MIGRATION ECOLOGY OF SHOREBIRDS ON THE NORTHERN GULF OF MEXICO AND EFFECTS OF THE DEEPWATER HORIZON OIL SPILL

AN ABSTRACT

SUBMITTED ON THE EIGHTH DAY OF MAY 2015

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

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FOR THE DEGREE

OF

DOCTOR OF PHILOSOPHY

BY

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ABSTRACT

The coastline of the northern Gulf of Mexico (NGOM) represents important non-breeding habitats for 28 species of migratory shorebirds. As processes of climate change accelerate, these habitats are expected to experience dramatic land loss. In addition, the NGOM has experienced several natural and human mediated disasters over the last decade, including Hurricane Katrina and the Deepwater Horizon Oil spill (DWH). Predicting the impacts of these events requires an understanding of the interactions between shorebirds and their habitats. However, the migration ecology of shorebirds on the NGOM has not been well studied. To better understand the effects of the DWH and the importance of NGOM habitats to the migration ecology of shorebirds I carried out two related studies. First, I investigated the potential for long term, large-scale effects of oil exposure to migratory shorebirds through both a literature review, and by investigating the exposure to DWH oil in seven species of shorebirds that winter or stopover along the NGOM. I found that through migratory carry-over effects, oil spills and other environmental disasters, have the potential to impact ecosystems far from the event. Exposure results suggest as many as 1 million shorebirds were impacted by direct exposure to oil, and many more may have been negatively affected by disturbance from cleanup activities in oiled habitats. Second, I investigated the migration ecology of three near-arctic breeding species of shorebirds (Semipalmated sandpipers (*Calidris semipalmatus*), Western Sandpiper (*C. mauri*) and Dunlin (*C. alpina*), by measuring within- and among-species variation in habitat use, stopover duration, and refueling rates, as measured by plasma metabolites, across 3 habitat types. I found that among species, shorebirds vary in their migration ecology according to the distance to the next stopover site, suggesting NGOM habitats may be particularly important to longer-distance “jump” migrants (Dunlin). I also found that while shorebirds are found across all habitat types sampled, the back bay habitats of barrier islands provided a higher quality habitat (as evidenced by higher prey biomass, and a higher refueling rate) than traditional coastal mudflats or remnant wetlands, highlighting the importance of considering shorebird ecology in barrier island restoration plans.

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This dissertation is dedicated to the magical city of New Orleans. Thank you, New Orleans, for providing a shelter in the storm. My hope is that my work here, and in the future, helps in returning the favor.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

Climates are changing worldwide, and in the United States the impacts of these changes are readily apparent in the wetlands of the northern Gulf of Mexico (NGOM). The state of Louisiana is experiencing the most severe land loss and barrier island erosion in North America (Penland and Ramsey 1990, Zervas 2009), due in part to the highest current sea level rise (SLR) rate in the USA (9.3 mm/year for 1947-2006; Miner 2009). As processes of climate change accelerate, the coastal areas of the northern Gulf are expected to experience increased levels of flooding and saltwater intrusion, leading to accelerated and dramatic land loss (FitzGerald *et al.* 2008). In addition to habitat loss from climate change, the NGOM has been especially vulnerable to other natural and human mediated disasters, such as Hurricanes Katrina and Rita, and the Deepwater Horizon oil spill (DWH). The wetlands affected by these events are important habitats for 34 species of shorebirds, including 28 migratory species that spend all or part of their non-breeding season on the Gulf coast. The ultimate goals of this dissertation were to investigate the effects of the DWH and establish the importance of the NGOM to migratory shorebirds given within and among species variation in migration phenology, habitat use patterns, and migration strategies. Improving our understanding of the migration ecology of shorebirds in NGOM habitats is important for developing models that can predict the potential population level effects of habitat loss and degradation in this group.

Migratory shorebirds are of high conservation concern as at least 61% of North American shorebird populations are declining (Andres et al. 2012). Research is under way to evaluate how shorebirds are responding to changes in their arctic breeding grounds (ALCC 2011), but as with many migratory species, less research has been conducted outside of the breeding season (Faaborg et al. 2010). Among migratory birds, conditions in non-breeding habitats have been linked to survival (Johnson *et al.* 2006) and reproductive success (Norris *et al.* 2004; Norris and Taylor 2006; Runge and Marra 2005). For shorebirds, there is some evidence that the migration period may be limiting populations (Piersma 1994, Ens *et al.* 1994, Baker *et al.* 2004, Newton 2006). Baker *et al.* (2004) and Mizrahi et al. (2012), for example, have attributed, in part, the population declines in the Red knot (*Calidris canutus rufa*) and Semipalmated sandpiper (*C. semipalmatus*) to the collapse of the horseshoe crab (*Limulus polyphemus*) population in the Delaware Bay, USA. The Delaware Bay represents a major stopover site for thousands of migratory shorebirds THAT rely on eggs from horseshoe crab spawning to fuel their long distance migration to high arctic breeding grounds. Galbraith *et al.* (2002) modeled the effect of SLR on 4 shorebird stopover habitats, and projected losses OF up to 70% of foraging habitat at some sites. If, as in the Red knot, other near-arctic breeding shorebird populations are limited during migration, habitat loss and degradation on the NGOM has the potential for major consequences to the stability of these arctic breeding populations.

Evaluating the effects of changes to migratory shorebird stopover habitats is challenging due to the variation in migration strategies demonstrated within and among species. Optimal migration theory, as posited by Alerstam and Lindstrom (1990) suggests that if birds seek to maximize their overall migration speed (time minimization hypothesis) they should minimize time spent on migration by bypassing lower quality sites. The competing energy-minimization hypothesis states that a bird will migrate to the next stopover site once its fat reserves allow it to make the journey safely, regardless of the intake rate (quality) at current or future sites. Evidence suggests that on spring migration shorebirds tend to exhibit time minimization behavior (Lyons and Haig 1995; Farmer and Wiens 1999) in an effort to reach northern breeding grounds and establish high quality breeding territories, whereas on fall migration such constraints are relaxed and, in some shorebird species, migrants tend to limit fat reserves, suggesting an energy-minimization strategy (Gudmundsson *et al.* 1991, Lyons and Haig 1995). How strongly a bird demonstrates a particular migration strategy can also vary according to environmental variables such as wind direction and speed, predation pressure, AND distance to subsequent stopover sites (Schaub *et al.* 2008; Delingat *et al.* 2008). Some coastal wintering shorebird species, such as Dunlin (*Calidris alpina*), are believed to use a “jump” migration strategy (Piersma 1987) - migrating long distances in the spring from coastal habitats on the Gulf of Mexico to the northern Prairie pothole region of North America without stopping (Skagen 1996). Other species, including the Semipalmated sandpiper (*Calidris pusilla*) and Western sandpiper (*Calidris mauri*) use a “hop” or “skip” migration strategy (Piersma 1987), stopping for shorter intervals at inland agricultural fields and natural wetlands along their migratory journey (Skagen 1996). Migration theory suggests that differences in migration strategy will result in variation in the requirements of migration physiology, as the longer the impending migration distance the larger the departing fat load predicted (Alerstam and Lindstrom, 1990, Alerstam and Hendenstrom 1998, Piersma 1998).

Variation in migration strategy for shorebirds may occur not only among species, but within species as well. As timing of arrival on the breeding grounds may be related to territory acquisition (Pitelka 1959, Farmer and Wiens 1999), male shorebirds often migrate before females. For example, Farmer and Wiens (1999) observed evidence of a time minimization strategy in male Pectoral sandpipers on spring migration, but a mixed time/energy-minimization strategy for females. In addition to migration strategy, habitat-use patterns while at stopover sites may also vary by sex and age class. Fernandez and Lank (2006) found female and juvenile Western sandpipers (*Calidris mauri*) use less preferred habitats more often than adult males during winter. Similar variation in habitat use within species has been observed across regional (Warnock 1990, Cresswell 1994, Shepherd and Lank 2004, Fernandez and Lank 2006) and latitudinal scales (Myers 1981, Shepherd *et al.* 2001, Nebel *et al.* 2002). Male Western sandpipers, for example, are predominant in northern non-breeding habitats on the Pacific coast, while the reverse occurs toward the southern end of the species' wintering range in Ecuador (Nebel et al. 2002).

Considering the complexities of migration ecology, predicting impacts of future environmental change at a non-breeding site to shorebird populations requires a detailed understanding of the variation in habitats used according to migration strategy and demographic differences, as well as the impact to migratory fitness of variation in habitat quality during stopover. Despite an increased awareness of the importance of many Gulf sites for significant concentrations of shorebirds following research surrounding the

Deepwater Horizon oil spill (M. Gutowski, Manomet, pers. communication), to date few researchers have investigated habitat use and migration strategies of non-breeding shorebirds on the NGOM (Withers 2002). The overall goals of this dissertation are accomplished in the form of four individual chapters (intended for separate publication) investigating the importance of the NGOM to migratory shorebirds. Following this introduction, Chapter 2 is a forum paper that uses the context of the Deepwater Horizon oil spill to discuss the populations of shorebirds using NGOM habitats, the effects of oil on birds, and the importance of improving our understanding of migratory connectivity in this group. Chapter 3 does a more detailed analysis of the effects of the Deepwater Horizon oil spill on seven species of shorebirds that use NGOM habitats. Shorebirds provide a good study system for evaluating exposure to oil because they vary widely in their habitat use, allowing for an assessment of effects from oil across the coastal landscape. In Chapter 3 I also discuss the variation in fuel stores and refueling rates according to site oil and disturbance level in one target migrant species, Dunlin. Chapter 4 analyses theoretically the variation in migration ecology of three species of shorebirds, Semipalmated sandpiper *(Calidris pusilla),* Western sandpiper (*C. mauri*), and Dunlin (*C. alpina*). In this chapter I applied one of the tenets of migration theory, that the timing of migration departure is limited by a bird's ability to acquire sufficient energy reserves to reach the next stopover site, to investigate variation in migration strategies among target species. I compared stopover duration, body condition (fat scores and size-adjusted mass), and refueling rate (plasma metabolite concentrations), after leaving the NGOM. I predicted that Dunlin, a jump migrant, would reach higher fuel loads, have higher refueling rates and/or stopover for longer periods on the NGOM than Semipalmated sandpipers and Western sandpipers, which make shorter distance skips or hops during their migration. In the final chapter 5, I investigated how habitat influences the migration ecology of the same three target species by examining the variation in habitat use across species, habitat partitioning within species, and relative habitat quality of three habitat types found on the NGOM. Habitat quality was measured using foraging habitat availability, resource abundance, and relative fattening rate as measured by plasma metabolites.

This research is particularly timely from a management and conservation perspective. The NGOM has experienced significant environmental degradation over the last 50 years, and faces increasing threats from climate change and an expanding energy industry (Needham et al. 2012, Gulf Research Program 2014). Additionally, a number of coastal restoration efforts have been proposed for the NGOM following the Deepwater Horizon oil spill (Gulf Coast Ecosystem Restoration Council, 2013). By establishing a clearer picture of the habitat use patterns and ecology of shorebirds on the NGOM, we will be better able to monitor the on-going effects of the Deepwater Horizon spill, and evaluate the impacts of proposed habitat restoration plans.

2. LARGE-SCALE IMPACTS OF THE DEEPWATER HORIZON OIL SPILL: CAN LOCAL DISTURBANCE AFFECT DISTANCE ECOSYSTEMS THROUGH MIGRATORY SHOREBIRDS? [1]

ABSTRACT

The 2010 Deepwater Horizon oil spill, the largest ever accidental release of oil into marine waters, affected hundreds of miles of US northern Gulf of Mexico coastline that is important habitat for migratory shorebirds. Shorebirds are particularly susceptible to oil contamination because of their subsurface probe-foraging behavior and reliance on intertidal habitat. More than one million migratory shorebirds representing 28 species were potentially exposed to Deepwater Horizon oil during their 2010–2011 nonbreeding season. Although only 8.6% of the shorebirds trapped from fall 2010 to spring 2011 showed visible signs of oiling, nonlethal effects and degradation of habitat can affect populations in ways that carry over into subsequent seasons. Here, we discuss how the spill could affect populations of migratory shorebirds through acute mortality, as well as through long-term and indirect pathways. We also discuss the potential impacts on ecosystems far from the spill, including prairie grasslands and the Arctic, where migratory shorebirds breed.

Keywords: shorebirds, migration, Deepwater oil well blowout, carryover effects

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INTRODUCTION

On 20 April 2010, the *Deepwater Horizon* (DWH) oil platform, situated 45 miles southeast of Venice, Louisiana, exploded and sank, causing the subsequent release of an estimated 4.9 million barrels of oil, the largest accidental marine oil spill in US history (Graham et al. 2011). More than 650 miles of the northern Gulf of Mexico (NGOM) coastline was directly affected by the spill (Graham et al. 2011), as a mixture of crude oil and chemical dispersants soiled beaches, mudflats, and coastal wetlands. Although much of the oil was collected, dispersed, or dissolved, as of July 2011, one year after the DWH oil well was capped, at least 490 miles of NGOM coastline remained contaminated by oil (as was reported by Polson 2011).

Shorebirds (order Charadriiformes, excluding suborders Lari and Turnici) are particularly vulnerable to oil spills, because they spend much of their time foraging in readily oiled, intertidal shoreline habitat (Peterson et al. 2003, OSAT-2 2011). Shorebirds are also of high conservation concern because many shorebird populations are declining (Morrison et al. 2006), and their habitat is vulnerable to sea-level rise and other effects of climate change. The beaches and wetlands along the NGOM affected by the DWH oil are important habitats for 34 species of shorebirds (Withers 2002). Of these, 6 species are considered resident and 28 are migratory species that spend all or part of their nonbreeding seasons on the NGOM coast. The breeding range of the nonresident species extends from the temperate prairie and wetlands of North America to the high Arctic (figure 2.1). For many species, the wetlands and barrier islands of the NGOM coast represent the first areas of suitable wintering habitat or stopover habitat between northern breeding grounds and distant wintering grounds in South America (Withers 2002).

Oil can affect birds in a variety of ways, and exposure to oil is not necessarily fatal. Instead, repeated exposure to oil within and between seasons may have sublethal effects that can lead to population-level impacts through diminished health and reproductive fitness. Some shorebirds have strong site fidelity to wintering and stopover sites (Drake et al. 2001), which makes them susceptible to repeated exposures as they return to contaminated habitats year after year. The importance of nonbreeding habitats to the conservation of migratory populations is becoming clearer as many species face increasing rates of habitat degradation and environmental change. In migratory birds, the conditions encountered in nonbreeding habitats can affect survival and reproductive success (reviewed in Harrison et al. 2011).

Relatively few oiled shorebird carcasses were collected during and immediately following the DWH spill; most of the bird carcasses found were from larger species (e.g., brown pelicans [*Pelecanus occidentalis*], northern gannets [*Morus bassanus*], laughing gulls [*Leucophaeus atricilla*]; USFWS 2011). However, out of the 220 shorebirds that we captured with mist nets between October 2010 and May 2011, 19 were visibly oiled. We also expect that a far greater proportion of shorebirds was exposed by oil ingestion, which cannot be detected through visual examination.

Although the Natural Resource Damage Assessment and Restoration program (NRDARR) includes components that are focused on shorebirds, including studies on the endangered piping plover (*Charadrius melodus*) and shorebird abundance surveys (NRDAR 2011), a better understanding of the extent that shorebirds were affected by the spill must wait until these data are released from the NRDAR confidentiality agreement. In addition, plans for a long-term assessment of the effects of the DWH oil on shorebird species are not apparent (NRDAR 2011). Shorebirds and nesting sea turtles are two groups of organisms identified by the US Coast Guard's Operational Science Advisory Team that face longer-term elevated risks of exposure from remnant beached oil (OSAT-2 2011). Although the immediate impacts of oil on shorebirds following smaller oil spills have been assessed (Burger 1997), the indirect and long-term impacts of oil on shorebirds have been measured in relatively few studies (but see Andres 1997). Our aim in this article is to explore the potential consequences of the DWH incident on migratory shorebirds across temporal and spatial scales and to highlight areas of further research necessary to address these effects.

POPULATIONS MOST AT RISK

Quantifying the impact of the DWH spill on shorebird populations is challenging, given the lack of baseline data regarding population sizes, habitat use, and migration strategies of nonbreeding shorebirds on the NGOM. Out of a total of 7258 live and dead birds recovered before 12 May 2011, 85 were shorebirds, and only 23 of those were identified as visibly oiled (USFWS 2011). However, given their small size and the difficulty of finding shorebird carcasses in sufficient condition to determine their oiling status (Burger 1997), we suspect that many more shorebirds were lost. Using population estimates compiled from several sources (see Table 2.1), we calculate that more than one million shorebirds migrate through the NGOM (from northern Texas to the Florida Panhandle). Considering that 8.6% of the shorebirds captured in the year following the

DWH spill showed some signs of visible oiling, as many as 86,000 shorebirds were potentially affected by trace or light oiling of their feathers. However, an unknown but substantially larger number of shorebirds was likely exposed through direct ingestion of tarballs while foraging or through the consumption of contaminated prey (Burger 1997).

During the nonbreeding season, the NGOM hosts more than 5% of the total North American population for 12 of the 28 migratory species that use its habitats (Figure 2.1, Table 2.1). Within the NGOM, there are three sites used by 10 of these species that are classified as regionally important, which means that more than 1% of at least one shorebird species' total population has been documented at the site (Table 2.1; Manomet 2010). For these populations, the potential effects from the DWH spill will be more severe if the same individuals that winter or stopover together on the GOM remain together during the breeding season. Unique-color banding of the endangered piping plover, one of the most intensively studied shorebirds, shows that a relatively large proportion of the breeding populations remain together throughout migration and winter (i.e., strong migratory connectivity; Gratto-Trevor et al. 2012). Although all four breeding populations (defined by their locations in the Canada Prairies, the Great Plains, the Great Lakes, and in Eastern Canada) of piping plover overwinter along the southeast Atlantic and GOM coasts, the eastern and western breeding birds remain relatively segregated during winter. Of the piping plovers color banded at the four breeding locations and resighted on their wintering grounds, 28% of the Great Plains birds and 26% of the Canada Prairies birds were observed in the NGOM (figure 2.2; Gratto-Trevor et al. 2012). In comparison, none of the Eastern Canada population and only 4.6% of the US Great Lakes population was observed in the NGOM. This highlights the importance of understanding migratory connectivity to better assess the impacts of disturbance to the nonbreeding grounds on a population. Given the already-degraded habitat, low population numbers (2959 individuals; Elliot-Smith et al. 2009[2]) and recent flooding of piping plover breeding grounds in the US Great Plains, the impact of the DWH spill on the Great Plains population is likely to be the most acute.

Our understanding of migratory connectivity in piping plovers allows researchers to focus impact studies on the most affected populations, optimizing the use of funding and increasing our chances of detecting population-level effects of the spill (NRDAR 2011). There is evidence of similar migratory connectivity in other declining, long-distance migrant shorebird species that are potentially affected by the spill. The breeding range of a subspecies population of dunlin (*Calidris alpina hudsonia)* known to overwinter on the NGOM coast is believed to be limited to northeastern Canada (Figure 2.2). However, we lack information on demographics and nonbreeding site fidelity along the GOM coast for this subspecies. Additional information regarding the migratory connectivity for shorebirds using contaminated GOM habitats during the nonbreeding season is necessary to make accurate predictions of population-level effects.

THE EFFECTS OF OIL ON MIGRATORY SHOREBIRDS

Migratory shorebirds provide a system for evaluating the direct and indirect effects of an oil spill on affected habitats and the potential for carryover effects to other ecosystems. The foraging ecology and habitat-use patterns of shorebirds make them particularly susceptible to oiling through a diverse set of contamination pathways

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[2] U.S. Northern Great Plains 2006 International Piping Plover Census population estimate (Elliot-Smith et al. 2009).

(Figure 2.3) and, since migration is energetically and physiologically demanding, the sub-lethal effects of oil may have severe consequences that lead to population-level effects. Migration also provides a mechanism whereby the effects of the spill may be transported to ecosystems far removed from those in the immediate vicinity of the contamination. Figure 2.1 shows the breadth of regions that are potentially affected by the DWH spill through migratory shorebirds. Below, we give a brief overview of the diverse effects of oil on migratory birds.

Lethal effects

Oil causes the direct, immediate mortality of birds through several pathways (Figure 2.3). Oil on feathers destroys their waterproofing and insulating capabilities, which leads to the birds' death from hypothermia (reviewed in Leighton 1993). Other effects of direct oil exposure include dehydration, starvation, arthritis, gastrointestinal problems, infections, pneumonias, cloacal impaction, and eye irritation (Briggs et al. 1996). Many of these effects are the result of oil ingestion, which can occur through the preening of oiled feathers (Leighton 1993, Briggs et al. 1996). However, in shorebirds, oil ingestion by foraging in contaminated habitats and consumption of contaminated prey may be a major contamination pathway and warrants further investigation (Burger 1997, NRC 2003, OSAT-2 2011). Mortality from ingested oil is primarily caused by acute toxic effects on the kidney, liver, and gastrointestinal tract (Briggs et al. 1996).

Diminished health

Ingested oil can have several sub-lethal toxicological effects, including hemolytic anemia, reduced reproduction, and immunosuppression. Hemolytic anemia in birds exposed to oil is caused by an oxidative process that forms Heinz bodies in red blood cells, which eventually destroys the cells (Leighton 1993). Although it is not necessarily lethal, Heinz-body anemia decreases a bird's ability to transport oxygen, which can be particularly detrimental to migratory birds because of the aerobic requirements of long-distance migratory flight and the heightened oxygen demands of the larger body mass of fattened migrating birds. Heinz-body anemia also reduces breeding success by preventing or impairing egg formation and egg laying (Leighton 1993). As a response to the destruction of red blood cells from oil ingestion, there is a compensatory increase in erythrocyte production, which results in immunosuppression and in a decline in white blood cell production. Another pathway through which the immune system may be affected by oil ingestion is damage and inflammation of the gastrointestinal tract (Briggs et al. 1996). This affects the function of the mucosal membrane, which is important in intestinal immune function. The gastrointestinal tract of birds is also important for T and B lymphocyte development. Indirectly, damage to the intestinal tract has negative impacts on nutritional uptake, which can also cause immunosuppression. In addition, oil exposure is associated with increased corticosteroid production, which has a negative impact on the effectiveness of circulating lymphocytes, which thereby decreases immune function (Briggs et al. 1996).

Oiled birds may also experience decreased foraging success due to a decline in prey populations following a spill (Andres 1997, NRC 2003) or due to increased time preening to remove oil from their feathers (Burger 1997). During both winter and migration, shorebirds spend much of their time feeding and depend on nonbreeding habitats to provide the fuel necessary for migratory flight (Withers 2002). Red knots (*Calidris canutus*) stopping over at Delaware Bay experience a decrease in refueling rates that has an impact on individual fitness for the remainder of the migration and may even be responsible for population declines (Baker et al. 2004). If oil from the DWH spill reduces foraging success and habitat quality for migratory shorebirds, subsequent weight loss and diminished health may delay the birds' departure, decrease their survival rates during migration, or reduce their reproductive fitness.

