

**IMPACT OF LOCAL CONDITIONS ON FACTORS THAT AFFECT LENGTH OF STAY AND WEIGHT
GAIN IN STAGING SEMIPALMATED PLOVERS (*CHARADRIUS SEMIPALATUS*) ALONG THE
NORTHUMBERLAND STRAIT**

BY

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Abstract

Staging sites are key refueling stops for migratory shorebirds as they travel great distances from their high-latitude breeding grounds to their tropical or subtropical non-breeding grounds. Semipalmated Plovers (*Charadrius semipalmatus*) breed in the Arctic and winter from the southern United States to South America. Eastern breeding populations use staging sites along the coast of Atlantic Canada, such as regions along the Northumberland Strait, to replenish fuel stores that consist of fatty acids, that are obtained from dietary triglycerides, which fuel their subsequent migration to their non-breeding grounds. Refueling rate and accumulation of fat stores are important indicators for how long birds must stay within the region. However, the ability to put on fat stores, and leave in a suitable amount of time to reach their non-breeding grounds successfully, can be impacted by environmental factors at their staging site, such as weather and prey availability. Climate change has increased the frequency and severity of storms, impacting Semipalmated Plover migration as it coincides with the Atlantic hurricane season. Currently, little is known about the effects of storms on the ability to refuel at stopover sites and how this in turn can impact the length of stay of these birds in the region.

Hurricane Fiona impacted the Northumberland Strait on September 24, 2022, and we looked at refueling of juvenile Semipalmated Plovers, both through changes in fat stores over time as well as plasma triglycerides in individuals captured before and after the storm. We found that birds that had encountered the storm either through being in the area during or after the storm had significant decreases in fat mass, losing almost 90% of their stored fats. We also looked at whether the storm had any impacts on local conditions, such as invertebrate abundance, for one of Semipalmated Plovers prominent prey items, and changes in sediment penetrability; both of which can affect prey availability and thus impact the ability of the birds to store fats.

To assess how the storm impacted migration decisions, we also looked at the minimum length of stay for birds at stopover sites. Birds that encountered the storm either through spanning the storm or arriving after, approximately doubled their length of stay. The ability to efficiently put on fuel stores and migration timing are closely linked with migration success. Juveniles are disproportionately affected by late season storms as they tend to migrate later than adult

Semipalmated Plovers so timing of storms may have more detrimental impacts on these shorebirds. If storms occur close to departure, it could limit their ability to refuel fast enough to be able to depart with the body condition necessary to survive migration and reach their destination. Lastly, the arrival conditions of Semipalmated Plovers from their breeding grounds may impact the extent that birds are affected by storms. Juveniles were arriving in better condition in 2022 than in 2021, meaning that they may have had more of a buffer for losing fat stores in 2022 than if the hurricane had been in a year where they were arriving in worse condition. This study emphasises the need for further research on storm effects on the refueling capabilities of migratory birds that encounter storms, as well as the various direct and indirect impacts storms may have on their staging ecology.

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Chapter 1: Introduction

Migration is an important life-history component for a wide range of species across multiple taxa, ranging from small insects to large land mammals (Alerstam *et al.*, 2003). Migration has evolved to facilitate exploitation of seasonal shifts in prey abundance, avoid harsh weather conditions, and offer access to less occupied and more stable habitats, typically for breeding (Alerstam *et al.*, 2003; Mathot *et al.*, 2007; Faaborg *et al.*, 2010). Some of the most well-studied migratory systems are among avian species, many of which have evolved specialized morphological and physiological traits to travel great distances between high-latitude breeding sites and subtropical or tropical wintering grounds (Alerstam *et al.*, 2003). Along the way, birds must often select resource-rich stopover or staging habitats to replenish fat or energy stores to fuel the remainder of their journey and subsequent life-stages, like breeding (Linscott and Senner, 2021). For these species, timing is critical to coincide with optimal environmental conditions that maximize resource availability and improve survival (Piersma, 1998; Alerstam *et al.*, 2003; Acácio *et al.*, 2022).

The Semipalmated Plover (*Charadrius semipalmatus*) is a medium- to long-distance migratory shorebird that breeds in the Arctic and Subarctic and spends the non-breeding season in coastal habitats from the southern United States to South America (Anderson *et al.*, 2019; Nol and Blanken, 2020). Migration for this species to non-breeding sites usually occurs from late-July to mid-October, with juveniles arriving at staging sites approximately 2-4 weeks later than adults (Anderson *et al.*, 2019; Nol and Blanken, 2020). Atlantic Canada hosts a large number of key staging habitat for migratory shorebirds (McKellar *et al.* 2020) and supports a large population of Semipalmated Plovers (Atlantic Canada Shorebird Survey, 2017).

The timing of departure from staging grounds is important for migratory birds because if they leave too early, they may not have enough fuel stored to make it to their destination (Senner *et al.*, 2014). Further, late season departures increase the risk of encountering unfavourable weather conditions that may increase energy demands, while also limiting their food availability (Richardson, 1978). Birds arriving at their non-breeding grounds in poor condition may also

experience carry-over effects, or cross-seasonal impacts on timing and body condition, that can influence reproductive success on the breeding grounds the following spring, if they do not have high-quality non-breeding sites that allow them to recover (Norris *et al.* 2004, Harrison *et al.* 2011, Senner *et al.*, 2014).

Staging ecology

Staging sites for migratory birds provide essential habitat that allows birds to refuel during their migration (Schaub and Jenni, 2000; Alerstam, 2011). Optimal staging sites consist of habitats with ample prey availability and low predation risk (Pomeroy *et al.*, 2006). There are multiple suggested strategies for optimizing fuel deposition and time spent at the staging grounds. The two most prevalent ones are time minimization and energy minimization, which are opposite ends of a spectrum; some strategies fall between the two (Alerstam, 2011; Sergio *et al.*, 2014). Time minimization is associated with more on-board fuel stores, higher refueling rate, and spending less time at stopover locations; whereas energy minimization involves carrying less fuel, having lower refueling rates, and staying longer at stopover sites (Alerstam and Lindström, 1990; Alerstam, 2011). This means energy minimizers may be able to be more selective of favourable departure conditions once they have reached the minimum amount of fuel, or energy threshold, that will allow them to reach their next location (Dänhardt and Lindström, 2001).

The coast of Atlantic Canada offers key stopover habitat for many different species of shorebirds. While the Bay of Fundy is an internationally recognized site of critical importance for Semipalmated Sandpipers (*Calidris pusilla*), other coastal sites in the region are also important to a range of shorebird species (Geldart, 2018; Mackellar, 2018; Doiron 2021, Linhart *et al.* 2023). Sites along the Northumberland Strait have been identified as important habitat for more diverse flocks of shorebirds that include Semipalmated Plovers (Bellefontaine and Hamilton, in press). However, less is known about how Semipalmated Plovers use these sites and how changing environmental factors may affect their ability to refuel and their length of stay within the region. Importantly, Semipalmated Plovers tend to return in subsequent years to the same staging locations (Smith and Houghton, 1984). Therefore, they may have limited

flexibility to use alternative sites in response to unfavourable conditions, which may require additional fuel stores to ensure safe arrival at the non-breeding grounds (Dänhardt and Lindström, 2001). As a result, habitat alterations or changing environmental patterns may have unforeseen impacts on refueling capacity and migratory success.

Fueling migration

Birds stop at staging sites during migration to refuel and replenish lost energy reserves. However, carrying fuel is energetically costly, so being able to maximize the energy obtained from fuel sources and minimize transportation cost, while also accounting for the cost of maintaining those stores, is crucial for long-distance flight (Jenni and Jenni-Eiermann, 1998). Depositing and burning fat as fuel meets those criteria; it provides eight to ten times more energy per gram of wet weight than other fuel types (Piersma, 1990; Jenni and Jenni-Eiermann, 1998). Fats also do not require water for storage in tissues, meaning that a bird can maximize energy with minimal weight costs that introduce drag while flying (Jenni and Jenni-Eiermann, 1998). Other fuels, such as protein, are still necessary for powering flight (e.g., in pectoral flight muscles), but the vast majority of metabolism for energy is done by using fats (Piersma, 1990; Jenni and Jenni-Eiermann, 1998).

Birds accumulate fat stores through their diet and can double their body weight during staging in a matter of days (Bairlein, 2002; McWilliams *et al.*, 2004). Most fats stored are in the form of 16 and 18-carbon unsaturated fatty acids (McWilliams *et al.*, 2004; Guglielmo, 2018). Fat is absorbed in the intestine and delivered through the circulatory system by lipid transporter proteins, portomicrons, to either the liver, where needed fatty acids are synthesized, or deposited as adipose tissue directly (Fraser *et al.*, 1986; Ramenofsky 1990; McWilliams *et al.*, 2004). Triglycerides, a source of fatty acids, have been found to increase in the blood plasma with mass gain and decrease with mass loss in Garden Warbler (*Sylvia borin*; Jenni-Eiermann and Jenni, 1994). Due to this feature, triglycerides found in the blood can be used to predict fat deposition in the preceding two days before capture, as seen in Western Sandpiper (*Calidris mauri*; Williams *et al.*, 1999), and have also been shown to reflect site quality for several species, indicating triglyceride storage (Guglielmo *et al.*, 2005).

Information surrounding fat storage during southbound migration in Semipalmated Plovers is limited. However, a recent study found that Semipalmated Plovers caught within Atlantic Canada had variation in the levels of plasma triglycerides within and among sites, perhaps owing to differences in environmental factors, food availability, or stopover strategies between sites (MacKeller, 2018; Doiron, 2021). In 2020, Semipalmated Plovers caught along the Northumberland Strait also had longer lengths of stay, around 25 days, corresponding with elevated levels of triglycerides (Doiron, 2021). This behaviour is similar to patterns observed in Semipalmated Sandpipers, in that both remained longer than necessary at stopover sites, and the prevailing hypothesis is that staging birds may be waiting to take advantage of favourable weather conditions (Dunn *et al.*, 1988; Doiron, 2021).

Diet and resource availability

Semipalmated Plovers are visual foragers that are often found running along damp substrate exposed by the tide (Nol and Blanken, 2020). Semipalmated Plovers consume a wide range of invertebrate food sources, but polychaetes and bivalves make up the largest portion of their diet (Recher, 1996; Rose *et al.*, 2016), both of which are abundant invertebrates along the Northumberland Strait (Linhart *et al.* 2023, Bellefontaine and Hamilton, in press). Foraging activity for these birds was highly correlated with invertebrate densities and biomass, and higher densities of birds were found at mudflats with the greatest numbers of invertebrates (Rose and Nol, 2010). Semipalmated Plovers are generalist foragers, but they have been observed to be selective when it comes to the size of their prey items, especially when prey is in high abundance, perhaps to maximize energy intake (Rose *et al.*, 2016).

Availability of invertebrates can be influenced by many different factors, including substrate penetrability (Colwell and Landrum, 1993). For shallow-feeding shorebirds, increasing the amount of sand over more packed mudflats reduced the amount of time that the birds spent foraging in those areas (Quammen, 1982). Reductions in the overall ability to seek out or capture prey items, as well as reductions in prey abundance due to sand deposition on original substrate (Quammen, 1982), may make stopover locations less able to support the large numbers of shorebirds. Changes in sediment composition from hard to soft substrates can occur

through wave action and even more so during storms which deposit and erode sediment (Palinkas *et al.*, 2014; Fegley *et al.*, 2020).

