Length of stay and habitat use of shorebirds at two migratory stopover sites in British Columbia, Canada

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Abstract

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Many species of shorebirds depend on stopover sites to rest and refuel during their long-distance migrations. To determine how shorebirds use migratory stopover sites, we tracked three species of shorebirds at two stopover sites in British Columbia from 2018-2021 during northward and southward migration using automated telemetry. Western Sandpipers (*Calidris mauri*) stayed longer at the Fraser River Estuary (4-8 days) compared to Tofino (2-6 days). We assessed habitat use of Sanderlings (*Calidris alba*), Semipalmated Plovers (*Charadrius semipalmatus)*, and Western Sandpipers between beaches and mudflat at the Tofino stopover site. Time spent at the beach and mudflat habitats varied by species, tidal period, time of day, migration period, and human disturbance. This study shows that different stopover sites, and habitats within stopover sites, offer a unique set of characteristics used by birds exhibiting varying migration strategies, highlighting the importance of conserving a diversity of migration stopover locations and habitats.

Keywords: shorebird, stopover site, migration, length of stay, habitat use, migration strategy, prey availability, human disturbance, coastal beaches, mudflat

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Chapter 1 – General Introduction

1.1 Shorebird migration and stopover sites

Shorebirds depend on stopover sites to rest and acquire sufficient food resources to fuel their migration between breeding and overwintering grounds (Myers 1987, Warnock & Bishop 1998, Warnock 2010). The Pacific Americas Flyway is a bird migration route along the west coast of North and South America that is used by millions of shorebirds, twice annually. A series of stopover sites are located along the coastal route, where the migration strategy of many shorebird species is to “hop” along these sites to refuel along the way (Iverson et al. 1996, Warnock & Bishop 1998). The availability of a continuous complex of wetland and mudflat habitats is critical for shorebirds to sustain these ~5,000 – 15,000 km-long migrations (Donaldson et al. 2000, Senner et al. 2016). A single stopover site can be used by millions of shorebirds in a short migration window of several weeks. For example, up to 50% of global Western Sandpiper (*Calidris mauri*) and Pacific Dunlin (*Calidris alpina pacifica*) populations stopover on the Brunswick Point mudflat in the Fraser River Estuary of southern British Columbia during spring migration (Drever et al. 2014). Therefore, disturbance or elimination of one critical stopover site can have detrimental effects on a species’ population (Studds et al. 2017).

Stopover sites include a mosaic of habitats such as coastal estuaries, tidal mudflats, sand beaches, and marshes (Burger et al. 1996, Long & Ralph 2001, McPeake et al. 2015). These habitats often contain an abundance of invertebrates and intertidal biofilm rich in fatty acids, important food sources that provide energy for fueling migratory flights (Placyk & Harrington 2003, Schnurr et al. 2020). However, anthropogenic disturbances and alteration of these habitats are rapidly increasing (Shepherd et al. 2003, Senner et al. 2016, Wang et al. 2022), where ~43% of global coastal wetlands have already been lost (Davidson, 2014). The loss and degradation of these critical stopover habitats can affect the availability of shorebird food sources and result in their inability to meet their energetic requirements during migration (Baker et al. 2004, Studds et al. 2017, Wang et al. 2022) - a potential contributing factor to the global decline in shorebird populations (Donaldson et al. 2000, Niles et al. 2009, Smith et al. 2023). Further, coastal stopover sites are often situated in areas that are also busy with people, and studies have shown that human activity can negatively impact shorebirds during migratory stopover (Pfister et al. 1992, Murchison et al. 2016). In North America, 68% of shorebird species are in decline with a net population loss of 37% from 1970 to 2019 (Rosenberg et al. 2019, Smith et al. 2023). Protecting a network of important stopover sites is a key component in the conservation of shorebird populations (Wang et al. 2022).

Decades of shorebird monitoring have determined major migratory stopover site locations and preferred habitats based on population counts and mark-recapture studies (Myers 1987, Warnock et al. 2004, Battley et al. 2012, Chan 2019). Although traditional tracking and resighting methods of individual shorebirds have helped to answer important questions about migration and stopover ecology (Iverson et al. 1996, Warnock et al. 2004, Warnock & Takekawa 2012, Henkel & Taylor 2015), these methods often come with limitations, such as the need to manually detect or observe birds in-situ, resulting in gaps across time and space (Kays et al. 2015, Taylor et al. 2017). Recent advancements in automated radio telemetry can help fill knowledge gaps in shorebird ecology as automated telemetry uses a network of stationary receivers that continuously detect tagged birds within range (Taylor et al. 2017). This tracking advancement is a useful tool in understanding shorebird migration and stopover ecology at varying spatial scales (Anderson et al. 2019, Aikens 2022, Neima et al. 2022). For example, detections from automated telemetry can determine minimum stopover length of tagged birds by detecting when a bird departs a stopover site (Anderson 2020, Neima et al. 2022), which is required for calculating accurate shorebird population estimates (Bishop et al. 2000, Drever et al. 2014, Hope et al. 2018, Macdonald et al. 2021). Examining stopover length is also an important part in understanding how shorebirds use stopover areas (Neima et al. 2022) as stopover length can help to understand species-specific migration strategies (Henkel & Taylor 2015, Duijns et al. 2019) and identify which stopover sites are important (Linhart et al. 2022a). Multiple receivers stationed at different habitats within a single stopover site can also show local movements and explain habitat use and site fidelity (Neima et al. 2020, Linhart et al. 2022b), which can identify important habitat(s) within a stopover site.

I used the Motus Wildlife Tracking System ('Motus'), an automated radio telemetry network, to track migrating shorebirds at two important stopover sites in the Pacific Americas Flyway situated on the west coast of British Columbia, Canada: Tofino and the Fraser River Estuary. Both stopover sites support large numbers of congregating shorebirds during migration and are composed of vast tidal mudflats, marshes, and at Tofino, sand beaches (Drever et al. 2014, Drever et al. 2016). The Western Hemisphere Shorebird Reserve Network (WHSRN) has recognized both Tofino and Fraser River Estuary as important stopover sites for shorebirds due to the high number of birds that use these areas during migration (WHSRN 2005, 2013). Shorebird migration and stopover has been well studied at the Fraser River Estuary since the 1980's (Butler et al. 1987, 2002), however few studies have been conducted at the Tofino stopover site. My thesis represents one of the first studies to use automated radio telemetry to examine shorebird habitat use, length of stay, and stopover ecology at these two sites.

1.2 Thesis objectives

The main objective of my thesis was to examine how shorebirds use stopover sites in the Pacific Americas Flyway during migration, by assessing environmental, morphological and/or physiological characteristics that influence their length of stay and habitat use. My specific goals were to i) determine length of stay of Western Sandpipers, an abundant sandpiper in the Pacific Americas Flyway, at two important stopover sites, ii) examine environmental, morphological, and physiological characteristics that affect Western Sandpipers' length of stay, iii) compare Western Sandpiper length of stay between two stopover sites with different site characteristics,

iv) examine habitat use and movements of shorebirds between two habitats at the Tofino stopover site and, v) determine if human disturbance affects habitat use of shorebirds at the Tofino stopover site.

1.3 Thesis structure

Two data chapters were written to examine the five thesis objectives. In Chapter 2, I determined length of stay of individual Western Sandpipers in Tofino and the Fraser River Estuary. I used invertebrate density to assess stopover site quality at both stopover sites. I investigated interactions between length of stay, stopover site location, migration period, and individual bird characteristics. I compared differences in length of stay and site characteristics between the two stopover sites and identified potential different migration strategies used by Western Sandpipers at these two locations. In Chapter 3, I examined shorebird habitat use at two different habitat types (beach and mudflat) in the Tofino stopover site. For this chapter I used detections from three species of shorebirds: Sanderlings (*Calidris alba*), Semipalmated Plovers (*Charadrius semipalmatus*), and Western Sandpipers. I used the measure of time spent at each habitat as a proxy for habitat use, and investigated interactions between time of day and tidal period to assess what drives habitat use at this site. I used invertebrate density to assess differences in habitat use between the beaches and mudflat. To assess human disturbance at the beaches of Tofino, I examined the relationship between number of visitors on the beaches and habitat uses.

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The following chapter has been submitted to the journal, Ecology and Evolution, and has been returned asking for resubmission. There are 8 co-authors. As it was a joint effort, throughout this chapter I use plural first-person pronouns instead of singular. Below I indicate the contributions of each co-author:

Anne Blondin[1]: Primary author. Conceived study. Conducted all aspects of the field research in 2021, and analyses and wrote the first draft of the manuscript.

Mark C. Drever[2]: Corresponding author. Helped to conceive study. Conducted field research from 2019 – 2021, contributed field data on tracked birds, provided guidance, and commented on manuscript.

Scott A. Flemming[2]: Helped to conceive study. Conducted field research from 2020 – 2021, contributed field data on tracked birds, provided guidance, and commented on manuscript.

Wendy Easton[2]: Conducted field research from 2019 – 2021, contributed field data on tracked birds and commented on manuscript.

Mark Maftei[3]: Conducted field research from 2018 – 2021, contributed field data on tracked birds and commented on manuscript.

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Chapter 2 – Length of stay and migration strategies of Western Sandpipers (*Calidris mauri*) during migration at two stopover sites in British Columbia, Canada

2.1 Introduction

Most species of North American shorebirds depend on stopover sites to rest and refuel during long-distance migrations between their Arctic breeding grounds and overwintering grounds in Central and South America (Myers 1987, Warnock & Bishop 1998, Warnock 2010). A single stopover site can be used by millions of shorebirds during migratory periods and these congregations can represent large proportions of global populations (Drever et al. 2014). Habitat loss or degradation at these key stopover sites can have detrimental effects on a species' population (Studds et al. 2017). Shorebird populations in North America have experienced a net decline of 37% in recent decades and these declines are accelerating (Rosenberg et al. 2019, Smith et al. 2020). Thus, understanding how shorebirds use stopover sites and maintaining a network of these critical areas is imperative for shorebird conservation efforts (Studds et al. 2017, Duan et al. 2022, Wang et al. 2022).

The total number of birds using migratory stopover sites is difficult to assess due to the continuous flow of birds in and out of the site throughout the migration period (Bishop et al. 2000). Length of stay is a key metric required to accurately estimate the total passage population of birds using a migration stopover site (Bishop et al. 2000, Drever et al. 2014, Hope et al. 2018, Neima et al. 2022, Macdonald et al. 2021). Understanding length of stay and its seasonal, annual, or interspecific variation is further complicated by a variety of factors. Habitat characteristics (e.g., prey availability or predation risk; Ydenberg et al. 2002, Lank et al. 2003, Taylor et al. 2007, Canham et al. 2021), individual physiology and biology (e.g., age, body condition, sex; Anderson et al. 2019, Herbert et al. 2022), environmental conditions (e.g., wind, beach width, human disturbance; Anderson et al. 2021, Herbert et al. 2022), and temporal variables (e.g., migration season, stopover arrival time) can all influence length of stay (Butler et al. 2002, Lank et al. 2003, Taylor et al. 2007). Therefore, understanding how length of stay can vary in space and time is important in determining the ecological processes that underlie changes in shorebird abundance at different stopover sites.

Length of stay can also reflect different migration strategies within or between populations (Henkel & Taylor 2015; Anderson et al. 2019). The 'time-minimizing strategy' hypothesizes that birds are under time constraints to reach their breeding grounds; they will reduce time spent during migration by flying farther distances between sites, even if it is more energetically costly. This strategy may be dominant during northward migration when birds are under selection pressure to obtain territories, mate and reproduce as early as possible (Warnock & Bishop 1998, Warnock 2010, Duijns et al. 2019). By contrast, the 'energy-minimizing' strategy hypothesizes that migrants reduce the energetic costs of migration when they are under reduced time constraints (Nilsson et al. 2014, Duijns et al. 2019). Birds using a 'mortality-minimizing' strategy will use tactics to avoid predator presence, such as site avoidance, and the alteration of migration phenology, stopover duration, fuel load, and migration speed (Ydenberg et al. 2004, Hope et al. 2011). Though an energy-minimizing strategy has historically been linked to southward migration (Nilsson et al. 2014), studies over recent decades have shown that shorebirds also implement a mortality-minimizing strategy during this post-breeding period (Lank et al. 2003, Ydenberg et al. 2004, Duijns et al. 2019).

Within these broader categorizations of migration strategy, shorebirds generally exhibit three patterns of migration depending on the distance travelled among stopover sites and energetic requirements to make the flights (Piersma et al. 1987, Warnock 2010). "Hop" migrants travel short to intermediate distances among stopover sites, have shorter lengths of stays, lower fueling rates, and depart to subsequent locations on their migratory route with smaller fuel stores; characteristics that are also associated with an energy-minimizing strategy. Conversely, "jump" migrants travel long distances among stopover sites, have longer lengths of stays, higher fueling rates, and depart to subsequent locations with larger fuel stores; behaviours associated with a time-minimizing migration strategy. "Skip" migrants travel intermediate distances among stopovers and exhibit migration behaviours somewhere between "hop" and "jump" migrants (Piersma et al. 1987, Warnock 2010, Henkel & Taylor 2015, Anderson et al. 2019).

Western Sandpipers (*Calidris mauri*) are the most abundant shorebird species in the Pacific Americas Flyway, numbering 3.0 – 4.5 million (Bishop et al. 2000), but their population appears to be declining (Hope et al. 2019, Canham et al. 2021, Warnock et al. 2021). This decline has been inferred from long-term monitoring of stopover sites. As such, a more detailed understanding of how the birds use these sites has become a priority for conservation. Length of stay of Western Sandpipers during northward spring migration has been calculated at numerous sites along the Pacific Americas Flyway, such as the Fraser River Estuary in southern British Columbia, using mark-recapture (re-sighting), ground and aerial telemetry, and hydrological modelling methods (Butler et al. 1987, Iverson et al. 1996, Warnock & Bishop 1998, Warnock et al. 2004, Drever & Hrachowitz 2017). Fewer studies have assessed Western Sandpipers' length of stay and factors influencing stopover duration during southward migration, including differences between adults and juveniles (Ydenberg et al. 2004, Hope et al. 2021). In addition to large estuaries, Western Sandpipers also stop in large numbers during northward and southward migration at smaller sites on the west coast of Vancouver Island (Drever et al. 2016), where relatively little information is known about their length of stay.

We used the Motus Wildlife Tracking System (Taylor et al. 2017), an automated radio telemetry network, to assess the length of stay of Western Sandpipers at two important migratory stopover sites in British Columbia, Canada: the Fraser River Estuary situated near Vancouver, British Columbia, and the Tofino Mudflats on the west coast of Vancouver Island, British Columbia (Fig. 2.1). The purpose of this study was to answer two main questions: (i)

What are the lengths of stays and migration strategies of Western Sandpipers at the Fraser River Estuary and Tofino stopover sites, and (ii) What variables affect their lengths of stay? We examined the relationship between length of stay and stopover site location, initial capture site location, migration season, age, sex, and body mass. We compared length of stay during the same migration periods at two sites that differed in habitat composition to establish how site attributes affect stopover behaviour of migrating sandpipers. We also assessed prey (benthic invertebrate) abundance at each site as an indicator of site quality, which might help to explain differences in stopover behaviour at our study sites. Sandpipers appear to have longer stopovers at higher quality sites (Herbert et al. 2022), and juveniles have shorter length of stay during years with lower prey density (Anderson et al. 2021). Based on higher shorebird counts at the Fraser River Estuary compared to Tofino (Drever et al. 2014, Drever et al. 2016), we predicted that the Fraser River Estuary would have greater prey abundance than Tofino, thus, we also predicted that sandpipers would have a longer length of stay at this site. To explore migration strategies during different migration seasons, we compared the length of stay of adult Western Sandpipers between northward and southward migration seasons. Since time-minimizing strategies are often associated with longer length of stays, as birds acquire large fuel loads to increase flight distance between stops and shorten the overall migration time (Piersma et al. 1987, Warnock 2010), we predicted Western Sandpipers would have longer stopovers during northward migration, as they would be under greater time constraints to reach their Arctic breeding grounds. We also tested whether length of stay varied between adults and juveniles during the southward migration. Juvenile sandpipers may use stopover habitats differently than adults as they have no prior migration experience and are potentially exposed to different environmental conditions during migration (Hope et al. 2011, Linhart 2021). Juvenile Western Sandpipers also migrate approximately one month later than adults, concurrently with Peregrine Falcons (*Falco peregrinus*), thus they may adopt different migration strategies (Hope et al. 2011). Since juvenile sandpipers can have both longer (Mann et al. 2017, Linhart et al.

2023) and shorter (Hope et al. 2011) stopovers than adult birds, depending on context, we therefore did not predict a direction of effect for the two age classes.

2.2 Methods

2.2.1 Study areas

The Fraser River Estuary (49.095 N, -123.125 W) (Fig. 2.1) is situated approximately 15 km south of the city of Vancouver in the Lower Mainland region of British Columbia, Canada. This site extends over approximately 22,000 ha at low tide and comprises three large intertidal mudflat habitats (Sturgeon Bank, Roberts Bank, Boundary Bay) and is mostly made up of sand, silt, and clay (Drever et al. 2014). This area receives significant freshwater input from the Fraser River, creating ideal conditions for intertidal biofilm; an important food source for migrating Western Sandpipers (Kuwae et al. 2008, Jardine et al. 2015). Industrial activity on and around the tidal mudflats includes a major shipping port, a ferry terminal, a sewage treatment plant, and river training dikes that stretch perpendicular from the shoreline into the Strait of Georgia (Atkins et al. 2016, Drever et al. 2023). The Fraser River Estuary is a stopover site of hemispheric importance (WHSRN 2005), and it is estimated that up to ~50% of the global Western Sandpiper population and 50% of Pacific Dunlin (*Calidris alpina pacifica*) populations use the Brunswick Point mudflat, where they exploit an abundance of invertebrates and biofilm (Drever et al. 2014, Hobson et al. 2022).