Prey and habitat switching

Oil can reduce invertebrate abundance or alter the intertidal invertebrate community that provides food for nonbreeding shorebirds (Andres 1997, NRC 2003). Reduced abundance of a preferred food may cause shorebirds to move and forage in other—potentially lower-quality—habitats. Following the 2003 *Prestige* oil spill off of the northwest coast of Spain, the reproductive performance of European shag (*Phalacrocorax aristotelis*) declined, their chick condition worsened, and the number of breeding adults decreased significantly (Velando et al. 2005). These changes were attributed to an indirect negative impact mediated by a more-than-25% reduction in the consumption of sandeel (family Ammodytidae), the preferred fish prey of European shag (Velando et al. 2005). Prey switching has not been documented in shorebirds following an oil spill. However, shorebirds will feed in alternative habitats when the intertidal zone alone cannot fulfill their energy requirements. For example, ruddy turnstones (*Arenaria interpres*) wintering in England switched from feeding on intertidal cockles to feeding on human-spilled wheat grain and fishmeal during periods of decreased cockle abundance

(Smart and Gill 2003). Nonbreeding shorebirds along the GOM coast will forage in agricultural fields during migration and throughout winter when the conditions are suitable (Vermillion 2011). A reduction in habitat quality and resource abundance in the intertidal zone by the DWH spill may increase the importance of agricultural fields as buffer habitats. This change could result in decreased fitness during the nonbreeding season and could also result in carryover effects, such as decreased breeding success. Gunnarsson and colleagues (2005) used carbon stable isotope ratios ($^{13}C/^{12}C$ expressed as delta ^{13}C ($\delta^{13}C$)) of feathers grown on the wintering grounds by black-tailed godwits (*Limosa limosa*) to measure the habitat quality of the wintering grounds. They found that individuals wintering in high-quality coastal habitats, characterized by high $\delta^{13}C$ ratios, had greater reproductive success than those wintering in poorer-quality inland habitats, characterized by low $\delta^{13}C$ ratios.

Diminished plumage quality

Birds wintering or stopping over in oiled habitats may show poor feather condition and dulled plumage before spring departure as a result of decreased health or diminished energy accumulation. The completeness and color of breeding plumage is a direct indication of physical condition (i.e., an honest signal of quality) in some birds (Piersma and Jukema 1993). Many shorebird species begin molting into breeding plumage before spring migration, which means that the quality of their breeding plumage can be influenced by the quality of their wintering or stopover habitats. Piersma and Jukema (1993) found a positive correlation between the completeness of breeding plumage and body mass in bar-tailed godwits (*Limosa lapponica*) during spring migration. Germain and colleagues (2010) measured the amount of breeding plumage in American redstarts (*Setophaga ruticilla*) and found a significant positive correlation between the amount of black breast plumage and birds wintering in high-quality habitat and a negative correlation between the amount of black breast plumage area and arrival time on the breeding grounds, both of which are indications of increased breeding success. Similar to redstarts, many shorebirds have melanic breeding-plumage coloration. A decrease in plumage quality or brightness could result in decreased breeding success for oil-affected birds and warrants further investigation.

Delayed migration

A bird's inability to obtain adequate resources delays its premigratory fattening and can delay the departure for its breeding grounds. Birds arriving on their breeding grounds earlier realize higher reproductive success through increased clutch size and offspring survival (for a review, see Harrison et al. 2011). If GOM coast habitats are sufficiently degraded by oil that premigratory fattening is slowed and birds delay departure for their breeding grounds, the individual effects could carry over into the breeding season and into distant breeding habitats.

LONG-TERM IMPACTS

Evidence from previous oil spills suggests that the impacts of the DWH incident are not likely to be limited to immediate or short-term effects (Peterson et al. 2003, Short et al. 2007). Oil contaminants, including polycyclic aromatic hydrocarbons (PAHs), which are some of the most harmful components of oil, can remain in the environment for decades. Sixteen years after the *Exxon Valdez* oil spill in Prince William Sound, Alaska, Short and colleagues (2007) identified slightly weathered oiled from the spill in subsurface sediments. Long-term exposure and ingestion of PAHs is carcinogenic, and there is evidence that PAHs may be incorporated into the food chain, although they do not biomagnify at higher trophic levels (NRC 2003, Peterson et al. 2003). Weathered oil has been shown to reduce hatching success in exposed mallard eggs (Finch et al. 2011), and adverse effects from the leaching of PAHs from weathered oil have been observed years after the *Exxon Valdez* oil spill (Esler et al. 2002, 2010). Documentation of the long-term effects of residual oil, however, is difficult and requires many years of research. For example, PAHs were found in yellow-legged gull (*Larus michahellis*) chicks 17 months following the *Prestige* spill (Alonso-Alvarez et al. 2007). These chicks were never directly exposed to spilled crude oil, and their parents showed no evidence of external oiling, which suggests that the contamination had been incorporated into the food chain. Given the warm climate of the NGOM and some evidence of increased microbial respiration (e.g., Edwards et al. 2011), it has been suggested that the persistent effects of oil observed following other large spills will not be as severe following the DWH spill. However, almost 500 miles of coastline remained contaminated by weathered oil a year after the oil stopped leaking (as was reported by Polson 2011).

The attribution of population-level effects to specific oil spills at longer temporal scales can be difficult and controversial. For example, although early studies suggested that the effects of the *Exxon Valdez* oil spill were short lived for most bird species, such as the harlequin duck (*Histrionicus histrionicus*; for a review, see Wiens et al. 2010), 10 years after the spill, female harlequin ducks that wintered in previously contaminated sites had significantly lower survival rates than those that wintered in uncontaminated sites (Esler et al. 2002). Other researchers, citing evidence that the numbers of harlequin ducks were lower in contaminated regions than in uncontaminated regions before the *Exxon Valdez* oil spill, have suggested that the different survival rates could be explained by differences in the intrinsic habitat quality of the two sites (for a summary, see Wiens et al. 2010). More recently, researchers have refuted this suggestion by demonstrating the return of winter survival rates in oiled sites 11–14 years after the *Exxon Valdez* oil spill to levels observed across the study period in the uncontaminated habitats (Esler and Iverson 2010).

Similarly, attribution to the *Exxon Valdez* oil spill of increased induction of cytochrome P4501A (CYP1A), a biomarker that is a sensitive indicator of exposure to PAHs, in harlequin ducks both a decade and two decades after the *Exxon Valdez* oil spill has been disputed (discussed in Esler et al. 2010). Some researchers have argued that although elevated CYP1A expression can indicate exposure to PAHs, there are many potential sources of PAHs in Prince William Sound that are not related to the *Exxon Valdez* oil spill (for a summary, see Wiens et al. 2010).

The debate about the attribution of effects from the *Exxon Valdez* oil spill appears to be driven, in large part, by a lack of baseline prespill data. The ecological risk-assessment approach used to quantify the intensity and duration of impacts to populations and ecosystems from environmental disasters requires the establishment of recovery endpoints that represent a return of a population or habitat to some prespill state. Without baseline data, endpoints are difficult to assess and are likely to be highly controversial. As in the case of harlequin ducks (Esler et al. 2002), very little is known about the prespill population densities, habitat use, or age:sex ratios of migratory shorebirds on the NGOM. If the changes in overwinter survival rates experienced by harlequin duck populations resulted from the *Exxon Valdez* oil spill, the site fidelity to nonbreeding habitats exhibited by shorebirds (Drake et al. 2001) would suggest that shorebird populations will continue to experience effects from the DWH spill for years to come. Attributing population-level effects in shorebirds potentially exposed to DWH oil will be difficult, given the many other threats facing shorebird populations, including climate change, habitat loss, and the background levels of oil present in the GOM as a result of natural oil seeps and an oil industry that has been in place for over half a century. A careful examination of environmental and spatial variation when comparing sites is necessary to assess the long-term effects of oil exposure. Therefore, to link changes in shorebird populations to the DWH spill, it will be essential to implement long-term research plans in which sources of variation other than contamination by DWH oil are accounted for. Unfortunately for shorebirds, no such studies appear to have yet been initiated in the damage-assessment plan (NRDAR 2011).

THE ECOLOGICAL COMMUNITIES AT RISK OUTSIDE THE GOM

Population declines of migratory shorebirds and reduced breeding productivity as a result of the DWH spill may have an impact on ecosystems outside the GOM (figure 2.1). In this section, we discuss the ecosystems most likely to be affected—those in which GOM shorebirds stop over during migration and spend the breeding season.

Stopover migration

Migrating shorebirds are a major food source for avian predators, including peregrine falcons (*Falco peregrinus*) and merlins (*Falco columbarius*). Although these avian predators are not likely to have direct contact with DWH oil, they may experience indirect impacts by consuming contaminated prey, such as shorebirds. A single merlin has been observed consuming an average of 2 shorebirds per day across the nonbreeding season, or about 295 shorebirds over a five-month period (Page and Whiteacre 1975). Following the 2002 *Prestige* oil spill, Zuberogoitia and colleagues (2006) found PAH concentrations from 21.20 nanograms per gram (ng/g) to 461.08 ng/g in eggs from peregrine falcon nests around the area of the spill. These high concentrations were probably the result of adults feeding on contaminated shorebird prey and passing the contamination on to embryos during egg production. PAH contamination was also observed at inland peregrine falcon nests, far from the spill, which suggests that it was from preying on contaminated shorebirds stopping over during migration at inland rivers (Zuberogoitia et al. 2006). A similar indirect exposure to predators could occur within ecosystems across the migration pathways of shorebirds in North America.

Upland prairie

Several species of shorebirds that overwinter and stop over along the GOM coast breed in the mixed-grass prairie habitats of North America (Gratto-Trevor 2006), which are threatened by conversion to agriculture. Prairie food webs are complex, and therefore, the effects of declines in shorebird abundance are difficult to predict. Shorebird and waterfowl nests are important food resources for predators in prairie ecosystems, and a decline in shorebird abundance can increase predation pressure on waterfowl that nest in the same region (Gratto-Trevor 2006). Such effects may be exacerbated by the extensive habitat loss and degradation that has already occurred in the prairie pothole regions of central North America, which has lead to waterfowl population declines (Gratto-Trevor 2006).

Arctic and subarctic regions

An estimated 30 million shorebirds breed in the high Arctic (Lanctot 2004), and another 7 million breed in the boreal forests of North America (Wells and Blancher 2011). The yearly influx of shorebirds into these ecosystems provides a vital food source for predators such as the snowy owl (*Bubo scandiacus*) and the arctic fox (*Alopex lagopus*). This is particularly true during low phases of the lemming (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*) abundance cycles, when shorebirds and waterfowl are the primary alternative prey for these predators (Gilg and Yoccoz 2010). Shorebird nest success can increase as much as 75% between high- and low-lemming-abundance years (McKinnon 2011), which indicates the potential importance of shorebirds as a buffer for Arctic predator populations. For example, the estimated home range of a male arctic fox is 10.22 square kilometers (km^2) (standard deviation= 6.18) (Anthony 1997). Using an upper limit of observed shorebird nest densities (80 per km^2; Cotter and Andres 2000) and an average of four eggs per nest, approximately 3270 shorebird eggs may be found in the territory of an arctic fox family. Careau and colleagues (2008) calculated the metabolized energy value of greater snow geese (*Chen caerulescens atlantica*) to the arctic fox's daily survival. Adjusting for shorebird egg size (one seventeenth the size of a snow goose egg; McKinnon 2011), we calculate that if every shorebird egg within a territory were consumed, this would be the caloric equivalent of 141 arctic fox pup rearing days (1112 kilojoules per day; Careau et al. 2008), or 1.48 additional pups. This suggests that any significant decrease in shorebird productivity could have a significant impact on arctic foxes, especially during low-lemming-abundance years. Because of the relatively low diversity of Arctic terrestrial vertebrate communities, any changes in community structure can quickly cascade through trophic levels (Gilg and Yoccoz 2010). Therefore, diminished availability and productivity of breeding shorebirds resulting from the degradation of their nonbreeding habitat has the potential to have a drastic impact on Arctic predators, and these impacts could cascade through Arctic food webs.

CONCLUSIONS

Shorebird populations of the NGOM coast are likely to experience both direct and indirect effects from the DWH oil. Shorebirds that use the NGOM are already facing a diverse array of threats, including habitat loss caused by wetland erosion from shipping, sea level rise, and human development. The DWH oil spill, occurring as it has in the context of these multiple other stressors, has likely added an additional burden to an already stressed system.

To monitor the impacts of the DWH disaster, it is important that researchers measure not only acute mortality in these species but also that they look for evidence of long-term, sublethal effects. Measuring these effects throughout the annual cycle in migratory species will be challenging, because migratory connectivity is difficult to discern and not well understood in many GOM coast species. Emerging technologies, such as stable isotope analysis, genetic markers, geolocators (global location sensors), and satellite telemetry, provide researchers with tools to uncover the connectivity of migratory populations (Robinson et al. 2010) and should be employed in efforts to quantify the effects of the DWH spill and other future environmental disasters. For example, Montevecchi and colleagues (2011) used geolocators to estimate the population size of adult northern gannets wintering in areas on which the DWH spill has had an impact. In comparison with band recoveries, their estimate increased by over 50,000 (53.7%) when they used information retrieved from geolocators.

As our knowledge of migratory connectivity grows, so does our understanding that ecosystem dynamics are not driven entirely by local events but, through migratory animals, can be influenced by events taking place in distant locations. The DWH oil spill is one such event that, through migratory shorebirds and other highly mobile species, may affect ecosystems far distant from the coastline along which the spill occurred. An increased awareness of the large temporal and spatial scales at which local habitat degradation can have measurable impacts on populations and ecosystems should be an important component of monitoring and planning for the effects of this and other future challenges, such as those presented by climate change, on migratory species.

ACKNOWLEDGEMENTS

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Table 2.1. North American and northern Gulf of Mexico (NGOM) population estimates for migratory shorebirds.

Species	**Conservation trend**[a]	**North American (NA) population**	**NGOM population**	**NGOM population percentage of NA population**	**Regionally important site**[e]
American golden-plover	Apparent population decline	150,000[a,d]	1851	0.92	Grand Terre, LA
American woodcock	Endangered or significant population decline	3,500,000[a,d]	49	<0.01	
Black-bellied plover	Apparent stable population or unknown	200,000[a,b]	12,500	6.25	
Buff-breasted sandpiper	Apparent population decline	40,000[a,b]	8360	20.9	
Dunlin	Apparent population decline	1,525,000[a,b]	97,692	6.41	Bolivar Flats, TX; Grand Terre, LA
Greater yellowlegs	Apparent stable population or unknown	100,000[a,b]	8250	8.25	
Hudsonian godwit	Apparent stable population or unknown	70,000[a,d]	206	0.29	
Least sandpiper	Endangered or significant population decline	700,000[a,b]	43,750	6.25	Bolivar Flats, TX
Lesser yellowlegs	Apparent stable population or unknown	400,000[a,b]	33,000	8.25	
Long-billed curlew	Endangered or significant population decline	100,000[a,b]	4620	4.62	
Long-billed dowitcher	Apparent population increase	1,000,000[a,b]	59,500	5.95	
Marbled godwit	Apparent population decline	171,500[a,d]	652	0.38	
Pectoral sandpiper	Apparent stable population or unknown	500,000[a,b]	37,800	7.56	
Piping plover	Endangered or significant population decline	8092[c,d]	582	9.39	Bolivar Flats, TX
Red knot	Endangered or significant population decline	120,000[a,d]	910	0.76	Bolivar Flats, TX
Ruddy turnstone	Apparent population decline	245,000[a,d]	811	0.35	Bolivar Flats, TX
Sanderling	Apparent population decline	300,000[a,d]	3565	1.18	Bolivar Flats, TX
Semipalmated plover	Apparent stable population or unknown	150,000[a,d]	1072	0.72	Bolivar Flats, TX
Semipalmated sandpiper	Endangered or significant population decline	2,000,000[a,b]	139,000	6.95	
Short-billed dowitcher	Apparent population decline	153,000[a,b]	9869	6.45	
Solitary sandpiper	Apparent stable population or unknown	150,000[a,d]	69	0.05	

Spotted sandpiper	Apparent stable population or unknown	150,000[a,d]	96	0.06	
Stilt sandpiper	Apparent stable population or unknown	820,000[a,b]	114,800	14.0	
Western sandpiper	Apparent stable population or unknown	3,500,000[a,b]	409,500	11.7	Bolivar Flats, TX
Whimbrel	Endangered or significant population decline	66,000[a,d]	3553	5.38	Anahuac N.W.R., TX
White-rumped sandpiper	Apparent stable population or unknown	1,120,000[a,d]	1687	0.42	
Wilson's snipe	Endangered or significant population decline	2,000,000[a,d]	1370	0.07	
Wilson's phalarope	Apparent population decline	1,500,000[a,b]	11,530	0.77	
Total			**1,006,643**		

[a] Morrison et al. 2006.
[b] Vermillion 2011.
[c] Elliot-smith et al. 2009.
[d] *www.ebird.org*.
[e] Used by more than 1% of the population (Manomet 2010).

Figure 2.1. Breeding ground distributions of migratory shorebirds species for which the northern Gulf of Mexico (NGOM) is used as wintering or stopover habitat. (a) Shorebird species of low to moderate concern (conservation trend rank 2–3; Morrison et al. 2006) in which less than 5% of the North American population uses the NGOM (see Table 2.1). (b) Shorebird species of low to moderate concern (conservation trend rank 2–3), in which more than 5% of the North American population uses the NGOM. (c) Shorebird species of high concern (conservation trend rank 4–5; Morrison et al. 2006) in which less than 5% of the North American population uses the NGOM. (d) Shorebird species of high concern (conservation trend rank 4–5) in which more than 5% of the North American population uses the NGOM. Distributions are adapted from data from the Birds of North America Web site (www.bna.birds.cornell.edu).

Breeding distributions of shorebird species with populations that overwinter or stop over in the Gulf of Mexico

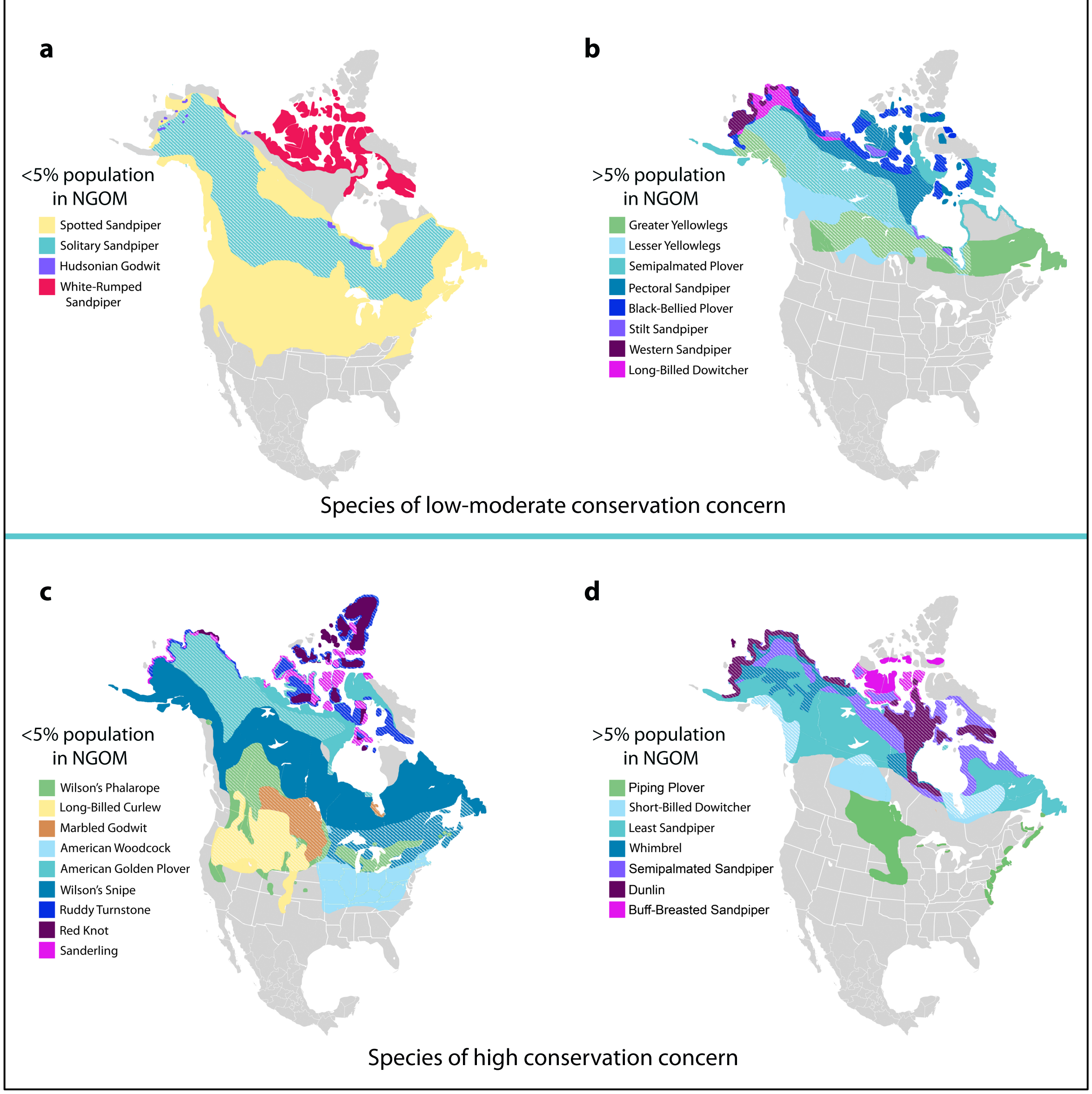


Figure 2.2. Breeding ground and wintering distributions of (a) Dunlin (*Calidris alpina*) and (b) Piping plover (*Charadrius melodus*), two shorebird populations assessed to be the most at risk to impacts from the Deepwater Horizon spill through migratory connectivity. Source: The distributions are based on data from the Birds of North America Web site (www.bna.birds.cornell.edu).