Weather effects on migration

Coastal habitats are highly vulnerable to extreme weather, such as from tropical storms and hurricanes. Besides causing direct mortality, weather events such as these can push birds off course during flight and cause damage to stopover habitat with strong winds and extensive precipitation over short periods (Dionne *et al.*, 2008; Toohey, 2021). Storm surges and high waves can also erode beaches or deposit sediment and wrack (Harris *et al.*, 2011; Palinkas *et al.*, 2014; de Santiago *et al.*, 2017; Hyndes *et al.*, 2022; Menicagli *et al.*, 2022). Previous studies have shown that severe storms that rearrange habitats can also affect food availability (Dobs *et al.*, 2009). Studies on the impact of these storms on stopover ecology of birds are rare and absent for birds in Atlantic Canada.

Study objectives and significance

Climate change is expected to increase the frequency and severity of storms that affect coastal ecosystems (Ranasinghe, 2020). Shorebirds that use stopover sites in Atlantic Canada are declining at an alarming rate (Smith *et al.*, 2023) and little is known about how these storms are impacting their refueling rate through alterations to stopover habitat. Further, long distance migratory shorebirds that are attempting non-stop, cross-Atlantic flights on their southbound migration are at an increased risk of encountering storms as their migration time corresponds with the Atlantic hurricane season (Watts *et al.*, 2021).

Given these knowledge gaps, in this thesis I have addressed the following questions: 1) Do fat mass and plasma triglyceride concentrations during stopover in migrating Semipalmated Plovers represent refueling differences across years and age groups? 2) How did hurricane Fiona impact Semipalmated Plovers' ability to store fat for migration? 3) Were there differences in the length of stay of Semipalmated Plovers that left before the storm and after the storm? 4) Are there changes to stopover habitat, including prey availability and sediment penetrability, that affect the ability of Semipalmated Plover's to refuel sufficiently to depart stopover sites?

Chapter 2: Materials and Methods

Study site and species

Juvenile and adult Semipalmated Plovers (*Charadrius semipalmatus*) were caught during 2021 and 2022 from a single site along the Northumberland Strait at Petit-Cap beach, NB (46.19°N, -64.15°W; Figure 1.1). Petit-Cap beach consists of a sand spit with two sides, an exterior and an interior, that is just under a kilometer long. The interior consists of a small cove with muddy substrate whereas the exterior is softer sand; either side has its own tide dynamics as the spit causes the tide to come in slower on the interior. Hurricane Fiona affected Petit-Cap beach on September 24, 2022.

Field methods

We captured birds at Petit-Cap between July 20 and October 5, 2021 (n = 146), and July 27 and October 13, 2022 (n = 124). Birds were caught using 12-m mist nets with four panels and 38-mm mesh. Nets were arranged on the intertidal flat, either on the exterior of the beach, facing the Northumberland Strait, or interior, facing Shemogue Harbour. Set up occurred prior to sundown and catching took place on the incoming tide, with estimated tide heights between 0.5 and 1.0 m as per the chart datum.

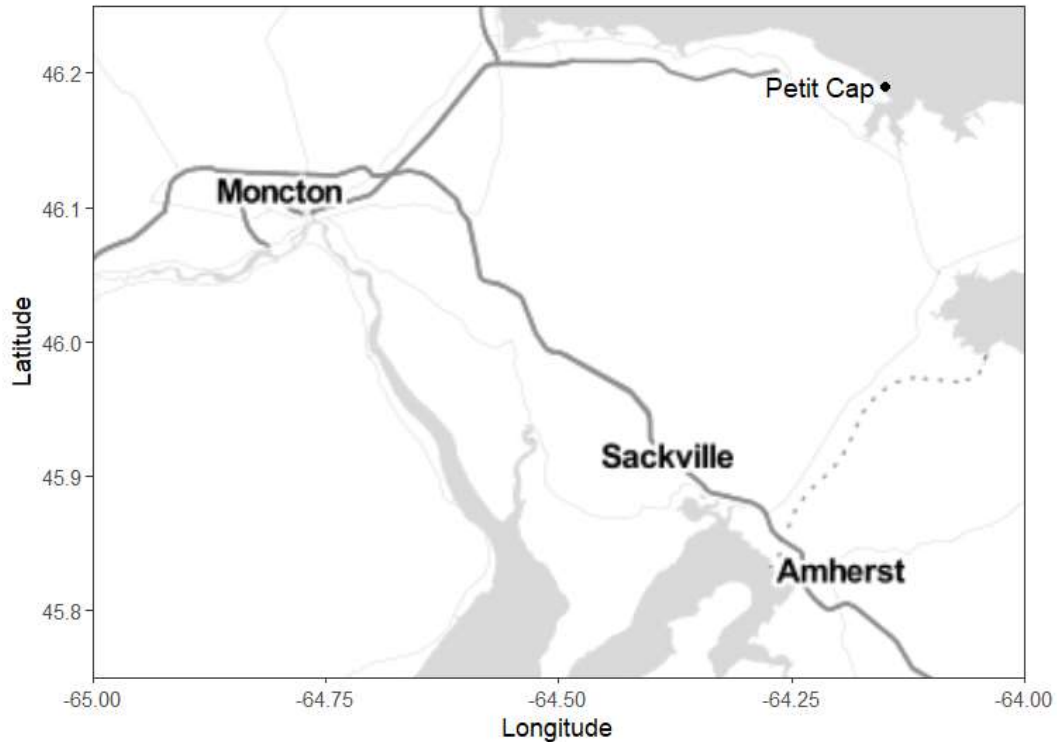


Figure 1.1: Petit-Cap beach NB (46.19°N, -64.15°W) on the Northumberland Strait, indicated by the point. Map plotted using ‘ggplot2’ and ‘ggmap’ (Wickham, 2016; Kahle and Wickham, 2013)

Upon capture, birds were extracted, immediately weighed and assigned a flag to their upper right leg with a three-digit alphanumeric code that is field readable for subsequent individual identification. We collected blood samples of up to 210 μ l (three 70 μ l capillary tubes) from birds heavier than 35 g, to ensure no detrimental effects from removing too much blood. We stratified the sampling across weights to ensure an even spread, and that we sampled roughly equal number of fat and thin birds. The brachial vein was pricked with a 27.5-gauge sterile needle and blood was collected within 20 minutes of capture to minimize the effects of stress on plasma metabolite levels (Guglielmo *et al.*, 2002). Blood was transferred to 200 μ l Eppendorf tubes and placed on ice until further processing. Within approximately 6 hours after blood was taken, it was centrifuged at 10,000 rpm for 1 minute and the plasma was extracted. Plasma and red blood cell samples were stored at -20°C until further analysis of plasma metabolites.

Following blood extraction, we used digital calipers to take morphometric measurements of the bill culmen (\pm 0.001 mm) and tarsus (\pm 0.001 mm), and a wing ruler to measure the flattened

and straightened wing chord length (± 0.5 mm). Birds were aged according to feather pattern and wear (Pyle, 1997). A fat score from 0-7 was given by blowing on the feathers in the furcular and abdominal regions to visually assess subcutaneous fat deposits (Meissner, 2009; Figure 1.2).

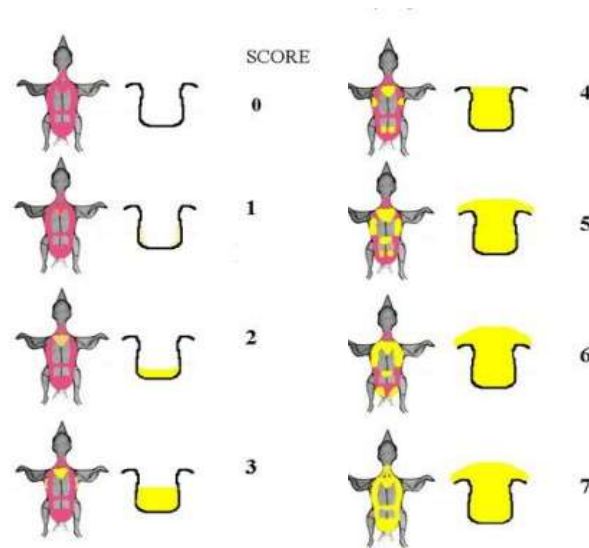


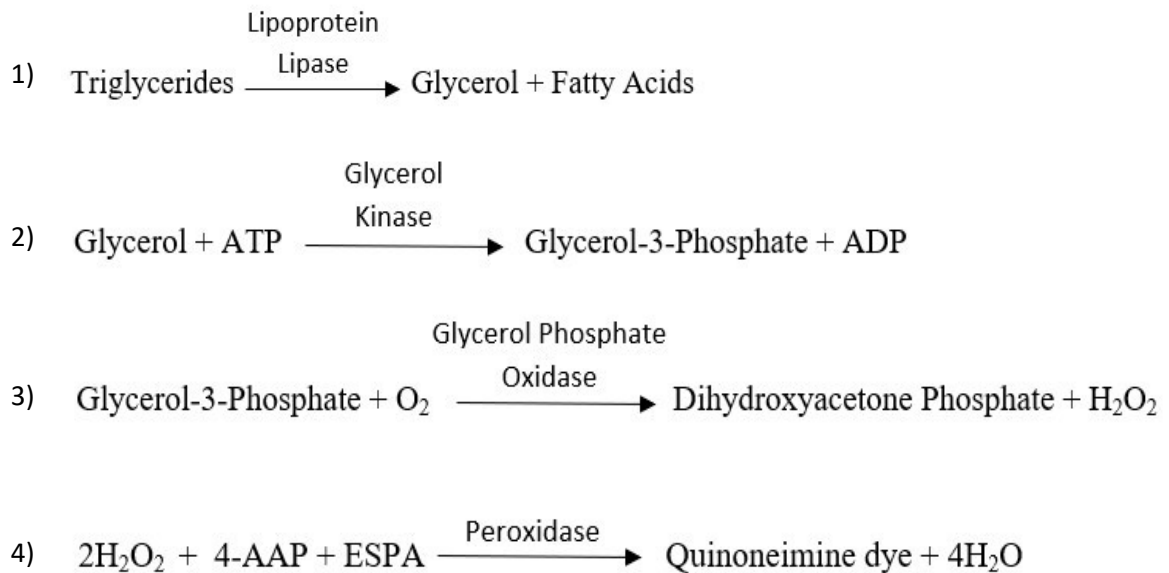
Figure 1.2 Scoring for subcutaneous fat from a scale of 0-7 based on visual assessment of a birds furcular and abdominal regions (Modified from Migration Monitoring Protocol, Log Point Observatory, 2019)

Each bird was fitted with a unique size 1A USGS aluminum band on their upper left leg. A subset of hatch year birds weighing less than 43 g received a Lotek avian nanotag (NTQB2-3-2, Lotek Wireless Inc., Newmarket, ON). The nanotags weighed less than 0.67 g and were attached with glue to the shafts of clipped dorsal contour feathers approximately 1 cm above the preen gland. After all samples and measurements were taken, birds were placed in cloth pens for ~15 minutes to reacclimate to the dark before they were released. 55 juveniles were caught pre storm, 20 of which received radio tracking tags and 22 birds were caught post storm, 17 of which received radio tracking tags.

