having individuals from different breeding colonies across South America (Mariano-Jelicich & Madrid 2014). Although counts did not vary much within month (Figure 7.3), results are based on scattered months of regular and ENSO data (Figure 7.2) and only a long-term monitoring could properly cover for possible inter-annual fluctuation in data. Moreover, the La Niña during this study was concentrated between November and January therefore conclusions must be cautious about its effect on the abundance of Black Skimmers in other months.

While the studies in Mexico (Carmona et al. 1995, Mellink 2003) verified an increase in breeding population and recruitment of the North American Black Skimmer, I detected a positive effect for the number of overstaging South American Black Skimmer individuals in southern Brazil. The difference between this study and the ones in Mexico demonstrates the same species can have different responses to climatic oscillations according to the geographic location and possibly different resource use. Concerning the use of estuarine areas, Murphy (1936) and Favero & Becker (2006) observed an influence of ENSO on the resource use by Red-necked Phalaropes (*Phalaropus lobatus*) and Common Terns (*Sterna hirundo*), respectively, with individuals foraging closer to estuarine areas during the El Niño phase. Individuals moving to other non-breeding areas during ENSO events have been recorded in several seabirds in the Pacific such as Inca Terns (*Larosterna inca*) to Colombia and South American Terns (*Sterna hirundinacea*) to Ecuador (Table 1.1, Haase 1997). The movement of individuals from sites with lower resources to the ones with higher resources would explain the higher aggregation of individuals I found during the non-peak season. Changes in foraging strategies in the non-breeding areas were already detected in other seabirds such as Humboldt Penguins (*Spheniscus humboldti*) and King Penguins (*Aptenodytes patagonicus*) in Chile and Antarctica diving deeper and farther from usual foraging areas, respectively (Culik et al. 2000, Bost et al. 2015).

The observed variation in abundance may not reflect changes in survival and recruitment. It could mean, for example, that individuals usually overstaging in other non-breeding areas aggregated in the study area during the El Niño. It is also possible however that the higher number of overstaging individuals indicates individuals had less propensity to breed during the El Niño. Black Skimmers could have failed breeding and returned to the non-breeding site due to flooded colony sites or other conditions inappropriate to breed. Antas et al. (2016) monitored a colony in Pantanal from 2006 to 2013 and covered one weak El Niño (2006) and one moderate El Niño Modoki (2009) when the number of colonies was less than 10 and 0 respectively while during regular years there would be greater than 15 colonies along the river sandbanks. Also, the river depth was higher in the El Niño than in regular years although river sandbanks were still available. Other possibility is that higher food availability caused by river runoff attracted juveniles and sub-adults from other overstaging areas to the study site as Favero & Becker (2006) assumed to be the reason why sub-adult Common Terns changed their timing leaving de La Plata estuary and reaching colonies in Germany. Garcia et al. (2001, 2003, 2004) found fish assemblages in Lagoa dos Patos 500 km south from the Island of Santa Catarina responded to the El Niño by replacing estuarine and estuarine-dependent fish, such as silversides and mullets that are Black Skimmer’s main prey item in the South Atlantic (Naves & Vooren 2006), to shallow sea waters. Unlike Lagoa dos Patos, the study sites are bays and the increased precipitation and river runoffs may have reduced the sea water salinity expanding the estuarine condition during the El Niño as observed in Galápagos by Romero & Wikelski (2001). In Chapter 6, I found Black Skimmers change the foraging resource use to estuarine fish during the peak season in an El Niño year however the number of individuals roosting in the study areas did not change significantly in this same season. Nonetheless, it is possible the changes in foraging resource use (see Chapter 6) affected the abundance of Black Skimmers during the non-peak season as a delayed response to prey availability. An alternative explanation is that weather conditions during ENSO would not favour individuals migrating to breeding sites due to the stronger winds and increased precipitation at the breeding sites. Guerra et al. (1988) found that Gray Gulls (*Leucophaeus modestus*) on the coast of Chile changed their timing of migration and moult delaying energetic-demanding activities during dry seasons and anticipating them during wet seasons. Macmynowski et al. (2007) and Calvert et al. (2009) showed migratory songbirds in the Northern Hemisphere are affected by ENSO and arrived earlier in warmer conditions. Although studies have detected changes in timing of breeding, migration, and moult during ENSO (Table 1.1), this is the first study I am aware of reporting a change in number of overstaging individuals.

This study corroborates that ENSO’s teleconnections across the globe affects marine predators also in the South Atlantic coast. The number of individuals in the study area was affected by ONI, minimum air temperature, and wind direction. Future anthropogenic change scenarios predict higher air and sea surface temperature in the next century (Easterling et al. 2000, IPCC 2007). Moreover, future ENSO are predicted to be more frequent and have higher intensities (Timmermann et al. 1999, Easterling et al. 2000, Collins et al. 2010, Cai et al. 2014). The number of Black Skimmers at the study sites were also affected by winds, with higher abundance during northern and eastern winds. The northern winds come mostly from mainland and are attenuated by the Atlantic Forest hills while the southern winds coming from the open sea are stronger but are also contained by hills on the island and do not directly reach the roosting sites (Vieira 2014, Pereira 2016). As temperature, future climate change scenarios predict changes in wind dynamics that can affect migratory birds (Sorte & Fink 2017) so staging sites protected from intense winds may play a key role in the conservation of this and possibly other migratory species. I found ENSO increased abundance of individuals during the non-peak season but that higher temperatures negatively affected the population. Therefore, a future change in intensity of ENSO events my lead Black Skimmers to lose their optimal environmental window. If ENSO becomes a constant and iterant climate state, dynamics in estuaries may dramatically change affecting the wildlife relying on it. Results found in this study highlight the value of exploring estuarine predators’ demographic parameters and responses to different environmental scenarios (Trathan et al. 2007, Bost et al. 2015).

Chapter 8: General Discussion

Introduction

The main aim of this study was to investigate the ecological responses of Black Skimmers to environmental changes in southern Brazil. In the process, I provided tools that could be widely used in ornithological studies despite researchers’ access to funds, and filled some gaps in the annual-cycle life-history and resource use by Black Skimmers. Throughout the thesis I investigated the reliability of using photographs, citizen data, and visual observation as affordable non-invasive methods to study Black Skimmer’s moult, identification of sexes and resource use. This study followed a large-scale approach in Brazil when using photographs, citizen data, and visual observation to assess the resource use by Black Skimmers during energetic-demanding activities in the non-breeding season. With data obtained from such methods, I could determine a specific site in southern Brazil – the Island of Santa Catarina – to collect feathers for stable isotope analysis and assess foraging resource use by Black Skimmers during regular and El Niño years. I also counted individuals and used data on the local environment to assess the effects of the El Niño Southern Oscillation (ENSO) on the abundance of Black Skimmers roosting at the Island of Santa Catarina.

Chapter 1 explored how ENSO affects seabirds in South America mostly by increasing rainfall and changing water temperature and salinity. Long-lived seabird species seemed to respond to the climatic extreme conditions by constraining, delaying, or skipping reproduction, changing habitat use due to lack of their normal prey resources, and prioritising adult survival by moving to farther areas and deserting nests and chicks. In general, species capable to move to farther sites looked for alternative areas during both breeding and non-breeding seasons. The Atlantic populations, however, were understudied. Chapter 2 then shows the Black Skimmer (*Rynchops niger*) occupies coastal and freshwater habitats that are highly affected ENSO and that Carmona et al. (1995) and Mellink (2003) found individuals had improved breeding performance and more individuals were found in resting areas near the breeding sites in Mexico during the El Niño. Most of studies about the Black Skimmer in South America addressed the breeding sites therefore I focused on their biology in the non-breeding season and especially while moulting. Because non-invasive methods were not available in literature, Chapter 3 assessed the use of photographs to study moult of primary feathers and found the repeatability of scores within- and between-observers was high suggesting the method was consistent. Chapter 4 then verified whether identifying sexes from photographs would be reliable and found the repeatability of visual identification of sexes in Black Skimmers was significant. Although I could not be completely sure which sex individuals in photographs had, it is known Black Skimmer males are significantly larger than females (Chapter 4, Burger & Gochfeld 1990, Shew & Collins 1990, Quinn 1990, Mariano-Jelicich et al. 2007, Scherer et al. 2013) with an overall difference between sexes around 20% which was big enough to reliably identify specimens from museums and individuals in images.