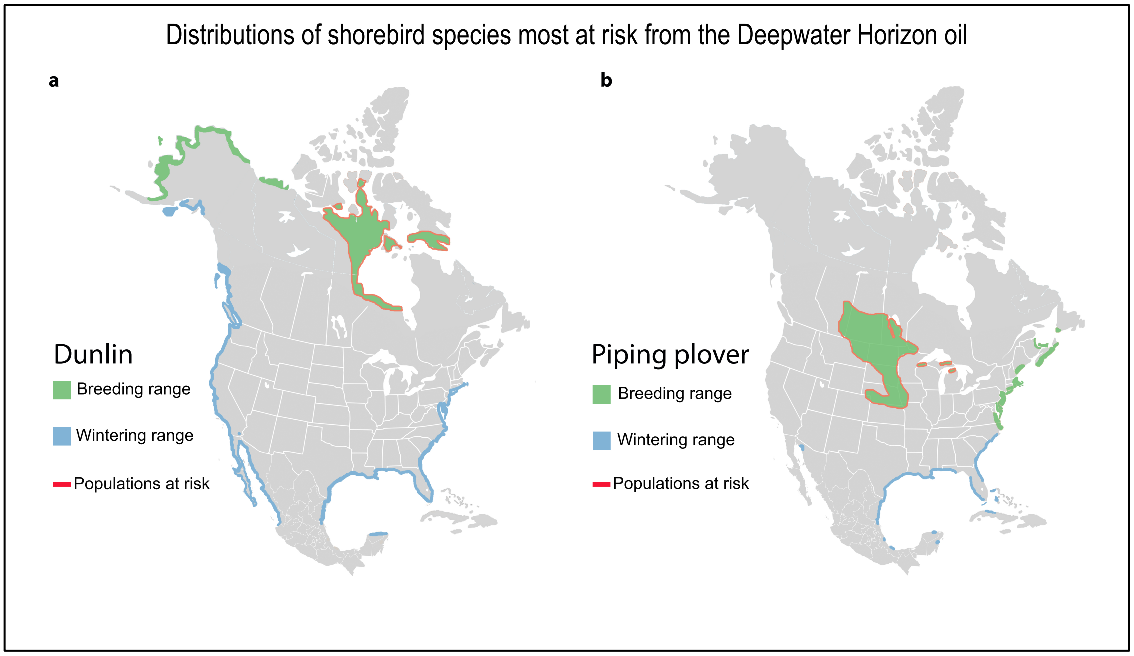
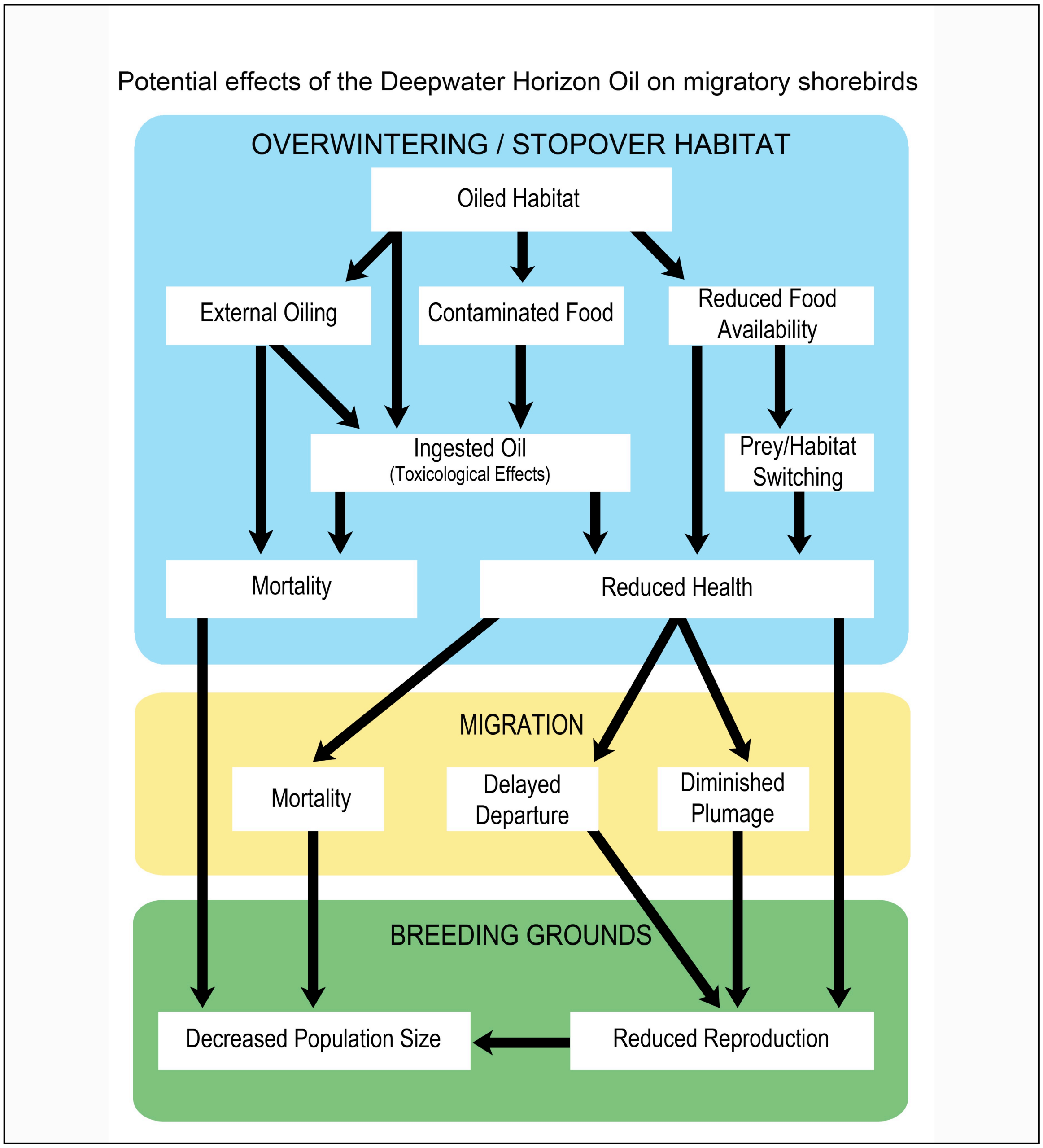


Figure 2.3. Oil contamination pathways and potential carryover effects at each stage of the annual cycle (overwintering or stopover habitat, migration, and breeding) for migratory shorebirds.



3. OILING RATES AND CONDITION INDICES OF SHOREBIRDS ON THE NORTHERN GULF OF MEXICO FOLLOWING THE DEEPWATER HORIZON OIL SPILL[1]

ABSTRACT

The coastline of the Gulf of Mexico in the United States is an important wintering and stopover region for migratory shorebirds. The Deepwater Horizon oil spill (April–August 2010) impacted more than 1700 km of this coastline and could potentially affect shorebirds through long-term exposure to toxins, degraded habitats, and altered food chains. We investigated the exposure to Deepwater Horizon oil of seven species of shorebirds that winter or stopover along the northern Gulf of Mexico. From October 2010 to May 2012, we captured and banded 691 shorebirds at six sites that experienced varying levels of oil contamination. Of birds sampled, 22 were lightly oiled, with species that forage on the coast having higher rates of oiling than those that forage in more estuarine habitats. Although only 8.6% of birds captured from October 2010 to May 2011 and 0.6% of the birds captured from August 2011 to June 2012 showed signs of oiling, an unknown, but potentially larger, number of shorebirds were likely exposed to indirect effects of the spill, such as decreased foraging time due to oiling of sites or disturbance

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from cleanup activities. Fuel stores and fattening rates of Dunlins (Calidris alpina) during spring migration, as measured using plasma metabolites, were not influenced by site oiling level. However, the level of disturbance at study sites was a significant predictor of both fuel stores and glycerol levels, suggesting that Dunlins stopping over during spring migration may have had difficulty reaching necessary fuel stores in spring 2011 due to disturbance from cleanup activity on oiled beaches. These effects from disturbance were only observed at sites with high cleanup activity, suggesting that the impact of oil-spill cleanup on shorebirds may be minimized by limiting cleanup activities to specific areas and times of day.

Key words: disturbance, fuel load, migration, refueling rate, plasma metabolites

INTRODUCTION

The beaches and wetlands of the northern Gulf of Mexico (hereafter GOM) are important habitats for 34 species of shorebirds (Withers 2002). During the nonbreeding season, these habitats host more than 5% of the total North American population of 12 species of migratory shorebirds (Henkel et al. 2012). Habitats of the NGOM face persistent threats from both environmental and anthropogenic change. Louisiana, for example, is experiencing the most severe land loss and barrier island erosion in North America (Penland and Ramsey 1990). Other threats include habitat loss due to shoreline development and erosion. Potential threats to shorebird populations using these vulnerable habitats were compounded when the Deepwater Horizon (hereafter DWH) oil platform exploded and sank on 20 April 2010, resulting in the release of 4.9 million barrels of crude oil (McNutt et al. 2012). Some of this oil washed up on the beaches and marshlands of the NGOM, subsequently stranding oil on 1773 km of coastline (Michel et al. 2013). Shorebirds were particularly vulnerable to this event because they forage in readily oiled, intertidal shoreline habitat (Peterson et al. 2003, OSAT2 2011).

The effects of oil on birds have been well documented (Leighton 1993, NRC 2003, Henkel et al. 2012). Extreme cases can include mortality due to a loss of waterproofing or to ingested oil, which may lead to toxicological effects, including hemolytic anemia, immunosuppression, and liver and kidney damage (Leighton 1993, Briggs et al. 1996). Although exposure to oil is not necessarily fatal, even limited exposure can negatively impact birds by reducing foraging success, either through a loss or degradation of food resources (Andres 1997, NRC 2003) or by reducing foraging time because of the need to preen oiled feathers (Burger 1997, OSAT2 2011). Cleanup activities following an oil spill can also increase disturbance and reduce foraging time for shorebirds. For example, following the Anitra oil spill off the New Jersey coast in 1996, Burger (1997) observed a significant reduction in foraging time and an increase in time spent foraging by shorebirds due to cleanup activities.

To understand the ongoing impacts of the DWH spill, methods are needed to measure long-term, sub-lethal effects. One method is to estimate mean energy stores of birds at stopover sites, measured through size-adjusted mass. Because large fuel stores are necessary for shorebirds departing on long-distance migrations (Warnock 2010), mean energy stores have been used to monitor changes in habitat quality at shorebird migration sites (Baker et al. 2004, Hicklin and Chardine 2012, Mizrahi et al. 2012).

Another potential method is to measure plasma metabolites. During spring, shorebirds minimize time spent migrating (Lyons and Haig 1995, Farmer and Wiens

1999) in an effort to quickly reach northern breeding grounds and establish breeding territories. One of the primary factors determining migration speed and success is the efficiency of refueling rates at stopover sites (Alerstam and Lindstrom 1990). Fattening rates of birds during migration may therefore be used as a proxy for habitat quality when comparing stopover sites because high refueling rates allow birds to continue migration faster. Plasma metabolites have been shown to be useful indicators of fattening rates in a variety of shorebird and passerine species (Jenni Eiermann and Jenni 1994, Williams et al. 1999, Guglielmo et al. 2005, Seaman 2005). Because levels of some plasma metabolites, such as triglycerides, increase during fat deposition and others (e.g., glycerol and β-hydroxybutyrate) increase during fat catabolism, metabolites can provide an instantaneous measure of the physiological state and energetic condition of birds. Plasma metabolites have been used as measures of habitat quality in a variety of studies where correlations between fattening rates, resource abundance, and availability of foraging habitat have been observed (Guglielmo et al. 2005, Seaman 2005, Seewagen et al. 2011). For example, Seamen et al. (2006) found that Western Sand pipers (*Calidris mauri*) using stopover sites with shorter mudflat exposure times (i.e., decreased foraging opportunities) had lower triglyceride levels during northward migration.

Different species of shorebirds use different habitats and microhabitats, facilitating assessment of contamination from oil across a coastal landscape. Sanderlings (*Calidris alba*), for example, forage primarily along tidal beach fronts (Burger and Gochfeld 1991), whereas other sandpiper species spend more time in estuaries or bayside wetlands (Holmes 1972, Baker and Baker 1973). Within habitats, shorebirds differ in their foraging behavior. Least Sandpipers (*C. minutilla*) tend to forage in brackish marshes and along the inner edge of mudflats between clumps of marine vegetation (Nebel and Cooper 2008, Mizrahi et al. 2012), whereas other estuarine species are more commonly found in open mudflat habitats (Wilson 1994, Hicklin and Gratto-Trevor 2010). Coastal wetland habitats used by shorebirds on the NGOM are primarily barrier islands (Withers 2002) where Gulf facing beaches are abutted by dunes, and the bayside/central portions of the islands consist of vegetated mudflats (Rosati and Stone 2009). These habitats experienced varying levels of oiling from the DWH oil spill. Gulfside habitats were more directly impacted by oil, but oil was also deposited in bayside habitats and vegetation by waves (Michel et al. 2013). Chapman (1984) investigated the vulnerability of a variety of shorebird species to oil spills following the Ixtoc I oil spill along the Texas GOM coast, and found that birds foraging in shoreline habitats of barrier islands were more vulnerable to oil exposure than those using the backshore.

We examined the potential indirect effects of the DWH oil spill on several species of migratory shorebirds and one species of resident shorebird over a 2yr period on the NGOM. Because birds can be impacted by even a small amount of oil, our objective was to expand on surveys conducted by the Natural Resource Damage Assessment to monitor oiling rates across species (NRDAR 2012) by examining birds in the hand so even trace amounts of oil could be detected. Our specific objectives were to quantify exposure across habitats and species with a variety of foraging behaviors, and to assess the degree to which variation in fuel stores and refueling rates could be explained by oiling and disturbance rates.

METHODS

Study sites. Beginning in October 2010, birds were captured and banded at six sites along the NGOM (Figure 3.1). These sites represented four habitat types commonly found on the GOM coast, including mudflats, back bays, sandy beaches, and remnant wetlands. These sites were selected because they host shorebird populations throughout the year and were monitored by the Audubon Coastal Bird Survey (Johnson 2011).

Site oiling level. The oiling level of each site was classified using maximum oiling categories (MAX) across 2010–2012 from Shoreline Cleanup Assessment Technique (SCAT) data from the National Oceanic and Atmospheric Administration, as well as by oiling levels following cleanup activities according to SCAT surveys from May 2011 and May 2012 (hereafter, post cleanup oil level or PC; Michel et al. 2013, Table 3.1).

Site disturbance level. The disturbance level of each site was categorized by the average number of times foraging shorebirds (both target and non-target species) were interrupted during 30min point count surveys conducted using the International Shorebird Survey Protocol (Manomet 2010). An interruption was counted if birds stopped foraging and flew > 30 m. Disturbance levels were categorized as low (0– 2 times), medium (3–4 times), and high (>4 times; Table 3.1). During fall 2010–spring 2011, high disturbance levels were only observed at sites with mechanical oil spill cleanup activities taking place. Mechanical cleanup included use of bulldozers for tar mat excavation, mechanical sand sifters (OSAT2 2011), and >10 all-terrain vehicles (> 50 individuals on the beach at least four days a week between 06:00 and 17:00; JRH, pers. obs.). Medium disturbance was associated with either manual cleanup activities, where workers were removing oil from intertidal sand with shovels and rakes (OSAT2 2011), or disturbance from activities on public beaches (including people and dogs).

Surveys. Surveys were conducted at the same sites as mist-net sampling (see Table 3.1) between 07:00 and 09:00 or 15:00 and 17:00 on or within one day of mist-netting. However, surveys were not conducted while mist-nets were set because that could have increased disturbance. Disturbance surveys were conducted in foraging areas with a minimum of 15 foraging birds present, although the median shorebird number during these surveys was 125. Foraging areas in habitats on the NGOM are highly localized, resulting in small areas with large numbers of birds foraging (Table 3.1).

Other data collected. In addition to disturbance level, other data collected during surveys included time of day, tidal height (according to nearest National Data Buoy; NDBC 2014), survey area, and predator abundance. Raptors, particularly falcons and accipiters, are the main predators of shorebirds during the nonbreeding season (Colwell 2010). We evaluated the effect of predation pressure at our study sites during sampling by counting the daily mean number of falcons (accipiters were not detected) observed during surveys days and trapping sessions (maximum number observed on any single day was 2, a single Merlin [*Falco columbarius*] and a single Peregrine Falcon [*F. peregrinus*]).

Study species. At our six study sites, we evaluated the oiling status of one resident shorebird (Wilson's Plover, *Charadrius wilsonia*) and six species of migrating shorebirds, including Sanderlings, Dunlins (*Calidris alpina*), Semipalmated Plovers (*Charadrius semipalmatus*), Western Sandpipers, Least Sandpipers, and Semipalmated Sandpipers (*C. pusilla*). Sanderlings primarily forage along Gulfside beaches (Burger and Gochfeld 1991). Dunlins and Semipalmated Plovers also forage along tidal beachfronts and are commonly found in back bay mudflat habitats. Least, Western, and Semipalmated sandpipers forage largely in estuaries or in back bay habitats, and rarely on Gulf side beaches (Holmes 1972, Baker and Baker 1973). Least Sandpipers preferentially forage along the edges of mudflats between clumps of marine vegetation (Nebel and Cooper 2008), and Western and Semipalmated sandpipers are more commonly found in open mudflat habitats (Wilson 1994, Hicklin and Gratto-Trevor 2010). We selected Wilson's Plovers as our target resident species because they are a species of high conservation concern (Brown et al. 2001, Zdravkovic 2013) that foraged and nested in coastal habitats while the DWH well was still leaking.

For Dunlins, we also measured mean fuel stores (size-adjusted mass) and refueling rates (as indicated by plasma metabolite levels) during spring migration (March–May) and compared the results for spring 2011 and spring 2012. Dunlins were chosen for this analysis because they are believed to use a "jump" migration strategy in the spring, making long migratory flights across the central United States from wintering or stopover sites on the NGOM en route to near-Arctic breeding grounds (Skagen et al. 1999). Because these long flights require large fuel stores, habitat quality of stopover sites on the northern Gulf may be especially important. Dunlins captured during fall migration were not included in these analyses because evidence suggests that shorebirds tend to exhibit time minimization behavior during spring migration (Lyons and Haig 1995, Farmer and Wiens 1999) in an effort to reach breeding grounds as soon as possible. Such constraints are relaxed during fall migration and, in some shorebird species, migrants tend to limit fat reserves, suggesting an energy-minimization strategy (Gudmundsson et al. 1991, Lyons and Haig 1995).

Bird sampling. Beginning in October 2010, shorebirds were captured at our six study sites (Table 3.1). Birds were captured primarily at dawn and dusk using six mistnets placed in foraging areas for 3–5 h. Birds were passively captured in nets that were monitored constantly so birds were retrieved from nets within 5–10 min. Captured birds were weighed (±0.1 g) using a digital balance, measured (wing chord, tarsus length, and exposed culmen), and banded with a USGS numbered band. Each bird was classified as adult or juvenile based on plumage characteristics (Prater et al. 1977), and fat scores were measured on a scale from 0 to 5 (Helms and Drury 1960). The level of oiling on each bird was measured using the Natural Resource Damage Assessment and Restoration (NRDAR) protocols, where birds are categorized as (1) not visibly oiled, (2) trace amounts of oiling (<5% of total body area covered with oil), (3) lightly oiled (5–20%), (3) moderately oiled (21–40%), and (4) heavily oiled (>40%; NRDAR 2010). We assessed mean fuel stores of Dunlins using an index of size-adjusted mass that adjusts body mass for size using the volumetric conversion of wing chord, that is, size-adjusted mass = mass/(wing chord)^3 × 10,000 (Winker et al. 1992, Mizrahi et al. 2012, Hicklin and Chardine 2012). Fat scores of Dunlins (corrected for Julian date) were significantly correlated with size-adjusted mass ($F_{1,184} = 50.8, P < 0.001$)[2], supporting our use of this as a measure of energetic condition. We present our results for size-adjusted mass instead of fat scores due to the subjective nature of fat scoring measurements.

Blood sampling and plasma metabolite analyses. To assess refueling rates of Dunlins, we collected blood samples (200–300 µl) from the brachial vein using a 26gauge needle and heparinized capillary tubes. Blood samples were stored on ice in the field and centrifuged within 2 h at 6000 rpm for 10 min. Plasma samples were stored in a −20°C freezer for 1 to 2 weeks and then stored at −80°C prior to analysis.

Lipid metabolites were assayed in 400 µl flat bottom 96well micro-plates (Greiner BioOne, Monroe, NC) in a micro-plate spectrophotometer (340EL, BioTek, Winooski, VT; Guglielmo et al. 2005, Williams et al. 2007). Due to small plasma volumes, not all metabolites could be determined for all individuals. Following previous studies (Schaub and Jenni 2001, Guglielmo et al. 2002, 2005), we prioritized triglyceride and glycerol assays. Total triglyceride (TRIG) and free glycerol (GLYC) were measured by endpoint assay (Sigma Diagnostics Trinder reagents A and B, Sigma Aldrich, St. Louis, MO; Williams et al. 1999). True triglyceride concentration (mmol L^{-1}) was calculated by subtracting glycerol from total triglyceride. Inter-assay coefficients of variation (CV) based on chicken plasma pools were 8.4% for TRIG and 9.9% for GLYC ($N = 9$ assays over 2 yrs.). β-Hydroxybutyrate (BOH) was measured by kinetic endpoint assay (kit E0907979, Biopharma, Lexington, MA; Guglielmo et al. 2005). The inter-assay CV for

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[2] $R^2 = 0.35, P < 0.001$

BOH was 13.4% (*N* = 9). All samples were run in duplicate or triplicate. Intra-assay CVs for TRIG, GLYC, and BOH 2011 were 6.2%, 4.4%, and 13.6%, respectively. Intra-assay CVs in 2012 were 3.6% for TRIG, 2.8% for GLYC, and 8.8% for BOH.

Statistical analyses. Fisher's exact test was used to test for differences in oiling rates between species and foraging habitats (coastal or back bay). We assessed the effects of site oil level (according to maximum oiling level and SCAT oiling levels in May 2011 and 2012) and site disturbance activity using general linear models with a backward selection procedure (a=0.1) to identify independent variables that contributed to differences among sites. Size-adjusted mass and metabolite concentrations were $\log_{10} + 1$ transformed to normalize the data. Independent variables of Julian date, time of day, tidal height, bleed time (time between capture and bleeding), mean predator abundance, size-adjusted body mass, and habitat type were assessed. We compared metabolite concentrations and size adjusted mass by site oil level or disturbance level with analysis of covariance (ANCOVA), with variables retained by the general linear model entered as covariates (Guglielmo et al. 2005). Results of the reduced models are presented, including significant covariates. We made all pairwise post-hoc comparisons using the Tukey's HSD test. We did not assess variation in disturbance levels between years because disturbance level was categorized (as described above) for individual sampling occasions (i.e., it varied within years and within sites). Although significant sex effects in stopover ecology have been reported in other studies (Warnock and Bishop 1998, Bishop et al. 2005, 2006), effects of sex or age have not been consistent across studies. For example, Guglielmo et al. (2002) and Seaman et al. (2006) reported no sex or age differences in triglyceride levels. For our analyses, samples were pooled across ages and sex due to small sample sizes. Values are presented as least-square means ± SE. All statistical analyses were conducted using R Software version 0.97.551 (R Core Team 2013).

RESULTS

Oiling rates across species and sites. From October 2010 to May 2012, we captured 691 shorebirds, with 76 captured during fall/winter 2010–2011, 146 during spring 2011, 37 during fall/winter 2011–2012, and 432 during spring 2012. Of birds sampled, 22 were visibly oiled. Most oiled birds (17/22) were captured at sites that were heavily oiled (Figure 3.2A and B). Oiled birds showed only light (2/22) or trace (20/22) amounts of oiling. From October 2010 to May 2011, 8.6% of captured birds (19/222) were oiled, and the percentage decreased to 0.6% (3/469) during the period from August 2011 to May 2012. Overall, 3.2% (22/691) of birds were oiled.

Among migratory species, Sanderlings had the greatest proportion of oiled individuals (5% of total captured; Figure 3.2C), followed by Dunlins (4.2%), Semipalmated Plovers (2.4%), and Least Sandpipers (2.3%). No Semipalmated or Western sandpipers were visibly oiled (Figure 3.2C). Seven of 16 Wilson's Plovers (43.8%) had visible signs of oil (Figure 3.2C). Oiling rates differed between foraging habitats (coastal vs. estuarine; Fisher's exact test, $P = 0.001$).

Residual size-adjusted mass and plasma metabolite levels. Size-adjusted mass was compared for 184 Dunlins captured during spring migration in 2011 and 2012. In multiple regression analyses of significant covariates, Julian date was the only significant predictor of mass across sites. Controlling for date, residual size-adjusted mass across years did not differ with either maximum ($F_{2,181} = 0.2$, $P = 0.8$) or post cleanup oiling levels ($F_{3,180} = 2.0$, $P = 0.12$). Mean residual mass did not differ among either maximum or post-cleanup oil levels within years (all $P > 0.10$, Figure 3.3A). Across years, residual mass differed with disturbance level ($F_{2,181} = 4.8$, $P = 0.01$), with Dunlins having lower residual mass at sites with high levels of disturbance than at sites with low (Tukey's HSD, $P = 0.04$) or medium ($P = 0.007$) levels. Residual mass of Dunlins did not differ between sites with medium and low levels of disturbance (Tukey's HSD, $P = 0.77$; Figure 3.3A). Plasma metabolite TRIG concentrations of 184 Dunlins were measured during spring 2011 and 2012. We found no relationship between TRIG and site maximum oiling level across or within years ($F_{2,181} = 1.2$, $P = 0.30$ across years; 2011: $F_{2,51} = 0.03$, $P = 0.97$ for 2011, 2012: $F_{2,127} = 1.7$, $P = 0.18$, controlling for Julian date and size-adjusted mass, with no other covariates significant in the full model; Figure 3.3B). There was also no relationship between TRIG and post-cleanup oil level across years ($F_{3,180} = 1.5$, $P = 0.21$) or within years (2011: $F_{3,50} = 1.0$, $P = 0.40$; 2012: $F_{2,127} = 1.4$, $P = 0.25$). Residual TRIG concentrations were not influenced by level of disturbance across years ($F_{2,181} = 0.8$, $P = 0.45$).

