BEHAVIOUR AND HABITAT USE BY LESSER YELLOWLEGS (*TRINGA FLAVIPES*) AT COASTAL AND INLAND SITES IN NEW BRUNSWICK

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A thesis submitted to the
Department of Biology
Mount Allison University
in partial fulfillment of the requirements for the
Bachelor of Science degree with Honours
April 15, 2023

Abstract

Staging sites provide essential habitat for shorebirds to build energy stores so they have enough energy to migrate. While staging in the Canadian Maritimes, Lesser Yellowlegs use both coastal and inland habitats, however, there is a lack of knowledge of many other aspects of their staging ecology. The population of Lesser Yellowlegs is declining due to many factors, but in part due to the loss of staging habitat. Without a clear understanding of which habitat or combination of habitats they use to meet the goals of staging, it is difficult to create effective conservation strategies. The aim of my study was to characterise foraging behaviour and habitat use, as well as diet, local movements, and length of stay in the region. Lesser Yellowlegs mainly used coastal sites for foraging and inland sites for roosting. There were also variations in the time spent foraging and inactive based on the amount of cloud cover and time of day. Pecking and probing rates were not different between sites, but they were correlated with wind speed, humidity, and air temperature. Pecking rate was higher overall than probing rate, and higher in the morning than at other times of day. On the coast, pecking rate also increased as invertebrate availability increased. Diet did not vary between birds caught on the coast or caught inland and showed a mainly marine influence, however, some birds had a diet consisting of mainly freshwater sources. Chironomids, oligochaetes, and aquatic detritivores appeared to make up the highest proportion of their diet, but this result should be taken with caution as it is likely skewed by missing data. There appeared to be two different patterns of movement around the region: coastal birds that primarily remained coastal and birds that moved between coastal and inland sites; however, the different patterns did not affect length of stay in the region. The results of my study help broaden our understanding of Lesser Yellowlegs' staging ecology by determining that coastal sites seem to be the most important for foraging, while inland sites may be primarily for roosting. Variability in staging habitat use among individuals suggest that the population of Lesser Yellowlegs may be more resilient to habitat loss than previously thought.

Acknowledgments

First, I would like to thank Dr. Hamilton and Dr. de Zwaan for being such amazing and dedicated supervisors. I am truly thankful for all of the support, guidance, and patience they gave me throughout this project. I feel so much more confident in my abilities and ready to move forward as a scientist because of their mentorship, and I hope that one day I can be even half as wonderful as they are. I do not think I would have been able to complete this project under the supervision of anyone else and I am extremely grateful for everything I have learned from them throughout this process. I would also like to thank Julie Paquet for all her contributions to field work, I do not think this project would have been possible without her expertise.

I also want to express my thanks to Mireille Savoie and the team at the Environmental Analytics and Stable Isotope Lab for analyzing my isotope samples. I would also like to acknowledge all of the lab volunteers that helped with catching shorebirds this summer.

Many thanks to all the mud lab members for their help with field work and processing samples, and for being some of the kindest people I have ever had the pleasure of knowing. I would like to extend a special thank you to Gianco Angelozzi-Blanco, Hilary Mann, and Allie Hjort for all their extra help with R, I am not sure I would have gotten through my analysis without them. I would also like to specially thank Mackenzie Warman, Kayla Fisher, and Erin MacMillan for their help processing my invertebrates, they would not have gotten done without their help. Also, a huge thank you to Sophia Fraser for her support and encouragement through all the stressful times, I cannot imagine going through this without you.

I would also like to thank my friends and family for their unwavering support and encouragement throughout this project.

Lastly, I want to acknowledge that this project was only possible due to the generous funding provided by NSERC, Mount Allison University, Project Learning Tree, and New Brunswick Wildlife Trust Fund.