The Tofino stopover site is situated on the west coast of Vancouver Island within the District of Tofino and Pacific Rim National Park Reserve (49.100 N, -125.852 W) and contains approximately 2,630 ha of exposed mudflats and sandflats (Government of British Columbia, n.d.). Collectively, these habitats are recognized as the Tofino Wah-nah-jus Hilth-hoo-is Mudflats, and include Chesterman Beach, Long Beach, and the mudflats along Browning

Passage on the north side of the Esowista Peninsula. Chesterman Beach and Long Beach are beach habitats that are exposed to the open ocean. Both beaches are frequently used by humans for recreational purposes from May to September (Murchison et al. 2016), and Long Beach is located within the Pacific Rim National Park Reserve boundary. The Tofino mudflats are a biologically diverse tidal mudflat complex of sheltered tidal channels, streams, marshes, and eelgrass beds, and peak counts during spring migration can see over 40,000 Western Sandpipers (Drever et al. 2016). The Tofino Mudflats have been designated as a locally important site for migrating shorebirds (WHSRN 2013) and are being considered for an elevated status given very high peak counts in 2019 to 2021 (M. Maftei 2023, unpub. data).

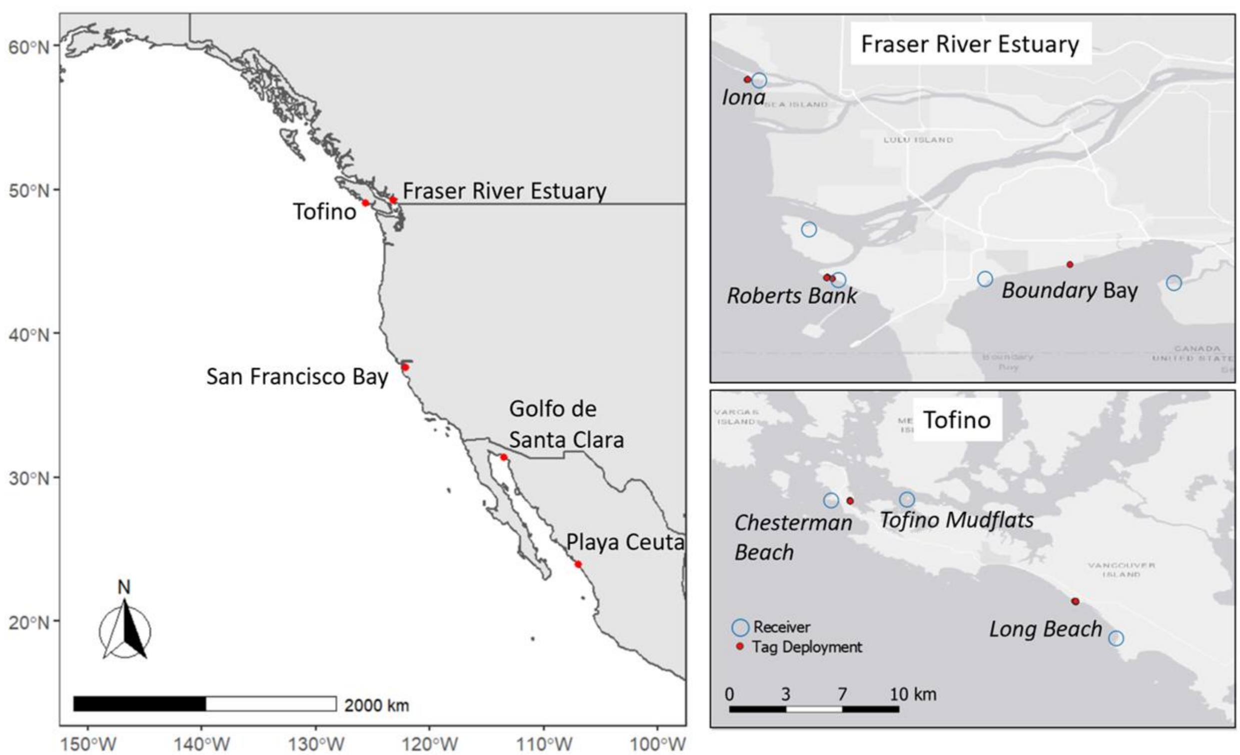

Figure 2.1 Western Sandpiper capture sites (red points) along the Pacific Americas Flyway (left map). Motus receiving stations (blue circles) and capture sites (red points) located within the Fraser River Estuary (top right map) and Tofino (bottom right map) stopover study areas.

2.2.2 Shorebird captures

We captured Western Sandpipers using mist-nets during northward and southward migration seasons from 2018 to 2021. Capture efforts corresponded to peak shorebird migration days, and timing of mist-netting sessions varied across the two study sites, seasons, and ages (adults and juveniles; Table 2.1).

Table 2.1. Capture dates and number of Western Sandpipers tagged with VHF radio transmitters in the Fraser River Estuary and Tofino stopover sites from 2018 to 2021.

	Northward migration				**Southward migration**			
	Fraser River Estuary		**Tofino**		**Fraser River Estuary**		**Tofino**	
Year	Tags Deployed	Capture Dates	Tags Deployed	Capture Dates	Tags Deployed	Capture Dates	Tags Deployed	Capture Dates
2018	0	-	0	-	0	-	23	Aug 08 – Sep 06
2019	15	Apr 25	34	May 01-07	0	-	36	Aug 01 – Sep 10
2020	0	-	37	May 01-08	78	Jul 11 – Aug 27	43	Jul 27 – Aug 22
2021	30	Apr 23-29	32	May 03-16	56	Jul 13 – Aug 24	11	Jul 20 – Sep 16
Total Tags Deployed	45		103		134		113	

For northward migration of adult birds, we conducted captures in late April in the Fraser River Estuary, and early May in Tofino. For southward migration, captures in the Fraser River Estuary were done in mid-July for adults and mid-August for juveniles. Southward captures in Tofino for both ages continued intermittently from late July through September. Northward shorebird captures did not occur in Fraser River Estuary in 2020 due to Covid-19 restrictions.

Upon capture, we banded each bird with a uniquely coded government-issued metal band, and we recorded mass (g), culmen (mm), and tarsus (mm). Wing chord (mm) was recorded at the Tofino capture sites, and wing chord (mm) and/or flattened wing (mm) were recorded in the Fraser River Estuary following methods in Prater et al. 1977. When possible, we recorded sex based on bill length (Sandercock 1998; Stein et al. 2008). We aged birds based on the colour of the inner medial covert feathers (O'Hara et al. 2006). We classified juveniles as birds hatched in that year, and adults as birds that hatched in or prior to the previous year. We attached small, digitally encoded Very High Frequency (VHF) nanotags to the skin on the backs of the shorebirds using cyanoacrylate adhesive. Feathers were trimmed to expose the skin just above the uropygial gland where the nanotags were attached. We used Lotek nanotag models NTQB2-3-2 (Lotek, Newmarket, Ontario, Canada), weighing 0.66 grams with a burst rate of 13.7 seconds. We deployed a total of 395 tags from 2018 to 2021 in Tofino and Fraser River Estuary (Table 2.1). To obtain length of stay estimates unbiased by handling time at capture sites (Warnock & Bishop 1998), we also deployed 108 tags on birds ~1,300 and ~3,200 km south of our main study sites, in San Francisco Bay, California, and the west coast of Sonora and Sinaloa, Mexico, respectively (Figure 2.1)

2.2.3 Automated radiotelemetry

We used the Motus Wildlife Tracking System ("Motus"; Taylor et al. 2017), a collaborative research network that uses automated radio telemetry, to determine the length of stay of shorebirds during migration stopover. The Motus system tracks wildlife using digitally encoded nanotags that are detected by stationary automated receivers that continuously scan for signals within detection range, a maximum of ~5-20 km depending on topography (Taylor et al. 2017). As the Fraser River Estuary and Tofino stopovers are approximately 200 km apart, the Motus detection ranges do not overlap between stopover sites in this study. Nanotags operated on a single frequency (166.380 mHZ), and individual tags were identified by a unique combination of sequence code and burst rates (Taylor et al. 2017). Motus receivers were strategically placed at each stopover site in areas where shorebirds congregate. The Fraser River Estuary study began with one receiving station in 2018, and the area had seven stations by 2021. The Tofino stopover site consistently maintained three receiving stations from 2018 to 2021 (Figure 2.1). Here, we refer to the receiving stations located within the two study stopover sites as the "project array".

2.2.4 Data cleaning

Telemetry data were downloaded from the Motus database using RStudio statistical software (v. 2021.09.0) following guidelines from the R Motus Book (Crewe et al. 2018). The data were cleaned using Motus' *filterByActivity* function (Crewe et al. 2018, Anderson 2021, personal comm.), resulting in 766,077 detections. Cleaned data were then filtered to only include detections by birds tagged in our study that were detected by receivers in our study areas. Filtered data were cleaned a second time by filtering detections with a run length (number of continuous detections) <4 and a mean standard deviation of frequency > 0.08 kHz, as values with these parameters typically indicate false detections (Bliss 2020). Tags with these criteria were also examined individually using signal plots to identify false detections, which were manually removed from the dataset. After all data cleaning and filtering processes were complete, we were left with 349,909 Western Sandpiper detections.

2.2.5 Length of stay

We calculated minimum length of stay (LOS) for individual birds that were detected at the two stopover sites during both migration periods. We refer to length of stay measurements as "minimums" because it was not possible to determine the elapsed time between the bird's arrival at the site and the time it was tagged. For birds first detected at their capture location (e.g., a bird that was both tagged and detected in Fraser River Estuary in the same migration season), length of stay was calculated within each stopover site as the duration of time from tag deployment to the last detection. For birds tagged outside their detection location [hereafter: "non-local birds" (e.g., a bird tagged in California but detected in Fraser River Estuary)], length of stay was calculated within each stopover site as the duration of time from first tag detection to last tag detection. Based on Western Sandpiper flight speeds of 1,017 km per day (Iverson et al. 1996), non-local birds with a length of stay <1 hour were removed from analysis, as this length of stay value indicates the bird likely transited the site without stopping.

2.2.6 Invertebrate prey availability

We collected sediment cores using a 5 cm x 10 cm corer (196.36 ml) and sieved them through a 0.5-µm mesh along 200 m-500 m transects to assess availability of invertebrate prey for migrating shorebirds, during both migration seasons in 2021. Northward samples were collected between April 18-May 29, and southward samples were collected between July 17-August 25. At the Fraser River Estuary, we collected sediment cores at 50m, 200m, 350m, and 500m distances from the high tide line along nine transects. At the Tofino mudflats, we collected sediment cores at 50m, 200m, and 350m intervals from the high tide line along five transects during northward migration, and four transects during southward migration. Beaches in Tofino were narrower and had distinct zones, therefore, we collected samples at the wrack line (visible high tide line), intertidal zone, and swash zone (active wave wash zone) along 9 transects. We collected sediment cores during the receding tide at all sites, however due to differences in tide levels and habitat availability, we collected samples within two hours of high tide at mudflat habitats and two hours of low tide at the beaches.

Invertebrates were counted and identified to the lowest taxonomic level possible. Sediment samples from mudflat habitats were processed within 24 hours, and samples from the beach habitat in Pacific Rim National Park near Tofino, were processed in-situ. A subset of invertebrates, as well as unidentified specimens, were preserved in ethanol for further classification.

2.2.7 Faecal collection and DNA metabarcoding

We collected faecal samples from Western Sandpipers in 2021 during both migration periods and used DNA metabarcoding to compare diet between stopover sites. During capture efforts, we placed individual birds in plastic holding bins lined with clean aluminum foil and collected any faecal matter remaining on the foil. Samples were stored temporarily at -20°C, and then stored in 95% ethanol and -20°C until submission to the Canadian Centre for DNA Barcoding (CCDB). We prepared 95 samples for analysis following methods from the CCDB (CCDB, 2018), and all samples were processed by the CCDB at the University of Guelph, Guelph, Ontario following extraction methods by Ivanova, Dewaard & Hebert (2006). Primers selected for analysis included annelids (193 bp), amphipods (193 bp), arthropods (157 bp), microalgae (168 bp) and mollusks (161 bp) as these taxa have been found to be food sources for migrating Western Sandpipers (Senner 1979, Hobson et al. 2022).

2.2.8 Data analyses

To compare length of stay between study sites, we used generalized linear models (GLM) for modeling northward and southward data. The length of stay data were positive-only and positively skewed, therefore we used a gamma error distribution with a log-link to fit the models (Kohlmann et al. 1999). We assessed multicollinearity of the predictor variables by inspecting the variance inflation factor score using the vif() function in RStudio. We visually inspected the residuals of final models using the "resid" function in R (version 2021.09.0) to confirm homoscedasticity.

We performed a discriminant function analysis (DFA) to assign sex to individual Western Sandpipers using culmen and tarsus measurements after Stein et al. (2008). If tarsus data were missing to use in the DFA (n = 168), we used the field-assigned sex, which was assigned based on bill length (Sandercock 1998; Stein et al. 2008).

We compared morphological variation in Western Sandpipers between stopover site locations using linear regression models on morphological data. Wing (mm), tarsus (mm), culmen (mm) and mass (g) were response variables with stopover site location, sex, age, and migration direction (mass model only) as predictor variables. Sex was included as a predictor variable in all models as there is sexual dimorphism in Western Sandpipers, where males are smaller than females (Stein et al. 2008). Age was included as a predictor variable to account for variability in size between adults and juveniles (O'Hara et al. 2006, Fernandez & Lank 2007).

We modelled northward and southward LOS data separately, since juveniles are only present during the southward period. Therefore, we included age as a predictor variable in the southward model only. To test the effect of migration season on length of stay, we ran a separate model with combined northward and southward data but with only adult birds. The tagging location variable was not included in the southward model as only one bird was detected during southward migration that was tagged outside its detection location. Since juvenile Western Sandpipers migrate southward approximately one month later than adults (Ydenberg et al. 2004; Hope et al. 2011), and timing of capture efforts differed between the two stopover sites, the "number of days since first tag" (hereafter 'days since first tag') variable was calculated as the number of days since the first tagged bird of each cohort. For example, if August 1 was the first day a juvenile Western Sandpiper was tagged in Tofino during southward migration, August 1 began as day 1 for all subsequent southward juvenile Western Sandpiper tagged in Tofino of that year.

The full LOS models for Western Sandpipers included individual minimum length of stay as the response variable, and mass, sex, tagging location (detected within or outside the capture site), detection location (Fraser River Estuary or Tofino), number of days since first tag, year as a factor and an interaction between detection location and mass as the predictor variables. The mass predictor variable was scaled using the scale() function in RStudio (v.

2023.06.1) to standardize the continuous variable. To test for difference in weight between stopover sites, an interaction between mass and stopover site was included in all models. To account for differences between locally and non-locally tagged birds, the northward model included interactions between tagging location and mass, and tagging location and days since first tag. To account for potential migration strategy and weight differences between ages, the southward model included an interaction between age and days since first tag, and age and mass. As the southward dataset only contained one non-locally tagged bird, that individual was removed from analysis. Along with interactions listed above for each migration season, we modeled all possible combinations of predictor variables, and compared Akaike's Information Criterion (AIC) values of each model to select the most parsimonious model by selecting the model with the lowest AIC value. We used AIC for model selection as AIC is better suited for complex models and modeling at an ecosystem scale, where BIC is best used for controlled experiments (Aho et al. 2014). To explore significant interactions between variables, we used the emtrends() function from the "emmeans" package in RStudio (v. 2023.06.1).

To compare prey availability and diet between study sites and shorebird migration periods we calculated the frequency of occurrence of invertebrates from sediment and faecal samples to taxonomic order. To assess invertebrate numbers between stopover sites and migration seasons, we used generalized linear models with a Poisson distribution. In these models we included the number of invertebrates per sample core (196.36 ml) as the response variable with stopover site and migration season as predictor variables. Models were separated by migration season to determine if there was an effect of stopover site, and by site, to determine the effect of migration season on the number of invertebrates. RStudio (v. 2021.09.0) was used to perform all statistical analyses. An alpha level of 0.05 was used to denote statistical significance.

2.3 Results

We tagged 395 Western Sandpipers from 2018 to 2021; 179 birds in Fraser River Estuary and 216 birds in Tofino. Ninety-six percent (379/395) of the tagged Western Sandpipers were subsequently detected by receivers in their respective project array. An additional 107 birds were tagged in Mexico and California during spring migration, and 39 of these birds (36%) were subsequently detected in the project arrays. We removed all birds with missing relevant attributes (i.e., mass, age, etc.) from models, which left a sample size of 385 Western Sandpipers for analysis.

2.3.1 Length of Stay

On average, minimum length of stay (LOS ± SE) of tagged Western Sandpipers across both stopover sites was 3.2 ± 0.2 days during northward migration, and 6.1 ± 0.4 days during southward. The LOS varied significantly between stopover sites; juvenile and adult Western Sandpipers detected at the Tofino study site stayed for ~2.0 to 2.5 days less than Western Sandpipers using the Fraser River Estuary, respectively (Figure 2.2, Table 2.2, Table 2.3). Length of stay was negatively correlated with body mass during both migration seasons, where lighter birds stayed for longer (Figure 2.3, Table 2.3). During northward migration, there was a significant interaction between capture location and mass, where mass was negatively correlated with length of stay for locally tagged birds but not for non-locally tagged birds. Males had significantly shorter stopovers than females during northward migration (Table 2.3). During northward migration, there was no effect of days since first tag, and no significant interactions between capture site and days since first tag or detection site and mass.

During southward migration, juveniles stayed longer than adults (Figure 2.2, Table 2.2), and there was a significant interaction between days since first tag and age where adults arriving earlier stayed longer (Table 2.3). In the southward models, there were no interactions between detection site and mass, age class and mass, and there was no effect of sex. In the model combining both migration periods with only adult birds, adults stayed at the stopover sites significantly shorter during southward migration compared to northward migration (Figure 2.3, Table 2.2, Table 2.3).

Table 2.2 Mean length of stay (LOS) in days of tagged Western Sandpipers by age and migration season in the Fraser River Estuary and Tofino migration stopover sites. LOS is calculated for each stopover site by subtracting the time of tag deployment from the time of last detection for birds that were both tagged and detected within the same stopover site, or by subtracting the time of first detection from the time of last detection for birds tagged outside the stopover site they were detected. Tagged indicates the number of birds tagged locally at the site, and Detected indicates total number of birds detected, including non-locally tagged birds with a stopover > 1 hour.