GLYC levels of Dunlins differed with both maximum and post-cleanup site oiling level across years ($F_{2,181} = 3.3$, $P = 0.04$ for MAX; $F_{3,180} = 2.7$, $P = 0.05$

for PC), after correcting for Julian date and time of day. GLYC levels at "lightly" oiled sites were lower than levels at "very lightly" oiled sites (Tukey's HSD, P = 0.04). No other post-hoc pairwise comparisons for MAX or PC showed significant differences. Within years, we found no difference in GLYC levels among either maximum (2011: $F_{2,52} = 0.2$, $P = 0.86$, 2012: $F_{2,127} = 2.3$, $P = 0.11$) or Post-cleanup (2011: $F_{3,50} = 0.6$, $P = 0.64$, 2012: $F_{2,127} = 1.8$, $P = 0.18$, Figure 3.3C) oil levels. GLYC levels of Dunlins differed with site disturbance level across years ($F_{2,181} = 3.3$, $P = 0.04$). Post hoc pairwise comparisons revealed higher GLYC levels at medium than at low-disturbance sites (Tukey's HSD, $P = 0.02$), but the difference in mean GLYC concentrations between high and low-disturbance sites was not significant ($P = 0.77$; Figure 3.3C).

BOH analyses ($N = 95$) were corrected for Julian date, bleed time, and habitat. No differences were observed in BOH levels by site maximum or post-cleanup oiling level either across (MAX: $F_{2,92} = 0.1$, $P = 0.94$, PC: $F_{3,91} = 0.1$, $P = 0.98$; Figure 3.3D) or within years (MAX, 2011: $F_{2,11} = 0.1$, $P = 0.91$, 2012: $F_{2,78} = 0.03$, $P = 0.97$; PC, 2011: $F_{2,11} = 0.0$, $P = 1.0$, 2012: $F_{2,78} = 0.02$, $P = 0.98$). Across years, BOH concentrations did not differ with site disturbance level ($F_{2,92} = 0.3$, $P = 0.73$; Figure 3.3D).

DISCUSSION

More than 1 million shorebirds migrate through habitats impacted by the Deepwater Horizon Oil spill (Vermillion 2012, Henkel et al. 2012). In two years following the spill, 8.6% (2010–2011) and 0.6% (2011–2012) of shorebirds captured on the NGOM had light or trace oiling, suggesting that the number of shorebirds potentially affected by oil during those years could have been as high as 100,000 birds (Henkel et al. 2012). Although oiled birds had only light or trace amounts of oil on their feathers, shorebirds with less than 15% of their body area covered with oil may have significantly reduced feeding times (Burger 1997). The number of oiled birds in our study may not have been as high as expected given the scale of the Deep water Horizon Oil spill, and one possible explanation for this is that we did not begin our study until October 2010, almost six months after the start of the spill. Additionally, our study sites were located where birds were foraging, and not necessarily where oiling levels were high. We did not expect to capture moderately or heavily oiled birds because they would probably either be too ill to forage or would have already perished.

Our results suggest that species of shorebirds using the outer coast, such as Sanderlings and Dunlins, were more likely to be oiled than more estuarine sandpipers, such as Western or Semipalmated sandpipers. Of 88 live shorebirds and shorebird carcasses captured or collected by USFWS personnel following the DWH spill, Sanderlings (*N* = 26) were the most common (4 visibly oiled, 20 not visibly oiled, and 2 with unknown oiling levels; USFWS 2011). Such microhabitat variation in oiling rates of birds is not surprising as many Gulfside habitats experienced higher oiling rates than bayside estuarine habitats (Michel et al. 2013).

Although they are not found in high numbers during the nonbreeding season in areas impacted by oil (Zdravkovic 2013), we found that a relatively high percentage of resident Wilson's Plovers had visible signs of oiling (43% of birds captured). This suggests that Wilson's Plovers and other resident species that spend most of the year on the NGOM were more likely to be exposed to oil. In a study of the effects of the Exxon Valdez oil spill on marine bird communities immediately after and during the year following the spill, Wiens et al. (1996) found that birds most impacted (significantly lower populations) were shoreline feeding species that either breed or winter on beaches or were full year residents in habitats that were oiled. Similarly, Andres (1997) observed fewer breeding pairs of Black Oystercatchers (*Haematopus bachmani*) and lower nest success in oiled habitats during the first summer after the Exxon Valdez spill. However, by 1991 (three summers after the spill), the breeding population in these areas had substantially recovered (Andres 1997). Like Black Oystercatchers, Wilson's Plovers in our study were nesting during the summer immediately following the spill, and the high oiling levels we observed suggests they, and other resident species of the GOM, may have been particularly negatively impacted by the DWH spill.

We found no evidence that oiling levels affected fattening rates and plasma metabolites of Dunlins. These results suggest that, although some variation in fattening rates may occur from high levels of oil in foraging habitat, on average, birds were fattening at the same rate regardless of the amount of oil in the environment. Therefore, food resources may have been adequate for attaining relatively high instantaneous refueling rates, even in heavily oiled habitats. One possible explanation for this could be increased abundance of prey in oiled habitats due to agitation of substrates during cleanup activity. Ferns et al. (2000) observed increased numbers of shorebirds and gulls feeding in intertidal habitats following disruption of sediment by mechanized cockle harvesters in South Wales. They suggested this (temporary) increase might have been due to a decrease in the amount of sand in the upper layers of the sediment, making prey detection or extraction easier. In heavily oiled habitats on the GOM, large machinery was used to dig up tar mats that formed as a result of the spill, and we observed that birds avoided these areas during active cleanup, but on multiple occasions flocks of birds (often >20 individuals) were observed foraging in exposed mats once human activity ceased for the evening (JRH, pers. obs.). Another potential explanation is that birds in our study were only captured while actively foraging. If so, even if refueling rates were diminished due to effects of the oil spill, plasma metabolites would not indicate this because they only provide a snapshot of what the bird was doing at that time. Williams et al. (1999) noted that, although studies of captive Western Sandpipers (*C. mauri*) suggest that metabolites reflect mass change over 1–2 days, plasma metabolite profiles in free living sandpipers may simply reflect instantaneous rates of mass change, or change over short time periods (0.5–1 day).

Our results indicate that disturbance from oil spill cleanup activities affected shorebirds. Across years, we found that Dunlins had lower energy reserves (as measured by size-adjusted mass) at sites with the highest level of disturbance (where mechanical cleanup was taking place), and lower GLYC concentrations (indicating fat catabolism) at sites with low levels of disturbance. TRIG and BOH concentrations did not differ with site disturbance level. This suggests birds may be able to maintain high instantaneous fattening rates (i.e., no difference in TRIG levels) at highly disturbed sites, but energy expended to avoid areas with high levels of disturbance may prevent them from attaining large fuel stores. Fuel stores of Dunlins did not differ between sites with medium (non mechanical cleanup as well as people walking on the beach) and low disturbance, suggesting that shorebirds can tolerate a limited amount of disturbance, but high levels are harmful. The lack of observed differences between medium and low disturbance sites may be the result of habituation to a more reduced human disturbance (Fitzpatrick and Bouchez 1998, Sutherland 2007 Dwyer 2010) or access to alternative foraging habitats (Gill et al. 2001, Gill 2007). During the demolition and cleanup of a mudflat in Jersey City, New Jersey, Burger (1988) observed lower foraging rates in shorebirds and gulls in the area of highest disturbance activity. However, during this cleanup operation, activity was limited to only 100m stretches of the beach at a time. Burger (1988) documented birds roosting and foraging on unoccupied areas of the beach, and returning to forage in the cleanup areas once workers left for the day, suggesting that restricting cleanup activity to a limited area allowed birds to continue foraging in undisturbed areas. Although care was taken by USFWS personnel to minimize the amount of disturbance at oiled sites, at our high disturbance study sites, we observed more than 30 all-terrain vehicles and three to four backhoes traveling up and down several kilometers of beach two to three times per day moving workers and oil-cleanup refuse. Sandpipers spend as much as 70–80% of their time foraging during spring stopover when preparing for migration (Davis and Smith 1998, De Leon and Smith 1999). If foraging is frequently interrupted by disturbance, birds may be delayed in attaining the fuel stores necessary for their long migratory journeys, thus delaying their departure for their breeding grounds (Morrison et al. 2006), which ultimately leads to decreased reproductive success through carry over effects (Baker et al. 2004, Harrison et al. 2011). The negative impacts of cleanup activities observed in our study might have been minimized by limiting such activity during the height of migration (e.g., April and May) or by limiting cleanup to hours of the day when shorebirds typically roost away from foraging areas.

Our results suggest that disturbance caused by oil cleanup activity may have a greater impact on shorebirds than the oil itself. Although we are not suggesting that cleanup activities should not have occurred following the DWH oil spill, taking into account the appropriate intensity and timing of such activities is important. Our results and those of other investigators suggest that the possible negative impacts of cleanup activities on shorebirds can potentially be minimized by restricting cleanup to specific sections of beach at a time (Burger 1988) or limiting cleanup activities to certain periods of the day (Stillman et al. 2007).

ACKNOWLEDGMENTS

Birds were captured, banded, and sampled under a USGS permit (22526), and capture, handling, and blood-sampling protocols were approved by the Tulane University Institutional Animal Care and Use Committee. Funding was provided by a National Science Foundation RAPID award DEB1060350 (PIs Taylor and Sherry), and the Environmental Protection Agency STAR Fellow ship Award FP91745701–0 (to JRH). Three anonymous reviewers provided helpful comments and suggestions on earlier drafts of the manuscript. Special thanks to D. Norman and F. Travica of the Wisner Foundation, and M. Strickland of the Town of Dauphin Island for access to study sites and field support.

Table 3.1

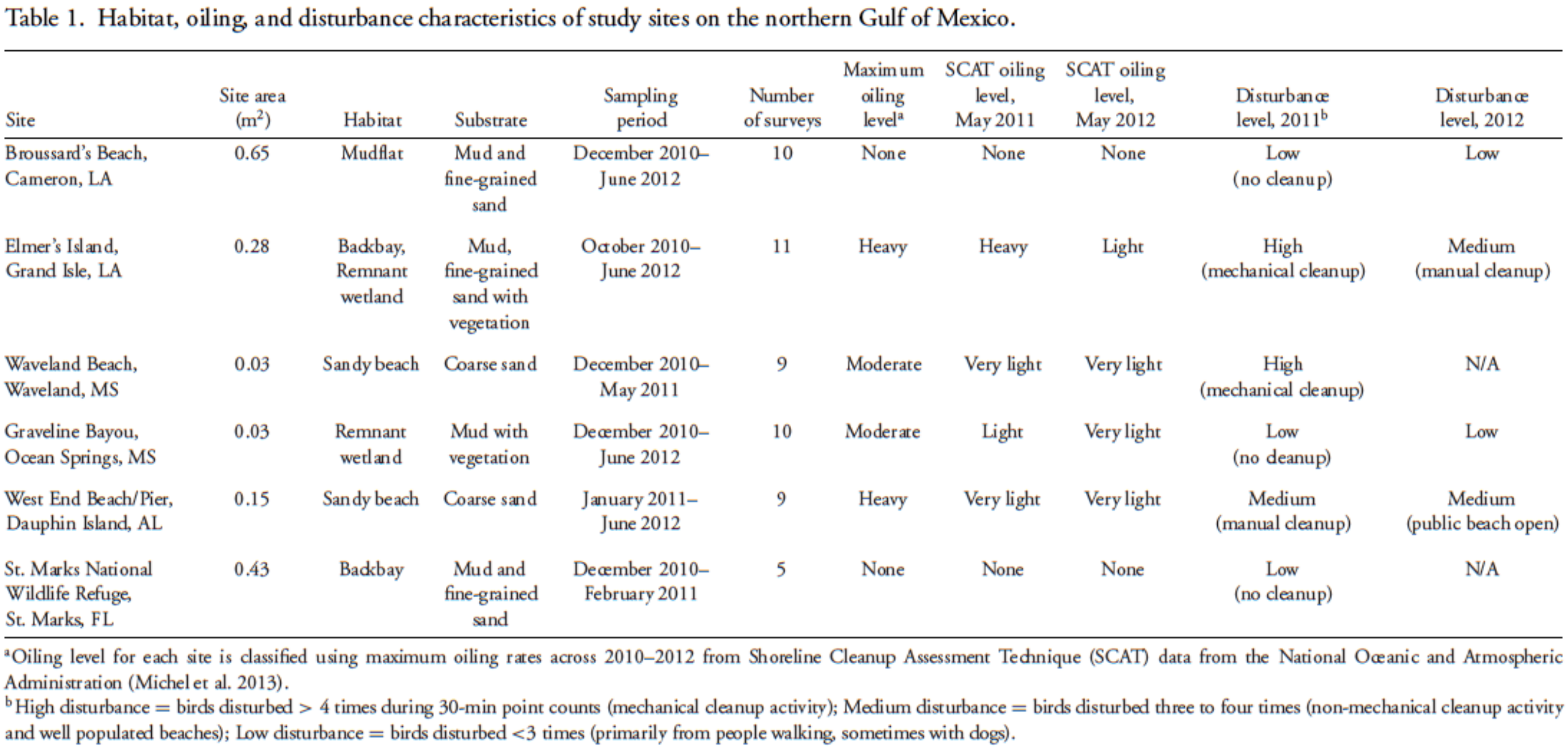


Table 1. Habitat, oiling, and disturbance characteristics of study sites on the northern Gulf of Mexico.

Site	Site area (m^2)	Habitat	Substrate	Sampling period	Number of surveys	Maximum oiling level[a]	SCAT oiling level, May 2011	SCAT oiling level, May 2012	Disturbance level, 2011[b]	Disturbance level, 2012
Broussard's Beach, Cameron, LA	0.65	Mudflat	Mud and fine-grained sand	December 2010–June 2012	10	None	None	None	Low (no cleanup)	Low
Elmer's Island, Grand Isle, LA	0.28	Backbay, Remnant wetland	Mud, fine-grained sand with vegetation	October 2010–June 2012	11	Heavy	Heavy	Light	High (mechanical cleanup)	Medium (manual cleanup)
Waveland Beach, Waveland, MS	0.03	Sandy beach	Coarse sand	December 2010–May 2011	9	Moderate	Very light	Very light	High (mechanical cleanup)	N/A
Graveline Bayou, Ocean Springs, MS	0.03	Remnant wetland	Mud with vegetation	December 2010–June 2012	10	Moderate	Light	Very light	Low (no cleanup)	Low
West End Beach/Pier, Dauphin Island, AL	0.15	Sandy beach	Coarse sand	January 2011–June 2012	9	Heavy	Very light	Very light	Medium (manual cleanup)	Medium (public beach open)
St. Marks National Wildlife Refuge, St. Marks, FL	0.43	Backbay	Mud and fine-grained sand	December 2010–February 2011	5	None	None	None	Low (no cleanup)	N/A

[a] Oiling level for each site is classified using maximum oiling rates across 2010–2012 from Shoreline Cleanup Assessment Technique (SCAT) data from the National Oceanic and Atmospheric Administration (Michel et al. 2013).

[b] High disturbance = birds disturbed > 4 times during 30-min point counts (mechanical cleanup activity); Medium disturbance = birds disturbed three to four times (non-mechanical cleanup activity and well populated beaches); Low disturbance = birds disturbed <3 times (primarily from people walking, sometimes with dogs).

Figure 3.1. Location of and levels of maximum oiling at study sites on the northern Gulf of Mexico.

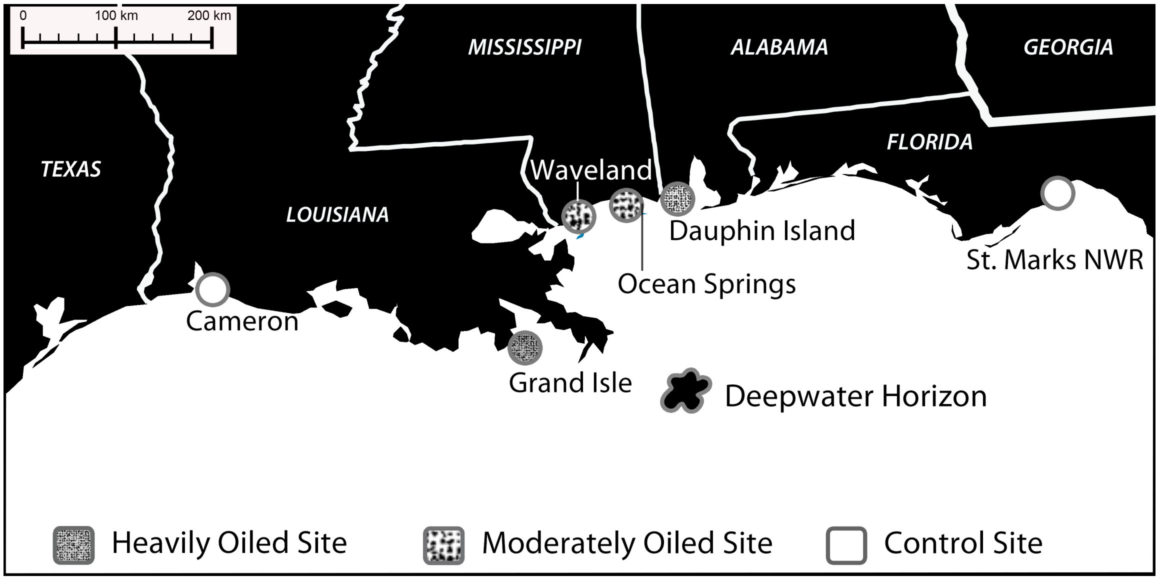


Figure 3.2. Proportions of total oiled shorebirds observed (A) across study sites, (B) by maximum site oiling level, and (C) by species. Numbers above bars indicate number of oiled birds relative to the total number captured.

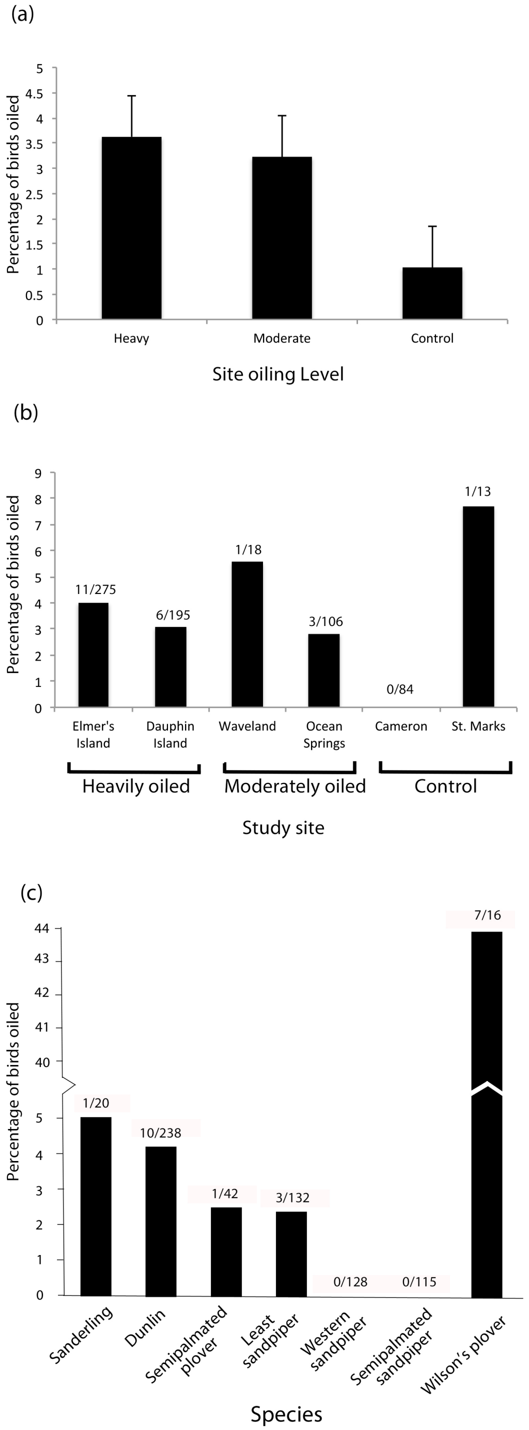
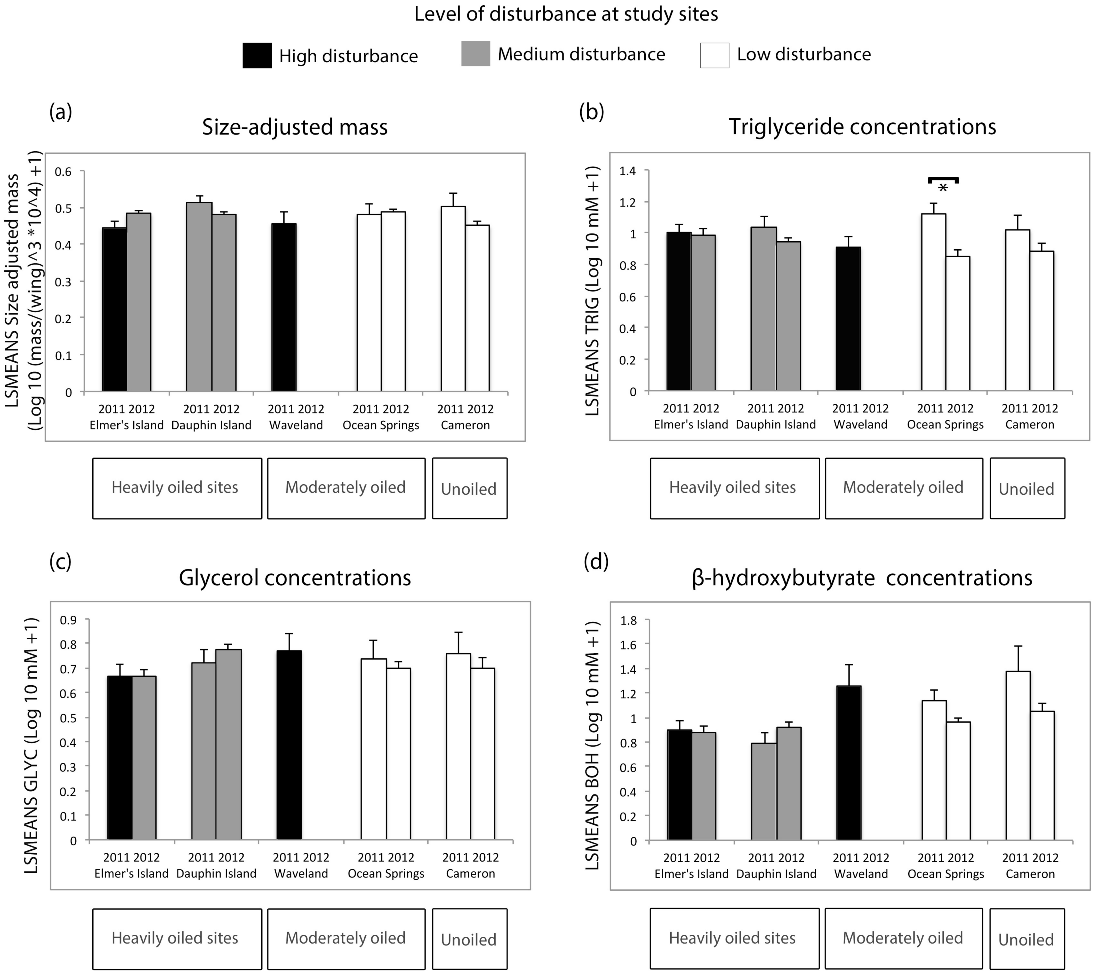


Figure 3.3. . Size-adjusted mass and plasma metabolite concentrations of spring migrating Dunlins during 2011 and 2012 across study sites on the northern Gulf of Mexico. (A) Residual size-adjusted mass (mass/[wing chord]^3 × 10,000) was significantly lower at high disturbance sites than at low or medium disturbance sites. (B) Residual Triglyceride levels showed no difference based on oil or disturbance status, but there was a significant difference between years at Ocean Springs. (C) Residual glycerol concentrations were significantly lower at lightly oiled sites than at very lightly oiled sites, and significantly higher at medium disturbance sites than at low disturbance sites. (D) Residual β-hydroxybutyrate levels did not differ based on oil or disturbance status. Values are least-squared means ± SE.