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Introduction

Each year, many species of shorebirds (order Charadriiformes) migrate thousands of kilometers from their Arctic or sub-arctic breeding grounds to their southern over-wintering grounds. Migration is an energetically expensive event; however, the risks far outweigh the benefits when shorebirds can exploit the highly productive summer habitat of the Artic to breed, and then migrate south to avoid inhospitable environmental conditions (O'Reilly & Wingfield, 1995, Alerstam et al. 2003, Cresswell et al. 2011, Winger et al. 2019). Subcutaneous fat is the main fuel source for long-distance migration (Alerstam and Lindstrom 1990, Lindstrom and Alerstam 1992), but shorebirds can only carry up to 50% of their body weight in fat while maintaining flight performance (Davidson, 1984). Fuel storage limitations mean shorebirds must make stops along the way to replenish energy stores (Lyons & Haig, 1995; Schaub & Jenni, 2000). These stops occur in habitat termed stopover or staging sites, depending on the migratory strategy of the species. Stopover sites are usually used for shorter periods of time and by species that make multiple stops along their migration route, while staging sites involve longer lengths of stay for birds to build fat stores to prepare for non-stop, long-distance flights over significant barriers where more frequent stops are not possible, such as trans-oceanic flights (Skagen & Knopf, 1994; Warnock & Bishop, 1998). Staging sites are therefore particularly critical to migratory success and survival, ideally providing habitat with a sufficient combination of predictable resources and environmental conditions for the birds to efficiently rest and refuel during migration (Warnock, 2010). Identifying key staging sites and habitat use within these sites is important to inform conservation decisions for species that rely on high-quality and predictable sites.

The importance of staging sites to survival during migration is disproportionate to the area and length of time birds spend there, and the quality of the habitat can have impacts on survival and population sizes (Studds et al., 2017). A low quality habitat could be one that has a lot of competition or predators, a low amount of food available, or a high amount of human disturbance (Pfister et al., 1992; Schaub & Jenni, 2001). Low quality staging habitat has the potential to greatly reduce survival during migration and reduce future breeding success (Baker et al., 2004).

Lesser Yellowlegs

Lesser Yellowlegs (*Tringa flavipes*) is a species of long-distance migratory shorebird that breeds in the boreal forest of North America and overwinters in the Caribbean and in Central and South America (Clay et al., 2012). During southbound migration, eastern-breeding Lesser Yellowlegs use Atlantic Canada and the northeastern United States as staging habitat before continuing their migration with a series of hops down the Atlantic coast (McNeil & Cadieux, 1972). However, individuals that are in excellent condition may attempt non-stop flights directly over the Atlantic Ocean to the Caribbean or northeastern South America (McNeil & Cadieux, 1972). At staging or stopover sites, Lesser Yellowlegs have been observed using salt marshes, mudflats, and beaches, but have also been observed in large numbers at inland freshwater habitats (Nisbet, 1959; Hicklin, 1987).

Diet and habitat use at staging sites

Refueling is a key goal of staging, but birds also use staging habitat to rest and roost, and studies of habitat use can be used to understand the relative importance of different sites for different staging activities (Ramer, 1985; Linscott & Senner, 2021). While migrating, birds are unable to sleep, so a habitat where they can safely sleep away from predators and return to their normal circadian rhythm is also important (Linscott & Senner, 2021). Given the varied uses of staging sites, it is unlikely that one site can meet all of the staging needs of a migrating bird and it is likely that individuals make use of multiple smaller sites within a region (Linhart et al., 2023).

Most research at staging sites has focused on foraging, and less attention has been paid to the importance of different sites for other activities in shorebirds (MacDonald et al., 2012; Linscott & Senner 2021). Lesser Yellowlegs that use the Canadian Maritimes as staging habitat have been observed using sand and mudflats to forage (Bellefontaine and Hamilton, in press), but there is no research on which areas are most important for them to rest. In other parts of their migratory range, Lesser Yellowlegs use wetlands as their primary staging site and habitat to refuel (McDuffie et al., 2022b), but again, there are no studies on the importance of wetlands in the Canadian Maritimes for staging activities. Another closely related species of shorebird, the Willet (*Tringa semipalmata*), has also been observed using both coastal and inland areas for staging activities, using tidal flats as their primary foraging habitat and inland salt marshes as

roosting habitat and as supplemental foraging habitat (Ramer, 1985), so it is possible Lesser Yellowlegs are using inland habitats primarily for resting as well. Lesser Yellowlegs are generalists and will feed on a wide variety of invertebrate prey (Bellefontaine, 2020), meaning they may be able to exploit resources in more varied habitats. A large proportion of their diet when foraging on the coast is made up of crustaceans, nereid polychaetes, and oligochaetes (Michaud & Ferron, 1990; Pérez-Vargas et al., 2016). In freshwater environments Lesser Yellowlegs primarily forage on Diptera, Coleoptera, and Ephemeroptera (Rundle, 1982; Smith et al., 2012). Understanding which habitats are important for which staging activities will let us know which areas are most important to conserve.

Foraging behaviour

Behaviour is the visual expression of how an animal is responding to its environment based on its physiological state (Sih et al. 2010). By studying animal behaviour, we can identify the needs of a population and predict how they may respond to changing environments (Cooke et al., 2014). Behavioural studies allow us to identify important habitat requirements and how animals are using the habitat, which can give insights into the best strategies for conservation (Sutherland, 1998).