Plasma triglycerides

Levels of free glycerol and triglycerides (TG) were measured using colorimetric assays of collected plasma samples. All assays were measured by absorbance of a colour indicator using a Spectramax Plus 348 spectrophotometer (Molecular Devices LLC, Sand Jose, CA).

We determined glycerol and triglyceride concentrations using reagents and protocols specified in the respective Cayman Chemical Colorimetric Assay Kits (Cayman Item No. 10010755 and 10010303, Ann Arbor, MI, USA). Plasma for glycerol and triglyceride assays was diluted 1:5, plasma to 1X Standard Diluent Assay Reagent, and assays were performed in duplicate. Any duplicate that exceeded a 20% difference between corrected absorbances were excluded from further analysis. We measured changes in absorbance at 540 nm for production of quinoneimine dye after a 1-hour incubation in the dark at room temperature. Concentrations of metabolites were calculated using standard curves derived from glycerol and triglyceride standards (0-20 mg/L and 0- 200 mg/dl, respectively). Change in absorbance was monitored at 540 nm according to the following reactions:



Where glycerol follows reactions 2-4 and triglycerides 1-4.

Diet analysis

Plasma samples were analysed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signatures at the Environmental Analytics and Stable Isotope Laboratory at Mount Allison University using an Isoprime Precision Isotope Ratio Mass Spectrometer (IRMS) (Elementar UK Ltd, Cheadle, UK) and Elementar PyroCube Elemental Analyzer (EA) (Elementar Analysensysteme GmbH, Hanau, Germany). Tin capsules were pre-weighed using a microbalance (Mettler-Toledo MX5; ± 0.001 mg) and 15 μl of plasma was inserted into each capsule for a minimum target weight of 0.500 mg. Prior to analysis with the EA and IRMS the samples were dried 24 hours at 70°C in an oven (Laboratory Oven Catalog No, 317-85, Lapine). Isotope signatures were determined using the following equation:

$$\delta^a X_{(sample)} = \left[\left(\frac{R_{(sample)}}{R_{(standard)}} \right) - 1 \right] * 1000$$

Where δ is the isotope signature, the relative isotope ratio of sample to international standards; a is the heavier isotope, X is the element of interest (N or C), and R is the ratio of the heavy to light isotope.

Prey availability

To assess effects of severe weather on prey availability, we collected prey samples before and after hurricane Fiona affected Atlantic Canada on September 24, 2022. Samples were collected at Petit-Cap beach on September 21st and October 2nd, 2022. We sampled using a stratified random approach with three transects perpendicular to the shore on the interior and the exterior of the sand spit (Figure 1.3). Each transect commenced at the high tide line, was 300 m long, and stratified into 100 m sections. Two samples were taken from each stratum with the meter number being determined by a random number generator.

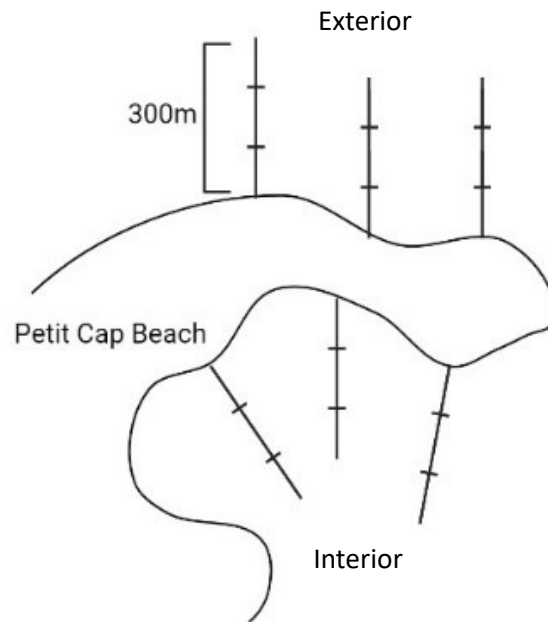


Figure 1.3 Schematic of transect orientation on the interior and exterior of Petit-Cap beach. Each transect was 300 m long and two samples were randomly taken from each 100 m stratum. Samples were collected using a vertical sampler which consisted of an 8 cm diameter ABS pipe that was divided in 0.5, 1.0, 1.5 and 2.0 cm depth layers using metal fins (Figure 1.4). The vertical sampler was pushed into the sediment until it was flush with the top of the core, fins were inserted and the top and bottom were covered with petri dish lids and secured with cable ties to prevent the loss of sediments. The penetrability (Kg/cm^2) was measured near where the sample was taken with a pocket penetrometer (Humboldt H-4200 Stainless Steel Soil Pocket Penetrometer, Item # UZ-99039-10).

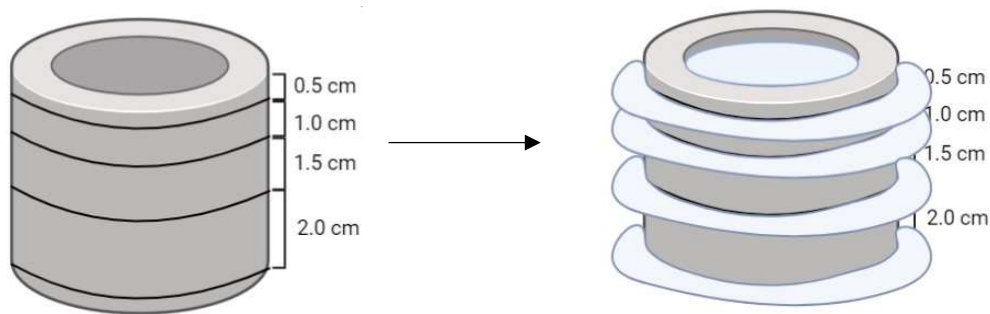


Figure 1.4 Vertical sampler used for extracting sediment cores. Metal fins sectioned the sediment at 0.5, 1.0, 1.5, and 2.0 cm depths. The diameter of the sampler was 8 cm.

Each layer was individually sieved (500 μm) and material with invertebrates retained was stored in 95% ethanol until later processing. Samples were sorted by taxa using a dissecting scope. For this study we included bivalves only, which are a common prey for Semipalmated Plovers (Bellefontaine and Hamilton, in press). Empty shelled invertebrates, which implies that they were not alive at the time of sampling, were not included. Bivalves were sorted into two size classes: (1) ≤ 2 mm, or (2) 2 - 6 mm.

Radiotracking

We tagged 31 hatch year birds in 2022 with Lotek avian nanotags, as described above. Nine tags had a burst rate of 19.7 seconds and anticipated battery life of 190 days. Two had a burst rate of 13.1 seconds, and the remainder had a burst rate of 10.3 seconds with an anticipated battery life of 294 days. Tags emit unique signal patterns that are detected by the MOTUS wildlife tracking array (Taylor *et al.*, 2017). Detection distance varies depending on conditions but can be up to 20 km (Taylor *et al.* 2017). The placement of the nanotag allows for it to be lost during molt, which typically occurs on the wintering grounds (Holmgren and Hedenström, 1995).

The Motus array covers most of the Atlantic flyway, but we focused on towers in Atlantic Canada to determine minimum length of stay, which was calculated from the date of tag deployment until the last detection within Atlantic Canada. Three birds were removed from the analysis due

to likely losing their tags prematurely: one had a length of stay of just over 3 days and a capture weight of 36.1 g, which is too light to have departed so quickly, while the other two had a length of stay less than one day. Two additional birds were last detected the day of the hurricane, and so were also removed from length of stay analysis as they most likely either perished through the storm or were blown into an area with no tower coverage.

Statistical analysis

Analyses were performed using R software, version 4.2.2 (R Core Team, 2022). Parametric assumptions were visualized using the 'ggfortify' package (Tang *et al.*, 2016) and formally tested using Shapiro-Wilk and multivariate Shapiro-Wilk tests for normality, and Levene's, NCV, and Box's M tests for homogeneity of variance (HoV). We also assessed potential multicollinearity using pair-wise correlation tests and calculating the Variance Inflation Factor (VIF) for each model. No factors were too correlated to include in the multivariate models ($r_p \sim 0.7$ or < 0.7). Variables were transformed if their distributions failed assumptions and otherwise non-parametric tests were performed if transformation was not possible. Data were plotted using the package 'ggplot2' (Wickham, 2016). For all analyses addressing annual variation, rather than storm effects, we removed birds caught after the storm from consideration.

Variation in fat mass among years

We estimated fat mass of 77 juvenile and 51 adult Semipalmated Plovers caught in 2022 by regressing body mass against predictors, wing length and subcutaneous fat score, separately for each age group. Wing length did not predict weight in either juveniles ($p = 0.995$) or adults ($p = 0.261$), so it was removed from the model. We used the intercept of the subsequent model for each age group to estimate lean mass. These values were subtracted from measured body mass at capture to estimate fat mass (g) for both 2022 and 2021 birds. Lean mass was comparable with estimates calculated following equations formulated by Anderson *et al* (2019).

Separate ANCOVAs were run for adults and juveniles to look at differences in fat mass between years, 2021 and 2022, using day of year as a covariate. To meet assumptions the data were square root transformed for juvenile Semipalmated Plovers.

Variation in plasma triglycerides among years

We analyzed plasma triglyceride values separately by age. For each age, we performed multiple regressions with triglyceride concentration [Trig] (mmol/L) as the dependant variable and fat mass (g), year (coded as a dummy variable where 2021 = 0 and 2022 = 1), and day of year as predictors. A single juvenile bird was determined to be an outlier and removed from analysis because it's fat mass was almost triple that of all others caught during the two-year study. The 2021 sample included 8 juveniles and 17 adults, and in 2022 we sampled 29 juveniles and 25 adults.

For juveniles, following removal of non-significant interactions between fat mass x day of year ($p = 0.724$) and year x day of year ($p = 0.956$), we detected a borderline interaction between fat mass x year ($p=0.055$), so the analysis was further separated by year. We took the same approach for adults, removing interactions of fat mass x day of year ($p = 0.835$) and fat mass x year (0.819). The year x day of year interaction ($p = 0.131$) was also removed, as the Akaike Information Criterion for small sample sizes (AICc) for the model with and without the interaction was similar (AICc ~ 122), and therefore we chose the most parsimonious model.

Effects of adverse weather on fat mass and plasma triglycerides

We used ANCOVA to compare fat mass of juvenile birds caught in 2022 before (pre; $n = 29$) and after (post; $n = 13$) hurricane Fiona affected the region on September 24th. Fat mass was the dependent variable, pre or post storm status was the independent variable, and day of year was a covariate. Plasma triglyceride concentrations [Trig] (mmol/L) of juvenile birds caught in 2022 before (pre; $n = 29$) and after (post; $n = 13$) hurricane Fiona were compared using a studentized t-test.

Length of stay

Tracking data were downloaded from the Motus Wildlife Tracking System website and cleaned following procedures outlined in the Motus R Book (Crew *et al.*, 2018). This included removing runs with less than three detections, as well as obviously false detections (e.g., in impossible

locations). Minimum length of stay (LoS) was estimated as the time between tagging and the last time a bird was detected by the Motus tower array within Atlantic Canada. While tagged birds arrived in the area prior to capture, and therefore this does not capture the full length of stay of all individuals, previous work on Semipalmated Sandpipers in the same area suggests that this approach provides a reasonable estimate of LoS (Neima *et al.* 2022). Birds were grouped by storm status into three categories: 1) pre-storm, which were captured and last detected before the storm (n = 12); 2) spanning, captured before the storm and last detected after the storm (n = 7); and 3) post-storm, captured and last detected after the storm (n = 13). We used ANCOVA to examine the effects of storm status (pre, spanning and post) on length of stay (dependent variable). The model also included covariates of fat mass and day of year, though fat mass was removed as it was unrelated to length of stay for any of the groups of birds ($p=0.27-0.86$). We found that the relationship of length of stay with day of year varied by storm status (interaction $p= 0.018$), precluding completing the ANCOVA. However, following removal of birds that spanned the storm, slopes were homogeneous, and we could proceed to compare pre- and post-storm birds. We also conducted a one-way ANOVA and post-hoc comparisons to directly compare length of stay for the three groups without accounting for day of year.