Level of disturbance at study sites
High disturbance
Medium disturbance
Low disturbance
(a)
Size-adjusted mass
LSMEANS Size adjusted mass (Log 10 (mass/(wing)^3 *10^4) +1)
0
0.1
0.2
0.3
0.4
0.5
0.6
2011 2012 Elmer's Island
2011 2012 Dauphin Island
2011 2012 Waveland
2011 2012 Ocean Springs
2011 2012 Cameron
Heavily oiled sites
Moderately oiled
Unoiled
(b)
Triglyceride concentrations
LSMEANS TRIG (Log 10 mM +1)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
*
2011 2012 Elmer's Island
2011 2012 Dauphin Island
2011 2012 Waveland
2011 2012 Ocean Springs
2011 2012 Cameron
Heavily oiled sites
Moderately oiled
Unoiled
(c)
Glycerol concentrations
LSMEANS GLYC (Log 10 mM +1)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
2011 2012 Elmer's Island
2011 2012 Dauphin Island
2011 2012 Waveland
2011 2012 Ocean Springs
2011 2012 Cameron
Heavily oiled sites
Moderately oiled
Unoiled
(d)
β-hydroxybutyrate concentrations
LSMEANS BOH (Log 10 mM +1)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2011 2012 Elmer's Island
2011 2012 Dauphin Island
2011 2012 Waveland
2011 2012 Ocean Springs
2011 2012 Cameron
Heavily oiled sites
Moderately oiled
Unoiled

4. MIGRATION STRATEGY PREDICTS STOPOVER ECOLOGY IN SHOREBIRDS ON THE NORTHERN GULF OF MEXICO[1]

ABSTRACT

Twenty-eight species of migratory shorebirds rely on the coastlines of the northern Gulf of Mexico (NGOM) to fuel migrations to near-arctic breeding grounds. As the processes of global change accelerate, habitats on the NGOM are expected to experience dramatic land loss. Shorebird species vary in their migration ecology: some species use a “jump” strategy, migrating long distances without stopping, while others use “skip” and “hop” strategies, stopping to refuel at shorter intervals along their journey. We compared stopover duration, body condition (fat scores and size-adjusted mass), and refueling rates (plasma metabolite concentrations), in three species of Calidrid sandpipers (*Calidris pusilla, C. mauri, C. alpina*) that differ in migration strategy after leaving the NGOM during spring. Results indicate that, while birds refueled at similar rates, *C. alpina,* a jump migrant, reached higher fuel stores before departing on migration than the shorter distant migrants, *C. pusilla and C. mauri. C. alpina* also spent more time on the NGOM than the other two species. Results indicate that NGOM habitats may be particularly important for migration success in *C. alpina*. This knowledge helps us understand the potential population level consequences of habitat loss on NGOM shorebird populations and conservation plans to mitigate these impacts.

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[1] This chapter has been written for submission for publication in Animal Migration.

Keywords: Sandpipers, refueling rates, plasma metabolites, fuel stores, migratory fitness

INTRODUCTION

At least 61% of North American breeding shorebird populations are declining (Andres et al. 2012) and their habitats face increasing pressure from anthropogenic and environmental change (Cox 2010). While shorebirds may be vulnerable at each stage of their annual cycle, evidence suggests that the migration period, in particular, may be severely limiting (Piersma 1994, Ens *et al.* 1994, Baker *et al.* 2004, Newton 2006). Precipitous population declines in the Red knot (*Calidris canutus rufa*) and Semipalmated sandpiper *(Calidris pusilla*) have been attributed, in part, to the collapse of the Horseshoe crab (*Limulus polyphemus*) populations in the Delaware Bay which represents a major stopover site for thousands of shorebirds who rely on eggs from horseshoe crab spawning to fuel their long distance migrations to high arctic breeding grounds (Baker et al. 2004, Mizrahi et al. 2012).

In the continental United States, the wetlands of the northern Gulf of Mexico (NGOM) are experiencing some of the highest global sea level rise rates (Miner 2009). During the non-breeding season these wetlands host 28 species of migratory shorebirds and more than 5% of the total North American population for 12 of those species (Henkel et al. 2012). However, despite the variety of species using the NGOM, the migration ecology of shorebirds in these habitats has been understudied demographically. As with Red knots using the Delaware Bay, some shorebird species may rely on northern Gulf habitats to provide the fuel necessary for spring migration to near-arctic breeding grounds. Developing a better understanding of the ecology of shorebirds during migration through northern Gulf habitats is an important step towards predicting the potential population level effects of continued habitat loss on the NGOM.

The consequences of changes to migratory shorebird stopover habitats will depend on migration strategies within and among species. Some species use a "jump" migration strategy, migrating long distances without stopping, whereas other species use a "hop" or "skip" strategy (Piersma 1987), stopping at shorter intervals in agricultural fields and natural wetlands during migration (Skagen 1999). Migration theory suggests that such differences in migration strategy will result in variation in the requirements of migration physiology and stopover behavior (Alerstam and Lindstrom, 1990, Alerstam and Hendenstrom 1998, Piersma 1998). Evidence suggests that, on spring migration, shorebirds exhibit time minimization behavior (Lyons and Haig 1995; Farmer and Wiens 1999) in an effort to reach northern breeding grounds early and establish high quality breeding territories. Under time-minimization, birds preparing for long migratory flights demonstrate high fueling rates, attain large fuel stores prior to departure, and stay for longer periods (i.e., weeks) at stopover sites (Jehl 1997, Piersma 1998, Warnock 2010). In comparison, high fueling rates and high fuel stores are not necessary in birds with a shorter distance to the next stopover, resulting in shorter durations (hours-days) at stopover sites (Warnock 2010), and higher selectivity for departure from stopover sites as soon as weather conditions, such as positive tailwinds, are favorable (Alerstam and Enckell 1979).

Variation in migration strategy for shorebirds may occur not only among species, but within species, between sex and age classes, as well. As timing of arrival on the breeding grounds can be related to territory acquisition (Pitelka 1959, Farmer and Wiens 1999), male shorebirds often migrate before females. Farmer and Wiens (1999) observed a time minimization-only strategy in male Pectoral sandpipers on spring migration, but a combination time/energy-minimization strategy for females, meaning that males migrated as soon as possible, whereas some females stayed at stopover sites longer and reached higher fuel stores. Patterns of habitat use while at stopover sites can also vary by sex and age class. Fernandez and Lank (2006) found female and juvenile Western sandpipers (*Calidris mauri*) use resource-poor habitats more often than adult males during winter. Within-species variation in habitat use has been observed at both local (Warnock 1990, Cresswell 1994, Shepherd and Lank 2004, Fernandez and Lank 2006) and latitudinal scales (Myers 1981, Shepherd *et al.* 2001, Nebel *et al.* 2002).

The goal of this study was to investigate variation in the migration ecology and behavior among and within three species of sandpipers that stopover on the NGOM: Semipalmated sandpipers (*Calidris pusilla*), Western sandpipers (*C. mauri*), and Dunlin (*C. alpina*). Populations of all three species use the central North American flyway *en route* to near-arctic breeding sites (Skagen 1996). Using survey data during spring migration through the central United States, Skagen et al. (1999) showed that after leaving the NGOM *C. pusilla* use a hop migration strategy, making several short migratory flights on their northern migration, whereas *C. alpina* used a jump migration strategy, generally skipping over habitats in the central United States. *C. mauri* used a combination "hop/skip" strategy. Therefore, we hypothesized that stopover duration, refueling rates, and response to favorable wind conditions in our target species would differ according to migration strategy. Specifically, we predicted that stopover duration would be longest in our jump migrant, *C. alpina*, shortest in the hop migrant, *C. pusilla*, and intermediate in the hop/skip migrant, *C. mauri*. We predicted that refueling rates of jump migrants would accelerate faster than hop or skip migrants, i.e., we predicted a steeper positive slope of fueling rates over time for *C. alpina,* than for *C. mauri* and a steeper slope for *C. mauri* than for *C. pusilla.* Although we did not expect to see a relationship between refueling rates and time in *C. pusilla*, given the shorter distance of their migratory flight following departure from the NGOM, we predicted that the hop migrant *C. pusilla* refueling rates would respond more strongly to positive wind effects than the species with longer distance flights.

As the key variable for these differences is distance to subsequent stopover site, we predicted that within species individuals would demonstrate the same migration behavior (hop, skip or jump), regardless of age or sex relative to the other species. However, due to variation in the selective pressures to reach breeding grounds, we also hypothesized that within species stopover duration and refueling performance by individuals would vary according to intrinsic factors. Given the strong pressure to arrive on breeding grounds and establish territories, we predicted that male sandpipers of all species would migrate through the northern Gulf earlier, depart with lower fuel stores, and stop over for shorter periods than females and juveniles. Finally, as juveniles often exhibit lower masses than adults due to lower foraging efficiency (Stillman et al. 2000) we predicted mean fuel stores and refueling rates would be lower for birds completing their first spring migration (SY birds).

METHODS

We studied spring shorebird migration at four study sites across the NGOM (Fig 4.1). These sites represent four habitat types commonly found on the NGOM coast: mudflats, back bays, sandy beaches, and remnant wetlands. At these sites we investigated the **phenology** of migration for *C. pusilla, C. mauri,* and *C. alpina* by capturing and banding birds from 3 March – 29 April in 2011, 29 February – 28 May in 2012, and recording capture date. We investigated the proportional age and sex classes of birds captured across three periods of migration. Migration periods were identified as "Early" (28 February – 28 March), "Mid" (29 March – 28 April), and "Late" (29 April – 28 May). In 2013, we measured variation in stopover duration by measuring **stopover site residence time** in birds captured at one study site, Dauphin Island, AL, between 1 March – 22 May.

We investigated the variation in **fuel stores and refueling rates** among and within species across all three years by measuring variation in size-adjusted body mass, subcutaneous fat scores, and plasma metabolite levels of triglycerides (TRIG) and β-hydroxybutyrate (BOH). Because some metabolites increase during fat deposition, such as triglycerides, while others increase during fat catabolism (e.g., glycerol and β-hydroxybutyrate), metabolites can provide an instantaneous measure of physiological state and energetic condition of individuals just prior to capture, and therefore have been shown to be useful indicators of fattening rates in a variety of shorebird and passerine species (Jenni-Eiermann and Jenni 1994, Williams *et al.* 1999, Guglielmo *et al.* 2002, Guglielmo *et al.* 2005, Seaman *et al.* 2005). As previous research suggests that of the fat catabolites, BOH is a better indicator than glycerol (GLYC) of fat catabolism in migrant birds (Guglielmo et al. 2005, Cerasale and Guglielmo 2006, Seaman et al. 2006, Thomas and Swanson 2013), we focused on TRIG and BOH as our target metabolites for this study.

Detailed Methods

Bird sampling - Birds were captured primarily at dawn and dusk using 6 mist-nets placed in foraging areas for 3-5 hours. Birds were passively captured in nets that were monitored constantly such that birds were retrieved from nets within 5-10 minutes. Captured birds were weighed (± 0.1 g) using a digital balance, measured (wing chord, tarsus length, and exposed culmen), and banded with a USGS numbered band. Each bird was classified as adult (ASY) or second year (SY) based on plumage characteristics (Prater et al. 1977), and fat scores were measured on a scale from 0-5 (Helms and Drury 1960). We assessed body weight using an index of size-adjusted mass that adjusts body mass for size using the volumetric conversion of wing chord (size-adjusted mass = mass/(wing chord)^3 *10,000; Winker et al. 1992, Hicklin and Chardine 2012, Mizrahi et al. 2012).

Residence Time - In addition to the bird sampling procedures described above, birds in 2013 were also banded with uniquely coded flags and color band combinations. All birds were released at their capture site after banding. We monitored residence time of shorebirds by re-sighting banded birds during twice daily surveys using binoculars and telescopes at the banding site (approx. 3.5 km^2), and a known nearby roosting site (6.5 km^2). Daily re-sighting effort was constant from 1 March through 24 May; however, analyses of stopover duration were limited to re-sighting data from 28 March – 24 May to account for differences in the migration phenology among species (i.e. *C. pusilla* do not arrive till late March).

Blood sampling, plasma metabolite and molecular analyses **-** To assess refueling rates we collected blood samples (75- 300 μl depending on the size of the bird) from the brachial vein using a 26-gauge needle and heparinized capillary tubes. Blood samples were stored on ice in a small cooler in the field and centrifuged within 2 h at 6000 rpm for 10 min. Separated plasma and red blood samples were stored in a -20°C freezer for 1–2 weeks and then stored at -80° C prior to analysis.

Lipid metabolites were assayed in 400-μl flat-bottom 96-well microplates (Greiner Bio-One, Monroe, NC) in a microplate spectrophotometer (Biotec 340EL) (Guglielmo et al. 2005, Williams et al. 2007). Due to small plasma volumes, not all metabolites could be determined for all individuals. Following previous studies (Schaub and Jenni 2001, Guglielmo et al. 2002, 2005), we prioritized triglyceride assays. Total triglyceride (TRIG) and free glycerol (GLYC) were measured by endpoint assay (Sigma Diagnostics Trinder reagents A and B; Williams et al. 1999). True triglyceride concentration (mmol L^{-1}) was calculated by subtracting glycerol from total triglyceride. Inter-assay coefficients of variation (CV) based on chicken plasma pools were 7.4% for TRIG and 8.6% for GLYC (N = 18 assays over 3 years). β-hydroxybutyrate (BOH) was measured by kinetic endpoint assay (kit E0907979, R-7 Biopharm, Guglielmo et al. 2005). The inter-assay CV for BOH was 12.9% (N = 18). All samples were run in duplicate or triplicate. Intra-assay CVs for TRIG, GLYC, and BOH 2011 were 6.2%, 4.4%, and 13.6%, respectively. Intra-assay CVs in 2012 were 3.6% for TRIG, 2.8% for GLYC, and 8.8% for BOH, in 2013 they were 5.4% for TRIG, 6.0% for GLYC, and 10.9% for BOH.

Molecular markers were used to confirm sex identification for all banded birds. We extracted DNA from red blood cells using a standardized protocol for the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA), then sexed the birds by standard PCR methods, using primers 2550F/2718R (Fridolfsson and Ellegren 1999). The bands were separated by gel electrophoresis in 2% agarose gels, stained with ethidium bromide, and visually analyzed under UV light. We compared the lengths of the bands to a size marker (1-kb DNA ladder, Life Technologies).

Environmental variables

Wind effect - To estimate the effect of wind on response variables, such that the effect is positive in tail winds and negative in head winds, we first calculated the expected ground speed (G) associated with ground wind speed and direction from the relationship:

$$G = \sqrt{}(A^2 - (W \bullet \sin\alpha)^2) + W \bullet \cos\alpha$$

Where A is the airspeed of the birds (assumed to be 17 m/s following Green and Piersma (2003), W is the wind speed and α is the angle between wind and track directions (with a track direction of 180°, and $\alpha = 0°$ corresponding to tail winds and $\alpha = 180°$ to head winds.) The wind effect was then determined as ground speed minus airspeed (($G - A$); cf. Piersma and Jukema 1990; Grönroos et al. 2012)).

Food availability - During Spring 2013, at Dauphin Island, AL core soil samples were collected to measure the biomass and diversity of benthic invertebrates. From 3 March through 23 May 2013, five sets of core samples, approximately 2-3 cm apart from each other were collected weekly in areas where all three species were observed foraging.

Core samples were collected from the mid-intertidal (the area regularly inundated under normal tidal cycles and weather conditions) using a 10-cm-diameter PVC pipe driven to a depth of 5 cm (see Sherfy *et al.* 2000). Cores were placed into glass jars and kept on ice until they were returned to the laboratory where they were stored at -30°C. Afterwards, the remaining sediment in the samples was sieved through a 500 µm mesh. The material remaining on the mesh was placed into 95% ethanol with 10% Rose Bengal dye added to facilitate sorting. Invertebrates were sorted from the sediment under a dissecting microscope and identified. Following identification of invertebrates the total invertebrate biomass of each sieved core was determined after drying for 24 hours at 60°C.

Predation pressure - Raptors, particularly falcons and accipiters are the main predators of shorebirds during the non-breeding season (Colwell 2010). To evaluate the effect of predation pressure at study sites during sampling, we calculated the average percent of surveys in which falcons (accipiters are not common along coastal NGOM) were observed during surveys that were conducted at study sites between 0700-0900 or 1500-1700 during active foraging on or within one day of mist-netting for 2011 and 2012, and during resight surveys during 2013.

Statistical analyses – We investigated variation in phenology within and among species by using *z* statistics to test for differences in proportions between species, and between age and sex classes within species caught by period of spring. We assessed the drivers of variation in residence time among and within species using mark–recapture analysis implemented in program MARK (White and Burnham 1999) through the RMark package for R (Laake, 2013). We used the Cormack–Jolly–Seber (CJS) open-population model framework to analyze encounter histories of individual birds re-sighted at least one time between 28 March and 24 May by examining a set of candidate models explaining two modeled response parameters, Φ (‘survival’ probability) and p (detection probability). In a model of residence time, survival probability is interpreted as the probability of remaining at the stopover site. To compare among species our set of candidate models included keeping response parameters constant (dot models) vs. allowing survival to vary by species alone, by age (ASY vs. SY), by sex, by capture date, by time since capture, size-adjusted mass and linearly by time. We also modeled for interactions between these variables. To investigate variation in residence time within species we ran separate analyses by species, which included allowing survival to vary by age, sex, age*sex, capture date, time since capture, and size-adjusted mass. We selected among models using Akaike’s information criterion adjusted for small sample sizes and lack of model fit (AICc) and the associated **Δ**AICc and Akaike weights (Burnham and Anderson 2002). To test that our data met expectations based on the assumptions underlying the model, we evaluated the goodness-of-fit of our global model using the program RELEASE GOF provided in program MARK to calculate $\hat{c}$ (variance inflation factor or lack of fit). We transformed the survival estimates into post-capture residence times according to Kaiser’s (1995) formula for life expectancy, residence time = –1/ln **Φ**. We report mean residence time ± 95% confidence intervals.

We assessed the drivers of variation within species in fat scores, size-adjusted mass, and plasma metabolites across periods of spring migration using multiple backward stepwise regression analyses. Size-adjusted mass and metabolite concentrations were

$\log_{10} + 1$ transformed to normalize the data. We tested the independent effects of migration period, age (SY or ASY), sex, migration period*age*sex, site, year, site*year, habitat type, time of day, bleed time (time between capture and bleeding), foraging area, wind effect (corrected for Julian date), and predation pressure. As data for weekly invertebrate abundance were only available for 2013, we also tested the independent effects of the variables listed above (minus site and year) in addition to weekly mean dried invertebrate biomass (corrected for Julian date) for 2013 alone. The variables retained in the full models at $P < 0.10$ (Guglielmo et al. 2005) were kept as covariates in an analysis of covariance (ANCOVA) to obtain marginal means for fat scores, size-adjusted mass, and plasma metabolites among migration periods by species classified by sex and age. Results of the reduced models, including significant covariates, were used to conduct pairwise post-hoc comparisons of variation between migration periods within species using the Tukey's-HSD test. Values are presented as least-square means ± SE. Statistical analyses were conducted using R Software version 0.97.551 (R Core Team 2013).

RESULTS

A total of 515 target species were banded and sampled during Spring migration 2011-2013: 177 *C. pusilla*, 121 *C. mauri* and 217 *C. alpina* (Table 4.1). 368 were captured in the morning (71%) 147 in the evening (29%). Proportionally more *C. pusilla* were captured than the other two species during Late spring (*C. mauri*: $z = 13.51$, $p < 0.001$, *C. alpina*: $z = 12.63$, $p < 0.001$, Table 4.1). There was no proportional difference in the number of *C. mauri* and *C. alpina* captured during Early and Mid spring; however, more *C. alpina* were captured during late spring ($z = 3.13$, p = 0.002).

Residence time - During the Spring of 2013, 76 *C. pusilla*, 34 *C. mauri* and 30 *C. alpina* were uniquely banded. Of these individuals 62% (87) were re-sighted more than once (37% (28) *C. pusilla,* 91% (31) *C. mauri*, 100% (30) *C. alpina*). After reviewing our resight data, our encounter records were constrained to only 56 days, beginning on 28 March, and ending on 24 May, to limit our analyses to periods of time when all three species were present at our study site. Tests of goodness of fit of the CJS model found no evidence of overdispersion ($\chi^2_{191} = 42.03$, p = 0.99). However, there was evidence of underdispersion of the data ($\hat{c} = 0.22$), or less variation than expected by chance. As there is currently no clear procedure for dealing with underdispersion in these models (Cooch and White 2005) we did not adjust $\hat{c}$ and proceeded with model selection using AIC_c scores. Our best model for post-capture residence time included variation in survival probability across species by capture date, with detection probability a function of species (Table 4.2a). Using estimates from this model *C. pusilla* exhibited shorter mean post-capture residence times (6.6 days) than *C. mauri* (9.3 days), and both species stayed for a shorter period than *C. alpina* (27.2 days, Table 4.3). Each individual was at the banding site for some undetermined amount of time prior to when it was captured, therefore residence time estimates in our study likely represent conservative estimates of how much time shorebirds actually spent on the NGOM after capture.

Environmental and wind patterns - Mean weekly dry weight biomass of invertebrates increased with Julian date at Dauphin Island in 2013 ($R^2 = 0.13$, $p = 0.004$, Figure 4.2a). Positive wind effects also demonstrated a linear increase with Julian date ($R^2 = 0.07$, $p = 0.001$, Figure 4.2b), as winds from the south, southeast and southwest became more common in Late spring on the NGOM. Predation pressure was low across all of spring migration at all study sites. The maximum number of falcons observed during any survey from 2011 – 2013 was two. The effect of environmental variables on fuel loads and refueling rates is reported by species below.

Semipalmated Sandpipers

Phenology and residence time - Of the 177 *C. pusilla* captured, none were captured during Early spring, and only 19.8% (35/177) were captured during Mid spring (Table 4.1). As most birds arrived in Late spring, no significant differences were observed between sexes and age classes in *C. pusilla* (Table 4.1). Using the best RMark model to assess variation among species (Table 4.2a) *C. pusilla* exhibited short post-capture residence times (6.5 days, Table 4.3). Analyses of within species models for *C. pusilla* show a stronger effect of sex than age or sex*age on stopover duration (Table 4.2b), with females staying on the NGOM longer than males on average (8.0 days vs. 3.8 days, Table 4.3). However, the AIC weight for the residence time model that varied by sex was not significantly greater than a model with no age/class variation for *C. pusilla* (Table 4.2b).

Fuel Load and Fat deposition - Neither fuel stores nor refueling rates were significantly influenced by migration period in *C. pusilla* (Table 4.4). Post-hoc tests indicate male *C.*

pusilla had lower fat scores during Mid spring than females (Tukey's HSD, p = 0.04, Figure 4.3a). Residual TRIG levels were slightly higher in SY *C. pusilla* across spring (Tukey's HSD, p = 0.09 for Mid Spring, p = 0.06 for Late Spring, Figure 4.3c). Fat catabolism as measured by BOH levels did not change by migration period in *C. pusilla.* Food availability (corrected for Julian date), foraging area and predation pressure were not significant predictors for any response variables for *C. pusilla*; however, residual TRIG levels in *C. pusilla* increased with increasing (+) wind effect (p = 0.01, Table 4.4).

Western Sandpipers

Phenology and residence time - More *C. mauri* were captured during Early (53.7%) and Mid (35.5%) spring than during Late spring (10.7%, Table 4.1). While the highest proportion of males (both ASY and SY) were captured during the Early spring period (Table 4.1), the only proportional differences observed within migration periods was between ASY males and SY females. More ASY males were banded during Early spring ($z = 2.37$, p = 0.02), and more SY females were banded during Late spring ($z = 2.15$, p = 0.03). There were no other differences between sex or ages classes by migration period (Table 4.1). The mean residence time for all *C. mauri* in 2013 according to the best AIC model (Table 4.2a) was 9.2 days (Table 4.3). Individual analyses of within species variation in residence time for *C. mauri* shows the top two candidate models as models with survival varying by capture date, and survival varying by an age*capture date interaction (Table 4.2c). Using parameter estimates from this top model ASY *C. mauri* were predicted to stay for longer (26.6 days) than SY birds (21.7 days, Table 4.3).