Lesser Yellowlegs exhibit a variety of foraging behaviours, but most commonly employ pecking and probing tactics (Bellefontaine and Hamilton, in press). Pecking, which is a visual method of foraging, is a short and quick motion to strike at the surface of the substrate or the water, compared to the tactile method of probing, which is a slower and deeper insertion of the bill into the water or substrate (Nol et al., 2014). An additional tactile method is sweeping, which is where a bird slowly walks through the water with their head down and bill open, while sweeping their head side-to-side to catch free-swimming prey (Nol et al., 2014). Lesser Yellowlegs have also been observed skimming, which is where they keep the tip of the bill touched to the sediment and use their tongue to pull in food (MacDonald et al., 2012; Bellefontaine, 2020). Lesser Yellowlegs share some of their foraging behaviours with other generalist shorebirds, but avoid competition by foraging primarily in deeper water, where smaller shorebirds cannot access (Bellefontaine and Hamilton, in press).

Each foraging behaviour targets different areas within the substrate, which likely contain different invertebrate assemblages. Rates of foraging behaviours have also been correlated with

invertebrate abundance (Beauchamp, 2009). Examining foraging behaviour can provide an indicator of the invertebrate community the birds are feeding on and their relative abundance. By examining the relative frequency of each foraging behaviour and how they change over time, we can gain a better understanding of important prey types and energy requirements while staging.

Population declines and habitat loss

Lesser Yellowlegs have experienced a significant population decline since the 1970's and have been identified as a priority for conservation in many areas in Canada (McDuffie et al., 2022a). Substantial long- and short-term declines have been noted in many areas of their range resulting in an overall decline of between 60-80% and a yearly decrease of 1.87% (Andres et al., 2012; McDuffie et al., 2022a, Smith et al. 2023). Declines are driven by a variety of factors, including habitat loss, exposure to agrochemicals, unregulated hunting, and climate change (Clay et al., 2012). One of the main threats for eastern-breeding Lesser Yellowlegs specifically is the substantial amount of unregulated hunting that occurs in many parts of the Caribbean and Brazil (McDuffie et al., 2022a). Lesser Yellowlegs that breed in the Eastern part of the Arctic had a greater probability of passing through and spending more time in countries with high levels of shorebird harvest, making them disproportionately affected by hunting compared to other breeding populations (McDuffie et al., 2022a). Conservation actions in Atlantic Canada will not directly reduce the impact of increased hunting on eastern-breeding Lesser Yellowlegs, but identifying and retaining high quality staging habitat can help to offset some of the effects, however, staging habitat is being lost in many parts of their range (Clay et al., 2012). Inland wetlands and marshes are primarily being lost to residential and agricultural settlements (Clay et al., 2012). Agricultural development is not as detrimental as residential development, as some crops like rice can be beneficial, but natural habitats will still be more beneficial (Clay et al., 2012). Loss of coastal staging habitat can often have a significant negative impact on shorebird populations, as this is often their primary foraging habitat during staging (Tong & Wilcove, 2020). Coastal habitat is being lost as sea levels rise due to climate change, eliminating the areas shorebirds currently use to forage, but also potentially creating new habitat as grasslands behind the coast flood (Clay et al., 2012). Staging is a critical part of migration and as staging habitat continues to be lost, it has the potential to negatively affect the entire population by decreasing migration success and survival.

Lesser Yellowlegs use both coastal and inland sites as staging habitat (Nisbet, 1959; Hicklin, 1987), but no research has been done on how much they move between them or the relative importance of each. Dependence on both types of habitat could make them more vulnerable to habitat degradation, so determining if constructed wetlands can supplement their use of natural wetlands could be beneficial for conservation decisions (Clay et al., 2012). There has been some evidence found to suggest that constructed wetlands can support the usage of natural wetlands. Langley et al. (1998) found that in a constructed wetland, there were multiple species, including Lesser Yellowlegs, that had larger flock sizes than they did in nearby natural sites. Alternatively, the ability to use both coastal and inland habitat could make them more resilient to habitat loss as it could suggest they are not reliant on one type of habitat to stage.

Objectives and significance

Very little is known about the staging ecology of Lesser Yellowlegs in the Canadian Maritimes. As their population continues to decline, conservation decisions need to be made to help minimize further declines, but such decisions must be made with an understanding of what is important to these birds. Detailed knowledge of their behaviour and habitat use is going to be critical in developing conservation strategies for them as staging habitat continues to be lost. There is a need to identify which habitats are most important to them and for what reasons before we can implement effective conservation strategies. Conservation strategies are often implemented with limited funding and so understanding whether a particular site or a combination of sites is most important to Lesser Yellowlegs is going to lead to more direct and beneficial conservation action.