Effects of adverse weather on prey availability

Bivalves were separated by size class (<2 mm and 2-6 mm) and densities per m² of each class in each of the top two sediment layers (0.0-0.5 cm and 0.5-1.5 cm depths) were calculated and rounded to the nearest whole bivalve. We examined differences in bivalve availability from before to after the hurricane using a MANOVA. Bivalves of the two size classes were dependent variables, and storm status (pre = 52 samples; post = 60 samples), sample depth, and side of Petit-Cap beach were fully crossed factors. Because of failed assumptions, we ran a semi-parametric repeated measures MANOVA using R package 'manovaRM' (10,000 iterations; Friedrich *et al.*, 2022). We evaluated significance using Wald-Type Statistics (WTS). Non-significant interactions ($p = 0.24-0.82$) were removed from the model. Post-hoc tests were run separately for both bivalve size classes using a generalized linear mixed effects model with

sample ID as a random intercept and a Poisson distribution using the 'lme4' package (Bates *et al.*, 2015).

Site penetrability

Penetrability was rounded to the nearest whole number to fit the model and was assessed using a generalized linear mixed effect model with nested random effects. Penetrability was the dependant variable with storm status as the independent variable and transect nested within beach side as the random effect. The model was fitted to a Poisson distribution. Transect 2 from after the storm was excluded from analysis.

Stable isotope analysis of diet

Stable isotope signatures for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were assessed to look at differences in diet in juvenile Semipalmated Plovers pre ($n = 11$) and post ($n = 5$) hurricane Fiona. A MANOVA was used from the 'jmv' package (Selker *et al.*, 2022) to analyse the data with nitrogen and carbon isotope signatures as the dependant variables and storm status (pre and post) as the independent variable. Pilli's trace was used as the test statistic as it is robust to violations of assumptions (Tabachnick and Fidell, 2007).

Chapter 3: Results

Variation in fat mass and plasma triglycerides between years

Both adult and juvenile Semipalmated Plovers gained fat mass as the season progressed, and while juveniles had differences in overall fat mass between years, adults did not. There was also a trend for the juveniles to arrive later than the adult birds, with the first juveniles being caught just after day 225, whereas we started catching adults just before day 210 (Figure 2.1). Juvenile and adult birds had within-year temporal trends in fat mass that were consistent across years (year x day of year interaction: $p > 0.10$), suggesting the rate of fat mass gain was similar between years (Figure 2.1). Juvenile fat mass was positively associated with day of year in both 2021 and 2022 (Figure 2.1, Table 2.1), and controlling for day of year the average fat mass

among individuals was greater in 2022 ($14.54 \pm 0.0.872$ g) than 2021 (9.39 ± 0.676 g) (Figure 2.1, Table 2.1). Fat mass also increased with day of year in both 2021 and 2022 for adult Semipalmated Plovers (Figure 2.1, Table 2.2). However, unlike juveniles, there was no difference in average fat mass among individuals between the two years (2021, 11.875 ± 0.855 g; 2022, 13.647 ± 0.925 g)(Table 2.2).

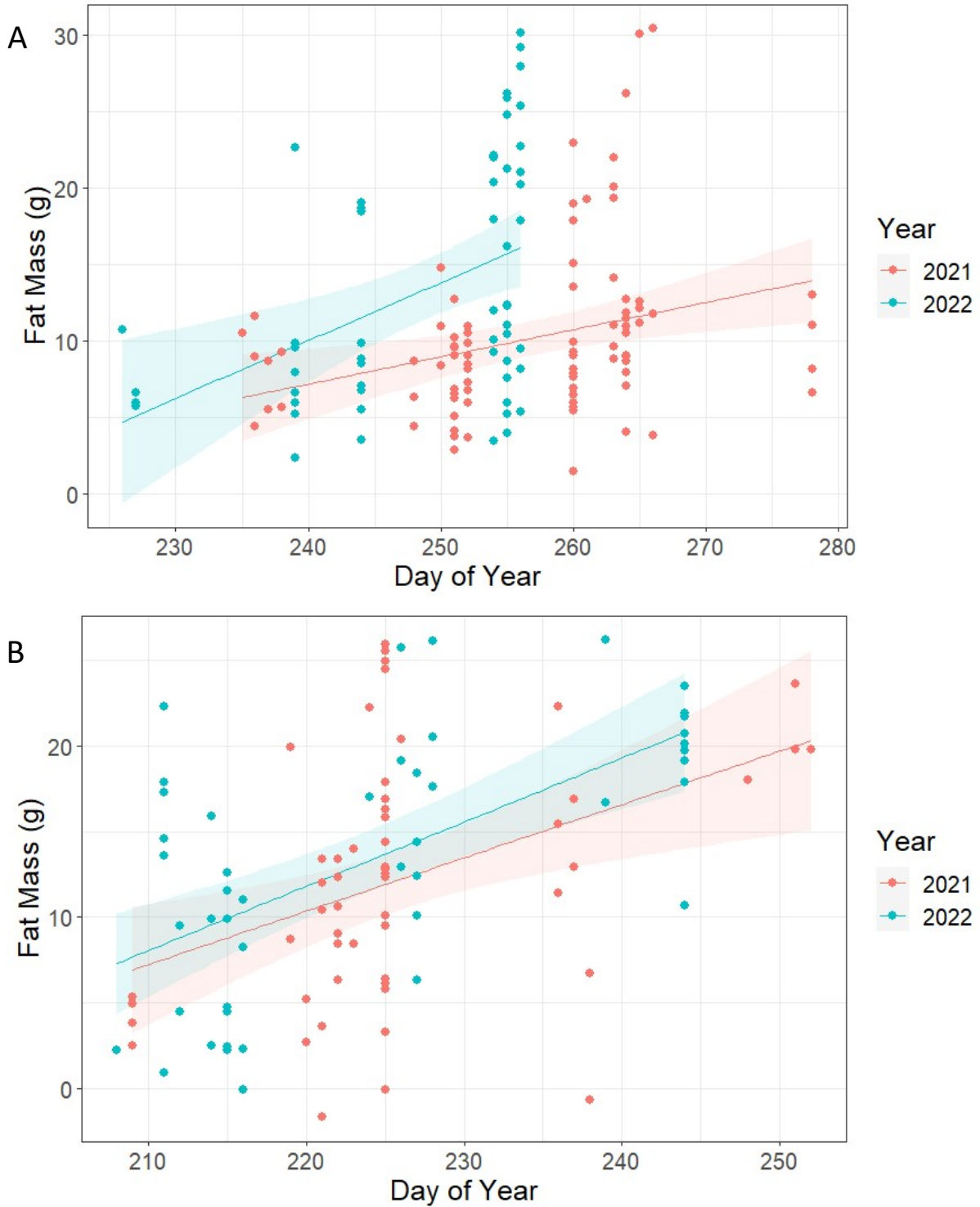


Figure 2.1 The relationship between fat mass (g) and day of year for 2021 (red) and 2022 (blue) in juvenile (A) and adult (B) Semipalmated Plovers captured at Petit-Cap beach, NB. The regression line for juveniles in 2022 is truncated prior to hurricane Fiona on day 267, as birds caught post-hurricane were excluded from this analysis. Statistical results are provided in Table 2.1 and 2.2 for juveniles and adults respectively.

Table 2.1 ANCOVA results for the relationship between square root transformed fat mass and year (2021, n = 88; 2022, n = 77), for juvenile Semipalmated Plovers captured at Petit-Cap beach, NB, with day of year as covariate. The interaction was not significant ($p = 0.116$), so was removed from ANCOVA model. MS is mean square, df is degrees of freedom. Significant p-values in bold.

Factor	MS	df	F value	<i>p</i> value
Day of Year	14.647	1	19.774	<0.0001
Year	13.271	1	17.918	<0.0001
Residuals	0.741	140		

Table 2.2 ANCOVA results for the relationship between fat mass and year (2021, n = 55; 2022, n = 51), for adult Semipalmated Plovers captured at Petit-Cap beach, NB, with day of year as covariate. The interaction was not significant ($p = 0.596$), so was removed from ANCOVA model. MS is mean square, df is degrees of freedom. Significant p-values in bold.

Factor	MS	df	F value	<i>p</i> value
Day of Year	1426.9	1	35.674	<0.0001
Year	78.800	1	1.969	0.164
Residuals	39.999	99		

Plasma triglycerides also varied between years and age categories, but to a lesser degree than fat mass. For juvenile birds, the relationship between plasma triglycerides and fat mass differed between years, though the interaction was borderline significant (fat mass x year interaction, $p = 0.055$; Figure 2.2A). Juvenile plasma triglyceride levels were strongly and positively associated with fat mass in 2021, but only marginally in 2022 (Table 2.3). The slope in 2021 was almost twice that of 2022 (Table 2.3), yet juveniles in 2021 reached only approximately half of the fat mass observed in 2022 (Figure 2.2A). Adult plasma triglyceride levels on the other hand were positively but weakly associated with fat mass in both years (Figure 2.2C), with a slope more similar to juveniles in 2022 (Table 2.3). Within years, plasma triglycerides were not associated with day of year for juveniles in either 2021 or 2022 (Figure 2.2B, Table 2.3). In contrast, adult plasma triglycerides declined with day of year and were significantly greater in 2021 compared to 2022 (Figure 2.2D, Table 2.4). There was no evidence for an interaction between day of year x year for either juveniles or adults ($p > 0.10$), indicating similar slopes between years.