Migration Direction	**Age**	**Stopover Site**	**Tagged (n)**	**Detected (n)**	**Minimum Estimated LOS (Days ±SE)**
Northward	Adult	Fraser River Estuary	45	46	5.0 ±0.4
		Tofino	103	104	2.5 ±0.3
Southward	Adult	Fraser River Estuary	47	44	4.4 ±1.0
		Tofino	11	10	1.9 ±0.7
Southward	Juvenile	Fraser River Estuary	84	84	7.9 ±0.7
		Tofino	102	100	5.9 ±0.6

Table 2.3. Top Generalized Linear Model coefficients and results of each model category (by migration season) selected using lowest AIC values. Minimum length of stay (LOS) in days is the dependent variable. Categorical predictor variables are capture site (captured within or outside detection site), days since first tag (capture day of year), stopover site (Tofino and Fraser River Estuary), migration direction (Northward and Southward), and year; continuous predictors are mass (g; Mass).

Model	**df**	**Predictor Variable**	**Estimate**	**Standard Error**	**t-value**	**p-value**
Northward	8	Capture site (Outside)	-1.35	0.28	-4.82	<0.01
		Mass	-0.27	0.08	-3.40	<0.01
		Sex (Male)	-0.41	0.16	-2.52	0.01
		Stopover site (Tofino)	-0.94	0.16	-5.80	<0.01
		Capture site (Outside) * Mass	0.71	0.34	2.04	0.04
Southward	10	Age (Juvenile)	0.30	0.19	1.59	0.11
		Days since first tag	-0.06	0.22	-2.82	<0.01
		Mass	-0.25	0.06	-4.03	<0.01
		Stopover site (Tofino)	-0.62	0.17	-3.64	<0.01
		Year (2019)	1.29	0.32	3.90	<0.01
		Age (J) * Days since first tag	0.05	0.22	2.11	0.04
North+South	5	Migration direction (S)	-0.38	0.19	-2.00	0.048
		Mass	-0.21	0.08	-2.72	<0.01
		Stopover site (Tofino)	-0.76	0.16	-4.80	<0.01

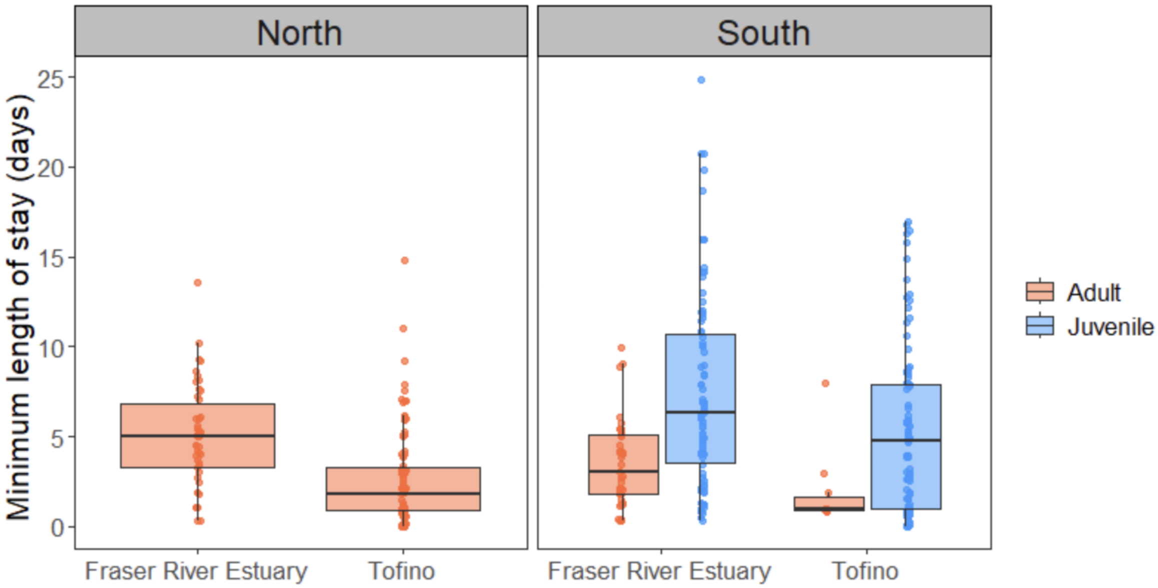

Figure 2.2. Minimum length of stay (LOS) of Western Sandpipers in the Fraser River Estuary (FRE) and Tofino stopover sites during northward (FRE = 46, Tofino = 103) and southward (FRE adults = 43, Tofino adults = 10; FRE juveniles = 84, Tofino juveniles = 100) migration seasons from 2018 – 2021. LOS is calculated for each stopover site by subtracting the time of tag deployment from the time of last detection for birds that were both tagged and detected within the same stopover site, or by subtracting the time of first detection from the time of last detection for birds tagged outside the stopover site they were detected. The boxplot denotes the median, and upper and lower quartiles of the data. The vertical lines extend to 1.5 x the interquartile range.

2.3.2 Non-local detections

Thirty-nine Western Sandpipers that were tagged in southern non-breeding sites in California and Mexico were detected by receivers in the project array in British Columbia. Only 28% of the southerly-tagged birds detected in our study sites were considered to have a stopover, where the remainder were deemed "flyovers" as their length of stay was < 1 hour. Though most of the southerly-tagged birds that were detected in our study areas during northward migration were detected in Tofino (tags detected in Tofino = 32, tags detected in the Fraser River Estuary = 7), these birds were significantly less likely to stop in Tofino (19%) and more likely to be flyovers, than the Fraser River Estuary (71%) ($z = -2.6$, $p < 0.01$). Western

Sandpipers tagged at southerly sites that stopped > 1 hour in Tofino stayed for 0.4 ±0.2 days (n = 6), which was a shorter length of stay than birds who stopped in the Fraser River Estuary, 2.1 ±0.7 days (n = 5). The northward length of stay of all southern-tagged Western Sandpipers that were detected at our study sites, including birds classified as flyovers (i.e., with stopovers < 1 h), was 0.08 ±0.05 days in Tofino (n = 32), and 1.5 ±0.6 days in the Fraser River Estuary (n = 7).

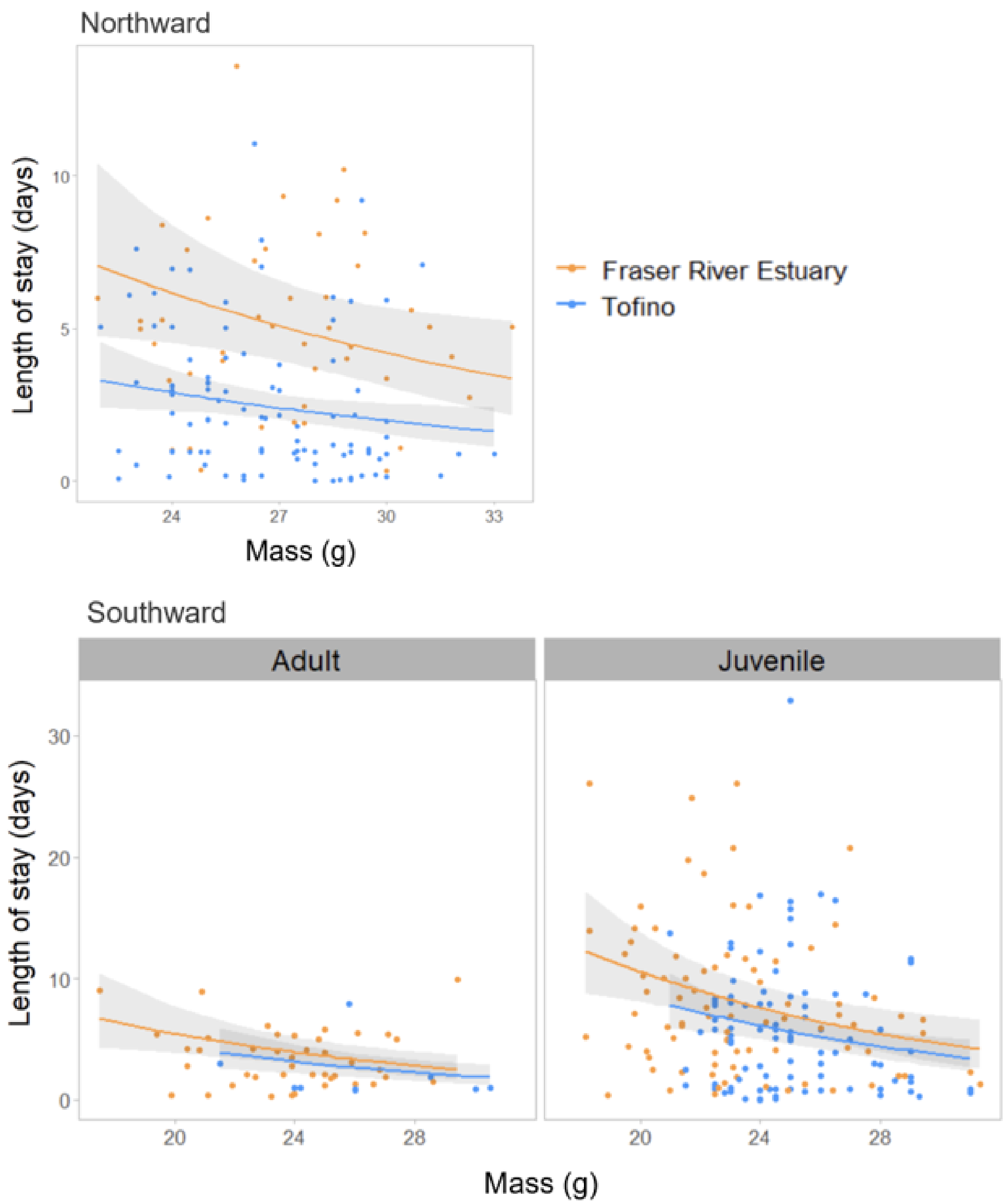

Figure 2.3. Relationship between mass and minimum length of stay in days of locally and non-locally tagged Western Sandpipers (n = 381) by stopover site during northward migration (top), and by stopover site and age during southward migration (bottom). Data points are raw values, and fitted lines are predicted values with 95% confidence intervals.

2.3.3 Morphology

The morphometrics of Western Sandpipers varied between the two stopover sites, migration season and with sex. Birds captured in Tofino were significantly heavier than birds captured in the Fraser River Estuary during southward migration [FRE n = 127, Tofino n = 102; df (3,225); t= 5.14, p < 0.01], but there were no significant differences in mass during northward migration [FRE n = 39, Tofino n = 102; df (2,138); t= -0.8, p = 0.4]. Males were also significantly lighter than females during both migration periods [Northward: female n = 61, male n = 80; df (2,138); t = -4.96; p < 0.01; Southward: female n = 104, male n = 125; df(3, 225); t = -7.04; p < 0.01], however this was likely due to sexual dimorphism in Western Sandpipers as males are smaller than females (Stein et al. 2008), and mass was not adjusted for size. Western Sandpipers that were captured in Tofino also had significantly shorter tarsi (mm) [FRE n = 148, Tofino n = 73; df (5, 215); Location (Tofino): t = -8.39; p < 0.01; Age (Juvenile): t = -3.21, p < 0.01; Sex (Male): t = -10.08, p <0.01] and wing lengths (mm) [FRE n = 177, Tofino n = 213; df(5, 363); Location (Tofino): t = -7.40, p < 0.01; Age (Juvenile): t = 1.99, p = 0.05; Sex (Male): t = -13.12, p < 0.01] than birds captured in the Fraser River Estuary (Figure 2.5). However, the difference in wing length between sites may be due to inconsistencies in wing measurement methodology in the FRE. There was no significant difference in culmen length between the two stopover sites [FRE n = 177, Tofino = 190; df = 5, 361; (Location (Tofino): t = -0.65; p = 0.5; Age (Juvenile): t = -1.67, p = 0.09; Sex (Male): t = -37.53, p < 0.01)]

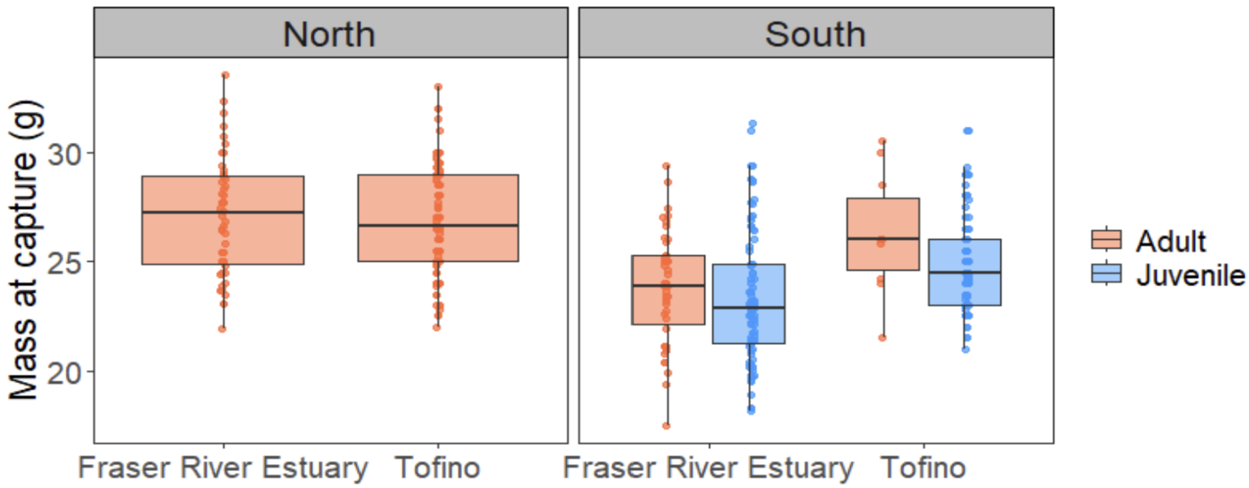

Figure 2.4. Mass by migration direction and age of tagged Western Sandpipers in the Fraser River Estuary and Tofino stopover sites. Boxplots represent raw data, and variables had significant statistical differences between stopover sites The boxplot denotes the median, and upper and lower quartiles of the data. The vertical lines extend to 1.5 x the interquartile range.

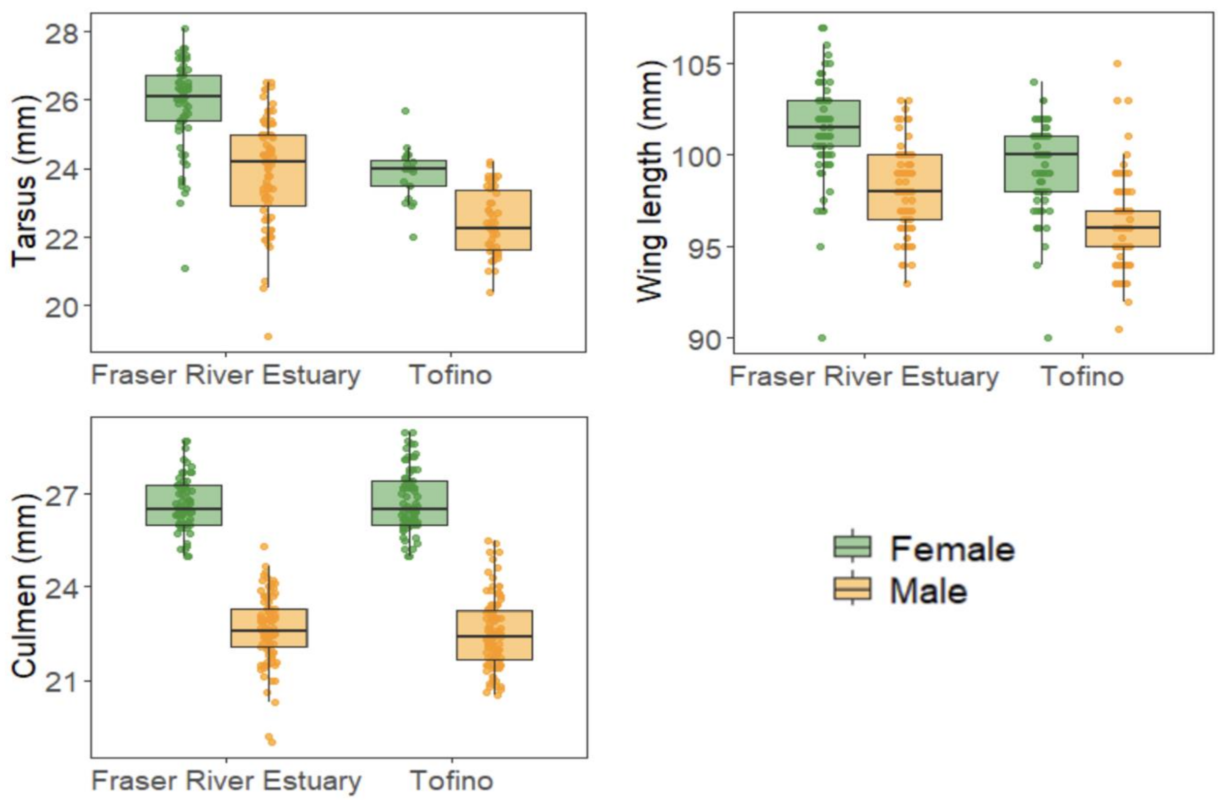

Figure 2.5. Tarsus (mm), wing length (mm), and culmen length (mm) of tagged Western Sandpipers in the Fraser River Estuary and Tofino stopover sites. Boxplots represent raw data and tarsus and wing lengths had significant differences between stopover sites. The boxplot denotes the median, and upper and lower quartiles of the data. The vertical lines extend to 1.5 x the interquartile range.

2.3.4 Invertebrate prey abundance & diet

We collected and processed a total of 216 sediment cores in the Fraser River Estuary and 222 cores in Tofino. Average invertebrate densities (number per 196.36 ml sample core) were nearly identical between the two sites (mean invertebrates per 196.36 ml; Tofino = 12.34 ±1.2, Fraser River Estuary = 12.29 ±0.9), although there were differences between the seasons. Tofino had a significantly higher density of invertebrates than the Fraser River Estuary during spring migration ($z = 7.08$, $p < 0.01$), and significantly lower density during southward migration ($z = -4.3$, $p < 0.01$). Invertebrate numbers differed by migration season, where there was a significantly higher invertebrate density during southward migration than northward migration at both the Fraser River Estuary ($z = -21.02$, $p < 0.01$) and Tofino ($z = -10.09$, $p < 0.01$).