Notably, very few ASY female *C. mauri* were captured during our study (29/121 for all three years, 3/34 in 2013) which may be influencing our results.

Fuel load and fat deposition - Migration period was a significant predictor of fat scores and size-adjusted mass in *C. mauri* (Table 4.4). Across age and sex classes fat scores and size adjusted mass were higher in Mid spring than Early (Tukey's HSD, $p = 0.003$, and $p = 0.09$, respectively) or Late spring (Tukey's HSD, $p = 0.10$, $p = 0.001$, Figure 4.3a,b). In Early spring the fat scores and size-adjusted mass of male *C. mauri* were significantly higher than females (Tukey's HSD, $p = 0.008$, $p = 0.02$), but these differences were not observed during any other period of spring Figure 4.3, a,b).

Migration period was also a significant predictor of residual TRIG levels across age and sex classes in *C. mauri* (Table 4.4, Figure 4.2 c, d). TRIG levels were higher in Mid spring than in Early and Late spring (Tukey's HSD, $p = 0.03$, and $p = 0.02$, respectively), but no difference was observed in TRIG levels between Early and Late spring (Tukey's HSD, $p = 0.45$). Residual BOH did not differ by migration period alone in *C. mauri*; however, during Late spring SY birds had higher residual BOH levels than ASY birds (Tukey's HSD, $p = 0.05$, Figure 4.3d). In 2013 residual TRIG levels in *C. mauri* showed some influence from increasing food availability ($p = 0.06$, Table 4.4), and BOH levels for *C. mauri* decreased significantly with residual wind effects ($p < 0.001$, Table 4.4), but there was no observed effect of predation pressure.

Dunlin

Phenology and residence time - More *C. alpina* were captured during Early (47.5%) spring than during Mid (27.7%) and Late spring (24.4%) (Table 4.1). The majority of males (both ASY and SY), and SY females were captured during the "Early" spring period (Table 4.1). As seen in *C. mauri*, fewer ASY females were captured than the other classes, and although not significant, more ASY females were captured during Late spring than ASY males ($z = 1.9$, $p = 0.057$). Proportionally more SY females were captured than ASY males during Late spring ($z = 2.36$, $p = 0.02$, Table 4.1). *C. alpina* exhibited the longest mean stopover duration of our three target species (27.2 days, Table 4.3). Analyses of within species models for *C. alpina* show a stronger effect of sex than age on stopover duration, however, the strongest model was one that held survival and resight probabilities constant (Table 4.2d). Parameter estimates derived from the top 3 candidate models show that in *C. alpina* females and ASY birds stayed longer on the NGOM than males and SY birds (Table 4.3).

Fuel Load and fat deposition - For *C. alpina* both fat scores and size-adjusted mass increased with migration period (Table 4.3, 4.2a, b). Residual fat scores differed between all periods of spring (Tukey's HSD, Early → Mid: $p = 0.006$, Early → Late, $p < 0.001$, Mid → Late, $p < 0.001$, Fig.3a). Residual size-adjusted mass differed between Early and Late spring (Tukey's HSD, $p = 0.05$), but differences were not significant between the other periods (Early → Mid, $p = 0.99$, Mid → Late, $p = 0.12$, Fig 4.3b).

All measures of refueling rates differed by migration period in *C. alpina* (Table 4.4). Residual TRIG levels were significantly higher in Late spring in comparison with Early spring (Tukey's HSD, p = 0.004, Figure 4.3c). These differences appear to be driven by high TRIG levels in ASY birds during Late spring in comparison with both Early and Mid spring (Tukey's HSD, p = 0.009, p = 0.05, respectively). Residual BOH levels were lower in Late spring in comparison with both Early and Mid spring (Tukey's HSD, p < 0.001 and p = 0.003, Figure 4.3d).

Within migration periods, differences were observed between *C. alpina* age classes during Late spring in both plasma TRIG and BOH concentrations (p = 0.005 and p = 0.05, respectively), with both male and female ASY birds refueling at higher rates than SY birds (Fig 4.3c, d). No differences were observed between the sexes. As observed in *C. mauri*, BOH levels were also influenced by wind, decreasing with increasing tail wind effect (p = 0.002, Table 4.3), but food availability and predation pressure were not significant predictors for any response variables for *C. alpina* (Table 4.3).

DISCUSSION

Among species variation in migration ecology - Before departing the NGOM migratory shorebirds exhibited stopover behavior consistent with behaviors predicted by optimal migration theory. Our prediction that our hop migrant, *C. pusilla,* would not need to increase fuel stores or stopover for extended periods was supported by brief stopover durations and fuel loads that did not change with migration period. *C. mauri,* a combination hop/skip migrant, and *C. alpina*, a jump migrant, demonstrated longer stopover durations, and significant differences in fuel stores among migration periods. How these species varied by migration period differed, however. While mean fuel stores in *C. alpina* increased linearly across spring, fuel stores in *C. mauri* were highest during Mid spring. These results likely reflect the differences in stopover duration and migration phenology between the two species. *C. alpina* appeared to spend the majority of the spring at a single site on the NGOM before departing, as reflected by long residence times and high fuel stores in Late spring. On average, *C. mauri* departed earlier, as reflected by low capture rates during Late spring and significantly higher fuel stores during Mid spring. There was wide variation in the migration phenology of our target species. While very few *C. pusilla* were captured or observed during Early and Mid spring, the majority of *C. mauri* and *C. alpina* were sampled during these periods. These results are corroborated by eBird surveys collected at coastal sites along the NGOM during the same three periods of spring from 2011-2013 for which the mean number of *C. mauri* and *C. alpina* observed per survey peak at 166.6 and 150.1 birds respectively during Mid spring, whereas *C. pusilla* numbers do not peak to 94.0 birds per survey until Late spring (eBird.org, 2014).

Although we cannot clearly differentiate between overwintering birds and birds arriving on migration from wintering grounds in central and Latin America, refueling rates of species before departing the NGOM further support variation in migration strategies. Plasma metabolite analyses for *C. pusilla* suggest that birds were refueling at the same rate regardless of migration period, supporting the hypothesis that the impending migratory journey for this hop migrant did not require rapid accumulation of fuel stores. On the contrary, variation in the refueling rates of *C. mauri* and *C. alpina* differed by migration period. For *C. alpina,* refueling rates increased throughout the pre-migration period consistent with the hypothesis that *C. alpina* was preparing to embark on a longer migratory flight than *C. pusilla* or *C. mauri.* In *C. mauri* refueling rates were significantly higher during Mid spring than in the other periods of migration, once again supporting the hypothesis that *C. mauri* was departing the NGOM before *C. alpina.*

While the lack of variation in fuel stores and refueling rates by migration period observed in *C. pusilla* could be attributed to small sample sizes in all but one migration period, additional support for *C. pusilla* behaving as a hop migrant is found in the species' response to wind. Optimal migration theory hypothesizes that species with multiple stopovers en route to breeding grounds will have more flexible migration strategies (Hendenstrom 2008), varying with individual differences in body condition and with temporal variation in resources and weather (Alerstam and Enckell 1979, Weber, Ens, and Houston 1998; Clark and Butler 1999). *C. pusilla* was the only species for which we observed a positive effect of tail wind on plasma TRIG levels, indicating that this species may be increasing refueling rates when weather conditions are beneficial for migration. In their research of songbird migration Covino et al. (2014) observed that birds with high refueling rates chose a more northerly migration route, while those with lower refueling rates selected a more westerly direction (closer to next available land mass). The relationship we observed between wind and refueling rates may similarly indicate that *C. pusilla* was taking advantage of positive migration conditions (tailwind), and fueling up for slightly longer migratory flights. Negative effects of tail winds were observed for plasma BOH in *C. mauri* and *C. alpina*, but no differences were observed in plasma TRIG, suggesting that while fat catabolism may slow when wind conditions are beneficial for migration, a converse flexibility in refueling given positive wind conditions is not occurring in these species.

Within species variation in migration ecology - Regardless of migration strategy, males of all species exhibited evidence of stronger time-selection than females. Fuel stores and plasma TRIG were lower, and estimated residence times for male *C. pusilla* were shorter than residence times for females. This suggests that, as Farmer and Wiens (1999) observed in male Pectoral sandpipers, after arrival on the NGOM male *C. pusilla* are demonstrating a more time-minimization strategy by departing sooner, with lower energy stores, in order to reach breeding grounds and establish breeding territories. Although their stopover durations were much longer than those of *C. pusilla,* we also observed female *C. alpina* stopping over for longer than males. These results may be driven by the extremely long mean minimum stopover duration (measure between banding date and day of last sighting) for the *C. alpina* ASY females (37.6 days, N=5). The mean minimum stopover duration for *C. alpina* ASY males was only 16.9 (N=6), indicating that although both adult males and females are stayed for relatively long periods on the NGOM, the adult males demonstrated a more time-minimized migration than adult females.

Our results for *C. mauri* are more difficult to interpret. While we found no effect of gender on stopover duration or refueling rate patterns*,* fuel stores in this species varied by sex during Early spring when males had higher fuel stores. By Late spring, however, fuel stores (particularly in ASY males) dropped off. These results may reflect that the majority of male *C. mauri* are departing the NGOM before Late spring, and that the few *C. mauri* moving through during Late spring are new arrivals, possibly in poorer condition, arriving from wintering grounds further south. Nebel et al. (2002) documented segregation during the non-breeding season in *C. mauri*, according to both sex and age, with adult males wintering further north than adult females, and second year birds wintering either at the northern or southern edge of the non-breeding grounds. High capture rates of males during early spring and longer stopover durations observed in ASY birds (26.6 days vs. 21.7) suggest the *C. mauri* captured during early spring were likely birds overwintering on the NGOM. The variation in winter site use by age and sex class observed by Nebel et al. (2002) may also explain the very low capture rate for *C. mauri* ASY females during this study. An alternative hypothesis is that ASY females were foraging in different habitats than studied here. Franks et al. (2013) found that at some non-breeding habitats female *C. mauri* occupy more freshwater-influenced habitats. As all of our study sites were located along the NGOM coastline, the *C. mauri* sampled in this study may better represent birds that preferentially forage in more saline environments. Therefore, results regarding *C. mauri* ASY females in this study should be interpreted cautiously. While significant sex differences in stopover duration were not detected by our strongest CJS models, only 3 ASY females were resighted during this study, and the mean minimum stopover duration was 8.6 days in comparison to the mean minimum stopover duration for ASY males of 28.2 days (N=9), suggesting that there may be sex differences in spring migration ecology for *C. mauri* that were not detected in this study due to small sample size.

Although we observed very few within-species differences in fuel stores and refueling rates, we did find higher plasma TRIG levels in ASY *C. alpina* during late spring than birds beginning their first spring migration. As Franks et al. (2013) observed in *C. mauri,* this could be the result of variation in foraging ecology among age classes, as SY *C. alpina* may also more readily forage in auxiliary terrestrial habitats than in high quality coastal habitats (Evans Ogden et al. 2005). Alternatively, in several shorebird species juveniles or SY birds appear to be less efficient foragers than adults (Goss-Custard and Durell 1987, Hockey et al. 1998, Evans Ogden et al. 2005), which could result in lower plasma TRIG levels, especially during late spring when *C. alpina* are accelerating their refueling to prepare for their jump migration. The decreased refueling rates observed in SY birds in this study may indicate that SY *C. alpina* are facing difficulties reaching the high fuel loads and refueling rates necessary for long distance migration to near arctic breeding grounds in coastal NGOM sites. Additional research on inter-annual survival rates among age classes in *C. alpina* and between habitat types on the NGOM is an important next step to addressing population level questions in this species.

Conclusions - Our research shows that at our study sites on the NGOM, *C. pusilla, C. mauri* and *C. alpina* are behaving as hop, skip, and jump, migrants, physiologically, and perhaps, behaviorally. However, their migration phenology and physiology varied somewhat within species by age and sex. Recent technological advancements in movement ecology such as satellite tagging and geolocation devices are beginning to provide our first glimpse of the mobility, site fidelity, and flexibility of shorebird migration ecology (Burger et al. 2012). While critical for developing our understanding of how highly mobile birds use sites within a region, understanding the importance of a stopover site also requires knowledge of the migration physiology of birds using that site.

Using models of potential sea-level rise for the NGOM Galbriath et al. (2002) predicted up to a 38% decline in tidal flats at Bolivar Flats, TX, by 2050. Bolivar Flats is a site on the NGOM categorized by the Western Hemisphere Shorebird Reserve Network as a site of hemispheric importance for shorebirds. Warnock (2010) predicted that the loss of a stopover site for a jump migrant can lead to consequences at the total population level. The subspecies of *C. alpina* found on the northern Gulf of Mexico is the *C. alpina hudsonia*. There are estimated to be only around 450,000 birds of this subspecies left (Andres et al. 2012), with at least 100,000 of the population using the northern Gulf during the non-breeding season (Henkel et al. 2012). Considering that *C. alpina hudsonia* populations were included on the 2015 list of Shorebirds of Conservation Concern (U.S. Shorebird Conservation Plan Partnership, 2015) understanding that this species may be particularly vulnerable to habitat loss along the Gulf is the first step in the development of plans to monitor changes in population size or ecology as the habitats of the northern Gulf of Mexico continue to change.

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Table 4.1. Number and percentage of total captured (in parenthesis) across species, age and sex by migration period.

Period of Spring	**Sex**	**Age**		**Species**	
			C. pusilla	*C. mauri*	*C. alpina*
Early (2/28-3/28)	**Male**	**ASY**	0	31 (63.3%)	32 (57.1%)
		SY	0	14 (51.9%)	36 (52.9%)
	Female	**ASY**	0	9 (47.4%)	8 (29.7%)
		SY	0	11 (42.3%)	27 (40.9%)
Mid (3/29-4/28)	**Male**	**ASY**	10 (14.5%)	15 (30.6%)	17 (30.3%)
		SY	8 (19.5%)	10 (37.0%)	13 (19.1%)
	Female	**ASY**	9 (24.3%)	9 (47.4%)	11 (40.7%)
		SY	8 (26.7%)	9 (34.6%)	19 (28.8%)
Late (4/29-5/29)	**Male**	**ASY**	59 (85.5%)	3 (6.1%)	7 (12.5%)
		SY	33 (80.5%)	3 (11.1%)	18 (27.9%)
	Female	**ASY**	28 (75.7%)	1 (5.3%)	8 (29.6%)
		SY	22 (73.3%)	6 (23.1%)	20 (30.3%)
Total			177	121	217

Table 4.2. Model selection results for Cormack-Jolly-Seber survival analysis to estimate residence time (stopover duration). Analysis was done on shorebirds detected multiple times at their site of capture. AIC_c (Akaike's Information Criterion adjusted for small sample sizes and lack of model fit) was used as our model selection criterion. For each model, **Δ** AIC_c = the change in AIC_c units between the top model and the model of interest; weight (w_i) = a measure of the relative support in the data for each model. Model selection results for among species comparisons are shown in (a); Model selection results for within species comparisons are shown in (b) for *C. pusilla,* (c) for *C. mauri,* (d) for *C. alpina.*

a. Among species models

Model	K	AIC_c	ΔAIC_c	w_i	Likelihood	Deviance
ϕ(Species*capture date) p(Species)	**9**	**2021.9**	**0.00**	**0.7999**	**1.000**	**2003.5**
ϕ(Species) p(Species)	6	2024.8	2.91	0.1867	0.233	1886.1
ϕ(Capture date) p(Species)	5	2031.0	9.17	0.0082	0.010	2020.9
ϕ(Sex*capture date) p(Species)	7	2033.4	11.49	0.0025	0.003	2019.2
ϕ(Age*capture date) p(Species)	7	2034.9	12.99	0.0012	0.002	2020.7
ϕ(Sex*Age) p(Species)	15	2035.6	13.70	0.0008	0.001	1878.1
ϕ(Species*capture date) p(.)	7	2046.4	24.50	0.0000	0.000	1915.4
ϕ(.) p(.)	2	2066.8	44.88	0.0000	0.000	1936.2

b. *C. pusilla* within species models

Model	K	AIC_c	ΔAIC_c	w_i	Likelihood	Deviance
ϕ(Sex) p(.)	**3**	**240.3**	**0.00**	**0.356**	**1.0000**	**209.8**
ϕ(.) p(.)	**2**	**241.1**	**0.77**	**0.242**	**0.6816**	**212.7**
ϕ(Age*capture date) p(.)	5	242.8	2.50	0.104	0.0001	236.8
ϕ(Capture date) p(.)	6	243.1	2.82	0.087	0.0000	230.7
ϕ(Age) p(.)	5	243.2	2.88	0.084	0.0000	212.6
ϕ(Time) p(.)	42	364.8	124.5	0.000	0.0000	174.5

c. *C. mauri* within species models

Model	K	AIC_c	ΔAIC_c	w_i	Likelihood	Deviance
ϕ(Age*capture date) p(.)	**5**	**802.0**	**0.00**	**0.490**	**1.0000**	**791.9**
ϕ(Capture date) p(.)	**3**	**802.2**	**0.23**	**0.436**	**0.8901**	**796.1**
ϕ(Age*sex*capture date) p(.)	9	807.1	5.10	0.038	0.0780	788.7
ϕ(.) p(.)	2	808.7	6.71	0.012	0.0350	749.4
ϕ(Sex) p(.)	3	810.3	8.05	0.009	0.0179	748.7
ϕ(Age) p(.)	3	813.2	11.2	0.002	0.0036	747.8

d. *C. alpina* within species models

Model	K	AIC_c	ΔAIC_c	w_i	Likelihood	Deviance
ϕ(.) p(.)	**2**	**962.5**	**0.00**	**0.346**	**1.0000**	**911.5**
ϕ(Sex) p(.)	**3**	**963.1**	**0.54**	**0.264**	**0.7630**	**910.0**
ϕ(Age) p(.)	**3**	**964.0**	**1.50**	**0.165**	**0.4776**	**910.9**
ϕ(Capture date) p(.)	3	964.5	2.01	0.126	0.3653	958.4
ϕ(Age*sex) p(.)	5	966.1	3.63	0.056	0.1629	909.0
ϕ(Size*capture date) p(.)	5	966.7	4.26	0.041	0.1191	954.4

Table 4.3. Estimated mean residence times (stopover duration) by species, and by sex and age classes. Estimates are derived from the top candidate model for among species and within species comparisons (see Table 4.2), results are omitted for within species comparisons where sex or age were not significant predictors of variation. Residence time estimates are calculated from mean values using Kaiser's (1995) formula for life expectancy, residence time = $-1/\ln \mathbf{\Phi}$.

Residence Time estimates			**Species**	
		C. pusilla	*C. mauri*	*C. alpina*
Among species		6.5 (1.6 – 33.0)	9.3 (5.3 – 16.6)	27.2 (16.3-45.5)
Within species	**Male**	3.8 (2.3-6.5)	-	20.5 (11.8 – 36.1)
	Female	8.0 (3.9-16.8)	-	34.6 (18.4-65.4)
	ASY	-	26.6 (12.3-58.2)	31.8 (16.7-61.0)
	SY	-	21.7 (12.2-39.0)	23.1 (13.3-40.3)

Table 4.4. Variables retained in the multiple regression models for migration period comparisons following backwards stepwise regression at the $p < 0.10$ level for each species and metabolite. Variables for which $p < 0.05$ are indicated in bold. Abbreviations: SESA = Semipalmated Sandpiper, WESA = Western Sandpiper, DUNL = Dunlin, MP = migration period, Time = time of day of capture, Bleed = bleed time following capture, Size = size-adjusted mass. Wind = Residual wind effect corrected for Julian date. Invert = Residual mean weekly dried biomass in 2013 at Dauphin Island corrected for Julian Date. Direction for effect, if applicable, is indicated by (+) for positive effect and (-) for negative effect.

Variable	SESA (N=177)	WESA (N=121)	DUNL (N=217)
Fat	**Sex**, Site, Year	**MP, MP*Sex**, Site, Site*Year	**MP**, Site, Year, Site*Year
Size-adjusted Mass	____	**MP, MP*Sex**	**MP**, Site, Year, Site*Year
Triglyceride	Age, **Wind (+),** Bleed (-)	**MP**, Site, Year, Site*Year, Invert (+), 2013))	**MP, MP*Age**, Site, Year, Site*Year, Time (+)
β - hydroxybutyrate	Year (N= 131)	**MP*Age**, **Wind (-),** Year, Bleed(+) (N=85)	**MP, Wind (-),** Site, Time(-), Bleed(+) (n=142)

Figure 4.1. Location of study sites across northern Gulf of Mexico.

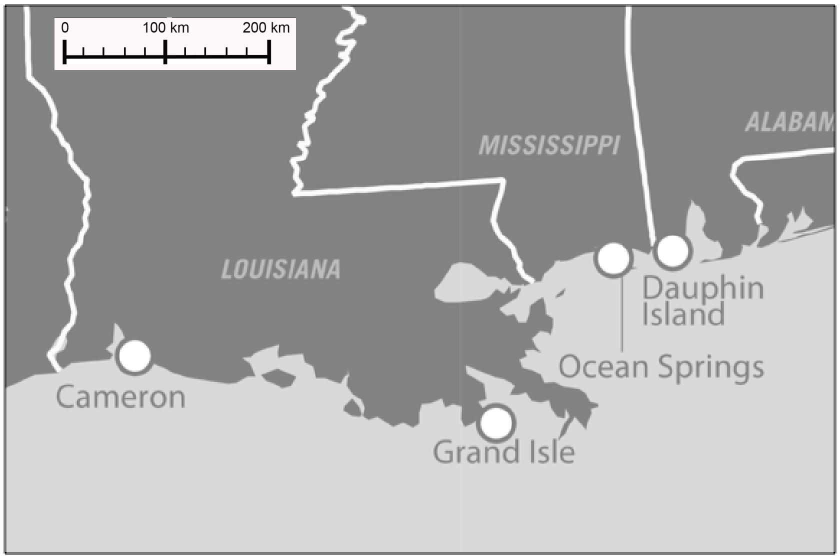


Figure 4.2 a) Change in weekly dry weight biomass (mg/mL^{-1}) at Dauphin Island, AL during Spring 2013, b) Change in daily wind effect across Spring 2011-2013.