I used methods from Chapter 3 and 4 to test if Black Skimmers had specific moulting areas within their coastal non-breeding range in Chapter 5. I also tested if there were differences between sub-species and found both South American and Amazonian sub-species moulted from austral spring to austral summer. In both sub-species, males started earlier than females, although this difference was more pronounced in the Amazonian sub-species. Both sub-species and sexes selected mostly the same productive estuarine habitats in southern latitudes to moult. Selection of mudflats and dunes differed between sub-species with South American Black Skimmers more likely to select dunes and less likely to select mudflats. After identifying sites used in southern Brazil, Chapter 6 focused on estimating the contribution of three different habitats to the assimilated diet of Black Skimmers moulting, and comparing their resource use in response to El Niño. Black Skimmers had a more constrained resource use with higher contribution from shallow marine habitats during regular years but changed to foraging in more estuarine habitats during the very strong El Niño event of 2015/2016. Results however are limited to a single very strong El Niño year so conclusions must be tentative until more data is available.

After finding El Niño would affect the foraging resource use of Black Skimmers, Chapter 7 assessed if ENSO could affect the non-breeding local population. There was an increase in the estimated abundance of Black Skimmers during the non-peak season in an El Niño event but a decrease during La Niña when compared to data from the regular year. During the non-peak season, South

American Black Skimmers normally leave the area to their inland breeding grounds. The number of individuals in the peak season however did not significantly change when comparing ENSO to regular events. Fluctuations in abundance were related to ONI, wind direction, and an interaction of minimum air temperature to ONI. During the South American Black Skimmer's non-peak season, the El Niño causes low austral winter temperatures (± 10ºC) to increase; and northern and eastern winds, which have less impact in the study area than southern winds, dominate (Grimm et al. 2000, Sutton et al. 2000, Grimm 2003) creating a climate similar to the one in the peak season of regular years when individuals are expected to concentrate in the study area. While the studies in Mexico (Carmona et al. 1995, Mellink 2003) verified an increase in breeding population and recruitment of the North American Black Skimmer, I detected a positive effect for the number of overstaging South American Black Skimmer individuals in southern Brazil.

The results answered the questions raised in this thesis however they opened other questions that demand more time and other methods to be fully addressed. For example, although my results were explained by ENSO and supported by other findings for seabirds and coastal web chains in the Pacific, I would gain much from addressing changes in Black Skimmers' movements during ENSO. Assessing how individuals change their movements between regular and ENSO years could improve conclusions in Chapters 6 and 7. I had access to 9-grams GPS-GSM PathTrack® devices to fix on Black Skimmers in Brazil however attempts to capture individuals were not successful mainly due to increased precipitation and thunderstorms caused by the very strong El Niño of 2015/2016. Also, the partnerships to try capturing individuals inland Brazil were cancelled due to economic and political instability in the country between 2015 and 2016. Nevertheless, I hope the remaining questions on Black Skimmers' movements will the addressed in future researches.

Affordable methods to study birds

In this thesis, I demonstrated that scoring feathers from photographs is reliable considering within- and between-observers repeatability which is backed by performance of data compared to other studies that scored bird feathers in hand. With specimens from museums, measurements from literature and citizen photographs, I also found identification of sexes in Black Skimmers using visual observation is reliable within- and between-observers. These findings allowed me to use citizen photographs from web databases to assess large-scale resource use by Black Skimmers in moult. Citizen platforms such as Wikiaves.com and e-Bird.org are of free scientific use and hold many photographs that could be used in studies in ornithology. My investigation on the resource use by Black Skimmer sub-species during moult was limited to Brazil because of Wikiaves' geographic range, which covered most of the South American Black Skimmer distribution but not the Amazonian Black Skimmer full extent. There is a lack of citizen platforms covering the entire South American territory with a reliable dataset of photographs. When this study was conducted, e-Bird.org expanded its coverage across the world but unlike Wikiaves.com it does not demand photographs therefore resulting in a low amount of data that could be used to score feathers and address large-scale resource use during moult when compared to Wikiaves.

The annual life-cycle of Black Skimmers in South America

The Black Skimmer is a coastal migratory bird with two sub-species in South America. The South American and Amazonian sub-species breed inland, and migrate to staging areas mostly at the coast. Black Skimmers have site selection affected by previous presence of species such as terns and plovers, and availability of sandbanks with high granulometry and short distance from calm shallow waters. Black Skimmers mostly feed on surface fish; and there is a diet segregation according to sex with males preying on larger fish than females (Mariano-Jelicich et al. 2008).

The main gaps in the annual life-cycle of Black Skimmers in South America were related to migration, moult, and resource use in the non-breeding season. Results in this study provided information on moult and resource use. I concluded that Black Skimmers moult during austral spring to summer, and that males take longer time to moult than females. The timing of moult differed between sexes and Amazonian males took a significant earlier and longer period to moult than Amazonian females and both sexes of the South American sub-species. Both Black

Skimmer sub-species moult while staging in coastal habitats mostly in southern Brazil. Black Skimmers select productive estuarine areas and are also likely to select sites near built-up areas. The South American sub-species selects less mudflats and more dunes while moulting.

Davenport et al. (2016) tracked Amazonian individuals from Peru and provided some interesting insights on routes, flight speed, and habitat range of Black Skimmers in South America. However, sample size was limited thus migration of Black Skimmer in South America still needs further studies. The occurrence data presented in Chapter 2 is a possible first step to assess migratory routes using species distribution models (SDM). The SDM approach is developing fast in ecology and can be useful to investigate migration based on presence-only data when the annual life-cycle is available for the species (Hayes et al. 2015). I collated aspects in the annual life-cycle of Black Skimmers, and gathered decent quality occurrence data to perform SDM in Chapter 2; but mainly due to time limitations I could not properly analyse and address the data. Nonetheless, I intend to present this analysis as an independent study.

Effects of ENSO on non-breeding Black Skimmers

It has been recognised that ENSO affects the climate South America by changing temperature, precipitation, wind speed, and wind direction (Grimm et al 2000, Sutton et al. 2000, Grimm 2003). Few studies have assessed effects of ENSO on coastal species in the South American Atlantic coast. Sathicq et al. (2015) found phytoplankton in La Plata estuary significantly decreases in biomass and density during the El Niño. Kelmo & Attrill (2013) found reefs in northeastern Brazil had significantly reduced densities with decreasing number of colonies during the El Niño. Garcia et al. (2001, 2003, 2004) investigated the effects of the El Niño on fish assemblage in an estuarine area in southern Brazil and found that abundance of individuals in the estuarine assemblage decreases with more freshwater species found due to higher precipitation causing river runoff, and changing salinity and water transparency. Favero & Becker (2006) assumed higher precipitation and river runoff increased prey availability justifying their findings on extended time of

Common Terns (*Sterna hirundo*) in the non-breeding site. Despite differences between locations, these findings in distinct levels of food chain in the South American Atlantic coast suggested to me that Black Skimmers would respond to ENSO by changing foraging resource use and locally altering timing of staging and abundance.

In Chapter 6 I found that Black Skimmers mostly foraged at marine habitats during regular years but changed the foraging use to a higher contribution of estuarine habitats in their assimilated diet during the El Niño of 2015/2016. However, in Chapter 7 the number of Black Skimmers resting in the same area did not significantly change during the non-breeding season. It is possible the changes in foraging resource use during the El Niño positively affected the numbers of Black Skimmers overstaging at the Island of Santa Catarina as a delayed response to prey availability. Unlike in Garcia et al. (2001, 2004), the study sites at the Island of Santa Catarina are bays and the increased precipitation and river runoffs may have reduced the marine water salinity expanding the estuarine condition during the El Niño as observed in Galápagos by Romero & Wikelski (2001). Moreover, the weather conditions during ENSO might not help individuals migrating due to the stronger winds and increased precipitation at the inland breeding sites. The higher number of overstaging birds during El Niño suggests a change in propensity of migration and staging. Results were based on a limited seasonal dataset thus conclusions must be cautious however most studies on ecological effects of ENSO are also based on limited events and yet provide a concise big picture of how species respond to extreme climate oscillations in South America (see Chapter 1).