Amphipods and polychaete worms comprised the highest proportion of invertebrate taxa in both sites (Table 2.4). Amphipods were the most abundant invertebrate taxa in Tofino during both migration periods, comprising 41.9%- 48.3% of samples, and were also the most frequently detected prey item in faecal samples from Western Sandpipers in Tofino during both northward and southward migration (Figure 2.6). During southward migration in the Fraser River Estuary, amphipods were the second most abundant taxa (32.1% of samples) and the most frequently detected prey item in faecal samples. Polychaetes were the most abundant invertebrate taxa in the Fraser River Estuary during both migration periods (42.2%-50.4% of samples), and yet were detected in only 20% of fecal samples during northward migration and were not detected during southward migration. Diptera were detected in >50% of fecal samples in the Fraser River Estuary during both migration periods, yet only 7 individuals were identified in sediment samples during southward migration (Figure 2.6, Table 2.4.).

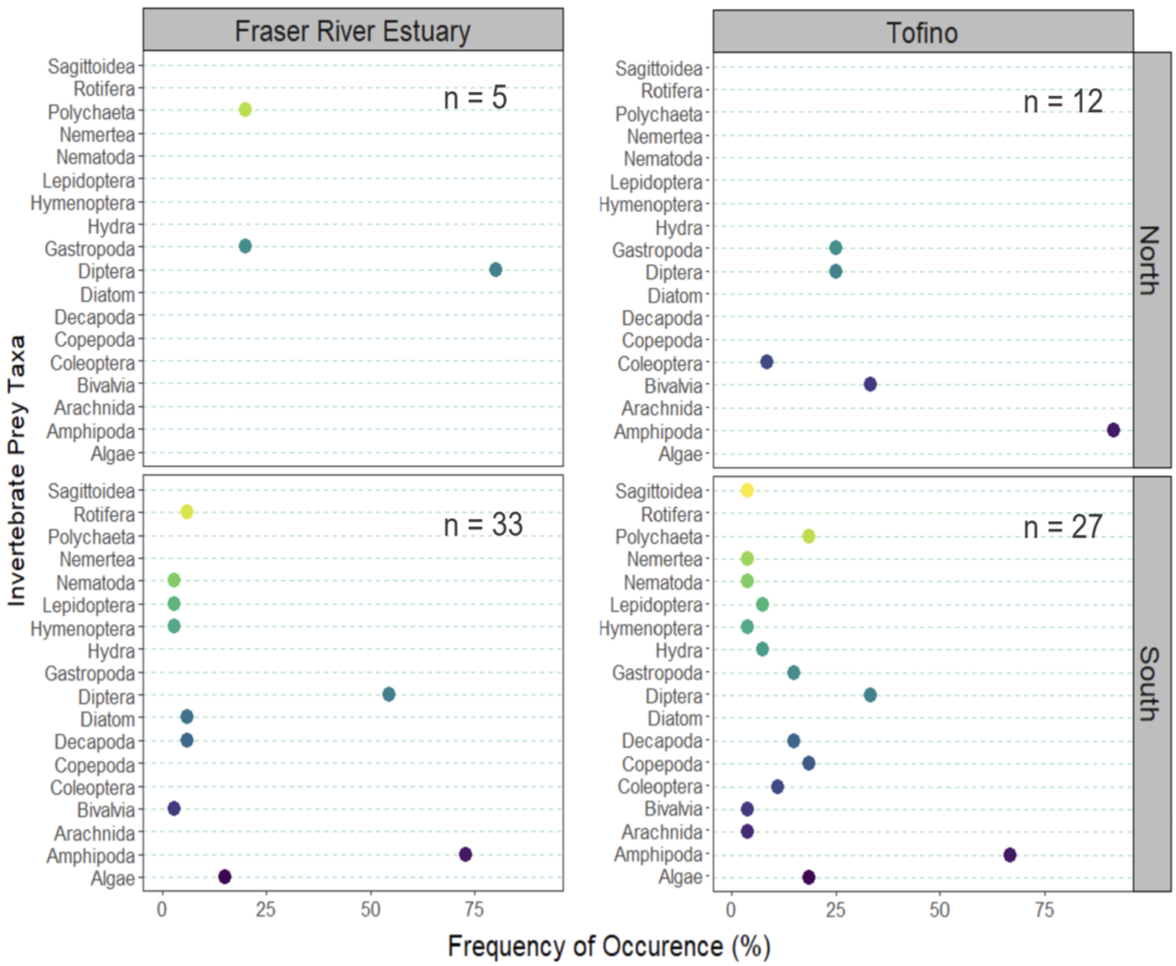

Figure 2.6. Frequency of occurrence (%) of invertebrate taxa found in the Western Sandpiper faecal samples using DNA metabarcoding

Table 2.4. Percent composition and number of invertebrates (N) from sediment core samples collected in the Fraser River Estuary and Tofino stopover sites during northward and southward migration in 2021. The same habitats and transects in each stopover site were sampled during both migration periods.

			Northward				Southward			
			Fraser River Estuary		Tofino		Fraser River Estuary		Tofino	
Phylum	**Class**	**Order**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**
Annelida	Clitellata	Oligochaeta	0.4	3	5.4	62	0.1	1	0	0
	Polychaeta	Spp.	50.4	387	34.1	395	42.2	796	33.8	535
	Unknown	Spp.	17.2	132	2.8	32	16.8	318	2.1	33
Arthropoda	Copepoda	Spp.	0.3	2	0	0	0	0	0.1	1
	Insecta	Diptera	0	0	0.8	9	0.4	7	0.3	4
	Malacostraca	Amphipoda	6.9	53	41.9	485	32.1	606	48.3	764
		Cumacea	11.7	90	0	0	1.3	25	0	0
		Euphausiacea	0	0	0	0	0	0	0.9	14
		Isopoda	0	0	0.6	7	0	0	11.9	188
		Tanaidacea	1.3	10	10.3	119	0.5	9	0.2	3
Molluska	Bivalvia	Spp.	11.1	85	2.9	34	5.2	99	2.4	38
	Gastropoda	Spp.	0	0	0	0	0.6	12	0	0
Unknown	Unknown	Unknown	0.8	6	1.2	14	0.8	15	0.2	3
Total number of sediment cores sampled			108		117		108		105	
Average number of invertebrates per sample core			7.1 ± 0.6		9.9 ± 1.3		17.5 ± 1.6		15.1 ± 2.0	

2.4 Discussion

Stopover ecology of Western Sandpipers along the Pacific Americas Flyway has been well studied, particularly during the spring migration season (Iverson et al. 1996, Warnock and Bishop 1998, Williams et al. 2007, Hope et al. 2018), but little has been done to track and compare strategies of Western Sandpipers between northward and southward migrations, or assess how migration strategies may differ (Carneiro et al. 2019, Duijns et al. 2019). We show that the length of stay of Western Sandpipers varied between stopover locations, migration seasons, and with age. Adults had shorter stopovers during southward migration compared to northward migration. This finding supports the idea that adult Western Sandpipers are more time constrained during northward migration relative to the southward migration, as they require higher fuel loads to increase distance between stopover sites during northward migration, thus shortening time spent during migration (Nilsson et al. 2013, Zhao et al. 2017). Western Sandpipers had shorter stopovers in Tofino compared to the Fraser River Estuary during both migration periods, supporting our prediction. Juveniles had longer stopovers compared to adults at both sites.

Southward migrating Western Sandpipers had a significantly longer stay in 2019 compared to other years, where only birds in Tofino were tagged during this migration period. Conditions were abnormally dry in the Tofino region in 2019 (Agriculture and Agri-Food Canada, 2024) which could create conditions that would lengthen stopover duration if prey were negatively affected. However, a moderate to severe drought also occurred in the region in 2018 and 2021 (Agriculture and Agri-Food Canada, 2024), and Anderson et al. (2021) found that a drought year did not extend length of stay in James Bay, Ontario, thus drought conditions were not likely the cause of longer length of stay in 2019. It is possible other environmental variables such as precipitation or wind caused the lengthened stopover (Herbert et al. 2022), though these data were not assessed in our study.

2.4.1 Length of stay compared to previous estimates

The estimated minimum length of stay of Western Sandpipers in the Fraser River Estuary using automated radio telemetry in this study [5.0 days northward, and 6.7 days southward (across age groups)] is longer compared to mean estimates from previous studies; 1

to 3.6 d for northward and 3 d southward (Butler et al. 1987, Iverson et al. 1996, Warnock & Bishop 1998). Length of stay of Western Sandpipers in the Fraser River Estuary may be longer than previous estimates due to differences in methods between studies. Previous studies in the Pacific Flyway mainly used handheld radio telemetry or resighting of flagged individuals (Butler et al. 1987, Iverson et al. 1996, Warnock & Bishop 1998), which can be limited by factors such as human effort, weather, and time of day, and size of the study area (Taylor et al. 2017). A capture/handling effect may have also resulted in longer LOS relative to previous studies, as northward birds in our study that were both tagged and detected at the same site stayed longer on average than birds that were tagged outside the detection site (Fraser River: 5.0 vs 2.1 days; Tofino: 2.6 vs 0.4 days). Though the sample sizes of non-locally tagged birds were low in the models (n = 11), the effect of tagging location (locally or non-locally tagged) was significant. A study by Warnock & Bishop (1998) using handheld radio telemetry estimated LOS of Western Sandpipers in the Fraser River Estuary during northward migration was 2.2 days (n = 25), where all birds were captured outside the Fraser River Estuary, thus there would have been no handling effect. Previous shorebird studies using radio-marked shorebirds showed mixed results of handling effects; some studies showed that handled birds stayed longer (Warnock & Bishop 1998, Warnock et al. 2004), where other studies showed no handling effect (Butler et al. 2002, Skagen and Knopf 1994). Gluing radio transmitters to shorebirds, as was done in our study, has fewer measured behavioural effects compared to other attachment methods such as implants and harnesses (Warnock & Takekawa 2012). Though the effects of nanotags on shorebird length of stay behaviour must be considered, due to a low sample size of non-local birds that had a stopover >1 hour (n = 11), the implications from this study remain unclear.

2.4.2 Differences in length of stay between stopover sites

Western Sandpipers in both age groups and migration periods had a significantly longer LOS in the Fraser River Estuary than in Tofino. The difference in LOS during southward migration may result from a difference in mean (arrival) mass between stopover sites. In our study, adult and juvenile Western Sandpipers captured in the Fraser River Estuary were significantly lighter than birds captured in Tofino. There was also a negative relationship between mass and LOS; as mass increased, LOS decreased. These results support findings from previous studies that indicate sandpipers with lower mass, body condition, and/or fuel load increased their length of stay (Skagen & Knopf 1994, Duijns et al. 2017, Herbert et al. 2022). However, this is in contrast to other sandpiper studies that found no relationship between body condition and length of stay (Warnock & Bishop 1998, Iverson et al. 1996, Linhart 2023) or that the effect varied depending on one or more factors (e.g., species, stopover arrival date, site location, predator presence, year; Skagen & Knopf 1994, Ydenberg et al. 2002, Anderson et al. 2019, Holberton et al. 2019), and does not explain the longer length of stay in the FRE during northward migration relative to Tofino, when there was no significant difference in mass between sites.

2.4.3 Site quality & prey availability

Variation in LOS and mass between individuals captured at the Fraser River Estuary and Tofino suggest a difference in site quality between the two stopover sites. Overall, shorebirds have longer lengths of stay at high quality stopover sites with a high abundance of prey (Warnock et al. 2004, Herbert et al. 2022). Though the composition of habitats that make up each study site could offer variable prey selection for Western Sandpipers, results from prey availability assessment in our study showed Tofino had a significantly higher density of invertebrates during spring migration compared to the Fraser River Estuary, and lower densities during southward migration. As birds had a longer stopover in the Fraser River Estuary during both migration periods, invertebrate numbers alone are unlikely to explain differences in LOS between sites, where our prediction of higher prey availability influencing longer stopover in the Fraser River Estuary was not supported during northward migration.

Our study found that amphipods (Order Amphipoda) are an important food source for Western Sandpipers in Tofino during both migration periods; not only were amphipods the most abundant taxon at this site, but the most frequently detected in faecal samples during both migration periods. This finding supports studies from other stopover sites along the Pacific Americas Flyway which similarly found that amphipods are one of the major prey items of Western Sandpipers (Franks et al. 2020, Wolf 2021). In the Fraser River Estuary during southward migration, amphipods were the most abundant taxon after polychaetes (Class Polychaeta) and the most frequently detected prey item in Western Sandpiper faecal samples, thus also likely an important food source at this site during this period.

Polychaetes were also abundant at both stopovers during both migration periods (33.8 % - 50.4% of samples), yet detection in fecal samples was relatively low (0-20% of samples); a surprising finding as polychaetes are a commonly identified food source of Western Sandpipers (Franks et al. 2020). The inconsistency of polychaete presence between sediment sample and faecal sample results could be due to a difference in sampling methods. Faecal samples were most often collected from captured shorebirds during rising and high tides and invertebrate sampling was conducted during the receding tides. The changes in sediment characteristics from sampling in different tidal levels may have resulted in differences in polychaete availability. For instance, Western Sandpipers were often observed foraging on *Thoracophelia* polychaetes during receding and low tides on the beaches of Tofino. These are the same tidal periods when *Thoracophelia* migrate vertically upward near the surface (Eikenberry 1966), and also when our invertebrate sampling occurred. By contrast, most faecal samples were collected during rising and high tides, which is concurrent with the downward movement of these polychaetes. As Western Sandpipers defecate relatively frequently (0.5 droppings per minute) compared to other shorebird species (Kuwae et al. 2008), it is possible the timing of faecal sample collection contributed to lower polychaete presence.

Diptera had a relatively high frequency of occurrence in faecal samples at both stopover sites during both migration periods, yet few specimens were found in sediment samples. This finding could be due to a gap in invertebrate collection methods; aerial dipterans (flies) were often observed on the surface of mudflats and beaches. However, these individuals likely escaped our samples as we used methods for sampling benthic invertebrates and not aerial insects. It is possible Western Sandpipers are consuming Diptera during migration which were not captured in our invertebrate samples. For instance, Anderson (2019) found that most of sandpiper diet in James Bay, Ontario consisted of prey items found in intertidal salt marshes (as opposed to mudflat), where dipterans were the most abundant taxa found in the samples. As faecal samples in our study were collected at incoming and high tide when sandpipers are more likely to use the salt marshes, they may have been consuming dipterans prior to capture. There are 17,000 ha of intertidal salt marshes in the Fraser River Estuary (Flynn et al. 2006), and this habitat was not sampled for invertebrates in our study, thus it is possible invertebrate prey availability is greater at this stopover site than what our invertebrate sample results suggest.

Intertidal biofilm has been identified as an important component of Western Sandpiper diet (Elner et al. 2005, Kuwae et al. 2008, Jardine et al. 2015). For instance, during spring migration in the Fraser River Estuary, Hobson et al. (2022) found that polychaetes contribute to about half of Western Sandpiper dietary protein, where intertidal biofilm contributes up to ~35%. Studies showed that the characteristics of the low-energy, estuarine mudflat habitats that makeup the Fraser River Estuary are ideal conditions for biofilm development (de Jorge & van Beusekom 1995, Kuwae et al. 2008), compared to sandy substrates that comprise much of the Tofino study sites. Although intertidal biofilm can be expected to be present at the Tofino sites, preliminary results suggest that the fatty acid content of surface sediment on the Tofino mudflats is lower than that of Roberts Bank in the Fraser River Estuary (Drever 2023, unpub. data). Given the longer length of stay and lighter mass (southward) of Western Sandpipers in the Fraser River Estuary, birds that stop at this site may be arriving after a long flight to target the essential fatty acids of both intertidal biofilm and invertebrate prey, thus staying longer to maximize fueling rates and gain higher fat stores (Schnurr et al. 2020, Hope et al. 2011). Conversely, Western Sandpipers who stop in Tofino may be arriving after a shorter flight (i.e., recently after a stopover at a nearby site), and thus do not require high fueling rates, and are able to gain sufficient fat stores from the availability of amphipods and large polychaetes (*Thoracophelia spp*) found at this site.

Site safety is an additional important factor influencing habitat during migration (Sprague et al. 2008). Predator presence, site width, and distance to nearest cover are characteristics used to measure site quality and selection for shorebirds, where predation danger becomes greater with decreasing site width (Pomeroy 2006, Sprague et al. 2008). Frequent, shorter stopovers are associated with a slower and safer migration strategy (Hope et al. 2011), and Ydenberg et al. (2004) hypothesized that Western Sandpipers using a site with a higher predation danger decreased their length of stay with increasing predator presence. The Tofino stopover site has physical characteristics that would suggest it is riskier than the Fraser River Estuary. Pomeroy et al. (2006) found that sandpipers foraged at a distance beyond 100 m or 150 m from the shoreline (depending on migration season) as a trade-off between site safety and prey availability at Boundary Bay in the Fraser River Estuary. At low tide, the width of beaches in Tofino is approximately 200 m wide, and the furthest distance to cover at the Tofino Mudflats is approximately 300 m. In the Fraser River Estuary, the mudflats are more expansive where the lowest tide mark can be over 5 km from shore (Government of British Columbia, 2020). Thus, the potentially greater predation danger at the Tofino site due to narrower site widths may be influencing the shorter length of stay at this site. As predators were not assessed in this study, further research investigating the differences in predation risk along the outer coast of Vancouver Island and the Strait of Georgia would be required.

2.4.4 Migration routes and strategies

Few individual birds in our study were detected in both the Fraser River Estuary and Tofino stopover sites, whether within or between migration seasons, suggesting that individuals tend to stop either exclusively in the Fraser River Estuary or Tofino. Our results show that Western Sandpipers migrating northward from California and Mexico ("southerly-tagged birds") were more likely to be detected in Tofino compared to Fraser River Estuary, however most of these southerly-tagged birds likely flew by Tofino and did not stop. Although fewer southern tagged Western Sandpipers were detected in the Fraser River Estuary, a greater proportion of birds that were detected at this location stopped for a longer duration, suggesting they were actively refueling. Migrating along the outer west coast of Vancouver Island may offer a more direct route for Western Sandpipers flying between their west coast wintering grounds and Arctic breeding grounds in Alaska (Figure 2.1). Since birds captured at the Tofino stopover had a higher mass during southward migration, it is possible that birds in better condition select the more direct migration route along the outer coast. As the Fraser River Estuary represents a slight eastbound detour for Western Sandpipers coming from the west coast of California and Mexico, birds that select this stopover may trade-off the increased distance to target the site for specific attributes such as the high fatty acid contents from intertidal biofilm (Schnurr et al. 2019, 2020).