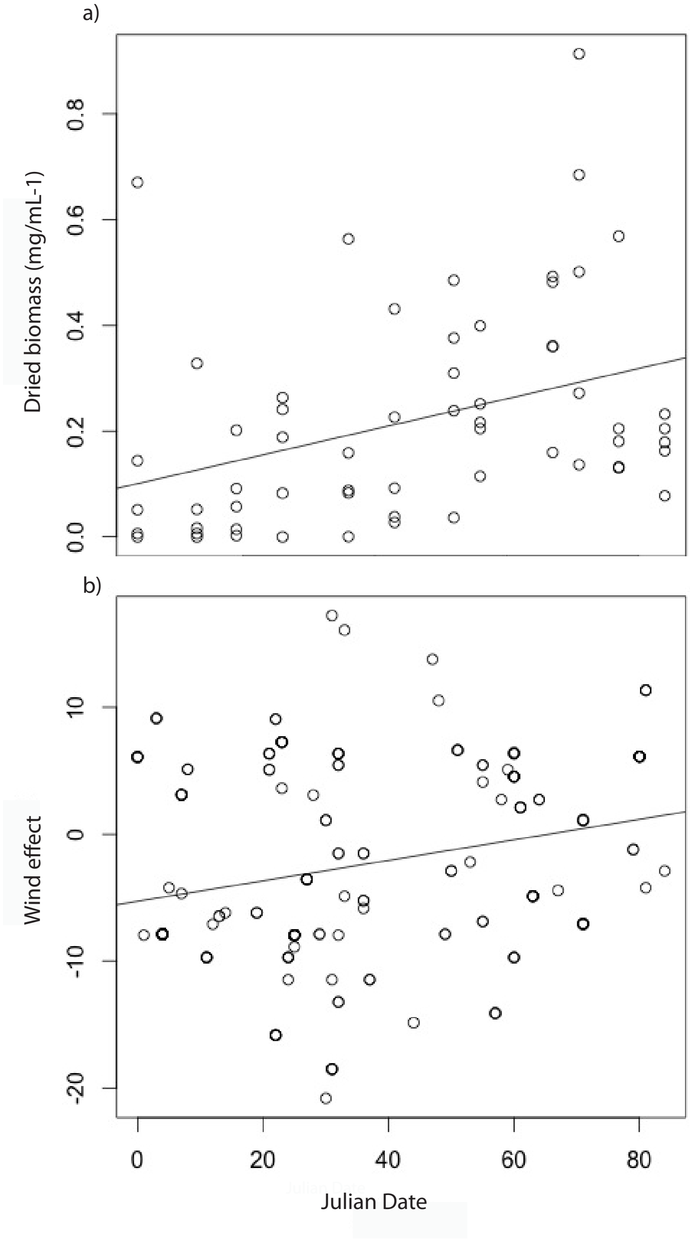
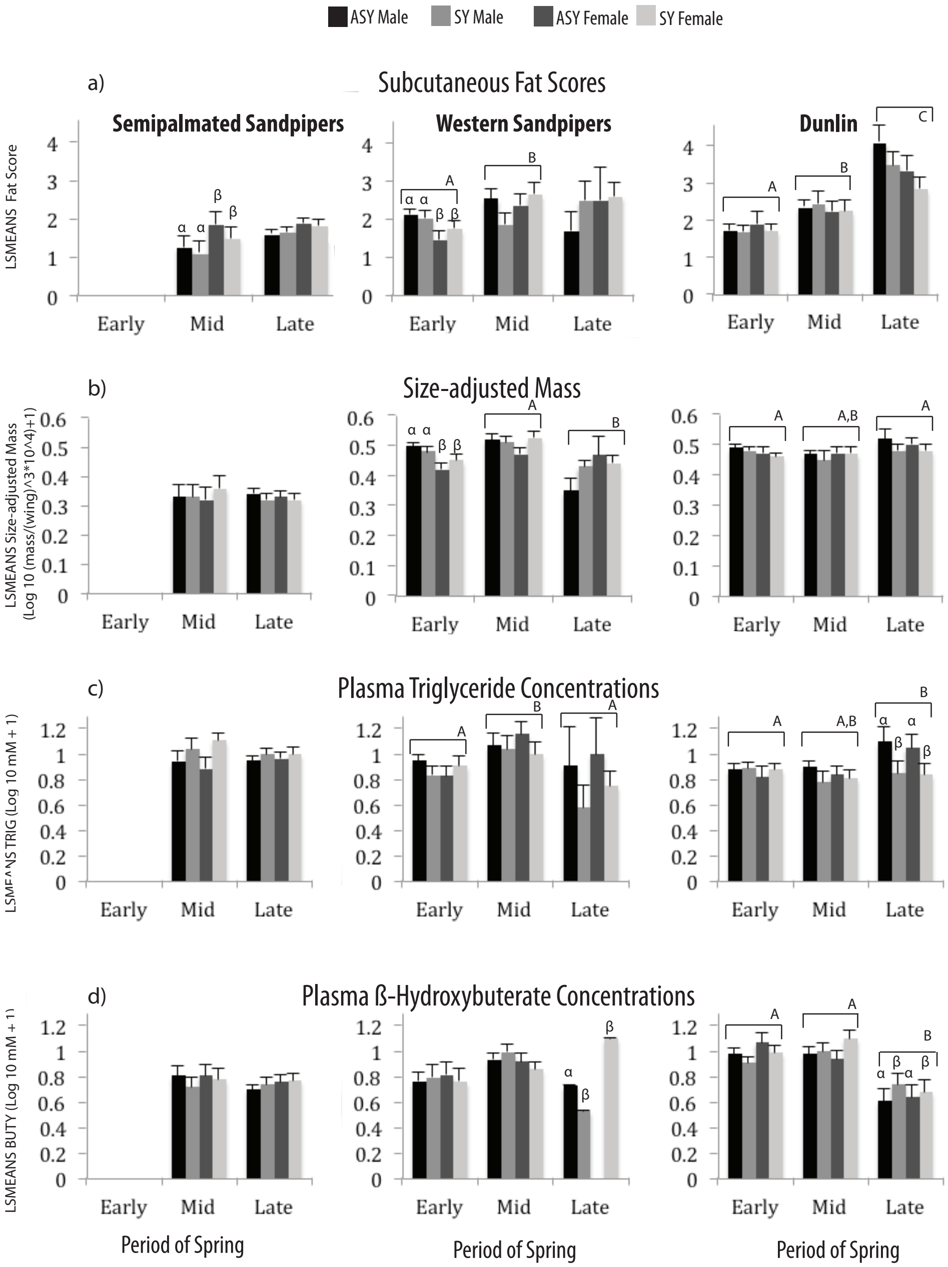


Figure 4.3. Residual least-squared means ± S.E. for a) fat score, b) size-adjusted mass, c) plasma triglyceride concentrations, d) β-hydroxybutyrate concentrations during 3 periods of migration by species, separated by age and sex classes. A,B, and C indicate within species differences among migration periods ($p < 0.05$). α, β indicated differences within species between age or sex classes ($p < 0.05$).



5. VARIATION IN DENSITY, REFUELING RATE AND POPULATION STRUCTURE OF THREE CALIDRID SANDPIPERS AMONG HABITATS DURING SPRING MIGRATION ON THE NORTHERN GULF OF MEXICO

ABSTRACT

We investigated variation in shorebird density, refueling rates and population structure among habitats on the Northern Gulf of Mexico during spring migration for three species of *Calidrid* sandpipers, the Semipalmated sandpiper (*C. semipalmatus*), the Western sandpiper (*C. mauri*) and the Dunlin (*C. alpina*). Three habitats were identified: barrier island back bay tidal flats, coastal mudflats and coastal remnant wetlands, which we ranked as of high, intermediate or poor quality based on resource abundance and availability, predation pressure and refueling rates (as measured by plasma metabolites). Bird densities were highest in the back bay habitats, the habitats with the highest prey biomass, but intermediate predation danger. For the Semipalmated sandpiper and the Dunlin there was evidence that birds on spring migration were also refueling at higher rates in the back bay habitats than the other habitats. Although proportionally more males were using the back bay habitats than females, and females tended to be observed in the "poorer" quality habitats, these differences were not significant, and there was no indication that males were refueling at higher rates in the back bay habitats than females. For Dunlin, second year birds were refueling at lower rates than adult birds in the back bay habitat, but additional differences within species were not observed among habitats. Overall, our findings support previous studies suggesting non-breeding population structure among shorebirds, and highlight the importance of barrier island back bay habitats for migrating shorebirds.

Key words: shorebirds, habitat quality, plasma metabolites, resource abundance, predation pressure

INTRODUCTION

Migrating shorebirds are among the longest-distant bird migrants. However, often they cannot carry enough fuel to complete the entire migration, and must stopover along their journey to rest and replenish fuel stores (Moore et al. 1995). The wetlands of the Northern Gulf of Mexico (NGOM) are important habitats for 28 migratory species that spend all or part of their non-breeding seasons on the Gulf coast. For many of these migratory species, the wetlands and barrier islands of the NGOM represent the first suitable stopover habitat between distant near-arctic breeding grounds and wintering grounds in South America (Withers 2002). The habitat use patterns and migration strategies of non-breeding shorebirds on the NGOM have not been well studied (Withers 2002). Our aim was to establish the importance of NGOM habitats to the migration ecology of three species of *Calidrid* shorebirds: Semipalmated sandpipers (*Calidris pusilla*, SESA), Western sandpipers (*C. mauri,* WESA), and Dunlin (*C. alpina*, DUNL). Populations of these three species stopover on the NGOM, and are believed to use the central North American flyway in route to near-arctic breeding sites (Skagen 1996). As shorebird species that use transcontinental migration routes can be more vulnerable to population declines than oceanic or coastal migrants (Thomas *et al.* 2006), a better understanding of the migration ecology of these species will be crucial for future conservation efforts.

The first objective of this study was to describe the habitat use patterns of our target shorebird species during spring migration across three coastal habitat types on the NGOM – barrier island back bay tidal flats, coastal mudflats, remnant wetlands. We investigated the quality of these habitats as measured by resource abundance (as measured through prey density and prey biomass), availability (how much suitable foraging habitat is available) and predation danger. Prey density and abundance for estuarine shorebirds has been shown to be a function of nutrient input, hydrology and sediment grain size (Colwell and Landrum 1993, Boettcher and Haig 1995, Coblentz et al. 2014). The level of predation includes both the abundance of predators, as well as distance to cover, as feeding closer to cover increases the risk of being attacked by an avian predator and of the attack being successful (Leger and Nelson 1982, Cresswell 1994, Dekker and Ydenberg 2004).

For migrating shorebirds, one of the primary factors determining migration success is how efficiently a bird can refuel at stopover sites (Alerstam and Lindstrom 1990). Therefore, fattening rates of birds on migration can be used as a proxy for habitat quality when comparing among stopover habitats. This is true for spring migrants utilizing a time-minimization migration strategy, as a high refueling rate at a high quality site will allow a bird to continue on its migratory journey faster than one stopping over at a poorer quality site with diminished refueling capacity. Some plasma metabolites, such as triglycerides, increase during fat deposition while others, such as **β** –hydroxybutyrate, increase during fat catabolism, allowing metabolites to provide an instantaneous measure of the physiological state and energetic condition of individuals just prior to capture (Jenni-Eiermann and Jenni 1994, Williams *et al.* 1999, Guglielmo *et al.* 2002, Guglielmo *et al.* 2005, Seaman *et al.* 2005). Plasma metabolites have been used to indicate habitat quality in a variety of bird studies where correlations between fattening rates and resource abundance and/or availability of foraging habitat have been observed ((Guglielmo *et al.* 2005, Seaman 2005, Seaman *et al.* 2006). In addition to measuring resource abundance and predation pressure among habitats, we investigated variation in habitat quality among habitats on the NGOM as reflected by differences in the refueling performance of shorebirds during spring migration. Our prediction was that plasma metabolite levels in target species would indicate higher fattening rates at sites with higher resource abundance, more foraging habitat availability, and reduced predation pressure.

The quality or importance of a habitat can vary not only among species but within species as well. As arrival time on the breeding grounds may be related to territory acquisition (Pitelka 1959, Farmer and Wiens 1999), male shorebirds often migrate before females. Patterns of habitat use while at stopover sites may also vary by sex and age class. Fernandez and Lank (2006) found female and juvenile Western sandpipers use less preferred habitats more often than adult males while overwintering in Mexico. Similar variation in habitat use within species has been observed at not only at this local scale, (Warnock 1990, Cresswell 1994, Shepherd and Lank 2004, Fernandez and Lank 2006) but across latitudinal scales as well (Myers 1981, Shepherd *et al.* 2001, Nebel *et al.* 2002). To account for the within species differences in migration ecology we also investigated variation in habitat use and refueling rates within species, by sex and age class. As migration theory predicts that given the strong pressure to arrive on breeding grounds and establish territories, adult males of all species will arrive earlier and have higher fueling rates than females at stopover sites, we predicted that within habitats on the NGOM adult males would have higher refueling rates than females of the same species. Similarly, juvenile shorebirds have been observed foraging in resource-poor habitats more often than adults (Evans Ogden et al. 2005, Fernandez and Lank 2006), and exhibit lower masses than adults due to lower foraging efficiency (Stillman et al. 2000). We, therefore, also predicted that the proportion of birds completing their first spring migration (SY birds) would be higher in poorer quality habitats and that mean refueling rates within habitats would be lower for this age class.

METHODS

Study Sites

This research was conducted across 4 known stopover sites along the Gulf of Mexico coast. These sites are representative of the 3 habitat types used by shorebirds on spring migration on the NGOM from Louisiana to Alabama (see Figure 4.1). Our westernmost site was located at Broussard's Beach in Cameron Parish, Louisiana. This site is located near the mouth of the Calcasieu River, which provides freshwater input. The habitat at this site (referred to herein as "mudflat") is composed of mud, fine-grained sand, with small fragments of shell hash. Our second site was located on the near-shore barrier island, Elmer's Island, in Louisiana (Figure 4.1). This site is on the back bayside of the barrier island. The habitat (referred to as "back bay") is characterized by standing water, which is replenished by tidal inundation. The sediment of Elmer's Island back bay is composed of mud and fine-grained sand topped by a thin algal mat. Freshwater input to Elmer's Island is provided by Barataria Bay and the Mississippi River. Our Ocean Springs site is a "remnant wetland" habitat site in coastal Mississippi. The sediment in the remnant wetland consists of both mud and medium-grained sand and contains the roots of dead vegetation. Freshwater input to Ocean Springs is provided by Biloxi Bay. Our final site was located on the backside of the far-shore barrier island, Dauphin Island, Alabama. The Dauphin Island habitat we sampled is also a "back bay" habitat, characterized by standing water that is replenished by tidal inundation. The sediment at Dauphin Island is layered with an algal mat that traps smaller sediment particles lying above a layer of large grained sand. Freshwater input to Dauphin Island is provided by Mobile Bay. All sites have variable salinity dependent upon recent weather conditions and the amount of freshwater input provided by nearby rivers and bays (sediment characteristics described in Coblentz et al. 2014).

Data collection

During the springs of 2011 and 2012 we estimated the density of our target species and benthic prey density and biomass in each habitat. Sandpiper density was estimated using 30-min point count surveys conducted using the International Shorebird Survey Protocol (Manomet 2010). The distance to cover and number of predators observed were noted during each survey. During the spring of 2012, core samples were collected at each site to measure the biomass and diversity of benthic invertebrates. From 29 February through 24 May 2012, five sets of core samples, approximately 2-3 cm apart from each other were collected every two weeks (approx.) in areas where all three species were observed foraging. Core samples were collected from the mid-intertidal (the area regularly inundated under normal tidal cycles and weather conditions) using a 10-cm-diameter PVC pipe driven to a depth of 5 cm (see Sherfy *et al.* 2000). Cores were placed into glass jars and kept on ice until they were returned to the laboratory where they were stored at -30°C. Afterwards, the remaining sediment in the samples was sieved through a 500 µm mesh. The material remaining on the mesh was placed into 95% ethanol with 10% Rose Bengal dye added to facilitate sorting. Invertebrates were sorted from the sediment under a dissecting microscope and identified. Following identification of invertebrates the total invertebrate biomass of each sieved core was determined after drying for 24 hours at 60°C.

Raptors, mainly falcons and accipiters are the primary predators of shorebirds during the non-breeding season (Colwell 2010). To evaluate the effect of predation pressure at study sites during sampling, we calculated the raptor encounter rate as the number of falcons (accipiters are not common along coastal NGOM) observed during surveys. During surveys we also estimated the distance from sandpiper foraging area to the nearest vegetation cover.

We investigated the variation in refueling rates among habitats and within species across all three years by measuring variation in size-adjusted body mass, and plasma metabolite levels of triglycerides (TRIG) and β-hydroxybutyrate (BOH). We trapped and surveyed our target species across our 4 study sites February – May 2011 and March – June 2012. From February – June 2013 we sampled our target species at only one study site, DIP. Birds were captured primarily at dawn and dusk using 6 mist-nets placed in foraging areas for 3-5 hours. Birds were passively captured in nets that were monitored constantly such that birds were retrieved from nets within 5-10 minutes. Captured birds were weighed (± 0.1 g) using a digital balance, measured (wing chord, tarsus length, and exposed culmen), and banded with a USGS numbered band. We assessed body weight using an index of size-adjusted mass that adjusts body mass for size using the volumetric conversion of wing chord (size-adjusted mass = mass/(wing chord)^3 *10,000; Winker et al. 1992, Hicklin and Chardine 2012, Mizrahi et al. 2012).

Plasma metabolite levels were measured from blood samples (75-300 ul) from the brachial vein using a 26-gauge needle and heparinized capillary tubes. Blood samples kept were kept cold and centrifuged within 2 h at 6000 rpm for 10 min. Separated plasma and red blood samples were stored in 20°C freezer for 1–2 weeks and then stored at -80° C prior to analysis. (See chapter 4 for a description of assay procedure and Inter and Intra-assay coefficients of variation.)

We also investigated the proportional age and sex classes of birds captured across habitats. Each bird was classified as adult (ASY) or second year (SY) based on plumage characteristics (Prater et al. 1977). Molecular markers were used to confirm sex identification for all banded birds. We extracted DNA from red blood cells using a standardized protocol for the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) then sexed the birds by standard PCR methods, using primers 2550F/2718R (Fridolfsson and Ellegren 1999). The bands were separated by gel electrophoresis in 2% agarose gels, stained with ethidium bromide, and visually analyzed under UV light. We compared the lengths of the bands to a size marker (1-kb DNA ladder, Life Technologies).

Statistical Analysis

To normalize distributions, bird and prey densities were log transformed prior to analysis. The effect of habitat on bird, raptor encounter rate, and prey densities was analyzed using mixed-model ANCOVA, with the effects of habitat and day of data collection as covariates, controlling for annual variation.

We assessed the drivers of variation in refueling rates across habitats by comparing variation in plasma TRIG and BOH from our target species controlling for year and Julian date. To eliminate samples from birds that may have been over-wintering on the NGOM (i.e. birds that were not a in a pre-migratory state), for these analyses we only analyzed samples from birds caught after March 28th of each year. Metabolite concentrations were $\log_{10} + 1$ transformed to normalize the data. Using multiple backward stepwise regression analyses we tested the independent effects of habitat type, size-adjusted mass, sex, age class, habitat type*sex*age class, time of day, site disturbance level (see chapter 2), bleed time (time between capture and bleeding), and wind effect (corrected for Julian date, see chapter 3) for each species separately. The variables retained in the full models at $P < 0.10$ (Guglielmo et al. 2005) were kept as covariates in ANCOVA to obtain marginal means for plasma metabolites among habitats by species. Results of the reduced models, including significant covariates, were used to conduct pairwise *post-hoc* comparisons of variation between habitat types within species using the Tukey's-HSD test. In cases where sex or age classes were significant covariates, analyses were rerun with variation within sex or age classes assessed independently.

We assumed that trapped birds were representative of the populations of using each habitat type. To assess variation in population structure among habitats across spring for each species we analyzed the proportion of each age each class within each sex, using a mixed-model analysis of covariance (ANCOVA) with the effects of habitat and day of capture as covariates, and controlling for annual variation. We also assessed variation in weight and size within habitats. We considered statistical test results significant at $p < 0.05$, except for interaction terms, which we considered significant at $p = 0.10$, as significance tests for interaction terms have lower power than those for main effects (Little et al. 1991). Values are presented as least-square means ± SE. Statistical analyses were conducted using R Software version 0.97.551 (R Core Team 2013).

RESULTS

Prey density, biomass and predation danger

The invertebrate community sampled from sediment cores consisted of invertebrates from five phyla, seven classes, and fifteen families across 110 sediment cores (Table 5.1). The remnant wetland habitat was a unique community and was dominated by tube-building tanaid crustaceans, but had high taxonomic richness including four families of polychaetes, three families of amphipods, and bivalves. 82.6% of the abundance consisted of tanaids, followed by 12.1% corophiid amphipods, and 1.9% polychaetes. The remainder was composed of gammarid and ischyocerid amphipods, the isopod family Idoteidae, and bivalves. The back bay habitats from Elmer’s Island and Dauphin Island were dominated by ephydrid fly larvae, which composed 40.6% of the abundance at Elmer’s Island and 41.3% of the abundance at Dauphin Island. At Elmer’s Island

33.2% of the abundance was represented by capitellid polychaete and nematode worms. At Dauphin Island, 11.3% of the remaining abundance was composed of insect larvae adapted to salt marsh conditions and 37.7.4% of the abundance was composed of capitellid polychaete and nematode worms. The mudflat habitat was dominated by haustoriid amphipods (67% of the abundance) and a number of gastropods and bivalves (32% of the abundance). Corrected for Julian date both prey density and prey biomass varied among habitats ($F_{2,107} = 8.4$, $p < 0.001$, and $F_{3,106} = 6.8$, $p = 0.002$, Table 5.1). However, while the density of invertebrates was higher in the remnant wetland habitat than the other habitat types (Mudflat, Tukey's HSD, $p = 0.002$; Back bay, $p < 0.001$), both the mudflat and remnant wetland habitats had lower total prey biomass than the Back bay habitat (Tukey's HSD, $p = 0.02$, and $p = 0.007$, respectively, Table 5.1).

Raptor encounter rates decreased with day of spring ($F_{1,109} = 8.46$, $p = 0.004$), but did not differ among habitats ($F_{2,108} = 0.19$, $p = 0.83$). In terms of habitat specific predation danger and available foraging area, the remnant wetland habitat was the closest to vegetation, and thus, potentially more dangerous for sandpipers ($F_{5,105} = 16.1$, $p < 0.001$, Tukey's HSD, $p < 0.001$) and had the least amount of available foraging area ($F_{2,108} = 26.6$, $p < 0.001$, Tukey's HSD, $p < 0.001$, Table 5.1).

Shorebird densities and refueling rates among habitats

Corrected for Julian date (day of survey) and controlling for annual variation the total densities of target bird species differed by habitat type ($F_{2,108} = 8.95$, $p < 0.001$, Table 5.1). Post-hoc comparisons of log-transformed densities show densities higher in the back bay and remnant wetland habitats than the mudflat habitats (Tukey's HSD, $p < 0.001$ and

$p = 0.005$). Although the back bay habitats also had higher densities than the remnant wetlands, these differences were not significant (Tukey's HSD, $p = 0.07$). The densities of SESA did not vary among habitats ($F_{2,68} = 1.7$, $p = 0.19$, Table 5.1), however the densities of WESA and DUNL differed by habitat ($F_{2,108} = 3.6$, $p = 0.03$, and $F_{2,108} = 12.1$, $p < 0.001$, Table 5.1). There were lower densities of WESA in the remnant wetland than the back bay (Tukey's HSD, $p = 0.02$), and lower densities of DUNL in the mudflat habitat than in both the back bay and remnant wetland habitats (Tukey's HSD, $p < 0.001$ for both comparisons, Table 5.1).

Across species, residual TRIG did not vary among habitats ($F_{2,336} = 1.4$, $p = 0.24$, Table 5.1), however there was an interaction effect of habitat*species (Table 5.2). While residual plasma TRIG did not vary among habitats for WESA ($F_{2,118} = 2.5$, $p = 0.09$) (Table 5.1), residual TRIG for SESA was lower in the remnant wetland habitat than both the back bay and mudflat habitats (Tukey's HSD, $p = 0.02$ and $p = 0.002$, Table 5.1, Figure 5.1). Residual plasma TRIG for DUNL did not vary among habitats when age and sex classes were analyzed together ($F_{2,118} = 2.5$, $p = 0.09$, Table 5.1), however, residual plasma TRIG varied by age ($F_{1,104} = 4.42$, $p = 0.04$) and with respect to age class and habitat (habitat x age: $F_{7,98} = 2.15$, $p = 0.05$). Due to the statistical interaction, subsequent analyses of plasma TRIG were conducted within age classes. Second year DUNL did not refuel at different rates in different habitats ($F_{3,121} = 0.17$, $p = 0.9$). Conversely, residual plasma TRIG for adult DUNL varied by habitat ($F_{2,40} = 5.02$, $p = 0.01$). Post-hoc analyses show adult birds of both sexes are refueling at higher rates in the back bay habitats than in the remnant wetland or mudflat habitats (Tukey's HSD, $p = 0.009$ and $p = 0.02$, Figure 5.1). Across species residual BOH did not differ among habitats ($F_{2,244} = 0.94$, $p = 0.39$), however residual BOH was higher in the mudflat habitat for DUNL than the back bay habitat ($F_{2,82} = 3.3$, $p = 0.04$, Tukey's HSD, $p = 0.02$, Table 5.1, Figure 5.1).

Within habitat variation in population structure and refueling rates

While proportionally more adult male SESA and more DUNL males of both age groups were found in the back bay habitat than the other habitats (Table 5.3), among habitats these differences were not significant ($F_{2,29} = 2.4$, $p = 0.11$ and $F_{2,53} = 1.9$, $p = 0.16$, Table 5.3).