Chapters 6 and 7 did not cover ENSO Modoki events. A continuous long-term monitoring would have better chances to investigate Modoki events which are so poorly understood and lack studies addressing related ecological responses. Although this thesis addressed important questions on how ENSO affects species in the South American Atlantic coast, other interesting topics could be further analysed. Considering the effects on overstaging and foraging of Black Skimmers in the non-breeding site, would be interesting to address effects of ENSO on the timing and duration of moult in Black Skimmers. Guerra et al. (1988) found the Gray Gull (*Leucophaeus modestus*) in Chile had moult either skipped or the timing of moult altered during drier conditions in the El Niño and more prolonged patterns during the La Niña. Also, Simeone et al. (2002) found only half of expected Humboldt Penguin (*Spheniscus humboldti*) adults and juveniles moulting in Chile during the El Niño. I could not analyse the effects of ENSO on Black Skimmers moulting in this thesis due to time limitation but this is certainly an interesting topic to be developed in future.

There is also a lack of studies on species with populations that depend on different aquatic habitats, and a broader field study on Black Skimmers could address such subject. For example, in terrestrial systems, Andean Condor (*Vultur gryphus*) populations respond in opposite ways to the same ENSO's phase depending on location (Wallace & Temple 1988). Condors living at high-elevation in the Andes had stable food supplies as weather conditions change little even during an El Niño. Populations in the foothills benefited from increased resources because rainfall was higher and mammals positively responded to enhanced vegetation. On the other hand, the coastal condors experienced low food availability and avoided breeding during El Niño. A similar pattern could happen to seabirds such as the Black Skimmers, gulls and terns occupying different offshore, coastal, and inland habitats but further studies are needed to address these possible differences.

Conservation and management action plans

Throughout the thesis I mentioned results from this study could be used in conservation and management action plans. Considering global changes have interfered on how species respond to the environment, understanding the patterns of resource use during key activities is fundamental to identify areas that should be prioritised for conservation, restoration, and suitable habitats for species translocations thus encouraging responsible management actions (Stephens et al. 2015). As concluded by Chapter 5, moult as an energetic-demanding activity demands high productivity habitats thus being an indirect bioindicator of habitat productivity. With the kernel and resource use function analysis in Chapter 5, important sites to the Black Skimmer during the non-breeding season were identified. Most of the areas matched with the highest wader biodiversity sites that

Butler et al. (2001) identified as priorities for conservation. The agreement between their results and mine backed the Black Skimmer as an umbrella species to other coastal birds such as gulls, terns and even waders. The Brazilian government revisited the forest code in 2012 and decreased the number of coastal habitats protected by law (Börner et al. 2014). Considering how society might have responded to these changes by increasing the pressure on coastal habitats, would be advisable to establish protected areas in the identified key areas and strengthen the management in the sites that are already protected.

One of the greatest challenges in current conservation is to manage areas not only to protect species now but to make sure refugia will be created and maintained in relation to future climate change scenarios (Root & Schneider 2006, Heller & Zavaleta 2009). Studies predict the anthropogenic climate change will resemble a conventional El Niño phase as a constant long-term condition (Easterling et al. 2000). Therefore, using the current ecological responses of species to ENSO is a useful tool to structure preventive action plans. The future is full of challenges concerning conservation and even the changes in ENSO itself with Modoki events are a completely new scenario to deal with. However, gathering the pieces of knowledge already published and improving long-term monitoring studies in other areas might underspin a guideline to identify and manage refugia.

Considering the conclusions from this thesis, the complex of estuaries at the Island of Santa Catarina and near mainland is an interesting refugia to be formally protected for Black Skimmers and possibly other species depending on the same resources. If El Niño prevents the species to breed, then overstaging in this area indicates adult population can at least survive and unsure a faster population recovery in the next breeding season. There are already few protected areas established in the island, such as the Carijós Ecological Station and the Pirajubaé Marine Extractive Reserve, however most of estuaries do not have formal protection and face constant pressure from residential and industrial developments, especially the Madre River estuary that was detached from the Serra do Tabuleiro State Park in 2009 (ALESC 2009).

If society has the real interest to protect biodiversity, studying responses to climate change should become a priority. Conservation in these scenarios implies a shift from being passive and simply observing changes in species populations to having proactive action plans, designing flexible management policies, reinforcing multiple target species for conservation and economical exploitation, monitoring environmental bioindicators (Bakun & Broad 2003). Managing ENSO’s effects on ecosystems is essential not only to the existence of species itself but also to macroeconomy.

Broad impact and future directions

Each chapter has a broader use helping in general studies in ornithology or explaining species’ ecological responses to ENSO. As already mentioned, scoring feathers from photographs could be used to address cost effective studies of geographic variation in moult patterns in widespread species and even large-scale resource use as in Chapter 5. The identification of sexes in Black Skimmers using visual observation allows researchers to gather more details on the species’ biology and support the testing of visual identification in other size-dimorphic species. The results confirm effects of ENSO on Black Skimmers in the South Atlantic but also open more questions about how this climate oscillation would affect other species. Because of their diet, it is likely terns respond to ENSO in similar ways to Black Skimmers. However, there are uncertainties on how coastal species with different diet and foraging strategies such as generalist gulls would respond to ENSO. Considering a big picture, would ecological effects of ENSO be more related to foraging strategies, diet, or habitat selection?

In a large-scale perspective, the ENSO reallocates the Walker cell and generates a cascade interplay between the atmospheric cells and the oceanic thermoclines changing marine currents around the world (Trenberth 1997). The theoretical framework based on climatic cells and ecosystems working as interconnected gears with alterations resulting in both top-down and bottom-up effects would result in populations of the same species in distinct locations having the same responses to ENSO. However, the literature review (Chapter 1) and results from this study (Chapters 6 and 7) suggest habitats also interfere in the species' responses to ENSO. For example, the position of estuaries related to bays or to open sea seems to play a key role in how species locally respond to environmental changes (Chapter 6, Romero & Wikelski 2001). The effect of habitat and local weather versus large-scale landscape and overall conditions during climate oscillations is another interesting topic. Findings could indicate key conditions for refugia that would guide how to establish protected areas and have more efficient conservation and management actions considering future climate change scenarios.

As Black Skimmers are aquatic top predators with widespread distribution associated with other species, their conservation is directly related to the conservation of others which turns them into suitable umbrella bioindicator. As top predators in coastal ecosystems, Black Skimmers are primarily affected by bottom-up effects in the non-breeding season through changes in prey availability caused by environmental conditions (Garcia et al. 2001, 2004). Using the Black Skimmer to assess the effects of environmental oscillations on aquatic species might open a new perspective for action plans considering future climate change scenarios.

In summary, I consider that this study provides useful and affordable non-invasive methods to study birds, a better understanding of the annual life-cycle and resource use by Black Skimmers, and how extreme climate events such as ENSO affect this species during the non-breeding season. Implications are important for scientific, conservation and management purposes. Through results found in this study and the new questions emerged, I hope to stimulate additional researches on other aspects of the ecological effects of ENSO on the biodiversity at the Atlantic coast.

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Appendices

Appendix 2.1. Literature used as source to map the occurrence and describe de annual-cycle life-history of Black Skimmers.

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Appendix 2.2. Location of South American and Amazonian Black Skimmer sub-species' breeding sites. Data retrieved from literature (Appendix 2.1), specimens at museums, and photographs on the Wikiaves database (WA followed by the voucher catalogue number).