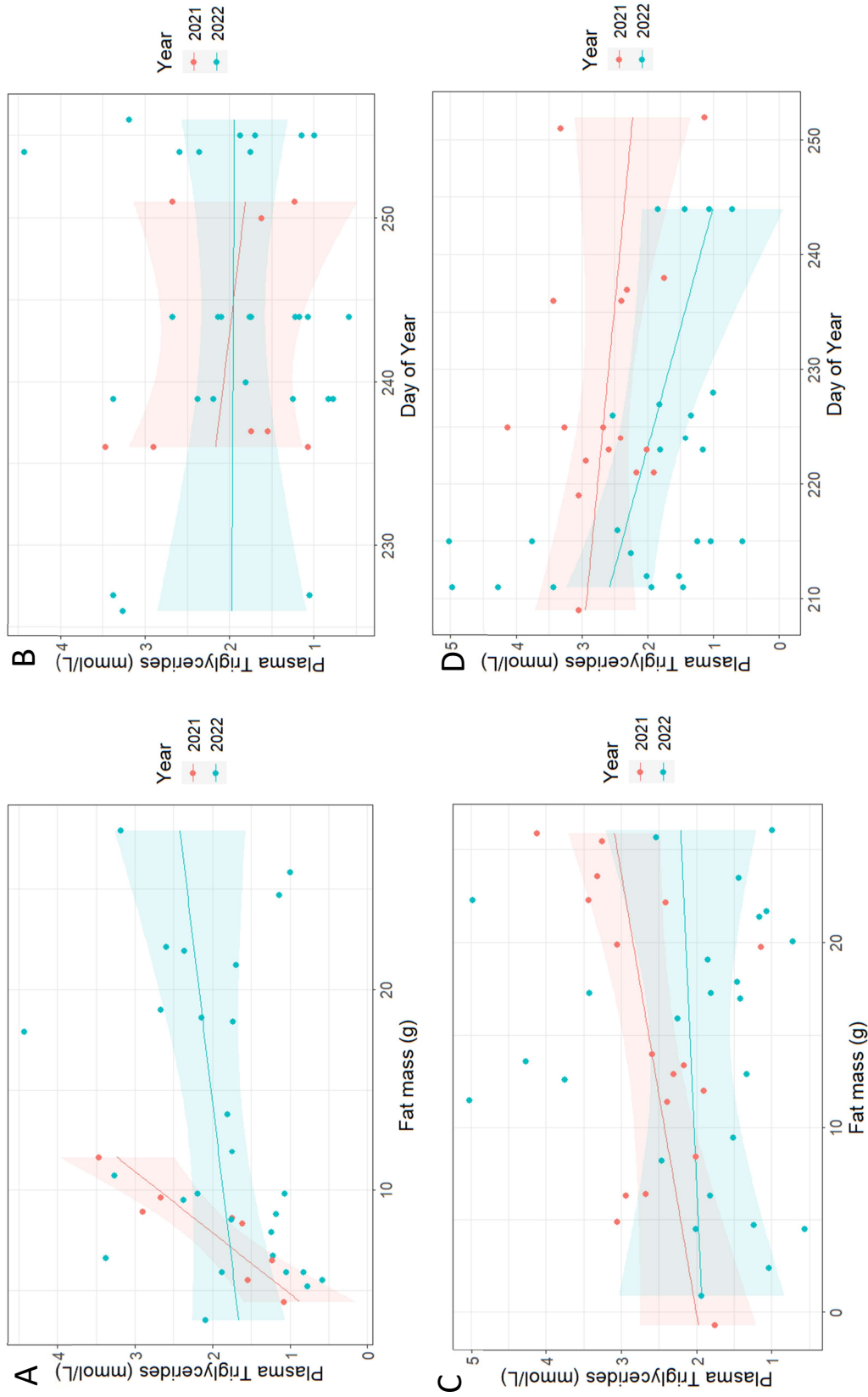


Figure 2.2 The relationship between plasma triglycerides (mmol/L) and fat mass (g) (A and C) and day of year (B and D) for juvenile Semipalmated Plovers (A and B) and adult Semipalmated Plovers (C and D) for 2021 (red) and 2022 (blue), captured at Petit-Cap beach, NB. Statistical results are provided in Tables 2.3 and Table 2.4 for juveniles and adults respectively. Juvenile birds caught after hurricane Fiona and excluded from analysis.

Table 2.3 Multiple regression results for the relationship between plasma triglycerides (mmol/L) and predictors fat mass (g) and day of year for juvenile Semipalmated Plovers (top: 2021, n = 8; bottom: 2022, n = 29) at Petit-Cap beach, NB. The interactions were not significant ($P > 0.5$) so were removed from the model. Significant p-values in bold.

Year	Factor	Std. Beta Coefficient	t value	p value
2021	Fat Mass	0.8995	5.118	0.004
	Day of Year	-0.2538	-1.444	0.208
2022	Fat Mass	0.4163	1.693	0.103
	Day of Year	-0.2757	-1.121	0.273

Table 2.4 Multiple regression results for the relationship between plasma triglycerides (mmol/L) and predictors fat mass (g) and day of year for adult Semipalmated Plovers (2021, n = 17; 2022, n = 25) at Petit-Cap beach, NB. The interactions were not significant ($p > 0.8$) so were removed from the model. Significant p-values in bold.

Factor	Std. Beta Coefficient	t value	p value
Fat Mass	0.4168	2.848	0.013
Day of Year	-0.2967	1.396	0.008
Year	3.7663	-1.326	0.001

Variation in fat mass and plasma triglycerides

Fat mass was positively associated with day of year both before and after the storm for juvenile Semipalmated Plovers (no adults were captured post-storm, so they are not included) (Figure 2.3, Table 2.5). Rate of fat mass gain over time was similar pre- and post-storm (storm status x day of year interaction, $p = 0.814$). However, after controlling for day of year, average fat mass was 17.8 g greater before the storm compared to afterwards, meaning that during the storm juveniles lost about 89% of their pre-departure fat mass (20 g, based on average fat mass of birds caught in the 2 weeks before the storm).

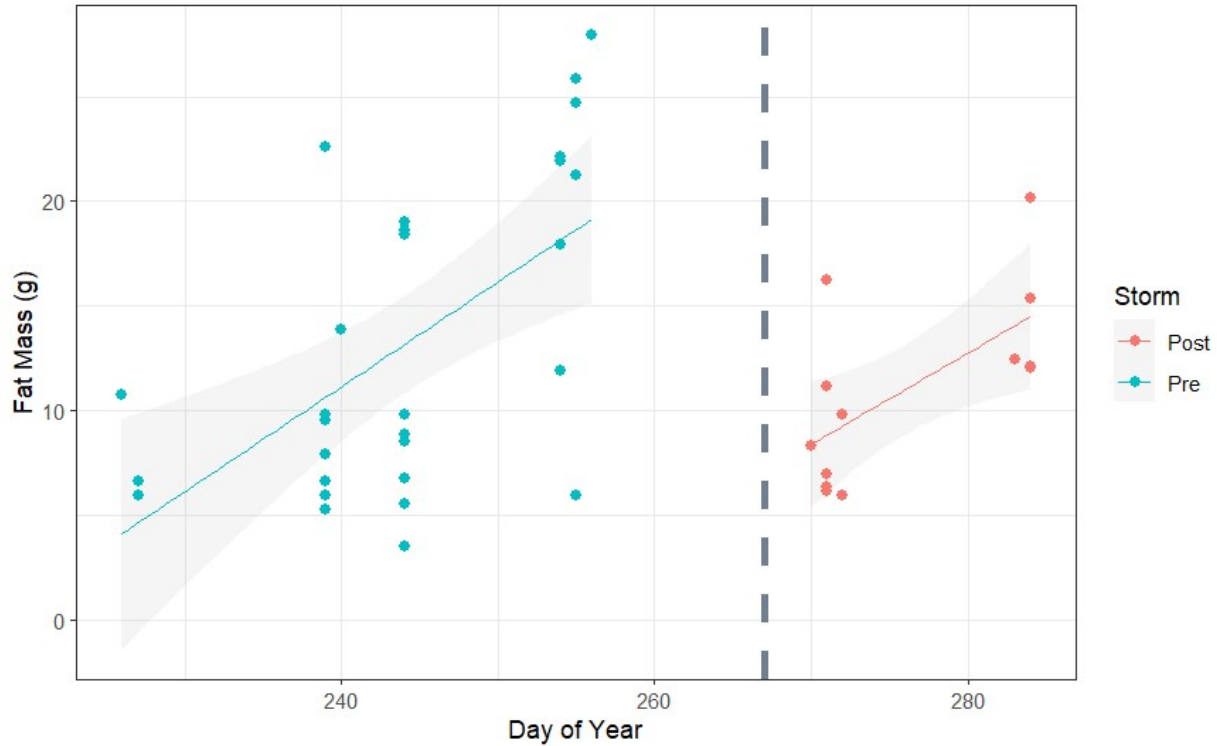


Figure 2.3 The relationship between fat mass (g) and day of year for pre (blue) and post (red) hurricane Fiona affected the region on September 24th (dashed line) for juvenile Semipalmated Plovers caught at Petit-Cap beach, NB in 2022. Results of statistical analyses are provided in Table 2.5.

Table 2.5 ANCOVA results for the relationship between fat mass and storm status (pre, n = 29; post; n = 13) for juvenile Semipalmated Plovers captured at Petit-Cap beach, NB, with day of year as covariate. The interaction was not significant ($p = 0.814$) so was removed from ANCOVA model. MS is mean square, df is degrees of freedom. Significant p-values in bold.

Factor	MS	df	F value	<i>p</i> value
Day of Year	625.63	1	21.178	<0.0001
Storm Status	635.10	1	21.499	<0.0001
Residuals	29.541	39		

Unlike fat mass, there was no significant difference in average plasma triglyceride levels before and after the storm ($t_{40} = -1.55$, $p = 0.13$). There was also no evidence of a relationship between plasma triglyceride and fat mass or day of year for pre- and post-storm juveniles (Figure 2.4)

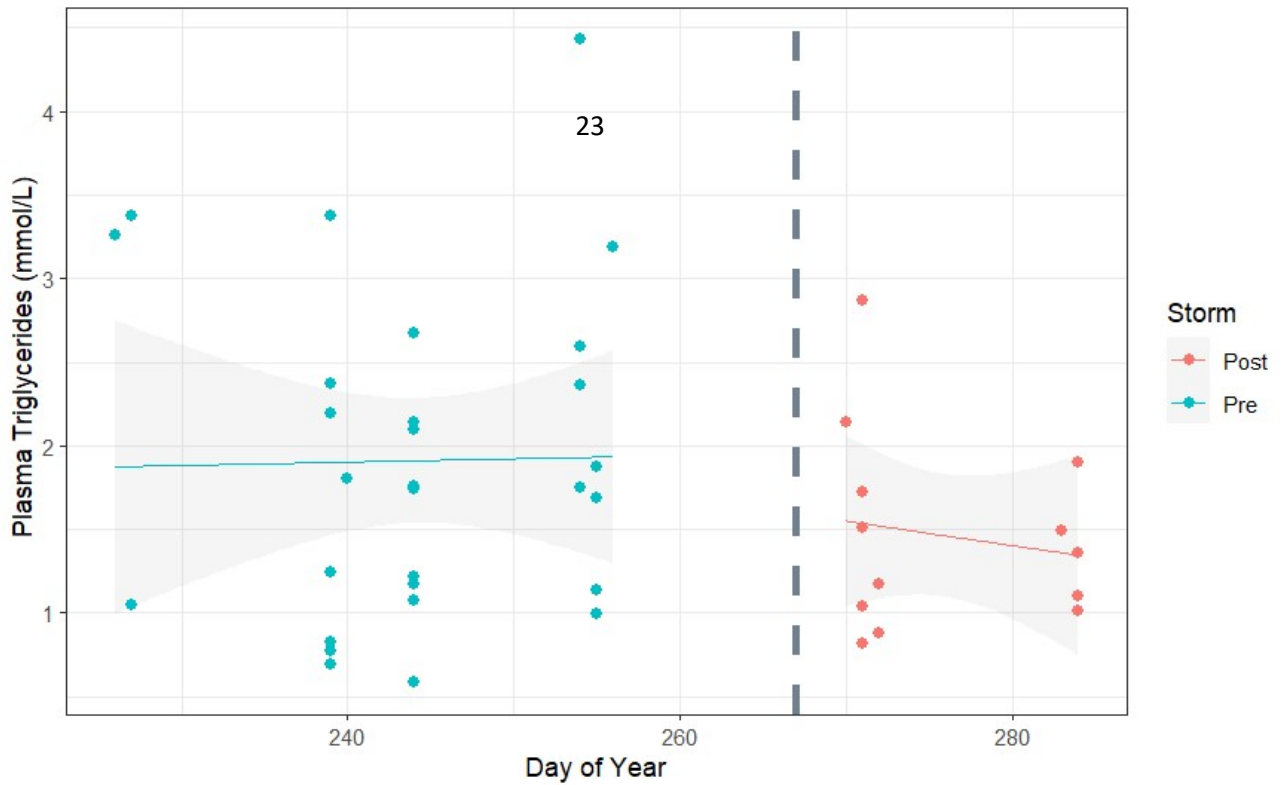


Figure 2.4 The relationship between plasma triglycerides (mmol/L) and day of year for pre (blue n = 29) and post (red, n = 13) hurricane Fiona affected the region on September 24th (dashed line) for juvenile Semipalmated Plovers caught at Petit-Cap beach, NB in 2022. Results of statistical analysis are provided in text.