Within habitats, the only variation we observed was that residual plasma TRIG was lower for SY DUNL in the back bay habitats than for adults (Tukey's HSD, $p = 0.012$, Figure 5.1).

DISCUSSION

Among habitat variation

We documented prey density and biomass, predation danger, refueling rates and the population structure of three shorebird species across four NGOM habitats during spring migration. Although prey density was highest in the remnant wetland habitat, this habitat also had the shortest distance to cover and least available foraging habitat. We, therefore, expected this habitat to be favored less than the back bay habitats which had the highest total prey biomass, second highest prey density, and the lowest raptor encounter rate. We expected the mudflat habitats to represent poorer habitats than either the back bay or remnant wetland habitats as the raptor encounter rates were higher, and the prey density, and prey biomass were lower in these habitats. Consistent with these rankings, the back bay habitat supported the highest densities of shorebirds of all species and had higher refueling rates for SESA and adult DUNL. Also consistent with this ranking was the higher plasma BOH levels for DUNL in the mudflat habitats, indicating birds were more rapidly catabolizing fat in this poorer quality habitat.

While prey biomass and refueling rates were higher in the back bay habitat, prey density was not. One possible explanation for this finding is that our sampling scheme may not have properly detected all the resources available in this habitat type. Recent literature investigating shorebird foraging patterns have focused on the foraging mode and dietary component of biofilm grazing. The biofilm layer, which contains a mixture of microbes and organic detritus is found on the surface of intertidal flats (Decho 1990). Western sandpipers and Dunlin have been found to feed heavily on unfiltered biofilm during spring stopover on the Fraser River delta, British Columbia, Canada (Kuwae et al. 2008, Mathot et al. 2010). The sediment of the back bay habitat type in which we sampled shorebirds was comprised of mud and fine-grained sand topped by a thin algal mat. The high density of shorebirds in this habitat may be a result of birds foraging on the biofilm layer of this algal mat. Additional research into the organic content of core samples, or stable isotope signatures of shorebird plasma, could help better elucidate the feeding patterns of migrating shorebirds in similar habitats on the NGOM.

Aside from the back bay habitat, however, there was no consistent pattern in densities or refueling rates among other habitats. For example, residual TRIG was lower in the remnant wetland habitats for both SESA, and adult DUNL*,* suggesting refueling rates were lower in this habitat. Conversely, while residual TRIG was highest for SESA in the mudflat habitat, residual TRIG was lowest in the same habitat for adult DUNL.

This difference may be a result of variation in food preference among species. SESA has been documented foraging in areas of high haustoriid amphipod abundance during spring migration through South Carolina (Thibault and Levison 2013), whereas the diets of DUNL during spring in similar habitats are more likely to be dominated by polycheates, insect larvae and ostracods (Weber and Haig, 1997). The core samples collected in mudflat habitats were dominated by amphipods, suggesting this habitat may provide superior food resources for SESA than DUNL.

The high variation in refueling rates among and within species also highlights the difficulty in using plasma metabolites as an indicator of habitat quality during spring migration. While plasma metabolite levels reflect an individual's refueling rate, these levels can also be influenced by many other factors, such as molt status (Jenni-Eiermann et al. 2002), and time since arrival or to departure (Taylor 2011). Due to the presence of overwintering birds at our study sites, individuals sampled in this study may have already begun migration, were about to migrate, or were staging depending on the species and the individual.

Another surprising result was the lack of any significant habitat interactions for WESA. The sample size for WESA in the remnant wetland habitat (n = 4), may have limited our power to detect differences in this and among habitat types in this species. Additionally, latitudinal segregation of male and female WESA during the non-breeding season has been well documented (Nebel 2005, Mathot et al. 2007). Supporting this, we captured very few adult female WESA throughout this study. Given that females in this species often winter further south than males (Nebel 2005, Mathot et al. 2007), their migration patterns through the NGOM may also differ, limiting our ability to detect differences among habitats in this species. A final explanation for this result may be the timing of migration in this species. WESA departs the NGOM before SESA or DUNL (See chapter 3). Although we did not observe differences in prey biomass or density as Julian date increased in this study, weekly core sampling at the Dauphin Island barrier island backbay habitat in the Spring of 2013 showed an increase in prey biomass with Julian date (See chapter 3). The differences observed in refueling rates for SESA and DUNL in the backbay habitat may reflect an increase in prey biomass in this habitat later in the season when WESA is no longer foraging in the habitat.

Within habitats variation

Although differences were not significant, the proportion of females and second year birds of all species tended to be higher in less preferred habitat. Additionally, adult residual plasma TRIG levels were higher for DUNL in the back bay habitat. These results may suggest asymmetry in competitive abilities among sexes and age classes (Marra and Holmes 2001). There is little evidence to support competitive asymmetries among classes in shorebirds, however. Stable dominance relationships are not common in small sandpipers, and adults do not necessarily win aggressive interactions with younger birds (Harington and Groves 1977, Warnock 1994). An alternative hypothesis is that habitat segregation is bill length dependent. Individual shorebirds occupying different foraging habitats according to morphology, preferred foraging mode or prey type is well documented (Harrington, 1982, Geritsen and Heezik, 1984, Fernandez and Lank 2008). However, while additional analyses of culmen length of birds sampled in this study (Appendix A) observed some differences in culmen length among age classes for all three species (ASY females generally had longer bills than SY females), no differences were observed within age classes or sexes that would indicate longer or shorter bills were preferential in any one habitat for any particular sex. The one exception to this finding was that second year female DUNL in the mudflat habitat had slightly longer bills than second year females in the remnant wetland habitats. Given the male dominated structure of the back bay habitat, and that the highest proportion of adult female DUNL were found in the mudflat habitat it is possible that the variation in culmen length observed in SY females is a result of SY females with shorter bills (i.e. closer in length to male culmen length) are preferentially foraging in the barrier island backbay habitat while SY females with longer bills (i.e. closer in length to adult females), are preferentially foraging in the mudflat habitat. Support for this hypothesis is given by Mathot et al. (2010) who observed female DUNL consuming more mollusks than males during spring migration. The mudflat sampled in this study had the highest proportion of mollusks (37%) of all habitats sampled, and may indicate a prey preference for longer billed females in this species. Future research into the population structure and foraging behavior of DUNL on the NGOM, for example, one including fecal and gut content analysis, could help strengthen this hypothesis. Given that sex-related differences in diet specializations can have population-level consequences, including differential susceptibility of subclasses of the population to habitat loss or degradation (Durell 2000), further investigation is warranted.

Conclusions

This study has shown evidence of non-random distribution of shorebird species across habitat types on the NGOM, and variation in the habitat quality at these sites. There is some additional evidence of habitat partitioning within shorebirds species according to sex and age classes during spring migration, however the mechanisms driving these differences are not clear. Overall, our finding that the barrier island back bay habitat provides an important habitat for migrating shorebirds, is significant in the context of continued sea-level rise and anthropogenic modification of barrier island habitats. Modern beach management practices often lead to further erosion of barrier island habitats, the loss of moist sediment habitat (Galbraith et al. 2002), and changes to infaunal macroinvertebrate distributions (Peterson et al. 2006), all of which can negatively impact beach reliant species, such as migrating shorebirds (Dugan et al. 2008, Seavey 2009). Effective conservation of shorebird populations using these habitats requires an *a priori* understanding of the population structure and ecology of birds stopping over in these habitats. Continuing to develop this understanding will allow for a better understanding of the costs and benefits associated with future beach management practices.

Table 5.1. Available resources (prey abundance, biomass and availability), predation pressure (raptor abundance and distance to cover), shorebird density, and refueling rates (Residual plasma TRIG and BOH) with respect to habitat type on the Northern Gulf of Mexico during Spring migration seasons of 2011-2013. Least-squares means (± 95% CI) are reported, controlling for annual variation and Julian date. Sample sizes are given in parentheses. Sample size for prey density/biomass = number of sediment cores, foraging area = number of surveys, raptor encounter rate = number/per survey, bird density = number of surveys, residuals plasma TRIG/BOH = total number of individuals sampled. * Denotes significant difference from other habitats, $p < 0.05$.

		Habitat Type		
		Back Bay	*Mudflat*	*Remnant Wetland*
Prey density (indv./ mL^{-1})		0.72 ± 0.29 (60)	0.46 ± 0.45 (25)	**2.74 ± 0.45 (25)* (+)**
Prey biomass (mg/mL^{-1})		**0.88 ± 0.22 (60)* (+)**	0.29 ± 0.35 (25)	0.23 ± 0.35 (25)
Foraging area (km2)		15.5 ± 4.2 (84)	59.2 ± 9.0 (10)	**12.5 ± 6.8 (17)* (-)**
Raptor encounter (#/survey day)		0.10 ± 0.08 (84)	0.13 ± 0.19 (10)	0.07 ± 0.14 (14)
Distance to cover (m2/survey)		112.0 ± 10.95 (84)	136.5 ± 23.58 (10)	**42.0 ± 33.2 (17)* (-)**
Bird density (birds ha^{-1})	*All Focal Species*	199.9 ± 40.1 (84)	**82.8 ± 86.3 (10)* (-)**	126.6 ± 63.7 (17)
	SESA	41.5 ± 33.9 (51)	13.6 ± 56.9 (9)	1.1 ± 49.4 (11)
	WESA	30.8 ± 17.4 (84)	16.8 ± 37.6 (10)	**8.9 ± 27.6 (17)* (-)**
	DUNL	136.9 ± 65.4 (84)	**76.6 ± 140.8 (10)* (-)**	117.1 ± 104.0 (17)
Residual TRIG	*All Focal Species*	1.02 ± 0.04 (243)	1.00 ± 0.08 (51)	0.95 ± 0.10 (45)
	SESA	0.99 ± 0.04 (132)	1.12 ± 0.10 (24)	**0.88 ± 0.10 (21)* (-)**
	WESA	1.1 ± 0.06 (103)	0.97 ± 0.17 (14)	1.14 ± 0.31 (4)
	DUNL	1.09 ± 0.06 (67)	1.04 ± 0.10 (19)	1.08± 0.10 (20)
Residual BOH	*All Focal Species*	0.77 ± 0.06 (185)	0.85 ± 0.09 (35)	0.78 ± 0.09 (53)
	SESA	0.75 ± 0.05 (67)	.76 ± 0.10 (21)	0.74 ± 0.13 (12)
	WESA	0.87 ± 0.06 (26)	0.84 ± 0.16 (3)	1.14 ± 0.34 (2)
	DUNL	0.83± 0.05 (92)	**1.01 ± 0.12 (11)* (+)**	0.94± 0.11 (39)

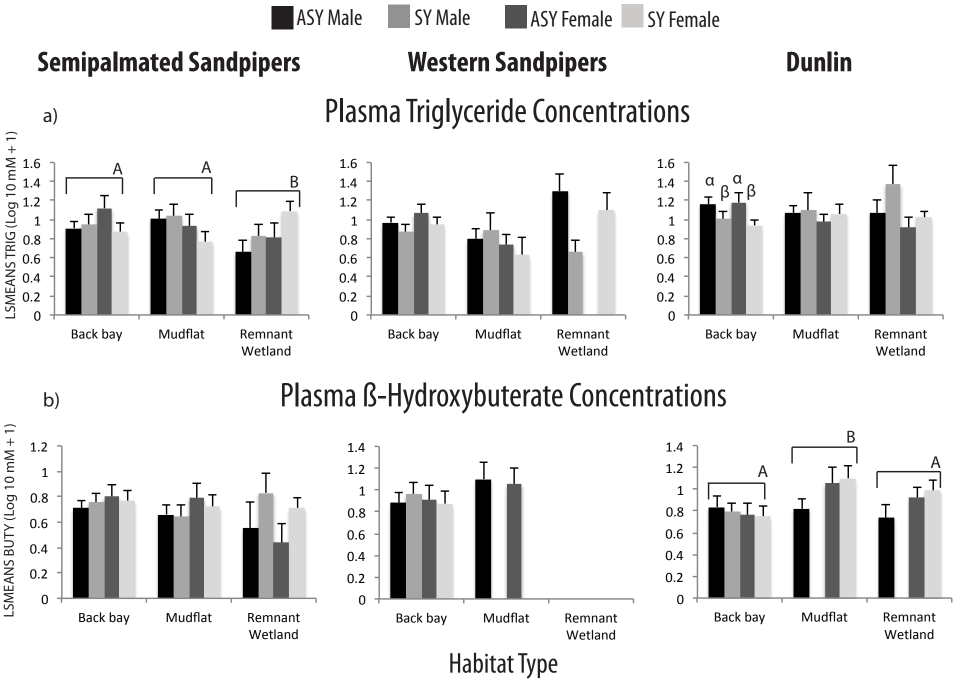
Table 5.2. Variables retained in the multiple regression models for habitat comparisons following backwards stepwise regression at the $p < 0.10$ level for each. Variables for which $p < 0.05$ are indicated in bold. Abbreviations: SESA = Semipalmated Sandpiper, WESA = Western Sandpiper, DUNL = Dunlin, Time = time of day of capture, Bleed = bleed time following capture, Direction for effect, if applicable, is indicated by (+) for positive effect and (-) for negative effect.

Variable	*Across species*	*SESA*	*WESA*	*DUNL*
Triglyceride	**Year, Size, Habitat*Species** (N = 339)	**Habitat** (N=178)	Julian Date, Year (N=55)	**Julian date (+), Year, Habitat*Age** (N=106)
β – hydroxybutyrate	**Julian date, Bleed (+),** Habitat*Species (N=85)	**Year,** Bleed (+) (N= 61)	Julian date (-), Bleed (+) Time (-) (N=11)	**Julian date (-),** Habitat (N = 13)

Table 5.3. Shorebird population structure with respect to habitat type on the Northern Gulf of Mexico during Spring migration seasons of 2011-2013. Least-squares means (± 95% CI) are reported, controlling for annual variation and Julian date. Sample sizes are given in parentheses. Sample size = number of birds captured.

				Back Bay	*Mudflat*	*Remnant Wetland*
Age composition (LS MEANS ± 95% CI)	SESA	Male	ASY	0.37 ± 0.13 (55)	0.26 ± 0.31 (9)	0.03 ± 0.32 (5)
			SY	0.22 ± 0.34 (31)	0.22 ± 0.28 (5)	0.20 ± 0.29 (5)
		Femal	ASY	0.22 ± 0.13 (31)	0.19 ± 0.3 (4)	0.24 ± 0.30 (3)
			SY	0.19 ± 0.16 (16)	0.34 ± 0.36 (6)	0.53 ± 0.37 (8)
	WESA	Male	ASY	0.45 ± 0.17 (39)	0.73 ± 0.44 (8)	0.45 ± 0.17 (1)
			SY	0.20 ± 0.15 (24)	0.06 ± 0.36 (1)	0.59 ± 0.51 (2)
		Female	ASY	0.12 ± 0.08 (16)	0.15 ± 0.19 (4)	N/A (0)
			SY	0.23 ± 0.12 (24)	0.05 ± 0.30 (1)	0.10 ± 0.43 (1)
	DUNL	Male	ASY	0.27 ± 0.12 (36)	0.33 ± 0.30 (8)	0.22 ± 0.49 (12)
			SY	0.34 ± 0.10 (49)	0.17 ± 0.25 (1)	0.07 ± 0.23 (13)
		Female	ASY	0.14 ± 0.11 (14)	0.41 ± 0.27 (6)	0.28 ± 0.23 (6)
			SY	0.25 ± 0.09 (36)	0.16 ± 0.25 (4)	0.43± 0.22 (22)

Figure 5.1. Residual least-squared means ± S.E. for a) Plasma triglyceride concentrations, b) Plasma β-hydroxybutyrate concentrations across 3 habitats on the Northern Gulf of Mexico by species, separated by age and sex classes. A,B**,** indicate within species differences among habitats ($p < 0.05$). α, β indicate differences within species and within habitats between age or sex classes ($p < 0.05$).



CONCLUSION

In this dissertation I have attempted to elucidate the ecological use of the northern Gulf of Mexico by migrant shorebirds. Relative to shorebird migration along the Atlantic and Pacific coasts, a very limited amount of work has addressed shorebird migration through the NGOM. Due to a lack of data it was unknown if NGOM habitats provide important stopover habitat for shorebirds. Following this, the effects of the environmental degradation that occurred as a result of the Deepwater Horizon oil spill were difficult to interpret due to a lack of baseline data. Field research for this study was conducted from October 2010 – June 2013 across sites from the Texas/Louisiana border to Florida, with a focus on spring migration for 2012-2013. In the following paragraphs, I provide a summary of the conclusions from this dissertation and provide some considerations for shorebird conservation and Gulf Coast restoration management.

Chapters 2 and 3 investigated the effects of the Deepwater Horizon Oil Spill from a large-scale (Chapter 2) and local scale (Chapter 3) perspective. In Chapter 2 I discuss the nonlethal effects of oil on birds, which include diminished health, diminished plumage quality, prey and habitat switching, and delayed migration. All of these setbacks can lead to reduced productivity in breeding shorebirds, which can impact ecosystems at a global scale. Chapter 2 also highlights the number and diversity of shorebird species using NGOM habitats. Chapter 3 takes a closer look at the level of oil exposure across seven of these shorebird species. Given that 8.6% of the birds handled in 2010-2011 and

0.6% of birds handled in 2012 showed visible signs of oiling, I predicted that as many as 100,000 shorebirds were directly exposed to oil. In the two years following the spill I also investigated how variation in foraging habitat impacted levels of oil exposure, and found that the more coastal foraging birds (i.e. Sanderlings and Dunlin) were more likely to be directly exposed to oil than the more estuarine foraging birds (i.e. Western and Semipalmated sandpipers). Perhaps the most surprising finding from my investigation of the effects of the oil spill was that there was more evidence of impact from oil-spill cleanup activities than from the oil spill itself. While biologists and managers at oil spill cleanup sites were careful to redirect cleanup traffic around nesting bird areas, less consideration was given to the disturbance this traffic may have been causing to the foraging birds also relying on those coastal habitats to fuel long distant migrations. This result should be carefully considered following future environmental disasters, and response plans should include migratory shorebirds as one of the species groups vulnerable to cleanup activities.

Chapters 4 and 5 used individual measures of physiology (size, fuel load, refueling rate) and behavior (stopover duration and phenology) to investigate variation in migration strategy and habitat use before departing the NGOM on spring migration. In Chapter 4, I compared the migration ecology of three species of Calidrid sandpipers and confirmed that Dunlin exhibited a “jump” migration strategy (long stopover duration, high fuel stores) while Semipalmated sandpipers exhibited a “hop” migration strategy (short stopover duration, lower fuel stores). Western sandpipers were found to be intermediate between these two species. In Chapter 5, I compared environmental variables and refueling rates with shorebird density and population structure across three habitat types found on the NGOM – back bay barrier island habitats, coastal mudflats, and remnant wetlands. I found that although prey density was highest in the remnant wetland habitat, prey biomass and foraging habitat availability was higher in the back bay habitats, suggesting the back bay habitats represented a better quality habitat. This finding was supported by higher density of shorebirds overall and higher refueling rates in the back bay habitat for Semipalmated sandpipers and adult Dunlin. While the refueling rate results from Chapter 5 supported the higher quality of the back bay habitat, few other results from plasma metabolites from this and other chapters throughout this dissertation were able to detect significant differences among habitats or within species, highlighting the difficulty in using plasma metabolites as an indicator of habitat quality. Instead, I would suggest, as suggested by Taylor (2011), that physiological metrics of migrating shorebirds (such as plasma metabolites) instead be used to confirm assessments of quality rather than as an independent indicator of habitat quality.

The results of Chapters 4 and 5 highlight two aspects of shorebird ecology on the NGOM, both of which have important implications for future research and management of NGOM habitats in regards to migratory shorebirds: 1) species-specific variation in migration ecology; 2) importance of barrier island back bay habitats. Estimates of shorebird population size (especially during aerial surveys on the difficult to navigate northern Gulf coasts) are sometimes reported by size category (e.g. "small shorebirds"), which can result in population estimates and impact assessments for oil industry or beach restoration activities that group suites of similar species together. However, this study has demonstrated the distinct variation in individual species' ecology during spring migration, and the effects of habitat loss or degradation of NGOM habitats will likely not be the same for all species. For example, this research has shown that the threatened NGOM habitats may be particularly important for migration success in the Hudson Bay breeding subspecies of Dunlin (*C. alpina hudsonia*). Future research should consider individual species ecology in these habitats before estimating population sizes and environmental impacts of management activities.

While other habitat comparisons of within species variation in habitat use were inconclusive, the importance of the back bay barrier island habitats to migratory shorebirds on the NGOM is critical considering the many threats barrier island habitats face. In particular, rising sea levels and beach erosion is leading to a coastal "squeeze" between human infrastructure and natural habitats (Defeo 2009). Humans have attempted to mitigate this shoreline retreat through beach nourishment (placement of sand fill on the beach), or the construction of dikes, and seawalls (Titus et al. 1991). These practices, however, can lead to further erosion and the loss of shorebird foraging habitat (Galbraith et al. 2002). Future beach restoration and management activities on the NGOM need to consider the importance of natural barrier island habitats to shorebirds and other beach dependent species when developing their impact assessment plans. This is especially important as the Gulf of Mexico prepares for a potential influx of money for coastal restoration work resulting from criminal penalties following the Deepwater Horizon oil spill (Gulf Coast Ecosystem Restoration Council, 2013). It is my sincere hope that restoration plans will carefully consider the findings of this dissertation research, and will work to develop proposals that are beneficial to both coastlines and coastally reliant species.

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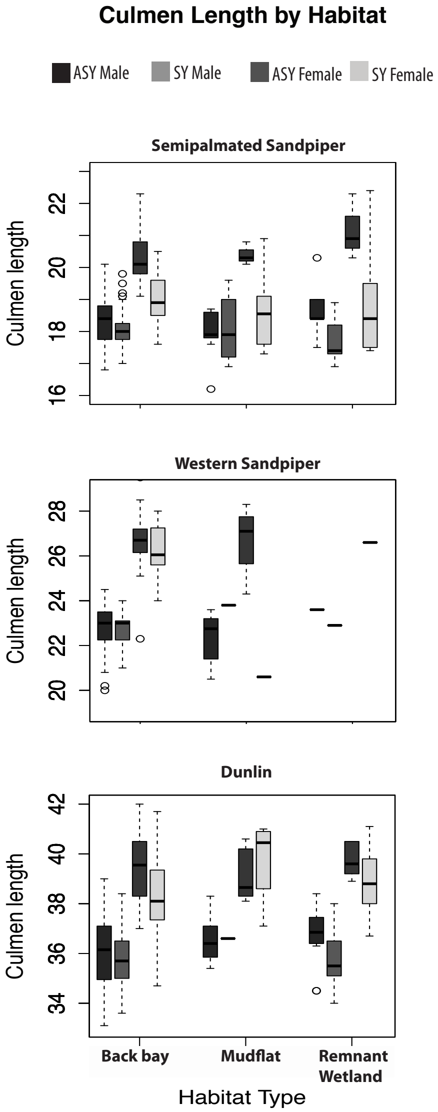
Appendix A

Figure A.1. Culmen lengths ± 95% C.I. for three species of *Calidrid* sandpipers sampled on the Northern Gulf of Mexico during Spring 2011-2013. Although differences were found among species and age classes, no significant differences were observed within sex or age classes among habitats.



BIOGRAPHY

Jessica Henkel is a Christine Mirzayan Science and Technology Policy Fellow with the National Academy of Sciences and a PhD candidate in the Department of Ecology and Evolutionary Biology at Tulane University. She has a B.A. in English from Stony Brook University and a M.S. in Conservation Biology from the University of New Orleans. Jessica is interested in how environmental and anthropogenic change and habitat degradation are impacting the coastal habitats of the U.S. Gulf of Mexico and the communities that rely on them. Her dissertation research investigated the migration ecology and physiology of near-arctic breeding shorebirds that stopover in coastal habitats on the Gulf of Mexico. When not wearing mud boots or waders, Jessica can be found advocating for coastal issues or marching in the Mardi Gras parades of her adopted city of New Orleans.