	Sub-species	**Location**	**Country**	**Longitude**	**Latitude**	**Year of Record**	**Source**
1	North American	Cerro Prieto, Baja California	Mexico	-115.2794566959612	32.41203619804309	1998-2005	Mellink et al. 2007
2	North American	Montague, Baja California	Mexico	-114.761585690771	31.7524800729947	1998-2005	Mellink et al. 2007
3	North American	Islet 8, Baja California Sur	Mexico	-114.1417721502748	28.04838974497471	1998-2005	Mellink et al. 2007
4	North American	Islet S1-A, Baja California Sur	Mexico	-114.0508967678208	27.64026525390614	1998-2005	Mellink et al. 2007
5	North American	Mar Muerto, Chiapas	Mexico	-94.50267047397298	16.21765879235717	1998-2005	Binford 1989, Mellink et al. 2007
6	North American	Islets, Colima	Mexico	-104.4871876154278	19.10464680493043	1998-2005	Mellink et al. 2007
7	North American	Cuyutlán, Jalisco	Mexico	-104.5984477966424	19.15531434318709	1998-2005	Mellink et al. 2007
8	North American	Agua Dulce, Jalisco	Mexico	-105.6905895851868	20.38988823527888	1998-2005	Mellink et al. 2007
9	North American	Pericos, Nayarit	Mexico	-105.5810084665616	22.14655298977387	1998-2005	Mellink et al. 2007
10	North American	El Raricho, Sinaloa	Mexico	-108.794797003196	25.39633013375666	1998-2005	Mellink et al. 2007
11	North American	Tres Tumbas, Sinaloa	Mexico	-105.6855638859742	22.63404129778911	1998-2005	Mellink et al. 2007
12	North American	Tobari, Sonora	Mexico	-109.9886188678455	27.06310885597097	1998-2005	Mellink et al. 2007
13	North American	Gulf, Tamaulipas	Mexico	-97.64068782206468	24.6731424019985	2000	Garza-Torres & Navarro 2003
14	North American	Alameda, California	USA	-122.2634874074654	37.73223297610414	1985	Molina 2008
15	North American	Elmore, California	USA	-115.76845437223	33.11949412573956	1972	Molina 1996
16	North American	Huntington Beach, California	USA	-118.0354501481994	33.68493353744941	1985, 1985-1990	Schew & Collins 1990, Molina 2008, Western Foundation of Vertebrate Zoology (Egg 163037, 182020-55, 185950-56)
17	North American	Johnson St, California	USA	-116.0502802224097	33.53905878634922	1972-1975	McCaskie et al. 1974, Grant & Hogg 1976, Molina 1996
18	North American	Kings, California	USA	-119.5636468749095	36.14568292971526	1995	Molina 2008
19	North American	Los Angeles, California	USA	-118.4528276351938	33.9607473101938	1998	Molina 2008

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
20	North American	Morton Bay, California	USA	-115.5886550155537	33.20623336960185	1972	Molina 1996
21	North American	Mullet Island, California	USA	-115.605994194999	33.22380083444002	1972	Molina 1996
22	North American	Obsidian Butte, California	USA	-115.6376202235238	33.17139375479393	1972	Molina 1996
23	North American	Orange, California	USA	-117.8100251921432	33.80377323307862	1995	Molina 2008
24	North American	Ramer Island, California	USA	-115.5017923996516	33.06179659903486	1972	Molina 1996
25	North American	Rock Hill, California	USA	-115.6220170707262	33.1828256760941	1972	Molina 1996
26	North American	San Diego, California	USA	-117.1753264106323	32.71145453454849	1976-1986, 1994	Molina 2008, Whelchel et al. 1996
27	North American	San Francisco Bay, California	USA	-122.3922484488879	37.83430487304324	1996	Layne et al. 1996
28	North American	San Mateo, California	USA	-122.3095516060294	37.57432089881321	1985	Molina 2008
29	North American	Bay, Florida	USA	-85.70415987919557	30.11701023017423	2005-2010, 2012-2015	FSD 2016
30	North American	Brevard, Florida	USA	-80.62346261723322	28.29226243719375	2009-2010, 2012-2015	FSD 2016
31	North American	Canaveral, Florida	USA	-80.72646095001564	28.7718769308494	1973	Downing 1973
32	North American	Charlotte, Florida	USA	-82.2537095250632	26.7921027590454	2005-2015	FSD 2016
33	North American	Citrus, Florida	USA	-82.65036514297215	28.88021669934494	2010	FSD 2016
34	North American	Collier, Florida	USA	-81.4783085669191	25.8514073370871	2005-2015	FSD 2016
35	North American	Duval, Florida	USA	-81.41007007350869	30.40612344336974	2005-2009, 2011-2015	FSD 2016
36	North American	Escambia, Florida	USA	-87.34834524807818	30.32600707472158	2005-2015	FSD 2016
37	North American	Franklin, Florida	USA	-84.6307687806124	29.79091837650321	2006-2015	FSD 2016
38	North American	Gulf, Florida	USA	-85.40266841537958	29.78976814563805	2006-2010, 2012-2015	FSD 2016
39	North American	Hillsborough, Florida	USA	-82.71947869370693	27.68095118907616	2005-2015	FSD 2016
40	North American	Lee, Florida	USA	-82.21526537522934	26.60126628737369	2005-2015	FSD 2016
41	North American	Manatee, Florida	USA	-82.69942923523767	27.47516409975717	2010	FSD 2016
42	North American	Marco Island, Florida	USA	-81.73489638241468	25.93657321729695	1973	Downing 1973
43	North American	Martin, Florida	USA	-80.16337761034322	27.18296649156265	2006, 2011	FSD 2016

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
44	North American	Mosquito Islet, Florida	USA	-81.27168410193822	25.65306492258941	1944	Wetmore 1944
45	North American	Naples, Florida	USA	-81.79742574537347	26.09050196221742	2013	WA1254750
46	North American	Nassau, Florida	USA	-81.45151908902217	30.53835267050572	2005-2012	FSD 2016
47	North American	New Port Richey, Florida	USA	-82.83779398692435	28.23229554696248	1973	Downing 1973
48	North American	Okaloosa, Florida	USA	-86.58275600136183	30.39691723824737	2010, 2013-2015	FSD 2016
49	North American	Palm Beach, Florida	USA	-80.5063511985763	28.00849051784341	2005, 2010, 2015	FSD 2016
50	North American	Pasco, Florida	USA	-82.84762894971276	28.19627905723306	2005-2015	FSD 2016
51	North American	Pinellas, Florida	USA	-82.82927978523796	27.9844951358266	2006, 2014	FSD 2016
52	North American	Polk, Florida	USA	-81.79759468222574	28.13686927817234	2005-2008, 2013-2015	FSD 2016
53	North American	Port St. Joe, Florida	USA	-80.76146936664742	28.48482449095777	1973	Downing 1973
54	North American	Sand Key, Florida	USA	-82.8355341705567	27.95107513185163	2005, 2010-2013	Forys et al. 2015
55	North American	Santa Rosa, Florida	USA	-87.05106026894664	30.37928406009093	2009, 2013-2015	FSD 2016
56	North American	Sarasota, Florida	USA	-82.5771363831204	27.31468617183601	2007-2011	FSD 2016
57	North American	Savannah, Florida	USA	-86.6344965984989	30.69389565001086	1973	Downing 1973
58	North American	St. George Island, Florida	USA	-84.84630412129916	29.67825026165754	1973	Downing 1973
59	North American	St. Johns, Florida	USA	-81.32525612075214	29.96640617060593	2013	FSD 2016
60	North American	Tampa, Florida	USA	-82.43644146679529	27.85920137498125	1973	Downing 1973
61	North American	Volusia, Florida	USA	-80.90592263434652	29.05421221726324	2014	FSD 2016
62	North American	Walton, Florida	USA	-86.1541581351553	30.45477451696574	2015	FSD 2016
63	North American	Atchafalaya Delta, Louisiana	USA	-91.3299346606693	29.41466159227034	1991	Pius & Leberg 2002
64	North American	Isles Dernieres Barrier Island Refuge, Louisiana	USA	-90.75920378328415	29.05214609287233	2009-2013	Owen & Pierce 2013, Furfey 2014
65	North American	Rockefeller Refuge, Louisiana	USA	-92.64378277961757	29.60829827687005	1959	Chamberlain 1959
66	North American	Gulfport, Mississipi	USA	-88.93305461088266	30.23277256860208	1979-1980, 2004-2005	Jackson et al. 1982, Dinsmore 2008
67	North American	Jackson County, Mississipi	USA	-88.58698776541148	30.2286423553208	2004-2005	Dinsmore 2008