Plasma isotope variation

There were no differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures for juveniles captured before and after the storm (Pre, n = 11; Post, n = 5) (MANOVA, $F_{2,13} = 0.1156$, $p = 0.8917$), suggesting that their diet remained consistent regardless of any storm effects on invertebrate availability.

Invertebrate availability

We evaluated variation in bivalve density in the upper layers of sediment before and after hurricane Fiona. Independent of the storm, densities of both size classes of bivalves (<2 mm and 2-6 mm) were higher in the top 0.5 cm of sediment than the next layer (0.5-1.5 cm; Tables 2.6 and 2.7, Figures 2.6 and 2.7). When bivalve size classes were considered together in multivariate analyses, there was no difference in densities between the exterior and interior of Petit-Cap beach (Table 2.6). However, when separated by size class there were fewer large bivalves on the exterior of Petit-Cap beach than the interior (Table 2.7). Small bivalve (<2 mm) densities did not differ with side of Petit-Cap beach. Independent of depth class and side of the beach, large bivalves occurred in lower densities after the storm than before the storm (Figure 2.6, Table 2.7). This effect was less pronounced for the smaller class of bivalves ($p = 0.055$), although densities still tended to be slightly lower post storm (Figure 2.5).

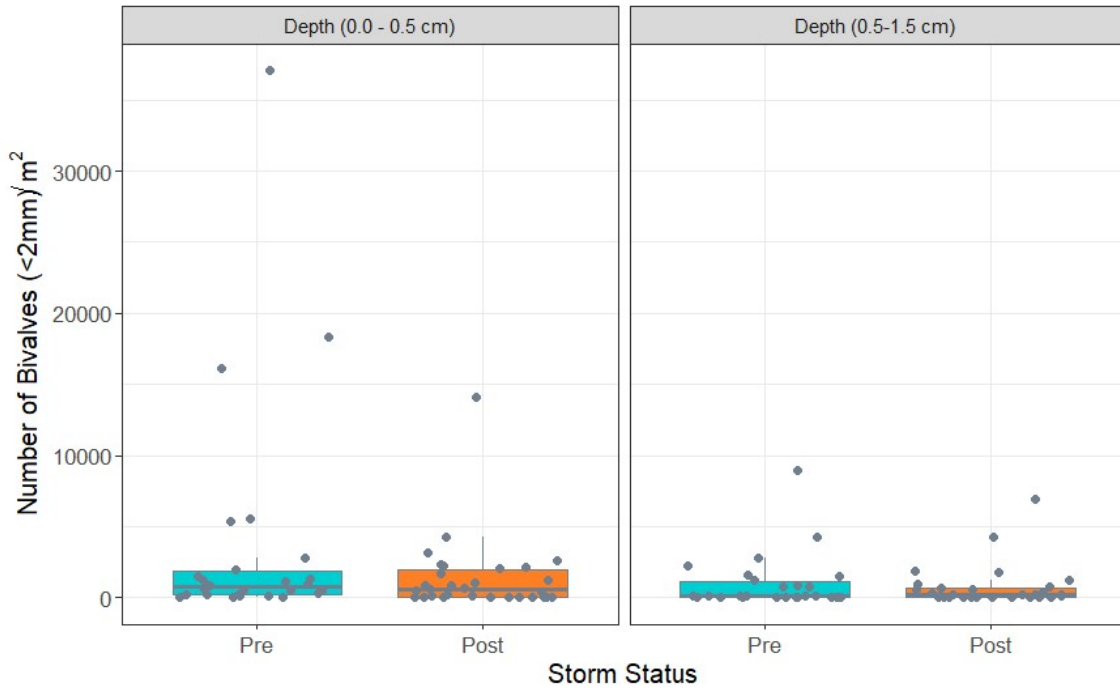


Figure 2.5 Number of bivalves <2 mm from two different depths, 0-0.5 and 0.5-1.5 cm, from pre (blue) and post (orange) hurricane Fiona impacted Petit-Cap beach on September 24, 2022.

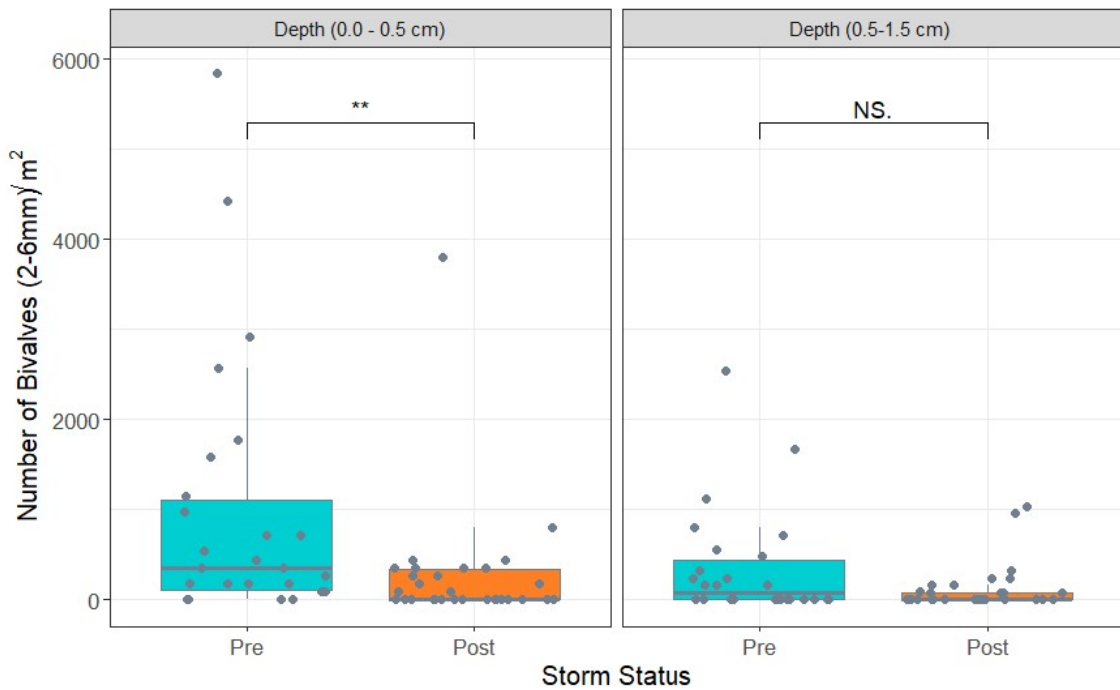


Figure 2.6 Number of bivalves 2-6 mm from two different depths, 0-0.5 and 0.5-1.5 cm, from pre (blue) and post (orange) hurricane Fiona impacted Petit-Cap beach on September 24, 2022. Asterix denotes significance, N.S is non-significant.

Table 2.6 Results of a semi-parametric repeated measures MANOVA evaluated using a Wald-Type Statistic with bivalve size classes (<2 mm; 2-6 mm) as dependant variables, and storm status, (pre, n = 52; post, n = 60), side of Petit-Cap beach, and depth of sample (0.0-0.5; 0.5-1.5 cm) as independent variables. Interactions ($p = 0.24 - 0.82$) were not significant and removed from the model. Significant p -values in bold.

Factor	df	t value	p value
Storm Status	2	4.916	0.086
Side	2	0.378	0.828
Depth	2	9.627	0.008

Table 2.7 Results from generalized linear mixed effect models of bivalve counts in each size class modeled using a Poisson distribution. Sample was a random factor, and fixed factors included storm status(pre, n = 52 ; post, n = 60), side of Petit-Cap beach, and depth. Estimates contain coefficients of effect sizes. Significant p -values in bold.

Bivalve Size (mm)	Factor	Estimate	Std. Error	z value	p value
<2	Pre Storm	1.627	0.848	1.918	0.055
	Petit-Cap Out	-1.108	0.848	-1.306	0.191
	Depth (0.5-1.5cm)	-1.059	0.005	-200.3	<0.0001
2-6	Pre Storm	2.645	0.940	2.814	0.005
	Petit-Cap Out	-2.454	0.417	-2.606	0.009
	Depth (0.5-1.5cm)	-0.974	0.010	-93.37	<0.0001

Site penetrability

Variation in substrate penetrability was greater between the sides of Petit Cap beach than among transects within the same side. Variance explained by random effects was 0.98 ± 0.31 and 0.18 ± 0.42 , respectively, with higher penetrability along the outer beach of Petit-Cap compared to the interior (Figure 2.7). Substrate penetrability was greater following the storm, regardless of beach side ($z = -1.89$, $p = 0.058$).

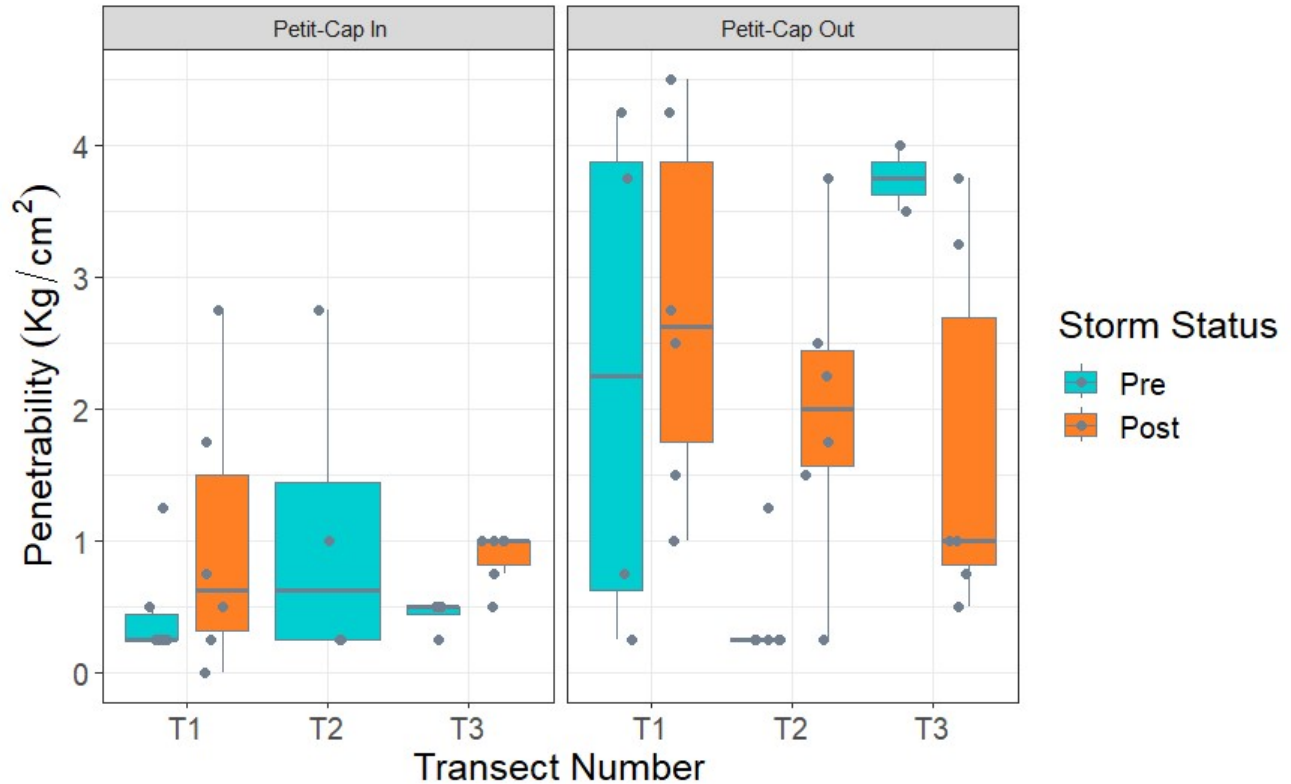


Figure 2.7 Penetrability (Kg/cm^2) for two different sides of Petit-Cap beach, NB , interior (in) and exterior (out), from three, 300 m transects from each side for pre (blue) and post (orange),hurricane Fiona affected the beach on September 24, 2022. Transect 2 for Petit-Cap beach for after the storm had to be excluded.