We found that Western Sandpipers stopping in Tofino were smaller based on body measurements. Though genetic differences among Western Sandpiper populations are unclear (Haig et al 1997, Álvarez-Sánchez 2011), there is evidence of morphological and sexual segregation on their wintering grounds (Nebel et al 2002, O'Hara et al. 2006). O'Hara et al. (2006) found that, within sexes, Western Sandpipers who overwinter in southern latitudes are morphologically larger than Western Sandpipers who overwinter in more northerly latitudes based on mean wing chord and culmen lengths. Though Western Sandpipers in Tofino had significantly shorter wing lengths, since there were inconsistencies in wing measurement methods in the FRE, inferences regarding the possibility of birds from differing latitudinal wintering grounds stopping at the different sites in our study cannot be made using tarsus alone.

The difference in stopover length between sites could be a result of differing populations and migration strategies. Shorter stopovers are associated with a slower migration strategy, both characteristics of "hop" migrants who fly short-to intermediate distances between stopover sites. The estimated peak passage of Western Sandpipers in Tofino (May 3 ±1.1) is approximately 4 days later than those stopping at the Fraser River Estuary (April 29 ±0.4) (Hope et a. 2018). Western Sandpipers who stop in Tofino may be using more of a "hop" migration strategy than birds who stop in the FRE, and as suggested by their later peak arrival time and shorter stopover duration, may be arriving from closer non-breeding sites. However, further studies assessing Western Sandpiper lengths of stay and morphology among multiple sites along the Pacific Americas Flyway would be required for inferences regarding population partitioning between sites on the outer Vancouver Island coast and the Strait of Georgia.

2.4.5 Age and migration direction

We found that Western Sandpiper adults and juveniles use similar migration patterns in both stopover sites during southward migration; adult Western Sandpipers have shorter LOS compared to northward migration, and juveniles have a longer LOS compared to adults during southward migration. The longer length of stay of adult sandpipers during northward migration supports the time-minimizing hypothesis. As northward birds are under greater time constraints to reach their Arctic breeding grounds, a longer length of stay allows for higher fuel loads and increased flight distance between stopover sites, which shortens migration time (Piersma et al. 1987, Nilsson et al. 2013, Zhao et al. 2017). However, the differences in stopover length between migration seasons could simply be a result of prey availability. We found that invertebrate prey density was significantly higher during southward migration at both stopover locations, thus Western Sandpipers may be staying shorter as they require less foraging time to gain sufficient fat stores. The longer stopover of juveniles compared to adults supports findings from previous studies on Semipalmated Sandpipers (Roques et al. 2020, Linhart 2021). Several previous studies have assessed Western Sandpiper length of stay in both age groups during fall migration in the Fraser River Estuary or nearby sites around 3 days for adults (Butler et al. 1987) and 3.8 – 12 days for juveniles (Hope et al. 2011, Drever & Hrachowitz 2017, Hope et al. 2021).

2.4.6 Predation danger

During southward migration, adult Western Sandpipers leave the breeding grounds before juveniles, and the adult migration precedes the Peregrine Falcon (*Falco peregrinus)* migration that occurs in late July (Ydenberg et al 2004, Hope et al. 2011). Juveniles remain in their breeding grounds longer than adults to continue to feed (Franks et al. 2020), putting them at increased predation risk during their southward migration that occurs concurrently with Peregrine Falcon migration (Lank et al. 2003). Further, adult Western Sandpipers molt their flight feathers upon arrival to their wintering grounds, leaving them at increased risk of predation during this event. The reduced LOS for adults during southward migration compared to northward in our study could be a result of the pressure to arrive to their southern wintering grounds prior to flight feather molt, yet ahead of the falcon migration front (Lank et al. 2003; Roques et al. 2020). As juveniles migrate concurrently with falcons, they may be using a more cautious strategy during stopover. However, our results of juvenile Western Sandpipers having longer length of stay than adults contradict findings from Hope et al. 2011, where juveniles shortened their length of stay to slow migration. Increasing vigilance while foraging and reducing fuel loads can decrease wing loading, which improves escape performance from predators (Burns et al. 2002; Ydenberg et al 2004; Hope et al. 2011). If juveniles are using more cautious behaviours than adults during stopover, it is possible their vigilant behaviour, along with their inexperience in migration and foraging, lengthens stopover duration as they may require more time to gain fat stores. Juveniles may also be able to afford this extension in time to migrate, as they do not molt their flight feathers on their wintering grounds (Lank et al. 2003; Roques et al. 2020).

Adult Western Sandpipers that arrived earlier at their stopover sites stayed longer in our study. As longer stopovers are associated with faster migrations (Piersma et al. 1987, Warnock 2010), it would be expected that stopover length would increase with later arrival times to stay ahead of the arriving falcon front (Hope et al. 2011, Anderson et al. 2019). Studies on migrating Western Sandpipers at the Fraser River Estuary have shown seasonal speed adjustments during southward migration, using a "caution – speed – caution" strategy. Earliest arriving sandpipers well ahead of the falcon migration can afford a slower and more cautious migration strategy, and as the "falcon front" approaches, migration speed increases with longer length of stays. The latest arriving sandpipers that are at greatest risk of predation once again slow their speed of migration, where stopover time is reduced (Hope et al. 2014, Ydenberg 2022). It is possible that adult Western Sandpipers captured earlier in our study coincided with the "speed" strategy, and later arriving adults who were at greatest risk of predation used a more cautious strategy. As lighter birds have improved escape performance from predators, it is also possible that later arriving adults who were at greater risk of encountering falcons reduced their stopover time to decrease fuel loads and maintain lower wing loading. Since we did not record predator presence in our study, it is unknown whether later arriving adult Western Sandpipers coincided with the arrival of falcons. However, the differences in stopover length between juvenile and adults, as well as the interaction between arrival time and stopover length of adults suggest that Western Sandpipers may be using a mortality-minimizing behaviour as part of their southward migration strategy. It is suggested that future studies assessing shorebird LOS include predator surveys, or it may be possible to assess predator abundance using available data (e.g., ebird counts).

2.6 Conclusions

Minimum length of stay of migrating Western Sandpipers at the Tofino and Fraser River Estuary in the Pacific Flyway varied depending on migration strategy, individual biology, site characteristics and location.

Western Sandpiper length of stay at the two stopovers showed some similarities in migration strategy between sites, supporting some hypotheses in optimal bird migration that shorebirds use a time-minimizing strategy during northward migration and mortality- and energy-minimizing strategy during southward migration (Alerstam et al. 1990, Lank et al. 2003, Duijns et al. 2019). At both stopover sites, adults had longer stopovers during northward migration, suggesting they are fueling for longer subsequent flights to arrive at their breeding grounds earlier. During southward migration, adults that arrived at the stopover sites earlier stayed longer than later arriving adults, suggesting their migration strategy changes with increasing predator risk (Ydenberg et al 2022) and/or the need to arrive at their overwintering grounds faster to molt (Roques et al. 2020). Juveniles also had longer stopovers than adults, suggesting that they experience different constraints than adults during southward migration, or may simply be a result of migration inexperience.

Our prediction that Western Sandpipers in the Fraser River Estuary (FRE) have longer length of stay due to greater prey availability was only supported during southward migration, when invertebrate density was higher and LOS longer in the FRE. However, the difference in prey availability between the two stopover sites may have been a result of our invertebrate sampling methods. Future studies assessing stopover site quality should include sampling both benthic and aerial invertebrates during different tidal periods and in all stopover habitats, including tidal marshes.

Western Sandpipers stopping in Tofino had a shorter length of stay across ages and migration seasons. Birds stopping in Tofino exhibit characteristics typical of “hop” migrants who travel shorter distances between stopover sites due to their shorter length of stay (Warnock 2010). As the beaches and mudflats at Tofino are less expansive than the FRE, the shorter stopovers may be a response to increased predation danger at this site. A possibility also exists that during southward migration the birds in better condition (higher departure body mass) select the shorter outer coastal route that would allow for a quicker arrival at non-breeding grounds, which also supports the possibility they are flying shorter distances and potentially destined to more northerly non-breeding sites.

Different stopover sites offer unique sets of characteristics used by birds exhibiting varying migration strategies, which highlights the importance of conserving both larger stopover sites like the Fraser River Estuary and smaller sites like those around Tofino. Our results also suggest that a more detailed understanding of population structure and connectivity across the Pacific Flyway would likely support more accurate assessment of population trends for this species.

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Chapter 3 – Shorebird habitat use at beach and mudflat habitats at the Tofino stopover site on Vancouver Island, Canada

3.1 Introduction

Many species of North American shorebirds depend on stopover sites to rest and refuel during their long-distance migrations between their Arctic breeding grounds and overwintering grounds in Central and South America (Myers 1987; Warnock & Bishop 1998; Warnock 2010). Stopover sites are high quality sites that contain abundant prey (Placyk & Harrington 2004, Schnurr et al. 2020) where shorebirds often gather in large numbers (Myers 1983, Myers 1987, Drever et al. 2014). Thus, disturbance or elimination of one critical stopover site can have detrimental effects on a species' population (Studds et al. 2017). Shorebird populations are in decline worldwide, where the loss and alteration of coastal habitat at migratory stopover and wintering sites is one of the main drivers (Stroud et al. 2006, Studds et al. 2017, Duan et al. 2022, Smith et al. 2023). The quality and availability of a variety of habitats during migratory stopover sites are important in sustaining shorebird populations (Burger et al. 1996, McGowan et al. 2011, Duan & Yu 2022). Understanding what influences shorebird movement and habitat use during migration stopover is an important component in implementing conservation measures.

Migratory stopover sites often consist of a mosaic of habitats used by shorebirds that can include beaches, tidal mudflats, and marshes (Burger et al. 1996, McPeake et al. 2015). The movement and use among different habitats at non-breeding sites is influenced by a variety of environmental factors. Shorebirds move with tide cycles as they forage in freshly exposed intertidal zones when their prey become available during receding tides (Helmers 1992, Erwin 1996, Rose & Nol 2010). When intertidal zones are flooded by incoming tides, shorebirds can seek alternate foraging habitats or congregate in high densities to roost (Colwell et al. 2003, Dias 2009, Basso et al. 2018). Time of day is also a driver of movement between habitats, where habitat use between night and day can vary due to changes in visual ability, predation risk, human disturbance, and prey availability (Robert et al. 1989, McNeil & Rodriguez S. 1996, Jourdan et al. 2020, Linhart et al. 2022).

Site safety and disturbance also influence shorebird habitat use. Increased site width has been linked to greater safety from predators (falcons), where shorebirds spend more time at expansive sites as they can forage away from cover where they are less vulnerable to surprise attacks (Pomeroy 2006, Sprague et al. 2008, Murchison et al. 2016). Human disturbance also plays a role in habitat use in many shorebird species, where studies show that shorebird abundance decreases at beaches with increasing levels of human disturbance (Pfister et al. 1992, Murchison et al. 2016). The complexity of factors affecting movements and habitat use show the importance of the availability of multiple habitats within stopover areas (Burger et al. 1996).

Thousands of migrating shorebirds stop to refuel in the coastal areas of Tofino, situated on the west coast of Vancouver Island in British Columbia, Canada (Drever et al. 2016). The Tofino stopover site offers an array of habitats used by shorebirds to rest and forage, including tidal mudflats, vast sand beaches and tidal marshes. The stopover site has been designated as regionally important by the Western Hemisphere Shorebird Reserve Network due to the high number of shorebirds during migration (WHSRN, 2013). Tofino is also a popular tourist destination which sees over 600,000 visitors annually, where the nearby beaches are the most popular attraction used by visitors (Tourism Tofino, 2019). Past studies in Tofino have shown that shorebird counts decreased with increasing human presence (Drever et al. 2016) and decreasing beach width (Murchison et al. 2016).

While shorebird count data is an effective method in assessing habitat use in Tofino, these count survey methods are generally limited to daytime and level of human effort and cannot easily account for individual movement between sites. To address these gaps in survey methods, we used the automated Motus Wildlife Tracking System ("Motus"; Taylor et al. 2017) to track individual movements and quantify habitat use of three species of shorebird at beaches and mudflats at the Tofino stopover site. The purpose of this study was to answer two main questions: i) What environmental variables affect shorebird movement and habitat use at two habitats (beach and mudflat) at the Tofino stopover site?, and ii) Does increased visitor use on the beaches of Tofino affect shorebird habitat use? Further, I determined prey density at the beaches and mudflat to investigate habitat use at the beaches and mudflats and predicted that shorebirds would spend more time at habitats with higher prey density. I also examined the relationship between tide level, time of day, and shorebird movements and habitat use. As past studies have shown a decrease in shorebird counts with increasing visitor use, we predicted that habitat use would increase at the mudflats with increasing human presence at the beaches, where nearly all humans occur. I also predicted that shorebirds would spend more time at the beaches at night when visitors were less frequent compared to daytime hours.

3.2 Methods

3.2.1 Study area

The Tofino stopover site is situated on the west coast of Vancouver Island within the District of Tofino and Pacific Rim National Park Reserve (PRNPR) (49.100 N, -125.852 W) and contains approximately 2,630 ha of exposed mudflats and sand beaches. We considered three shorebird habitats at the Tofino site, two sand beaches and one mudflat complex. The "North Beaches" are two connected sand beaches (Chesterman Beach and Cox Bay) located only 3 km south of the town site of Tofino. Long Beach is a 10 km long sand beach located within Pacific Rim National Park Reserve. Both the North Beaches and Long Beach are wave-washed sand beaches exposed to the open ocean and see high numbers of visitors during the summer months. The Tofino Mudflats (Wah-nah-jus Hilth-hoo-is Mudflats) are a biologically diverse tidal mudflat complex of sheltered tidal channels, streams, marshes, and eelgrass beds (Figure 3.1), and peak counts during spring migration can see over 40,000 Western Sandpipers (Drever et al. 2016). In this study, I refer to the Tofino Mudflats as “mudflat” and the North Beaches and Long Beach as “beach(es)”. The Tofino Mudflats have been designated as a locally important site for migrating shorebirds (WHSRN 2013) and are being considered for an elevated conservation status by WHSRN given very high peak counts in 2019 to 2021 (Maftei 2023, unpub. data).

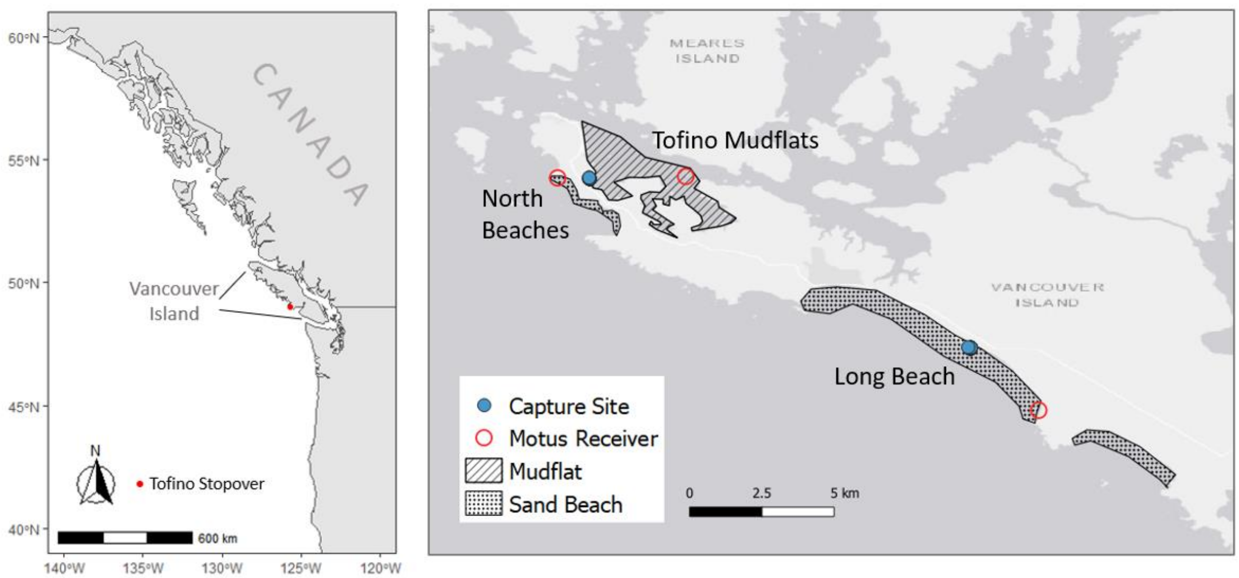

Figure. 3.1 Tofino stopover site (red point) on the west coast of Vancouver Island, British Columbia, Canada (left map). Motus tag deployment locations (blue points) and Motus receiving station locations (red circles) at three study areas within the Tofino stopover site. Small-scale map (left) created in RStudio software version 4.0.5 using ggspatial package, and large-scale map (right) created in QGIS version 3.16.2.

3.2.2 Shorebird tagging and tracking

We captured 314 shorebirds using mist nets (60 mm and 32 mm) and attached radio transmitters (“tags”) in the Tofino region, during northward and southward migration between 2018-2021 (Table 3.1). Dates of capture for northward migration were from early to mid-May, whereas dates of capture for southward migration ranged from early August to mid-September (Table 3.1). Target species included Sanderlings (*Calidris alba*), Semipalmated Plovers

(*Charadrius semipalmatus*), and Western Sandpipers (*Calidris mauri*). All three species were captured during northward and southward migration. An additional 107 Western Sandpipers were tagged in Mexico and California by research collaborators during northward spring migration, where 32 of these birds were subsequently detected in Tofino.