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
68	North American	Pascagoula, Mississipi	USA	-88.57808183387273	30.31338926960676	1973	Downing 1973
69	North American	Biloxi, Mississipi	USA	-88.84286412478437	30.38366014905002	1891, 2001	The Field Museum of Natural History (Egg 385), Western Foundation of Vertebrate Zoology (Egg 43297)
70	North American	Anglesea, New Jersey	USA	-74.79150613983562	39.01163469424164	1925-1926	Gillespie 1931, Western Foundation of Vertebrate Zoology (Egg 167432)
71	North American	Barnegat Bay, New Jersey	USA	-74.09537485929296	39.85993930821248	1955, 1976-1988, 2005-2007	Burger 1982, Burger & Gochfeld 1990, Burger et al. 2010, Western Foundation of Vertebrate Zoology (Egg 123421)
72	North American	Brant Beach, New Jersey	USA	-74.1996078017736	39.61036756933162	1929	Gillespie 1931
73	North American	Brigantine, New Jersey	USA	-74.37471492442997	39.40428010607804	1921-1923, 1930	Gillespie 1931, The Museum of Vertebrate Zoology at Berkeley (Egg 5768), Western Foundation of Vertebrate Zoology (Egg 1652, 165111)
74	North American	Cape May, New Jersey	USA	-74.91389006924879	38.93258751284069	1867	British Museum of Natural History (1941.4.6.1036)
75	North American	Ham Island, New Jersey	USA	-74.22518746388963	39.59916816101786	1965	Frohling 1965
76	North American	Wildwood, New Jersey	USA	-74.81218307948022	38.9836165825831	1929	Gillespie 1931
77	North American	Cedar Beach, New York	USA	-73.3102429437366	40.62714771542507	1969-1988	Gochfeld 1979, Burger 1981, Safina & Burger 1983, Burger & Gochfeld 1990
78	North American	Shinnecock Bay, New York	USA	-72.49063697946241	40.84864716811498	1968	Hays & Donaldson 1970
79	North American	South Oyster Bay, New York	USA	-73.43582984534132	40.63508935109209	1934	Vogt 1934
80	North American	Beaufort, North Carolina	USA	-76.65728856986199	34.6905657304661	1973	Downing 1973
81	North American	Brant Island, North Carolina	USA	-75.84664031097378	36.32616028803184	1980, 1982-1983	Grant et al. 1984
82	North American	Hatteras, North Carolina	USA	-75.68954077274728	35.21361060750224	1973	Downing 1973
83	North American	North Core Banks, North Carolina	USA	-76.46356631712841	34.70162946084064	2010-2011	Hillman 2012
84	North American	Sunset Beach, North Carolina	USA	-78.50235398679772	33.87004136775728	1973	Downing 1973
85	North American	Bay Point Shoal Seabird Sanctuary, South Carolina	USA	-80.63210358491489	32.26940505518132	1975-2009	Snipes & Sanders 2012
86	North American	Bird Key, South Carolina	USA	-79.98545533890604	32.63706533592585	1975-2009	Snipes & Sanders 2012

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
87	North American	Bosun's Point, South Carolina	USA	-79.23347253389287	33.38962114742389	1975-2009	Snipes & Sanders 2012
88	North American	Cape Romain National Wildlife Refuge, South Carolina	USA	-79.40592591087027	33.0562447144229	1971-2010	Snipes & Sanders 2012, Brooks et al. 2014, Western Foundation of Vertebrate Zoology (Egg 193222-44)
89	North American	Charleston, South Carolina	USA	-79.89586139459649	32.71233844918051	1900, 1926, 1973	Sprunt 1926, Downing 1973, Western Foundation of Vertebrate Zoology (Egg 60109)
90	North American	Crab Bank, South Carolina	USA	-79.72252246083043	32.83356565246427	1975-2009	Snipes & Sanders 2012
91	North American	Deveaux Bank, South Carolina	USA	-80.18776557130444	32.54882598980417	1961, 1973, 1975-2009	Snipes & Sanders 2012, Western Foundation of Vertebrate Zoology (Egg 193199, 30294)
92	North American	Egg Bank Island, South Carolina	USA	-80.48703892314711	32.47176987183152	1932, 1975-2009	Snipes & Sanders 2012, Humboldt State University Vertebrate Museum (3201)
93	North American	Harbor Island, South Carolina	USA	-80.43373214337308	32.39991266976175	1975-2009	Snipes & Sanders 2012
94	North American	Huntington Beach, South Carolina	USA	-78.78499017582082	33.76371310188558	1975-2009	Snipes & Sanders 2012
95	North American	Joiner Bank, South Carolina	USA	-80.66324313306257	32.20388908854113	1975-2009	Snipes & Sanders 2012
96	North American	Kiawah Island, South Carolina	USA	-80.07738036066792	32.60612434910708	1975-2009	Snipes & Sanders 2012
97	North American	Litchfield Beach, South Carolina	USA	-79.04167502687939	33.52895385110357	1975-2009	Snipes & Sanders 2012
98	North American	North Island, South Carolina	USA	-79.1663658594528	33.29849178195661	1975-2009	Snipes & Sanders 2012
99	North American	North Santee Bar, South Carolina	USA	-79.28404267496664	33.15497109956157	1975-2009	Snipes & Sanders 2012
100	North American	Sand Island, South Carolina	USA	-79.19216407146097	33.18869006454504	1975-2009	Snipes & Sanders 2012
101	North American	Savannah Spoil Sites, South Carolina	USA	-80.97451650942459	32.07951963149989	1975-2009	Snipes & Sanders 2012
102	North American	South Island, South Carolina	USA	-79.23107784555745	33.17972428434203	1975-2009	Snipes & Sanders 2012
103	North American	Sullivan's Island, South Carolina	USA	-79.83476571884069	32.76486500065916	1975-2009	Snipes & Sanders 2012
104	North American	Tomkins Island, South Carolina	USA	-80.87426868836838	32.11052136398921	1975-2009	Snipes & Sanders 2012
105	North American	Arroyo Colorado, Texas	USA	-97.19473414041481	26.28621476706722	1978-1981	White et al. 1984
106	North American	Chorpus Christi Bay, Texas	USA	-97.16178402273792	27.77883240022335	1978-1989, 1926, 2012-2013	White et al. 1984, Fern 2013, Chicago Academy of Sciences (Egg 1470-1472, 1916), Western