Length of stay

Minimum length of stay for juvenile Semipalmated Plovers was related to both day of tagging and storm status (pre-storm, spanning storm, and post-storm; Figure 2.8, Table 2.8). Minimum length of stay declined with date of tagging for both pre- and post-storm birds, but not birds that spanned the storm. A significant interaction between day of year x storm status became non-significant when spanning birds were removed ($p = 0.998$), suggesting the rate of decline in minimum length of stay over time did not differ between pre- and post-storm birds (Figure 2.8). However, controlling for date of tagging, post-storm birds remained in the region approximately 3.5 days longer than those that were tagged and left before the storm (Table 2.8). Without

controlling for date of tagging and keeping storm-spanning birds in the model, storm-spanning birds remained in the region for approximately 22 days longer than pre-storm birds ($p < 0.001$) and approximately 18 days longer than the post-storm birds ($p < 0.01$; ANOVA: $F_{2,31} = 11.76$, $p = 0.0002$, Figure 2.9).

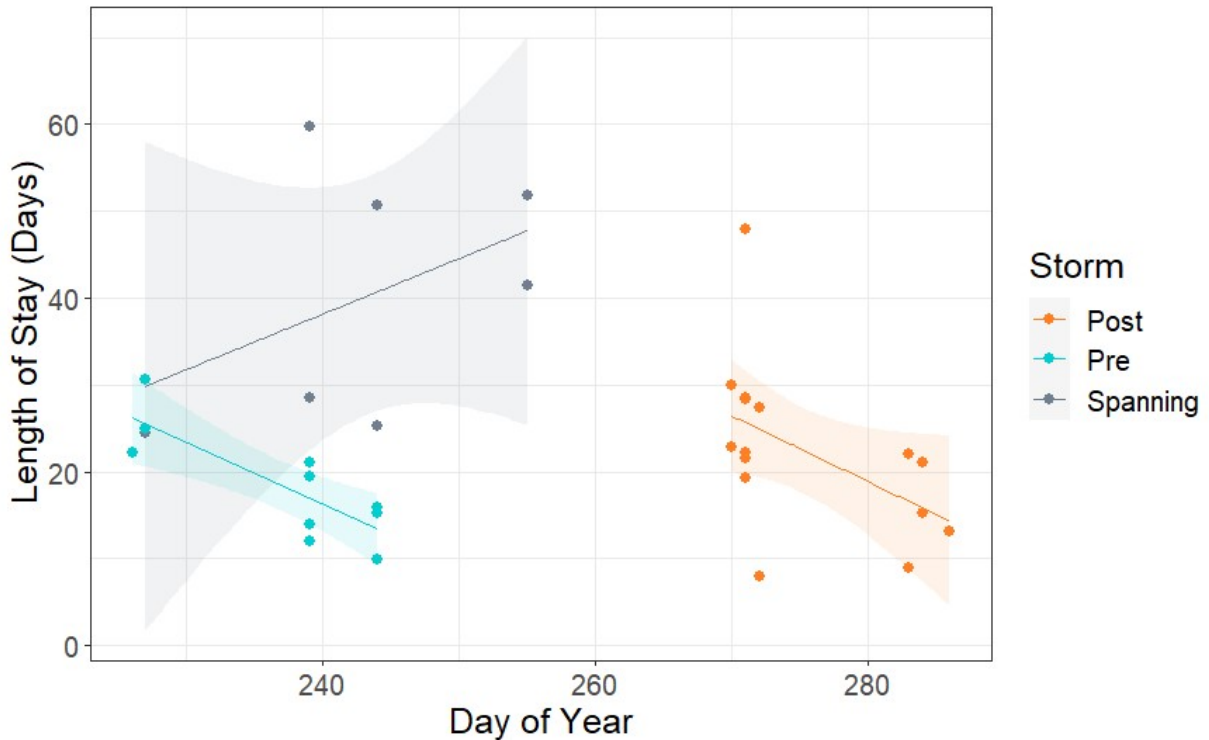


Figure 2.8 The relationship between minimum length of stay (days) and day of year for juvenile Semipalmated Plovers captured at Petit-Cap beach, NB. Birds separated by storm status, pre (blue), spanning (orange) and post (gray), hurricane Fiona affected the region on September 24, 2022. Statistical results are provided in Table 2.8.

Table 2.8 ANCOVA results for the relationship between minimum length of stay (days) and storm status (pre, $n = 12$; post, $n = 13$) hurricane Fiona for juvenile Semipalmated Plovers captured at Petit-Cap beach, NB, with day of year as a covariate. MS is mean square, df is degrees of freedom. Significant p -values in bold.

Factor	MS	df	F value	p value
Day of Year	6.8515	1	11.726	0.002
Storm Status	7.7131	1	13.2	0.001
Residuals	0.5843	22		

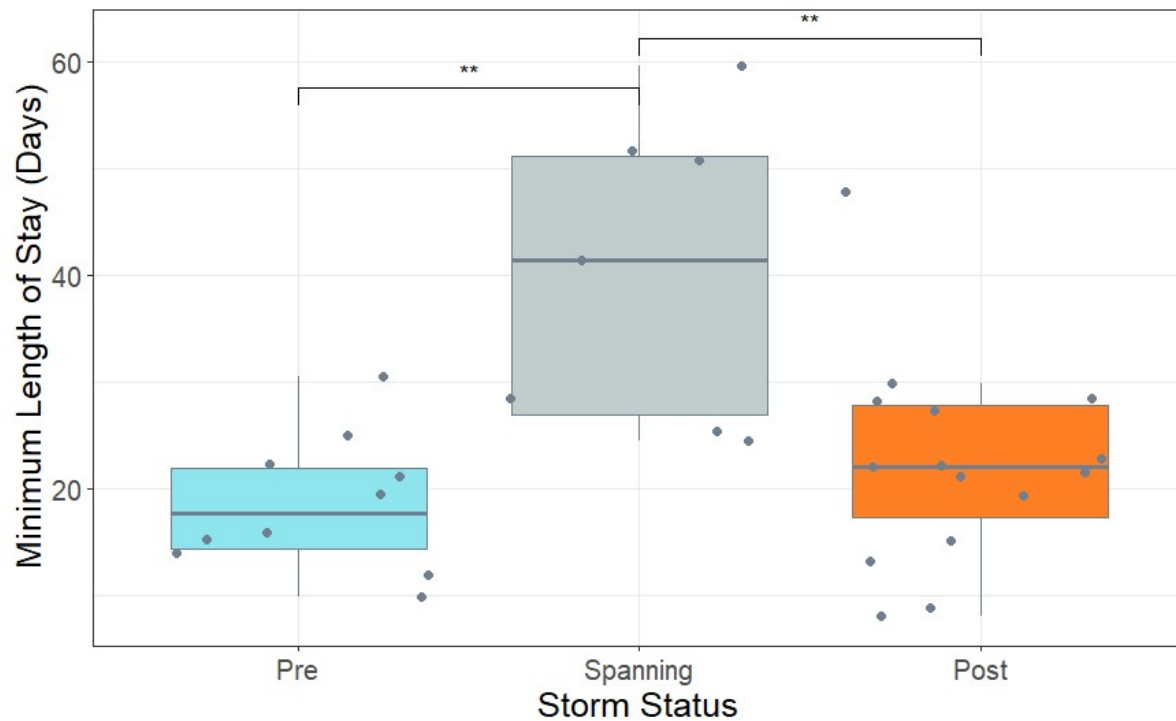


Figure 2.9 Minimum length of stay (days) for juvenile Semipalmated Plovers captured at Petit-Cap beach, NB for pre (blue), spanning (grey) and post (orange), hurricane Fiona affected the region on September 24, 2022. Asterix denotes significance.

Chapter 4: Discussion

Overview

Staging sites are critical for migration success, as they provide the resources necessary for migratory birds to replenish fuel stores that will carry them to non-breeding sites (Nol and Blanken, 2020; Linscott and Senner, 2021). The ability to accumulate fat stores while at staging sites is closely tied to the overall timing and migration success of birds (Schaub *et al.*, 2008). In addition to accumulating fat, staging sites should also provide a safe habitat for birds to recover from high intensity flight, build flight muscles, and avoid predators while waiting for favourable weather conditions for trans-oceanic flights (Linscott and Senner, 2021).

Small staging sites along the coast of Atlantic Canada, particularly those along the Northumberland Strait, have previously been highlighted for their importance to shorebirds as areas that provide rich habitat for refueling during southbound migration (Linhart *et al.*, 2022, 2023). However, most of these studies have been focused on Semipalmated Sandpipers and less is known about how other species use these sites to refuel. Based on limited previous work, we know that small coastal staging sites in Atlantic Canada are important to a range of shorebird species (Doiron 2021, Bellefontaine and Hamilton in press), with 21 sites recommended as key habitats for shorebirds within the Western Hemisphere Shorebird Reserve Network (WHSRN; McKellar *et al.* 2020,). Semipalmated Plovers make extensive use of these sites during their annual southbound migration from the Arctic and Subarctic to the Southern United States and South America (Nol and Blanken, 2020). Previous work suggests that they use multiple strategies. Some use sites within relatively small areas (e.g., the Acadian Peninsula), whereas others move more broadly (Geldart, 2018). Individuals that stage along the Northumberland Strait have been found to remain longer in the region than some other species of shorebirds, alluding to the importance of sites within this region (Doiron, 2021).