Upon capture, I banded each bird with a uniquely coded metal band and recorded mass (g), wing chord length (mm) and culmen (mm). When possible, I recorded sex based on bill length for Western Sandpipers (Prater et al. 1977, Sandercock 1998, Stein et al. 2008), and facial markings (lore, forecrown) and breast stripe for Semipalmated Plovers (Teather & Nol 1997). I aged birds during southward migration based on colour of wing coverts (Cramp and Simmons 1983, O'Hara et al. 2006). We recorded juveniles as birds that hatched that year, and adults as birds that hatched on or prior to the previous year, thus all birds captured during northward migration were recorded as adults (Table 3.1). We attached digitally encoded Very High Frequency (VHF) nanotags (Lotek, 2023) to the skin on the backs of shorebirds using cyanoacrylate adhesive. Feathers were trimmed to expose the skin just above the uropygial gland where the nanotags were attached. We used nanotag model NTQB2-4-2S weighing 1.0 grams with a burst rate of 13.7 seconds for Sanderlings [average mass at capture (g): 55.8 northward; 52.0 southward] and Semipalmated Plovers [average mass at capture (g): 49.7 northward; 44.4 southward], and we used nanotag model NTQB2-3-2 weighing 0.68 g for Western Sandpipers [average mass at capture (g): 27.3 northward; 25.0 southward] (Lotek 2023).

I used the Motus Wildlife Tracking System ('Motus') to detect signals from the tagged shorebirds. Three automated radio telemetry receivers were stationed at each study area within the Tofino stopover site to detect their movements and habitat use: one at the north end of the North Beaches, one on Dinner Island at the Tofino Mudflats, and one on the south end of Long Beach in PNRPR (Figure 3.1).

Table 3.1. Number of tagged shorebirds in the Tofino stopover site during northward and southward migration between 2018-2021. Species include Sanderling (SAND), Semipalmated Plover (SEPL), and Western Sandpiper (WESA).

	Northward				**Southward**			
Year	Capture Dates	SAND	SEPL	WESA	Capture Dates	SAND	SEPL	WESA
2018	-	-	-	-	Aug 08 – Sep 06	6	4	23
2019	May 01-07	1	10	34	Aug 01 – Sep 10	7	2	36
2020	May 01-08	0	7	37	Jul 27 – Aug 22	0	0	43
2021	May 03-16	5	5	32	Jul 20 – Sep 16	22	4	11

3.2.3 Data cleaning

Telemetry data were downloaded from the Motus database using RStudio software (v. 2021.09.0) following guidelines from the R Motus Book (Crewe et al. 2018). The data were cleaned using Motus' *filterByActivity* function (Crewe et al. 2018, Anderson 2021, pers. comm.). Cleaned data were filtered to include detections of target species by receiving stations located in the study areas identified by station name (i.e., "Wickaninnish Inn", "Kwisitis Visitor Centre, PRNPR", and "Dinner Island"). Filtered data were cleaned a second time by filtering detections with a run length <4 and mean standard deviation of frequency > 0.08 kHz, as values with these parameters indicate false detections (Bliss 2020). Tags with these criteria were also examined individually using signal plots to identify false detections, which were manually removed from the dataset.

3.2.4 Habitat use

I calculated elapsed time of individual tagged birds at each Motus receiver as a measure of habitat use. To calculate elapsed time, I first sorted the detection data by tag ID, timestamp, and receiver name, subtracted the time (in minutes) between detections and summed the differences to calculate the duration of time spent at each receiver (habitat) by each tag at each receiver. I included short gaps in detections (0-60 minutes) as time spent at the receiver as it is possible that Motus tags may not get detected depending on location or situation of the bird (e.g.

tag is not facing the receiver, the bird is in tall grass, etc.). Gaps in detections > 1 hour were not included in the elapsed time as this indicated that the tagged bird may have left the receiver detection range (Linhart 2021). Detections from the Long Beach and North Beaches receivers were classified as "beach" and detections by the Tofino Mudflats receiver were classified as "mudflat". Daily sunrise and sunset times were determined using the sunRiseSet() function in the "Motus" package in RStudio (v. 2021.09.0). Detections with timestamps between sunrise and sunset were classified as "day" and detections between sunset and sunrise were classified as "night". Tide level data were downloaded from tides.gc.ca, classified as "low", "rising", "high" and "falling", and merged with the shorebird detection data based on the timestamps. A 1.5 hour window on either side of the highest and lowest tide heights were used to classify "high" and "low" tidal periods. I grouped shorebird detection data by individual bird (Motus tag ID), habitat (beach or mudflat), time of day (day or night), and tide level (low, rising, high, falling), and summed the elapsed time for each habitat, daytime period, and tidal period combination. To summarize habitat use of all three species, I calculated the mean elapsed time spent at the beach and mudflat habitats during northward and southward migration.

3.2.5 Human disturbance

To model effects of human disturbance on habitat use, I summarized visitor survey data provided by PRNPR to average number of visitors per hour for each day surveyed. Shorebird habitat use data were then grouped by individual bird (Motus tag ID), detection date, habitat (beach or mudflat; Western Sandpipers only), and time of day (day or night). The daily average number of visitors per hour data were merged with the shorebird habitat use data by detection date in RStudio software, and only shorebird daytime detection data occurring on days with visitor surveys were included in the analysis. As there were very few visitors recorded during surveys in spring 2020 due to a lack of visitors resulting from Covid-19 lockdowns, I removed northward migration 2020 data from analysis.

3.2.6 Movements between habitats

To investigate frequency of movements between habitats, I determined the number of moves between the beaches and mudflat. One move was counted when a bird was detected at one receiver, and subsequently detected at a different receiver. I removed movements with very short durations (<60 s) that were detected between receivers; movements within this timeframe suggest that the bird was flying and simultaneously being detected by two different towers. As a method of quality control, a subsample (12 tags) of filtered movement data (<60 s) was compared to a subsample of manually inspected signal plots. Northward migration data include movements in 2020-2021, and southward migration data are from 2018-2021.

Two movement strategies were determined for Western Sandpiper analysis, "beach to mudflat" and "mudflat to beach". Movements between the two beach receivers (beach to beach) were removed from the analysis. The time-of-day variable included sunrise and sunset, which was 30 minutes before and after the rise/set times (Linhart et al. 2022). Day was the time between "sunrise + 30 minutes" and "sunset - 30 minutes", and night was time between "sunset + 30 minutes" and "sunrise - 30 minutes).

3.2.7 Invertebrates

I collected sediment cores along 13 transects during both migration seasons in 2021 at the Tofino Mudflats (4 transects), North Beaches (5 transects), and Long Beach (4 transects). Samples were collected between May 1 – May 31 during northward migration, and July 1 – August 30 during southward migration. Samples at the beach habitats were collected along transects at the wrack line (visible high tide line), intertidal, and swash zones (active wave wash zone). At the North Beaches, the intertidal and swash samples were collected at an average distance from the high tide line of 50 m and 110 m, respectively. At Long Beach, samples at the intertidal and swash zones were collected at an average of 65 m and 165 m from the high tide line, respectively. As the mudflat habitat contained fewer distinct beach zones, samples at the mudflat were collected at set distances from the high tide line: 50 m, 200 m, and 350 m. Sediment samples were collected using a corer (volume=196.36 ml) and were sieved through a 0.5 um mesh. Invertebrates that remained in the mesh were counted and identified to the lowest possible order. Sediment samples from the mudflat habitat and North Beaches were processed within 24 hours, and samples from Long Beach in Pacific Rim National Park were processed in-situ. A subset of invertebrates, as well as unidentified specimens, were preserved in ethanol for further classification.

3.2.8 Statistical analysis

I used RStudio (v. 2021.09.0 and 2023.06.1) to perform all statistical analyses. I used Shapiro-Wilks tests and visually inspected histograms with kernel density and normal curves to check for normality of the data. I inspected the residual spread of the models using the resid() function in RStudio to confirm homoscedasticity.

I ran models for each species separately to account for differences in species biology and behaviour. For Semipalmated Plovers and Western Sandpipers, I first modeled northward migration and southward migration combined to check for differences in response variables between the two migration periods. If significant differences occurred between migration periods, I then ran models for northward and southward migration separately. Analyses for Sanderlings were performed for southward migration only as the sample size was insufficient (n = 6) for analysis of northward migration. For Western Sandpipers, only data from 2020-2021 were included in northward analyses, as the mudflat receiver was not functional in spring 2019, eliminating the ability to compare between beaches and the mudflat. For Sanderlings and Semipalmated Plovers, analyses included beach detections only as preliminary results suggested that these two species spent little time at the mudflat, thus I was unable to compare significant differences between the two habitats.

To investigate habitat use, I ran generalized linear mixed-effects models (GLMM) with elapsed time (in minutes) as the dependent variable, time of day, habitat (Western Sandpiper only), and tide level as predictor variables, and individual tag number as a random effect. To explore differences in habitat use between migration seasons, we ran a GLMM with elapsed time (in minutes) as the dependent variable, time of day and migration direction as predictor variables. Individual bird (Motus tag ID) was included as a random effect as individual birds may have multiple observations in the dataset (up to one observation for each tidal period, daytime period, and habitat combination). As the elapsed time data were positive-only and positively skewed, we used a gamma distribution with a log-link to fit all models.

For visitor disturbance models, I ran separate GLMMs with elapsed time (in minutes) as the dependent variable. Predictor variables included habitat type, average number of visitors per hour, and migration direction, and an interaction between time of day, tide, and habitat. Individual bird (Motus tag ID) was included in the model as a random effect as individual birds may have multiple observations in the dataset (up to one observation per day for each daytime and habitat combination). The elapsed time data were positive-only and positively skewed, thus I used a gamma error distribution with a log-link to fit the models. As Western Sandpiper data contained sufficient detections in both beaches and mudflats, the habitat predictor variable contained detections from both locations to investigate the effects of beach visitors on shorebird habitat use. As Sanderlings and Semipalmated Plovers had limited detections in the mudflat, only beach detections were included in the models, and the habitat predictor variable was removed from the GLMMs. Since mudflat detections were removed from visitor use analysis for Sanderlings and Semipalmated Plovers, northward data also contained detections from 2019 as the broken mudflat receiver did not affect the analysis. Significant interaction effects were explored by inspecting plots using the emmip() function from the package “emmeans” in RStudio (v. 2023.06.1)

To assess movements between habitats, I ran a binomial general linear model with movement strategy (1 = beach to mudflat, 0 = mudflat to beach) as the response variable and time of day (sunrise, sunset, day, night), and tide level (low, rising, high, falling) as predictor variables. I used t-tests with a Poisson distribution to test for differences in the number of movements of Western Sandpipers between northward and southward migration, as well as between adults and juveniles. I first tested for equal variances using the var.test function from the "stats" packaged in RStudio (v. 2023.06.1).

I ran an ANOVA to compare invertebrate densities between habitats (North Beaches, Long Beach, Tofino Mudflats) for each migration period with invertebrate count per sample core as the response variable and site as the predictor variable. As the data were not normally distributed (Lilliefor's, $p < 0.01$), we used a Kruskal-Wallis test and a Dunn's test with method "holm" to explore differences between sites. To determine if distance from shoreline (high tide line) influenced invertebrate density, I ran generalized linear models (GLM) with a Poisson distribution. Number of invertebrates per core was the response variable, and distance from shoreline was the predictor variable. I ran GLMs separately for the beach and mudflats as the distances were measured differently (zones for beaches and set distances for mudflats) and cannot be compared within the same model. As there are significant differences in invertebrate densities between northward migration and southward migration (Chapter 2), I ran the ANOVAs and GLMs separately for each migration season.

3.3 Results

3.3.1 Habitat use

The time that shorebirds spent on the beaches and mudflats in Tofino varied by species, migration season, tide, and time of day. Western Sandpipers spent more time at the mudflat than the beaches (Table 3.2), and there was a significant interaction between habitat and tide level during both northward and southward migrations (Table 3.3). Western Sandpipers spent more time at the mudflat than beaches during low, rising, and falling tides. At high tide, Western Sandpipers spent significantly less time at the mudflat and slightly more time at the beach (Figure 3.2, Table 3.3). In the southward model, there was also a significant interaction between time of day and habitat type. Western sandpipers spent more time at the beach at night than during the day and more time at the mudflat during the day than at night (Figure 3.2, Table 3.3).

During southward migration, Sanderlings spent significantly more time on the beach during falling tide, and during the day than at night. There was a significant interaction between time of day and tide, where Sanderlings time on the beach during rising tide decreased at night and increased during the day (Figure 3.3, Table 3.3).

Semipalmated Plovers also spent more time on the beach during the day compared to night during both migration periods. There was also a significant interaction between time of day and tide level during both migration periods. During northward migration, time spent on the beach at low tide decreased during the day and increased at night, where the opposite trend occurred for falling tide. During southward migration, time spent at falling and rising tides increased during the day and decreased at night, where the opposite trend occurred at high tide (Figure 3.3, Table 3.3).

Table 3.2. Mean duration of time (hours) spent by shorebirds per habitat type in each migration period. Northward data contains tags deployed in 2020-2021, and southward data contains tags deployed from 2018-2021. Data were grouped by tag (individual bird) and habitat. “N Dep” is the number of tags deployed in each habitat (beach, mudflat), and “N Det” are the number of tags that were detected in each habitat. As tagged birds move between habitats during stopover, N Det may be greater than N Dep.

		Sanderling			**Semipalmated Plover**			**Western Sandpiper**		
Migration Direction	Habitat	N Dep	N Det	Mean time (hrs ±SE)	N Dep	N Det	Mean time (hrs ±SE)	N Dep	N Det	Mean time (hrs ±SE)
Northward	Beach	5	5	10.6 ±3.4	12	12	11.3 ±5.0	29	71	1.3 ±0.4
	Mudflat	0	4	0.2 ±0.1	0	6	0.2 ±0.1	40	69	3.0 ±0.6
Southward	Beach	35	35	12.7 ±2.5	10	10	12.8 ±7.0	97	96	1.9 ±0.3
	Mudflat	0	3	0.2 ±0.1	0	2	0.05 ±0.04	16	57	16.7 ±2.3

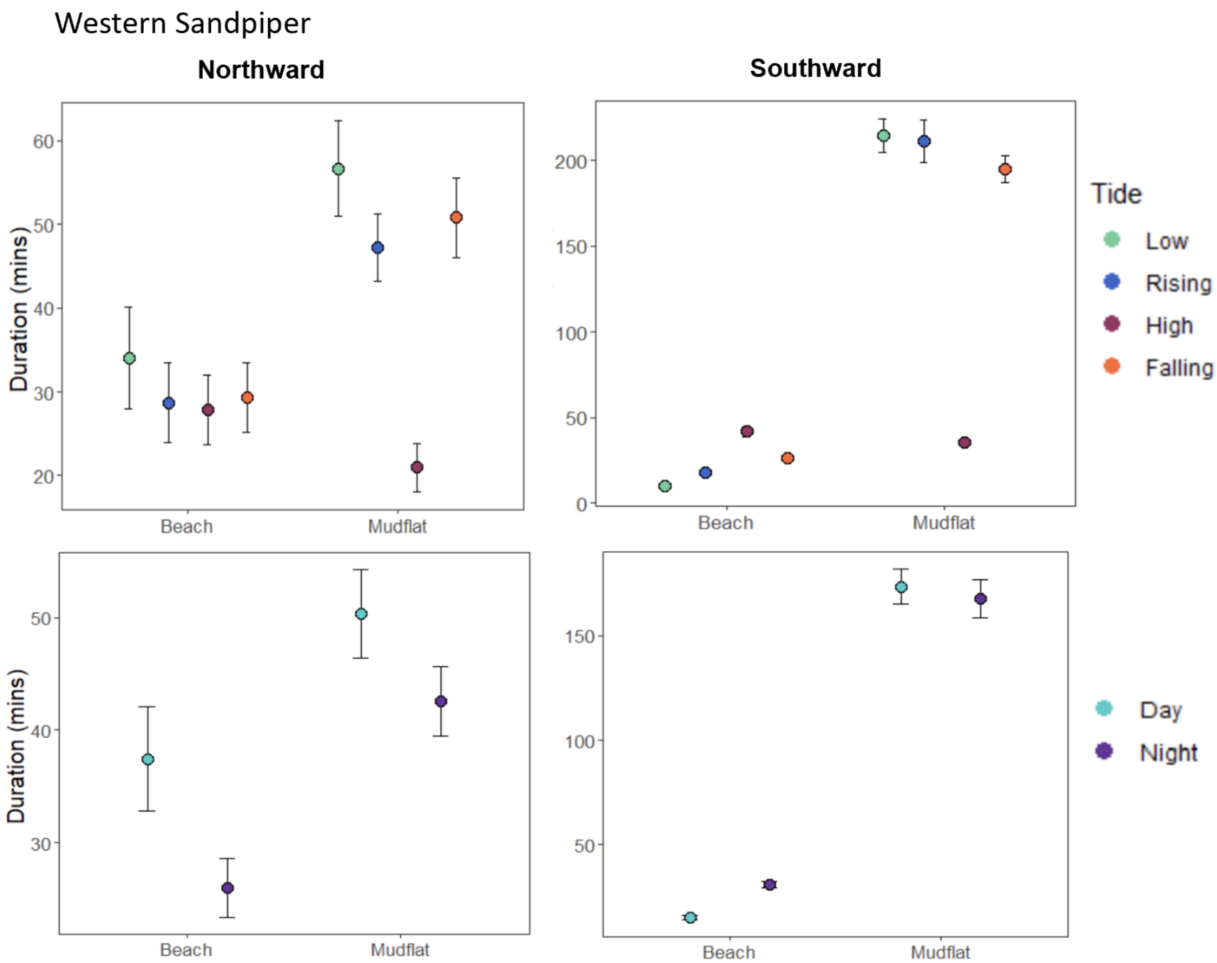

Figure 3.2. Mean duration of time of Western Sandpipers spent at beaches and mudflats by tidal level (top) and time of day (bottom) during northward (left) and southward (right) migrations. Data were grouped by tag (individual bird), habitat, time of day, and tide. Points are means from predicted values generated from generalized linear mixed-effects models, and errors bars are standard error from the means.