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
							Foundation of Vertebrate Zoology (Egg 204122, 114734)
107	North American	Laguna Madre, Texas	USA	-97.44323385899625	26.8001948651619	1920-1921, 1978-1981	White et al. 1984, Western Foundation of Vertebrate Zoology (Egg 1654-55, 43333, 100323)
108	North American	Laguna Vista, Texas	USA	-97.29179588178469	26.08712428927831	1921, 1978-1981	White et al. 1984, Western Foundation of Vertebrate Zoology (Egg 1654-55)
109	North American	Lavaca Bay, Texas	USA	-96.46307045732749	28.5905132669655	1982-1983	Quinn 1990, Quinn et al. 1994
110	North American	Nueces Bay, Texas	USA	-97.5092457831131	27.85626514613311	1978-1981	White et al. 1984
111	North American	Port Mansfield, Texas	USA	-97.43360632803315	26.52628951161993	1978-1981	White et al. 1984
112	North American	Galveston, Texas	USA	-94.71086311545683	29.42523361518179	1890, 1940-1966	British Museum of Natural History (1926.12.2.82-95), Western Foundation of Vertebrate Zoology (Egg 204121, 88087)
113	North American	Assateague Island, Virginia	USA	-75.19967977656469	38.07958133295416	1990-1991	O'Connell & Beck 2003
114	North American	Cardwell Island, Virginia	USA	-76.00877628262893	37.823865452689	1933	Pettingill 1937
115	North American	Cedar Island, Virginia	USA	-75.60834809270342	37.65096274918262	1990-1991	O'Connell & Beck 2003
116	North American	Cobb Island, Virginia	USA	-76.84528867680646	38.25696750609642	1881-1991	British Museum of Natural History (1900.6.25.25, 42-77), The Field Museum of Natural History (Egg 4872, 17873-18023, 18101-102, Western Foundation of Vertebrate Zoology (Egg 204089-93, 43385, 118430), O'Connell & Beck 2003
117	North American	Conjers, Virginia	USA	-75.73515554541766	37.49842698860486	2001-2002	Rounds et al. 2004
118	North American	Fisherman Island, Virginia	USA	-75.9666312810625	37.09328983949467	1973-1974	Downing 1973, Erwin 1977a, b, 1979
119	North American	Man & Boy Island, Virginia	USA	-75.86870062736782	37.2814834923439	2001-2002	Rounds et al. 2004
120	North American	Metomkin Island, Virginia	USA	-75.56801379941366	37.73948054953736	1990-1991	O'Connell & Beck 2003
121	North American	Parramore Island, Virginia	USA	-75.62798169999998	37.5387464	1990-1991	O'Connell & Beck 2003
122	North American	Wire Narrows, Virginia	USA	-75.42715651259083	37.88150175133821	2001-2002	Rounds et al. 2004

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
123	North American	Dawson Shoals, Viriginia	USA	-75.61919480522828	37.60047695653579	1990-1991	O'Connell & Beck 2003
124	North American	Hog Island, Viriginia	USA	-75.69602298540637	37.4126951140506	1881-1886, 1927, 1953, 1990-1991	O'Connell & Beck 2003, The Field Museum of Natural History (Egg 18099-100), Western Foundation of Vertebrate Zoology (Egg 118441, 132423, 204073, 160967)
125	North American	Little Pine Island, Florida	USA	-82.20192068449616	26.61989418401909	2006-2014	FSD 2016
126	North American	Saint Lucie, Florida	USA	-80.25793365346659	27.38244832963924	2005-2015	FSD 2016
127	North American	Boston, Massachusets	USA	-70.92353369492309	42.32694190297365	1944	Wetmore 1944
128	North American	island 15-miles off coast, Virginia	USA	-75.48989968825745	37.15749063094119	1917	Bales 1919
129	North American	Salina Matijs, Bonaire	Antilles	-68.36762364563769	12.27825251947813	1872	The Field Museum of Natural History (Egg 384, 573, 1877)
130	North American	Isla San Sebastian, Usulutan	El Salvador	-88.40213023140827	13.17536296132149	2008	Herrera et al. 2009
131	North American	Allen's Island, Virginia	USA	-76.440514297978	37.24808297717066	1900	Western Foundation of Vertebrate Zoology (Egg 204098), The Field Museum of Natural History (Egg 16227-32)
132	North American	Amelia Island, Florida	USA	-81.45021703664315	30.68207582369058	1881, 1906	The Field Museum of Natural History (Egg 4864-71)
133	North American	Aransas Island, Texas	USA	-97.05874409810653	27.88817952983851	1899, 1923-1926, 1930	Western Foundation of Vertebrate Zoology (Egg 204069, 54225), The Museum of Vertebrate Zoology at Berkeley (Egg 8497, 5774)
134	North American	Beach Haven, New Jersey	USA	-74.26143021599884	39.53561489027509	1882	Western Foundation of Vertebrate Zoology (Egg 176538)
135	North American	Bull's Bay, South Carolina	USA	-79.62470399720466	32.93651873795754	1901-1933	Western Foundation of Vertebrate Zoology (Egg 125996, 166579), Denver Museum of Nature & Science (Egg 832-33, 1399-1405), The Field Museum of Natural History (Egg 20572, 22349), The Museum of Vertebrate Zoology at Berkeley (Egg 3786, 5773)

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
136	North American	Buzzard's Bay, Massachussets	USA	-70.8694882300901	41.460082510402	1911	Western Foundation of Vertebrate Zoology (Egg 204119)
137	North American	Caldwell Island, Maine	USA	-69.29760070956361	43.9332399133643	1924	Western Foundation of Vertebrate Zoology (Egg 28612)
138	North American	Cape Charles, Virginia	USA	-76.04544637948366	37.27114716668741	1881	The Field Museum of Natural History (Egg 18093-98)
139	North American	Cartwells Lump, Massachussets	USA	-70.64779718524112	41.72717403208715	1920	The Museum of Vertebrate Zoology at Berkeley (Egg 5770)
140	North American	Chincoteague Island, Virginia	USA	-75.36458194717206	37.94418111788607	1886	University of Colorado Museum of Natural History (Egg 687)
141	North American	Destin, Florida	USA	-86.52971263249368	30.39043608898907	1973	Western Foundation of Vertebrate Zoology (Egg 191999)
142	North American	Edisto Island, South Carolina	USA	-80.29728820828596	32.55030662114019	1898	Denver Museum of Nature & Science (Egg 2432)
143	North American	High Island, Texas	USA	-94.39000067751971	29.55736623613591	1921	Western Foundation of Vertebrate Zoology (Egg 100322)
144	North American	Imperial Beach, California	USA	-117.1281524866833	32.55554037761353	1980	Western Foundation of Vertebrate Zoology (Egg 120441)
145	North American	Little Beach Island, Virginia	USA	-75.64318775163744	37.53094560739769	1934	Western Foundation of Vertebrate Zoology (Egg 17089)
146	North American	Longport, New Jersey	USA	-74.54562362625408	39.31204050444384	1949	Western Foundation of Vertebrate Zoology (Egg 123609)
147	North American	Matagorda Island, Texas	USA	-96.74920306445134	28.16636714205216	1940	Western Foundation of Vertebrate Zoology (Egg 83174)
148	North American	Mussel Reef, Oregon	USA	-124.3591108009302	43.34372897249598	1963	Western Foundation of Vertebrate Zoology (Egg
149	North American	Mussel Reef, Oregon	USA	-124.3591108009302	43.34372897249598	1905	Western Foundation of Vertebrate Zoology (Egg 54237)
150	North American	Ocean City, New Jersey	USA	-74.58557252537247	39.26891428196228	1955	Western Foundation of Vertebrate Zoology (Egg 128618)
151	North American	Ocracoke Island, North Carolina	USA	-75.96300117696997	35.1112778157047	1933	Western Foundation of Vertebrate Zoology (Egg 188532)
152	North American	Robinson Island, Alabama	USA	-87.55380263769919	30.28588969799601	1922	Western Foundation of Vertebrate Zoology (Egg 43343)
153	North American	Rockport, Texas	USA	-97.03287203169072	28.03539365544503	1927	The Museum of Vertebrate Zoology at Berkeley (Egg 8498)
154	North American	Rogue Island, Virginia	USA	-75.73717783779631	37.3861191106405	1945-1946	Western Foundation of Vertebrate Zoology