Coastal habitat is highly vulnerable to climate change effects (Ranasinghe, 2020), including increases in the frequency and severity of storms (de Santiago *et al.*, 2017). These increasing risks make it essential for us to understand how Semipalmated Plovers are using coastal habitats and how storms affect both their habitat and staging activities. To assess these knowledge gaps, we first examined variation in fat storage among years for adult and juvenile Semipalmated Plovers, as well as if there were differences in diet between the two age groups. Then, as a way of investigating effects of extreme weather on staging, we examined impacts of hurricane Fiona on refueling, diet, and prey availability. Finally, to integrate effects of the storm on staging, we investigated the relationship between the storm and overall migration timing to determine whether encountering a storm could extend length of stay at a staging site.

Annual variation in refueling

Based on the observed rate of increase in mass over time, we found that both adults and juveniles accumulated fat mass at a consistent rate between 2021 and 2022. However, on

average, juveniles had higher fat mass in 2022 than 2021, while there was no difference for adults. This suggests that juveniles were arriving in better condition in 2022 compared to 2021, while adults maintained consistent body condition upon arrival. Arrival condition at staging sites has been correlated with body condition at the preceding departure location; birds in better condition on arrival were likely to have had better departing weather conditions and were seen to stay a shorter period of time at staging sites than those that arrived with depleted fat reserves (Moore and Kerlinger, 1987). While few studies have looked at how factors on the breeding grounds influence migration, in certain songbird systems, birds that finished breeding later leave the breeding grounds later and have faster migration speeds (de Zwaan *et al.*, 2019; Imlay *et al.* 2021). This suggests potential added costs to delayed departure that would need to be made up for along their migration route, including at stopover or staging sites, and highlights both the potential for carry-over effects and the importance of staging sites in buffering negative effects at a previous location (Briedis *et al.*, 2018; Gow *et al.*, 2019).

We also found evidence of differences in fat mass deposition among years. There was a borderline significant increase in triglycerides for a given gain in fat mass in 2021 suggesting that juvenile Semipalmated Plovers may have been more metabolically active while refueling, as a higher level of triglycerides in the blood was required to store the same amount of fat found in 2022. This could mean that while birds in 2021 were ingesting high levels of fat, less was being stored for later use during migration. Birds encountering stressors such as cold temperatures can be forced to increase their metabolic rate, which would lead to slowed or halted fat deposition, even with increased feeding (Klaassen and Biebach, 1994). Another possible explanation for the increased fat deposition in 2021 is that birds could have been eating prey items rich in fatty acids, but not necessarily 16 and 18 mono and polyunsaturated fatty acids, which are the main types of fatty acids that are being stored (McWilliams *et al.*, 2004; Guglielmo, 2018).

For the adult Semipalmated Plovers, day of year and fat mass had inverse relationships with plasma triglycerides, being negatively and positively correlated respectively, with 2021 having higher plasma triglycerides in both cases. This suggests that as adults approach departure they are not as actively foraging, similar to Bar-tailed Godwits (*Limosa lapponica*), which showed

similar decreases in triglyceride levels when inactive (Landys *et al.*, 2005). It has been found previously that sandpipers will stay longer than necessary at staging sites to gain the required fat stores to make their flight, possibly because they are waiting for optimal departure conditions (Roques *et al.*, 2021 Linscott and Senner, 2021, Neima *et al.* 2022, Linhart *et al.* 2023). During these extended stays, birds should not put on more mass than needed due to carrying costs during flight (Alerstam and Lindström, 1990;). Thus, if Semipalmated Plovers are extending their stay to track prevailing weather conditions, we would expect a decrease in the rate of refueling closer to departure (Alerstam and Lindström, 1990), possibly reflected in the plasma triglyceride values we observed.

Refueling with adverse weather

Exposure to Hurricane Fiona had a dramatic negative effect on fuel reserves of juvenile Semipalmated Plovers, and since juveniles tend to migrate later than the adults (Nol and Blanken, 2020), they will be disproportionately affected by late season tropical storms and hurricanes (Wood *et al.*, 2020). When adjusting for day of year, birds exposed to the hurricane lost an estimated 18 g of fat, which comprises approximately 60% or greater of their expected fuel load upon departure. This means that birds that would have almost been ready to leave would have had to essentially start refueling again. Further, birds that arrived just prior to the storm may have been at increased risk of death because they would have lacked fuel stores and may not have been able to withstand the fasting that was induced by the hurricane, or the weather itself. While there are limited studies on storm impacts on birds, it has previously been shown that high amounts of precipitation negatively impact small birds, and particularly juveniles, as they may be more inexperienced at foraging and so less capable of finding food during lulls in storms (Boyle *et al.*, 2010). If foraging time is compromised due to excessive rainfall, not obtaining enough energy could lead to starvation (Boyle *et al.*, 2010). Storms can also lead to significant direct mortality. For example, during hurricane Wilma, over 727 Chimney Swifts were reported dead in the province of Quebec and the total estimated population there decreased by approximately 50% (Dionne *et al.*, 2008). In fact, two of 9 Semipalmated Plovers

(22%) that we tracked with radiotelemetry tags disappeared during the storm, likely representing mortality events.

While there was a dramatic weight loss related to the hurricane, birds resumed refueling shortly after the storm at a rate consistent with what we observed before the storm. This suggests that after the storm they were still able to find sufficient food sources to resume gaining weight.

Based on stable isotope analyses of blood plasma, diets appeared to be consistent before and after the hurricane. Severe disturbance can have significant effects on the prey bases (Dobbs *et al.*, 2009; Harris *et al.*, 2011), so we anticipated that carbon and nitrogen signatures may differ from before to after the storm. However, that was not the case, either because the same prey items were available, or they were replaced with items having similar isotopic signatures.

However, these results should be taken with caution because we had low sample sizes after the storm and so we may have not been able to detect a shift in the isotope signatures. This small sample size was also biased towards heavier birds, as we avoid running blood samples from light birds to ensure that the samples reflect foraging in the region (see Quinn and Hamilton 2012). However, in this case birds may have been light because they lost fat as a result of the storm, and samples from these light birds may have yielded different results. We also observed a significant decline in bivalve availability from before to after the storm, so we suggest that birds may have replaced prey items with similar isotopic signatures, and we cannot in fact conclude that their diets did not change. However, the observed similarity in refueling rates from before to after the storm would be consistent with the birds finding and exploiting alternative prey items.

Bivalve populations within the 2-6 mm range, which would be attractive to shorebirds due to their high nutrient content (Mogle, 2021), significantly decreased in response to hurricane Fiona. After hurricane Fiona, visibly softer sand was deposited on Petit-Cap beach. This is consistent with the aftereffects of hurricane Irene (Palinkas *et al.*, 2014). Penetrability at our site significantly increased after the storm, meaning that the sediment was less resistant to pressure, indicative of finer sediment. It would be easier for birds to penetrate the softer sediment and find prey items. However, sediment deposition may have been one of the reasons that bivalve numbers decreased, as invertebrate populations have been known to change with

increases to sedimentation in a size- and species-dependant manner (Peterson, 1985). Increased sedimentation elevated mortality for suspension feeders, and larger clams had higher mortality because they could not move closer to the surface, remaining at their original sediment depth, whereas the smaller bivalves could migrate up within the sediment column (Peterson, 1985).

It is positive that weight gain resumed shortly after the storm. However, given that it was late in the season and birds had lost substantial fat mass needed for successful migration, it is notable that they did not increase their rate of mass gain. They may have already been at their maximum rate for fat deposition before the storm, either through a physiological limitation or an inability to acquire sufficient food. Maximum fuel deposition rates are dependent on the time available to forage, foraging efficiency, and food availability, so with abundant prey, birds may already be operating at their maximum refueling rate (Lindström, 1991). Alternatively, the lower numbers of bivalves could be one of the reasons why they did not elevate their refueling rate to compensate for lost fuel stores. The higher penetrability after the storm could have allowed for more efficient prey capture but with lower prey availability, whereas lower penetrability and higher prey abundance before the storm may have evened out the refueling rates to be relatively equal, as our results suggest. Regardless, a lack of compensatory refueling may have major implications for the timing of storms. Storms occurring later in the season could mean that the birds would not have sufficient time to recover from lost fat stores before factors such as winter conditions forced them to depart for migration with depleted fuel stores (O'Neal *et al.*, 2018). Birds that are departing from staging sites at a suboptimal mass may not be able to reach the non-breeding grounds or not be able to recover once they have made it there.

The plasma triglyceride analysis was consistent with our observation of similar refueling rates before and after the storm, as there was no significant difference between triglyceride levels. There was a tendency of triglycerides to be slightly lower after the storm, but without further assessing other plasma metabolites, it is difficult to interpret this trend. Triglycerides in the blood are quickly turned over and so only reliably reflect the preceding two days of refueling (Williams *et al.*, 1999). Given this, and the fact that we sampled birds five days after the hurricane, refueling commenced quickly. If we had been able to sample immediately after the

storm, we might have seen lower circulating triglycerides from birds not being able to feed throughout the storm. However, their triglycerides and weight gain over time remained consistent so it is likely that they were not hindered by lack of prey availability but were already refuelling at maximum capacity. Conversely, there are many potential reasons for their consistent refueling rate that requires further research to elucidate why this is a trend.

Length of stay

Hurricane Fiona substantially increased time birds spent in Atlantic Canada, with estimated lengths of stay approximately doubling for birds that were present during the storm. This result is consistent with the observed large losses in fat stores and the apparent inability of birds to increase their refueling rate, as evidenced by no change to their rate of fat mass gain or plasma triglycerides. There is very little, if any, current research that has been done on movement decisions of migratory birds in response to encountering an extreme weather event. Having to leave later puts the birds at high risk of not having sufficient fuel and unfavourable weather conditions for their cross-Atlantic flight, or not being able to leave before cold temperatures become a potential limitation (Richardson, 1978; Newton, 2006; Senner *et al.*, 2014). On a more encouraging note, the fact that they are staying longer and still refueling at the same rate could mean that they are able to withstand some level of extreme weather and reduction in their available prey items and still be able to make a successful migration.

Conclusions

Staging sites on the Northumberland Strait provide essential habitat for refueling migratory shorebirds, including Semipalmated Plovers (Doiron, 2021). With climate change exacerbating the effects of storms (Ranasinghe, 2020), it is critical to understand how these adverse conditions are affecting migrating shorebirds. Hurricane Fiona had severe effects on Semipalmated Plovers staging behaviour, drastically decreasing their fuel loads and increasing their length of stay. However, their ability to maintain the same refueling rates as they had before the storm, and their apparent capacity to adapt to changes in their prey base, suggests that these birds can still be resilient against storms. However, 2022 was a “good” year for

Semipalmated Plovers, with high breeding success (E. Nol. Pers comm via D. Hamilton), and birds arriving in better condition than they had in the previous year. If severe storm events and poor arrival condition were to coincide, the negative impacts may be compounded, leading to cascading limitations on refueling behaviour, departure condition, and thus migration success. Further, if they are not able to increase their refueling rates, as these data suggest, late season storms may be especially detrimental as individuals will not be able to leave their staging region in time to make it to their destination safely (Newton, 2006). This also highlights the importance of non-breeding sites and their conservation, as birds encountering storms at staging sites may arrive in poor condition, and without good quality non-breeding sites, the effects of the storm may have carry-over effects to future years (Senner *et al.*, 2014). Migration presents a unique challenge for shorebird conservation as they require multiple habitats across a wide geographical range that each present their own risks for survival. This research highlights the potential impacts of late season hurricanes on the staging of shorebirds along the Northumberland Strait and the growing need to foster resilient habitat that is critical for continued refueling and migration success.

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