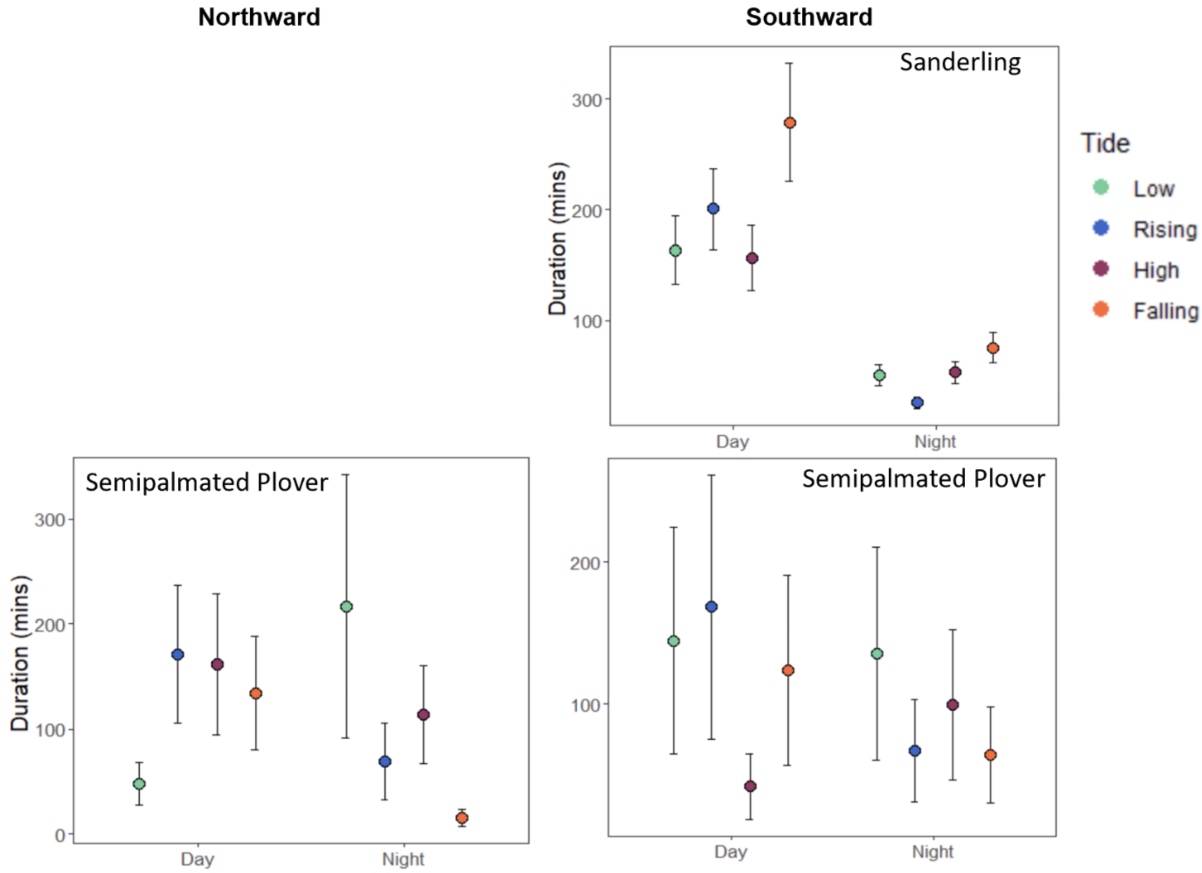

Figure 3.3. Mean duration of time of Sanderlings (top) and Semipalmated Plovers (bottom) spent at beaches and mudflats by tidal level during northward (left) and southward (right) migrations. Data were grouped by tag (individual bird), time of day, and tide. Means are predicted values generated from generalized linear mixed-effects models, and errors bars are standard error from the means.

Table 3.3. Generalized linear mixed-effects model coefficients and results of each species' model by category (migration season), dependent variable is duration of time (mins) spent by shorebirds

Species	Model	Predictor Variables	Estimate	Df	Std. Error	t-value	p-value
Sanderling	Southward	Time of Day (Day) * Tide (Rising)	0.8	10	0.4	1.99	0.04
Semipalmated Plover	Northward	Time of Day (Day) * Tide (Low)	-3.23	10	0.81	-3.97	<0.01
	Southward	Time of Day (Day) * Tide (High)	-1.36	10	0.67	-2.03	0.04
Western Sandpiper	Northward	Habitat (Beach) * Tide (High)	0.87	12	0.35	2.51	0.01
	Southward	Habitat (Beach) * Tide (High)	2.2	12	0.25	8.67	<0.01
		Habitat (Beach) * Tide (Low)	-1.01	12	0.27	-4.14	<0.01
		Habitat (Beach) * Time of Day (Day)	-0.78	12	0.19	-4.04	<0.01

3.3.2 Visitor use

There was a significant interaction between visitor use (daily average visitors per hour) and habitat use for Western Sandpipers (est = 0.02, se = 0.003, t = 6.22, df = 6, $p < 0.01$); as visitor use increased at Long Beach, Western Sandpipers spent more time at the mudflat and less time at Long Beach (Figure 3.4). There was no significant interaction effect for Western Sandpipers between migration season and visitor use, and no significant effects for Sanderlings or Semipalmated Plovers.

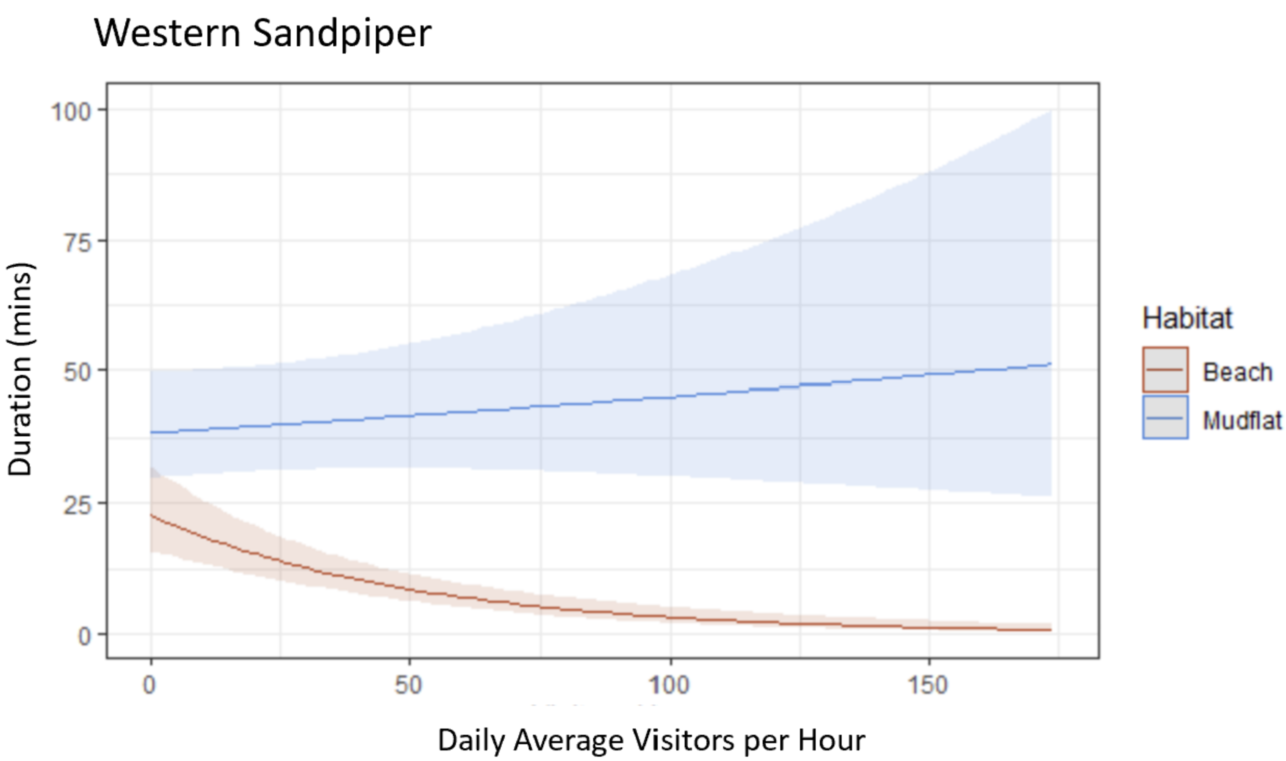

Figure 3.4. Plotted generalized mixed-effects model (GLMM) interaction (visitors per hour * habitat) and predicted values of duration (mins) by Western Sandpipers at the Tofino stopover site during northward and southward migration. Plots were created using the plot_model function in the sjPlot package in RStudio v. 2021.09.0.

3.3.3 Movements between habitats

Western Sandpipers moved most between habitats, followed by Semipalmated Plovers, then Sanderlings (Table 3.4). The proportion of Western Sandpipers that moved between habitats at least once during migration stopover were the same during northward migration and southward migration; approximately 46% of individual tagged birds (northward = 32/69; southward = 53/113) were detected at least once at both beach and mudflat receivers (Table 3.4). Western Sandpipers moved significantly more during southward migration ($t = -4.7$, $df = 123$, $p < 0.01$), and juveniles moved significantly more than adults ($t = -5.1$, $df = 111$, $p < 0.01$), where the average number of moves between habitats was 4.8 ±0.8 for juveniles and 0.6 ±0.2 for adults. Movement strategy ("beach to mudflat" or "mudflat to beach") was also similar during both migration periods. Out of the Western Sandpipers that moved between habitats, 61% and 52% of movements were from the beach to mudflat during northward and southward migration, respectively.

There was an effect of tide level on Western Sandpipers' movement strategy during southward migration, where movements from the beach to the mudflat were more frequent during falling tide ($z = 2.67$, $df = 3$, $p < 0.01$). There were no significant effects of time of day (sunrise, sunset, day, night) on movement strategy during northward or southward migration.

Table 3.4. Summary of shorebirds movements in the Tofino stopover site where "n" is the number of tagged birds, "% Move" is the proportion of birds that moved at least once, and "Mean Moves" is the mean number of movements by birds that moved at least once between radio-telemetry receivers stationed at two different habitat types (two beaches, one mudflat).

Migration	**Species**	**n**	**% Move**	**Mean Moves**
Northward	Semipalmated Plover	12	25	1 ±0
	Western Sandpiper	69	46.4	2 ±0.2
Southward	Sanderling	35	8.5	1.6 ±0.7
	Semipalmated Plover	10	20	1.5 ±0.5
	Western Sandpiper	60	46.9	9.4 ±1.2

3.3.4 Invertebrates

The mudflats had a significantly higher density of invertebrates (number of invertebrates per 196.36 ml core), approximately 2-3 x higher, than the beaches during both migration periods (northward: df = 2, z = -5.8, p <0.01; southward: df = 2, z = -5.1, p <0.01), and no differences between the two beach habitats (Table 3.5). The number of invertebrates were higher at all three sites during southward migration compared to northward where the difference was significant at Long Beach (df = 1, z = 1.8, p = 0.03) and the Tofino Mudflats (df = 1, z = 2.6, p < 0.01) (Table 3.5).

Table 3.5. Mean number of invertebrates per sample core (196.36 ml) and number of samples collected at each of the three study habitats within the Tofino stopover site.

Site	Northward		Southward	
	Mean Invertebrates ±SE	Number Samples	Mean Invertebrates ±SE	Number Samples
Long Beach	3.9 ± 1.0	36	8.5 ± 1.9	35
North Beaches	7.1 ± 2.6	45	9.4 ± 3.1	43
Tofino Mudflats	19.4 ± 2.0	36	32.7 ± 4.0	27

There was a significant effect of distance from shore on invertebrate numbers at both the mudflat and beaches. At the beaches, the number of invertebrates were significantly greater at the wrack zone (North: $z = 4.18$, $p < 0.01$; South: $z = 14.93$, $p < 0.01$) and lower at the swash zone (North: -7.08, $p < 0.01$); South: -4.98, $P < 0.01$) during both migration periods (Figure 3.6). At the mudflat, the number of invertebrates increased with distance from the high tide line during both migration periods (North: $z = 5.09$, $p < 0.01$; South: $z = 5.42$, $p < 0.01$) (Figure 3.5).

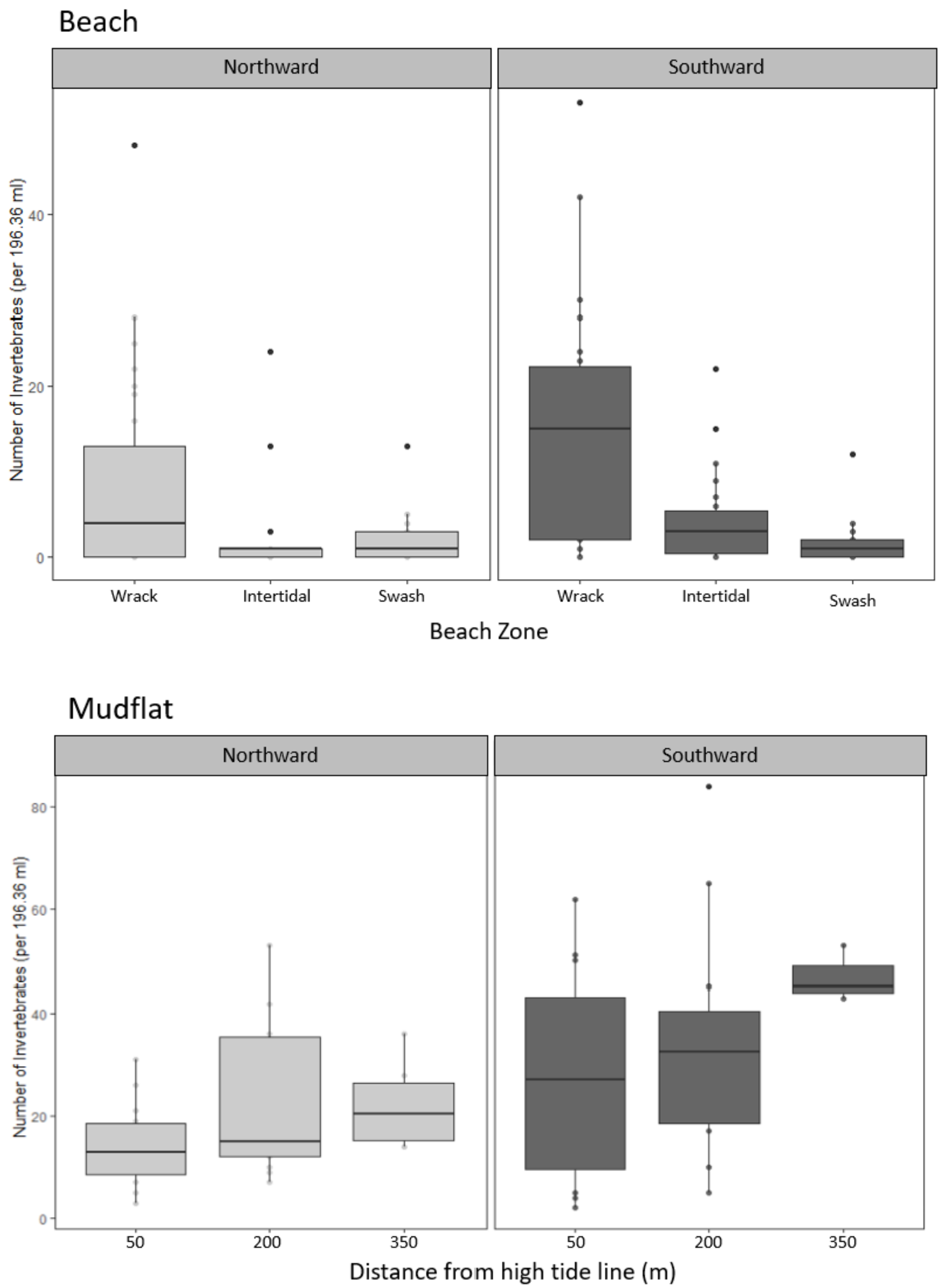

Figure 3.5. Number of invertebrates per sample core (196.36 ml) (y-axis) along increasing distances from shore (x-axis) at the beaches (top) and mudflats (bottom) at the Tofino stopover site during northward and southward shorebird migration seasons. At the beaches, wrack is the high tide line, swash is the active wave zone, and intertidal is the region between wrack and swash.

3.4 Discussion

Habitat use by shorebirds in this study was affected differently by migration season, tidal period and time of day. Western Sandpipers used both mudflats and beaches in the Tofino stopover during migration, and their habitat use was mainly driven by tidal period. Sanderlings and Semipalmated Plovers used the beaches almost exclusively, and more often during the day than night. Beach use by these two species was affected by a combination of both tide period and time of day. Visitor use also influenced habitat use. Western Sandpipers spent less time on Long Beach with increasing visitor use, and Semipalmated Plovers had the same negative trend, but only during northward migration.

3.4.1 Habitat use & movements

3.4.1.1 Western Sandpipers

Western Sandpiper habitat use was driven by the daily tide cycle during both migration periods. This species spent significantly more time at the mudflat than the beaches at every tide level except for high tide, where at high tide their time increased at the beach. This finding was also supported by results from the southward movement analyses where significantly more movements from the beaches to the mudflat occurred during falling tide – indicating they departed the beaches for the mudflat after high tide.

Daily tide cycles affect shorebird habitat selection during non-breeding periods; when high tides inundate intertidal areas, shorebirds must seek alternate habitats to roost or forage (Rogers et al. 2006, Dias 2009, Rosa et al. 2006, Linhart et al. 2022). Previous studies exploring habitat use among exposed sand beaches and sheltered mudflats found that many shorebird species use mudflats to forage during low tides and use exposed beaches to roost at high tide (Placyk & Harrington 2004, Rose & Nol 2010). A study in New Jersey found that peak densities of Western Sandpipers occurred at a sheltered mudflat around low tide, where densities became lowest at high tide (Burger et al. 1977). The Tofino Mudflats are completely inundated at tide levels > 2.7 m (Y. Zharikov pers. comm). In contrast, the upper area of the beaches remain available during high tide, and thus it is likely that Western Sandpipers use the beaches at high tide as a potentially important roost site.

Western Sandpipers' response to tidal periods at the Tofino stopover may also be explained by prey availability. Results from our prey analysis found that prey density at the mudflat increased with increasing distance from shore, and the inverse trend was found at the beaches where the greatest density was at the wrack zone. Western Sandpipers likely leave the mudflat at high tide as prey availability decreases when it is covered by water during this tide period yet remains available at the beach. Further, amphipods made up the highest proportion of invertebrates found in Western Sandpiper faecal samples collected at the Tofino stopover (Chapter 2), suggesting this is the preferred prey item at this site. As amphipods were the most abundant prey item found at the mudflat, and polychaetes were greatest at the beaches, Western Sandpipers may prefer to use the mudflat when amphipods are available, and once they become inaccessible at high tide, move to the beaches to roost or prey on polychaetes. While my study was unable to detect behaviour of individuals (e.g. roosting, foraging, etc.), further observations of marked individuals might confirm this use of the beaches by Western Sandpipers during high tide.