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
							(Egg 53576, 58818)
155	North American	Saint Augustine, Florida	USA	-81.3071765613654	29.90511747859952	1929	Western Foundation of Vertebrate Zoology (Egg 163510)
156	North American	Shell Island, North Carolina	USA	-76.21004044968565	34.96707301765548	1896, 1900	Denver Museum of Nature & Science (Egg 76), Western Foundation of Vertebrate Zoology (Egg 43309)
157	North American	Skyline Causeway, North Carolina	USA	-75.7131978417024	36.10479617265887	1959	Western Foundation of Vertebrate Zoology (Egg 79547)
158	North American	Smith Island, North Carolina	USA	-75.90462310339495	36.54089195089234	1886	Western Foundation of Vertebrate Zoology (Egg 124237)
159	North American	St. Helena Sound, South Carolina	USA	-80.53241692737316	32.52984987342364	1916	The Museum of Vertebrate Zoology at Berkeley (Egg 4689)
160	North American	Stone Harbor, New Jersey	USA	-74.75627000032253	39.05234900834965	1931	Western Foundation of Vertebrate Zoology (Egg 165105)
161	North American	Timbalier Island, Louisiana	USA	-90.49431217992603	29.07109831343169	1896	Western Foundation of Vertebrate Zoology (Egg 204099)
162	North American	Titusville, Florida	USA	-80.78293555100262	28.62950541623443	1968	Western Foundation of Vertebrate Zoology (Egg 79550)
163	North American	Marsh Island, Lousiana	USA	-91.88126646157677	29.57520458649408	1896	The Field Museum of Natural History (Egg 4863)
164	North American	Wreck Island, Virginia	USA	-75.80567582963423	37.24154581291182	1910-1920	The Museum of Vertebrate Zoology at Berkeley (Egg 1073-74), Western Foundation of Vertebrate Zoology (Egg 43386, 43292, 90715)
165	South American	Rio Uruguay, Entre Rios	Argentina	-58.1533678735529	-32.01271873939618	1984, 2009	Klimaitis & Moschione 1984, Mariano-Jelicich & Madrid 2014
166	South American	Sao Francisco River, Bahia	Brazil	-42.90932590800716	-10.94176997361926	2014	Antas in litt. 2014
167	South American	Cuiba River, Barao de Melgaco	Brazil	-56.41015698982822	-16.54475347902286	2001-2015	Mariano-Jelicich & Madrid 2014, Antas et al. 2016, WA1840044
168	South American	Sao Lourenco River, Barao de Melgaco	Brazil	-56.02963925963802	-16.71296262925089	2012-2014	Antas et al. 2016
169	South American	Sao Miguel do Araguaia, Goias	Brazil	-50.59087455073898	-13.12171288352565	2013	WA1099164
170	South American	Caceres, Mato Grosso	Brazil	-57.70412607133584	-16.00436062112081	2012	WA1694101
171	South American	Paranaita, Mato Grosso	Brazil	-56.56669333584909	-9.398524201075974	2014	WA1468941
172	South American	Pocone, Mato Grosso	Brazil	-56.59005980250915	-16.4635149108832	1982-1986, 2005-	Valente et al. 2011, WA100125, WA6792, WA647763,

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
						2006, 2010-2015	WA1601911, WA1023581, WA1425010, WA1858680
173	South American	Vila Bela da Santissima Trindade, Mato Grosso	Brazil	-59.97021259410166	-14.98538863761069	2014	WA1495632
174	South American	Aquiduana, Mato Grosso do Sul	Brazil	-55.85352281299352	-20.42089925674418	2007, 2011, 2014	WA1724671, WA23383, WA458243
175	South American	Corguinho, Mato Grosso do Sul	Brazil	-54.78366542158651	-19.79960905372107	2015	WA1893099
176	South American	Corumba, Mato Grosso do Sul	Brazil	-57.59196403691525	-18.97379004803958	2003, 2012	WA192107, WA786406
177	South American	Ibicui River, Rio Grande do Sul	Brazil	-55.62516278377959	-29.56465307855553	1998, 2010	Efe et al. 2001, WA244560
178	South American	Lagoa da Confusao, Tocantins	Brazil	-50.62073666815581	-10.8978925708217	2011	WA396574
179	South American	Palmas, Tocantins	Brazil	-48.37666555337739	-10.07626017542027	2014	WA1275819
180	South American	Pium, Tocantins	Brazil	-49.94595391576842	-10.43766797019358	2006, 2010-2012	WA104327, WA229404, WA473038, WA797399
181	South American	River Paraguay	Paraguay	-58.2295912213026	-20.26766538223132	1920	Griscom 1935
182	South American	Colonia Risso, Concepcion	Paraguay	-57.87516473645084	-22.33073602815365	1909	British Museum of Natural History (1910.7.9.1-24)
183	South American	Rio Negro	Uruguay	-58.20316944444445	-33.00143333333333	2015	Martin Abreu, in litt. 2016
184	South American	Alta Floresta, Mato Grosso	Brazil	-55.95777420580921	-9.636550161635142	2014	WA1491828
185	South American	Santa Maria das Barreiras, Pará	Brazil	-49.8059042182994	-8.97790703869315	2011	WA404185
186	South American	Caseara, Tocatins	Brazil	-49.95045223466763	-9.205982902355272	2008	WA1630388
187	Amazonian	Manoel Urbano, Acre	Brazil	-69.24916148266264	-8.859506328348564	2014	WA1440625
188	Amazonian	Anavilhanas Archipelago, Amazonas	Brazil	-60.74468715793627	-2.702913774499155	2006-2009	Valente et al. 2011, Zarza et al. 2013
189	Amazonian	Careiro da Varzea, Amazonas	Brazil	-59.81693518434155	-3.207082731888237	2009	WA96563
190	Amazonian	Iranduba, Amazonas	Brazil	-60.25385094864903	-3.274974125224791	2015	WA1921347
191	Amazonian	Alto Alegre dos Parecis, Rondonia	Brazil	-61.91351174287495	-13.42613917485183	2011	WA406614, Renato Moreira, in litt. 2016
192	Amazonian	Itacoatiara, Amazonas	Brazil	-58.55913954258602	-3.233751075000917	2011, 2014	Kirwan et al. 2012, WA1613382
193	Amazonian	Labrea, Amazonas	Brazil	-64.88616707504392	-7.278093766253987	2010	WA661929
194	Amazonian	Nova Olinda do Norte, Amazonas	Brazil	-59.0859431217205	-3.855001813095646	2014	WA1563168

	Sub-species	Location	Country	Longitude	Latitude	Year of Record	Source
195	Amazonian	Piranhas Island, Amazonas	Brazil	-65.41659890575575	-2.450016310190182	1961	Preston 1962
196	Amazonian	RDS Amana, Amazonas	Brazil	-64.66405504703664	-2.656538461775867	2003-2004	Valente et al. 2011
197	Amazonian	RDS Mamiraua, Amazonas	Brazil	-65.20752775784752	-2.28363973551777	1998-2001, 2003-2005, 2012-2014	Raeder & Bernhard 2003, Valente et al. 2011, Mariano-Jelicich & Madrid 2014, Bianca Bernardon in litt. 2016, WA1854925, WA1896275
198	Amazonian	RDS Piagacu-Purus, Amazonas	Brazil	-62.30121726719828	-3.889688027544448	2004	Valente et al. 2011
199	Amazonian	Trombetas River, Amazonas	Brazil	-56.30533404503174	-1.475126101822909	1982	Krannitz 1989
200	Amazonian	Comodoro, Mato Grosso	Brazil	-60.39705537130618	-13.45247783031406	2014	WA1558896
201	Amazonian	Itaituba, Para	Brazil	-56.54832640781009	-4.679095805725306	2012	WA780799
202	Amazonian	Porto de Moz, Para	Brazil	-52.20158093447394	-1.618351415523531	2010	WA193722
203	Amazonian	Santarem, Para	Brazil	-54.87145671491872	-2.047842167572697	2014	WA1239384
204	Amazonian	Senador Jose Porfirio, Para	Brazil	-52.02129750239146	-2.770055837019256	2015	Felipe Gomes & Bianca Vieira pers. obs. 2015
205	Amazonian	Cabixi, Rondonia	Brazil	-60.57314050104736	-13.55128839904095	2014	WA1504723, João Ribeiro in litt. 2016
206	Amazonian	Corumbiara River, Rondonia	Brazil	-61.01523984754824	-13.1148789032623	2014	João Ribeiro in litt. 2016
207	Amazonian	Alta Floresta d'Oeste, Rondonia	Brazil	-63.02402090222109	-12.78402052780303	2014	João Ribeiro in litt. 2016
208	Amazonian	Rolim de Moura do Guapore, Rondonia	Brazil	-62.283608608693394	-13.08797670555805	2014	João Ribeiro in litt. 2016
209	Amazonian	Guapore River, Rondonia	Brazil	-63.77604317223789	-12.43601632448114	2001	Mariano-Jelicich & Madrid 2014
210	Amazonian	Manu River, Madre de Dios	Peru	-71.16525570460115	-12.03737652252865	1992, 2012	Groom 1992, WA1607101
211	Amazonian	Cocha Cashu Biological Station, Manu	Peru	-71.3988619065523	-11.8907106805742	2012-2014	Davenport et al. 2016
212	Amazonian	Playa Garza, Manu	Peru	-71.03713606923955	-12.15999019045667	2012-2014	Davenport et al. 2016
213	Amazonian	Ucayali River, Ucayali	Peru	-74.32282156681148	-7.849390730736681	1865	British Museum of Natural History (1891.5.10.43-53, 1902.1.10.312-315), Sclater et al. 1866
214	Amazonian	Alto Purus River, Esperanza	Peru	-74.45341924061697	-8.324835713405745	1963	Western Foundation of Vertebrate Zoology (Egg 168821)

Appendix 5.1. Summary of the forward stepwise model selection for the final resource selection function model (in bold) by Black Skimmers in moult as a function of individual, habitat, location, and effort across the Brazilian coastline. The stepwise selection considered the log-likelihood (LL), the Bayesian information criteria (BIC), and the Hosmer and Lemeshow goodness of fit test (X^2-value, DF = degrees of freedom, *P[GOF]*-value). *P[GOF]*-values were considered significant if ≥ 0.05 (in bold). I also present the estimate (β), standard error (SE), *z*-value and *P[z]*-value for the last covariate added in the model. *P[z]*-values were considered significant if ≤ 0.05 (in bold). Description of variables are available in Table 5.2.

Model	**LL**	**BIC**	**X^2-value**	**DF**	***P[GOF]*-value**	**β**	**SE**	***z*-value**	***P[z]*-value**
0/1 ~ abund * eff	-2055	4126	7.28	8	**0.50**	0.0001	0.0003	0.100	0.920
0/1 ~ lat*ssp	-1969	3955	11.17	8	**0.19**	-0.033	0.022	-1.501	0.133
0/1 ~ chl * ssp	-2036	4089	11.5	8	**0.19**	-0.0005	0.0001	-0.439	0.660
0/1 ~ dstE * ssp	-1889	3794	4.34	8	0.82	-0.022	0.025	-0.891	0.373
0/1 ~ dstM * ssp	-1989	3996	6.85	8	0.55	0.049	0.024	2.071	**0.038**
0/1 ~ dstM * ssp + dstD * ssp	-1920	3868	9.52	8	**0.30**	-0.013	0.005	-2.505	**0.012**
0/1 ~ dstM * ssp + dstD * ssp + dstU * ssp	-1868	3774	5.77	8	0.67	-0.021	0.015	-1.399	0.162
0/1 ~ dstM * ssp + dstD * ssp + dstD * sex	-1914	3867	7.43	8	**0.49**	0.0001	0.004	0.025	0.98
0/1 ~ dstM * ssp + dstD * ssp + dstM * sex	-1913	3865	6.13	8	0.63	-0.003	0.004	-0.759	0.447
0/1 ~ dstM * ssp + dstD * ssp + chl * sex	-1858	3760	8.30	8	**0.40**	-0.0001	0.0001	-1.611	0.107
0/1 ~ dstM * ssp + dstD * ssp + dstE * sex	-1761	3567	12.99	8	**0.11**	0.034	0.023	1.489	0.136
0/1 ~ dstM * ssp + dstD * ssp + lat * sex	-1739	3523	19.78	8	**0.01**	0.031	0.369	0.861	0.389
0/1 ~ dstM * ssp + dstD * ssp + dstU * sex	-1877	3798	5.77	8	0.67	0.028	0.015	1.843	**0.056**
0/1 ~ dstM * ssp + dstD * ssp + dstU * sex + dstE	-1745	3541	10.7	8	**0.21**	-0.117	0.011	-10.58	**<0.001**
0/1 ~ dstM * ssp + dstD * ssp + dstU * sex + dstE + chl	-1691	3438	8.04	8	**0.42**	0.0005	0.0001	8.864	**<0.001**
0/1 ~ dstM * ssp + dstD * ssp + dstU * sex + dstE + chl + lat	-1567	3195	10.18	8	**0.25**	-0.139	0.015	-9.096	**<0.001**
0/1 ~ dstM * ssp + dstD * ssp + dstU * sex + dstE + chl + lat + abund	-1559	3185	10.21	8	**0.25**	0.009	0.002	3.760	**<0.001**
0/1 ~ dstM * ssp + dstD * ssp + dstU * sex + dstE + chl + lat + abund + eff	**-1518**	**3108**	**10.28**	**8**	**0.24**	**0.012**	**0.001**	**8.255**	**<0.001**

Appendix 6.1. Stable isotope ratios for δ^{13}C, δ^{15}N and δ^{34}S (mean ± SD) of three internal laboratory standards (MSAG2, M2 and SAAG2) and four international standards (USGS40, IAEA-S1, IAEA-S2 and IAEA-S3) used to normalise raw stable isotope ratios.

	δ^{13}C	**δ^{15}N**	**δ^{34}S**
MSAG2			
First run	-21.32 ± 0.12 (n = 32)	2.24 ± 0.12 (n = 30)	6.15 ± 0.23 (n = 31)
Second run	-21.43 ± 0.09 (n = 32)	2.18 ± 0.09 (n = 32)	6.09 ± 0.43 (n = 32)
Third run	-21.35 ± 0.07 (n = 32)	2.53 ± 0.17 (n = 32)	6.37 ± 0.38 (n = 32)
International accepted values	-21.23 ± 0.12	2.24 ± 0.09	6.23
M2			
First run	-34.2 ± 0.05 (n = 23)	32.69 ± 0.14 (n = 23)	14.42 ± 0.19 (n = 23)
Second run	-34.13 ± 0.10 (n = 25)	32.69 ± 0.19 (n = 25)	14.66 ± 0.45 (n = 24)
Third run	-34.19 ± 0.08 (n = 25)	32.94 ± 0.31 (n = 25)	14.33 ± 0.5 (n = 25)
International accepted values	-34.28 ± 0.11	32.70 ± 0.27	14.60
SAAG2			
First run	-5.7 ± 0.06 (n = 18)	4.57 ± 0.07 (n = 20)	0.07 ± 0.19 (n = 20)
Second run	-5.58 ± 0.18 (n = 15)	4.6 ± 0.05 (n = 23)	0.12 ± 0.3 (n = 22)
Third run	-5.69 ± 0.07 (n = 23)	4.75 ± 0.87 (n = 23)	0.17 ± 0.35 (n = 23)
International accepted values	-5.78 ± 0.12	4.55 ± 0.06	-0.16
USGS40			
First run	-26.34 ± 0.01 (n = 3)	-4.37 ± 0.04 (n = 3)	
Second run	-26.37 ± 0.03 (n = 4)	-4.49 ± 0.10 (n = 4)	
Third run	-26.39 ± 0.01 (n = 4)	-4.43 ± 0.06 (n = 4)	
International accepted values	-26.39 ± 0.09	-4.52 ± 0.12	
IAEA-S1			
First run			0.12 ± 0.17 (n = 4)
Second run			-0.54 ± 0.31 (n = 3)
Third run			-0.31 ± 0.01 (n = 3)
International accepted values			-0.3
IAEA-S2			
First run			23.01 ± 0.25 (n = 4)
Second run			22.39 ± 0.84 (n = 3)
Third run			22.39 ± 0.46 (n = 3)
International accepted values			22.62 ± 0.2
IAEA-S3			
First run			-32.76 ± 0.22 (n = 4)
Second run			-32.61 ± 1.1 (n = 3)
Third run			-33.21 ± 0.86 (n = 3)
International accepted values			-32.49 ± 0.2