Western Sandpipers spent more time on the beaches and mudflats during the day than night during northward migration. During southward migration, an interaction occurred between time of day and habitat where their time at the beach decreased during the day and increased at night. Fluctuations in temperatures can affect prey availability; marine invertebrates can increase their depth under sediment as temperatures increase to avoid desiccation (Kensler et al. 1967, Somero 2002). Western Sandpipers can adjust their foraging behaviour to changes in prey availability (Nebel et al. 2004). The Tofino stopover experiences higher temperatures during southward migration (July and August) than northward migration (early May), and as the wrack zone at the beaches remains exposed throughout the daily tidal cycles, it is possible that invertebrates bury deeper into the sediment during the day to avoid higher temperatures. A downward migration of invertebrates may reduce prey availability for sandpipers, resulting in Western Sandpipers spending less time at the beach during the day and increasing use at night. However, as our invertebrate sampling only occurred during the day, it is not possible to compare prey availability from the day to night in our study. Western Sandpipers' decrease in daytime beach use during southward migration may also be a result of the increase in daytime human visitors during this migration period (see below).

Although the proportion of Western Sandpipers that moved between habitats was similar during both migration periods, the average number of movements increased during southward migration. Higher visitor use was expected to increase movements during southward migration, and our study suggests this increase in moves was likely due to the presence of juveniles, whose average number of moves was nearly 4x greater than those of adults. Juvenile Western Sandpipers are more vigilant than adults during southward migration and fly farther and longer than adults when disturbed by falcon silhouettes, however juveniles are less disturbed by approaching humans than adults (Hope et al. 2014). As juveniles migrate concurrently with falcons during southward migration, the expected increase in predator disturbance may result in the greater numbers of movements between habitats that were seen in our study. Juvenile sandpipers also use a greater variety of sites than adults during stopover (Linhart et al. 2023), and as they are inexperienced in migration, they may be moving more between habitats.

3.4.1.2 Sanderlings

During southward migration, Sanderlings used the beaches almost exclusively compared to the sheltered mudflat. Sanderlings spent more time at the beach during falling tide compared to all other tide levels, and time at the beach increased during the day during rising tides.

Sanderlings are known to use sand habitats (Connors et al. 1981, Placyk et al. 2004, Burger et al. 2018), where they forage in water-covered sand in the wave-wash zone (Burger et al. 1977; Myers et al. 1980). Their habitat use at the Tofino stopover is consistent with findings from other studies which found Sanderlings used sand beaches over nearby backwater mudflats and marshes (Burger et al. 1977, Placyk et al. 2004) and their numbers peaked during falling and rising tides (Burger et al. 1977, VanDusen et al. 2012, Burger et al. 2018). Sanderlings also use multiple habitats within one site, where they move from outer beaches to sheltered sand flats during the lower part of falling tides (Connors et al. 1981, VanDusen et al. 2012). As exposed, wave-washed beaches are the main type of sand habitat available at the Tofino stopover, Sanderlings may limit habitat use to these beach types, resulting in a greater reliance on Long Beach and other sand beaches around this stopover site.

Sanderling beach use was also significantly greater during the day than night, and time on the beach during rising tides increased significantly during the day compared to night. A study found that beaches used by Sanderlings during the day saw few or no individuals at night (Maron & Myers, 1984). As this species uses both visual and tactile foraging methods (Myers et al. 1980, Van Dusen et al. 2012), Sanderlings may simply be spending greater amounts of time foraging during the day to maximize both methods of foraging. Connors et al. (1981) hypothesized that Sanderlings make use of the diurnal period by foraging sequentially in more than one sand habitat. As Sanderlings in our study seldom used the mudflat, it is possible that they exploit daytime foraging at the beach by foraging in the swash zone during daytime rising and falling tides, and forage at night during falling tides if their energetic requirements were not met during the day (McNeil & Rodriguez, 1996).

3.4.1.3 Semipalmated Plovers

Semipalmated Plovers at the Tofino stopover site spent most of their time at the beaches and little time at the mudflat. Previous studies have found that Semipalmated Plovers use a variety of habitat types during non-breeding periods, including tidal mudflats, mangroves, and sand beaches (Smith & Nol. 2000, Rose & Nol 2010). Burger et al. (1977) compared shorebird use among outer beach, inner beach, and mudflat habitats, and found that Semipalmated Plovers used all three habitats regularly. It is not known why Semipalmated Plovers were found to spend relatively little time at the mudflat compared to the beaches at the Tofino study site. Studies have shown polychaete worms to be the most consumed prey item during non-breeding periods (Strauch & Abele 1979, Rose et al. 2016). However, a study in the Bay of Fundy also showed that nearly half of this species' diet was made up of amphipods, which are abundant at the Tofino mudflat (Napolitano et al. 1992). Semipalmated Plovers were frequently observed foraging on *Thoracophelia* polychaetes in 2021 (A. Blondin, pers. obs.), which was the most abundant prey item at the Tofino beaches. It is possible that Semipalmated Plovers in Tofino choose *Thoracophelia* polychaetes over amphipods when available. However, since faecal samples were not assessed for this species in this study, preferred prey items at the Tofino site remain unknown.

Semipalmated Plovers spent more time at the beach during the day compared to night during both migration periods. Diurnal activities of Semipalmated Plovers during non-breeding periods in other studies are inconsistent; a study in Venezuela found they were more active during the day (Morrier & MacNeil 1991), another study in Venezuela found that they forage more actively at night (Robert et al. 1989), where a study in California found their nocturnal activity increased during the fall (Dodd & Colwell 1998). Semipalmated Plovers are strictly visual hunters (Strauch & Abele 1979), and they may be using the beaches in Tofino during the day to visually hunt for polychaetes. Semipalmated Plovers spend most time foraging at low tide (Strauch & Abele 1979, Rose & Nol 2010), which is consistent with our results, except during northward migration where a significant decrease of time spent at the beach at low tide occurred during the day. Time spent at low tide could be explained by the vertical movements of the abundant *Thoracophelia* polychaetes found at the Tofino beaches. This genus of polychaete migrates upwards to the sand-surface interface during low tide and burrows downward as the tide rises (Eikenberry 1996, Dafoe et al. 2008), making *Thoracophelia* easy prey for Semipalmated Plovers as they mostly peck from the surface with their short bills (Rose & Nol 2010). However, this does not explain the decreased use of beaches at low tide during northward daytime, which remains unclear.

3.4.2 Human disturbance

The number of beach visitors negatively affected beach use of Western Sandpipers. As the number of visitors at the beach increased, Western Sandpipers spent significantly less time at the beach and more time at the mudflat. A 2016 study at Long Beach near Tofino found that human activity affected shorebird beach use, where an increase in number of people resulted in shorebird absence from beaches, and disturbance increased with proximity to people and speed of human activity (Murchison et al. 2016). Our study is consistent with Murchison et al. (2016), and detection from the Motus receivers supports evidence that Western Sandpipers used the mudflat more as visitor use increased at the beach, suggesting they seek alternative habitats with less human disturbance when the beaches become busy with people. Thus, this consistency suggests that Motus data have the potential to accurately reflect habitat use of shorebirds at multiple habitats. This finding of influence of human visitors on Western Sandpipers use of beaches and mudflats was also supported by an interaction in our habitat use analysis, where Western Sandpipers spent less time at the beach during the day during southward migration. As the number of visitors on Long Beach double during southward migration in July and August (Murchison et al. 2016), Western Sandpipers may be using the beach less during the day during this migration period when visitor numbers are high.

An increase in human presence at Long Beach showed no significant effects for Sanderlings or Semipalmated Plovers. Semipalmated Plovers are known to be less disturbed by people than other shorebird species (Pfister et al. 1991, Murchison et al. 2016, Nol & Blanken, 2020), and unlike the plovers, Sanderlings can be negatively impacted by human disturbance. For example, Burger et al. (2007) found that after a human disturbance event at a beach, only 20% of Sanderlings returned after 1 minute. Sanderlings increase their foraging time at night as a method to avoid human disturbance (Burger & Gochfeld 1991, McNeil & Rodriguez S. 1996), and as our study shows that Sanderlings used the beaches during falling tide at night, this may be a response to avoid daytime beach visitors.

The lack of negative effects of human disturbance on Semipalmated Plovers and Sanderlings during migration in our study may be due to the nature of these two species' habitat use preferences, in combination with the Motus tracking methods. At the Tofino stopover, Semipalmated Plovers and Sanderlings spent most of their time at the beaches, using the mudflat only seldomly in our study. Although disturbance events at the beach may result in these species leaving the immediate area, Long Beach is extensive, and these individuals can simply move to another area of the beach after a disturbance event. As the Motus receiver on Long Beach monitors the beach's entire length, disturbances may not be well captured for beach species if the birds are not leaving the antenna's range. Further, tagged birds are more likely to be detected by Motus receivers while in flight than on the ground (Taylor et al. 2017). Studies have found that Sanderlings spent more time flying than roosting with increased level of human activity (Morton 1996, Macwhirter et al. 2020). Thus, if time spent in flight increases with human activity, detections by Motus towers may increase with increasing disturbance, such as what was found with Semipalmated Plovers during southward migration in this study. This caveat may not be an issue with Western Sandpipers as they were found to spend more time at a different habitat also monitored by Motus.

3.5 Conclusion

Habitat use in shorebirds is complex - I found that it varies by species, and by tide, time of day, migration season, or combination of these factors, as well as human presence. The effect of tide on movements and habitat use of Western Sandpipers in our study shows the importance of maintaining availability of different habitats in the Tofino Stopover for this species. Though Western Sandpipers overall spent more time at the mudflat, likely due to the availability of amphipods, the beach remains important for this species particularly at high tide. The decreasing amount of time that Western Sandpipers spent at the beach as visitors increased suggests they also move to the mudflat to avoid human disturbance. Although it is useful for Western Sandpipers to access alternate habitat to avoid disturbance, increased movements can be energetically costly (Nudds & Bryant 2000, Lilleyman et al. 2016) at a time when good fat stores are imperative for a successful migration (Dunn et al. 1988).

Sanderling's and Semipalmated Plover's almost exclusive use of the beaches in Tofino highlights the importance of Long Beach and nearby sand beaches for migrating shorebirds. As these beaches become busy with people in the summer months, it is important to consider the effects on migrating shorebirds, especially since past studies on the west coast of Vancouver Island have shown decreased foraging rates with increased human disturbance (Yasué 2005, Murchison et al. 2016). However, using Motus in this study to detect absence from the beach as a proxy for human disturbance was likely not effective for these two species, as they seldom were detected at the mudflats, suggesting it is not the preferred habitat at this stopover site.

There were several limitations of Motus that made local detections difficult to assess in this study. In addition to the possibility of roosting birds not being detected, and flying birds likely having increased detections, the overlap of antennae ranges from different receiving stations in Tofino made habitat location difficult to pinpoint. However, as Motus technology improves and simultaneous detections become simpler to decipher in large datasets such as in this study, it has the potential to be a valuable tool for detecting local movements due to its autonomous and relatively non-invasive method for tracking shorebirds (Taylor et al. 2017, Linhart et al. 2022).

3.6 References

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Chapter 4 – General Discussion

Using Motus detection data allowed me to answer important questions about shorebird stopover ecology in the Pacific Americas Flyway. In Chapter 2, I found that Western Sandpiper's length of stay varied between stopover sites situated at different coastal locations and with different habitat characteristics. The shorter length of stay of birds who stop at Tofino suggest birds using this site may be using a "hop" migration strategy (flying shorter distances between stopover sites) compared to birds that use the Fraser River Estuary. These characteristics also indicate the potential that Tofino is a riskier site due to the narrower site width of the beaches and mudflats compared to the Fraser River Estuary. We also found some similarities in Western Sandpiper's length of stay behaviour between the two stopover sites. Adult Western Sandpipers had longer stopover during northward migration at both stopover sites, suggesting they are using a time-minimizing strategy during northward migration. Juveniles also stayed longer than adults during southward migration, indicating they are using a different migration strategy than adults, or the longer stays could result from inexperience in refueling during migration.

We were able to provide an updated length of stay of Western Sandpipers at these sites: 2-6 days at Tofino and 5-8 days at the Fraser River Estuary (depending on migration season). These minimum estimates will allow researchers to better estimate Western Sandpiper populations as they pass through these stopover sites, which comes at a critical time at the Fraser River Estuary. The Port of Vancouver is situated on an important mudflat at this site and has been recently approved for expansion, where the effects on intertidal biofilm and impacts to Western Sandpipers remain relatively unknown (IIAC, 2020). Thus, maintaining a network of Motus receivers at the Fraser River Estuary can help researchers monitor potential effects of the port expansion on shorebird length of stay and populations, where long-term monitoring is increasingly important as global shorebird populations decline. This study is also one of the first to assess length of stay at the Tofino stopover site, and recent survey counts suggest that

Western Sandpiper numbers at this site are increasing or are higher than what was previously estimated (M. Maftei 2022, unpub. data). Thus, an accurate length of stay of Western Sandpipers in Tofino during both migration periods, along with recent survey count data, can assist researchers in determining new population estimates for this important site.

I also found that Western Sandpipers that were tagged outside the study sites had significantly shorter stopovers, possibly due to a handling effect from capture and the application of the nanotags. Though the sample size of non-locally tagged birds was too low for proper assessment in this study, the potential handling effect should be taken into consideration for future Motus work, as the capture event itself may be increasing length of stay of sandpipers that were tagged at their detection site. Further work to investigate differences in length of stay of shorebirds that were tagged (with nanotags) both within and outside their detection location could help address this potential issue and validate current length of stay results. Until then, I suggest that birds be tagged prior to their arrival at the study areas of interest to reduce risk of handling effects.

In chapter 3, I found that shorebird habitat use at a stopover site with two distinct habitat types – beaches and mudflats - is affected by tide, time of day, and visitor use, depending on species. As Western Sandpipers used both habitats that were monitored by Motus, we were able to compare use between the two habitats. Investigating habitat use of Sanderlings and Semipalmated Plovers was more challenging as they did not tend to use the mudflats, which limited our analysis to the beaches only.

Using Motus to measure habitat use comes with caveats; as the receiver ranges in our study area only covered three habitats, there was always a possibility that shorebirds used other areas in the Tofino stopover that were not monitored by Motus receivers. Further, as tagged birds are more likely to be detected during flight than while on the ground (A. Anderson, pers comm. 2023, Taylor et al. 2017), their chances of detection may increase during active foraging or following a disturbance event. Thus, a lack of detection by Motus receivers may not only be attributed to the absence of a tagged bird from a study site but may also indicate roosting or resting behaviour.

Using elapsed time as a proxy for habitat use in this study was found to be effective, since analysing only detections could have been misleading; as a bird foraging with a tag facing a receiver would usually result in many more detections than a bird foraging with a tag facing away from the receiver, even though their time at the habitat was the same. It is also possible that overlapping antenna ranges from different Motus receivers at this site may have affected results. Though comparing elapsed time of individual tags at different receivers with corresponding signal plots was found to be relatively accurate, it is possible some error remained in the data. However, overlapping receiver detections usually occurred when a bird was flying within range of two receivers, and since elapsed time between two different receivers was not calculated in our habitat use dataset, these data would not have been included in our analysis. Future work when investigating local movements and habitat use could follow triangulation methods to first determine accurate locations of birds, as outlined in a Lenske & Nocera (2018) study.

The effects of visitor use were apparent for Western Sandpipers in our study, as Western Sandpipers were found to increase their time at the mudflats when the beaches became increasingly busy with people. Investigating the effect of visitor use on Sanderlings and Semipalmated Plovers was more challenging. As our habitat use results showed the almost exclusive use the beaches by these two species, it is unknown if a response to visitor disturbance by these species would lead to i) increased detections by the Motus receiver as the bird increases movements with disturbance, or ii) by an absence of detection as the bird leaves the beach. Motus may not be an effective way to determine human disturbance of shorebirds species that show strong habitat preference and/or site fidelity and may be better assessed using tracking methods like miniaturized GPS. These tracking devices have become small enough to outfit on small-bodied shorebirds, where a recent habitat use study using miniaturized GPSs on Piping Plovers (*Charadrius melodus*) was shown to be effective (Stantial & Cohen 2020).

Invertebrate and faecal sample analysis in my study provided some insight about prey availability and Western Sandpiper diet at the Tofino and Fraser River Estuary stopover sites. Amphipods were an abundant and an important prey item at both stopovers, and invertebrate density significantly was significantly higher during southward migration than during northward migration. Although prey availability did help explain habitat use between the beaches and mudflats in Tofino, it did not explain differences in length of stay between the two stopover sites. Sampling habitats at the same tidal periods and only during the day did not show a complete picture of prey availability, which also made comparison with faecal samples difficult since these were collected at different tidal periods and times of day than invertebrate samples. Further, the relatively frequent detection of dipterans in faecal samples was not reflected in the invertebrate sampling results, probably because invertebrate sampling did not include aerial insects nor samples from marshes, which usually have higher numbers of dipterans (Anderson 2020). Future work investigating shorebird prey availability and consumption should consider collecting both invertebrate and faecal samples across tidal periods, all stopover habitats, and during both day and night.

As North American shorebird numbers decline (Smith et al. 2023), it is increasingly important to conserve critical stopover areas required for shorebirds to complete their life cycle. Our study showed that different stopover sites may offer distinct characteristics for migrating Western Sandpipers who may use these sites differently based on migration strategy, overwintering location, and body condition. Maintaining a network of diverse stopover sites across a hemispheric scale essential for migrating shorebirds, as well as maintaining a mosaic of habitats *within* stopovers as birds respond to fluctuating tides, changing patterns of daylight, and human disturbance. As human populations and anthropogenic disturbance increase around important stopover sites, limiting habitat loss during development planning stages and implementing measures to reduce human disturbance are imperative to prevent further shorebird declines.

4.1 References

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