The objective of my project is to quantify movement, habitat use, and behaviour of Lesser Yellowlegs during staging in the Canadian Maritimes by looking at three main questions:

1) Do Lesser Yellowlegs move between coastal and inland areas, and if so, does it impact their length of stay in the region? I predict that some birds will move around between coastal and inland sites and others will remain restricted to just coastal areas. I also predict that birds that move around a lot will have longer lengths of stay than those that remain in one habitat (Linhart et al., 2023).

2) How does behaviour and habitat use differ between coastal and inland areas? I predict that coastal sites will be used primarily for foraging and inland sites primarily for resting (Ramer, 1985; Placyk & Harrington, 2004).

3) Do foraging rates vary with prey availability? I predict that foraging rate will increase as prey availability increases (Beauchamp, 2009).

To answer these questions, I caught Lesser Yellowlegs and used the Motus wildlife tracking network to track their movement in the area. I also observed foraging behaviour to determine if there were differences in activities and foraging rates, as well as correlations with prey availability. The results of my study will give us more insight into the activities of Lesser Yellowlegs while in this region, which can be used to help develop future conservation plans.

Methods

Study Sites

I used two coastal and two inland sites in my study of the behaviour and habitat use of Lesser Yellowlegs. The coastal sites were Petit-Cap beach, NB (46.1931° N, -64.1624° W) and Carleton Cove, PEI (46.2742° N, -63.7066° W), hereafter referred to as Borden-Carleton, which both consist of sand flats. The inland sites I used were the Lorne Street Stormwater Mitigation Pond, Sackville, NB (45.893313° N, -64.364688° W) and Beaubassin East, NB (46.2112° N, -64.4225° W). The Stormwater Mitigation Pond, hereafter referred to as the Retention Pond, is a constructed wetland within the town of Sackville and Beaubassin is a salt marsh that is currently part of a re-naturalisation project to return it to its original state. We caught Lesser Yellowlegs at all four sites, but I only conducted behavioural observations at three: Petit-Cap, Borden-Carleton, and the Retention Pond.

Collection of invertebrates for diet analysis

I collected sediment samples where I had previously observed birds foraging. This was done to better reflect the invertebrate community available to the foraging birds and to ensure we had a large enough sample size to minimise potential temporal changes in isotope values if I had to collect samples on multiple days. To obtain potential prey samples for stable isotope analyses,

I collected scoops of surface sediment from Petit-Cap and the Retention Pond. I also used a sweep net at the Retention Pond to catch any potential prey that was living in the water column instead of the sediment. I sieved sediment with a 500 μm sieve and sorted the live invertebrates by taxon. I tried to obtain three samples of each taxon, but some were not abundant enough and only one sample could be obtained. I froze each sample in glass scintillation vials at -20ºC for future processing.

To prepare invertebrates for isotope analysis, I removed molluscs from their shells and placed them in separate aluminum weigh boats by taxon. All other invertebrates were also placed into aluminum weigh boats by taxon and dried in a drying oven at 70 ºC for at least 24 h. The dried samples were crushed with a mortar and pestle and 1-1.5 mg was placed into an aluminum capsule. All instruments used to grind and measure each sample were cleaned after each use with 90% ethanol to prevent cross-contamination.

Dried and crushed invertebrates were pre-weighed using the Mettler-Toledo MX5 microbalance (± 0.001 mg), with a target weight of 1.000 mg for each invertebrate sample. For blood plasma isotopic analysis, I pipetted 15μl of plasma into each pre-weighed aluminum capsule, which were then dried at 70 ºC for at least 24 hours to meet the target weight of 0.8000 mg. Invertebrate and plasma samples were analyzed with the Elementar PyroCube Elemental Analyzer (EA) (Elementar Analysensysteme GmbH, Hanau, Germany) and an Isoprime Precision Isotope Ratio Mass Spectrometer (IRMS; Elementar UK Ltd, Cheadle, UK) for $\delta^{13}C$ and $\delta^{15}N$ at the Environmental Analytics and Stable Isotope Laboratory at Mount Allison University. Delta values of isotope signatures are a relative isotope ratio of the sample to international standards, calculated using the following formula:

$$\delta^{a}X_{(Sample)} = \left[\frac{(\,R_{(Sample)}\,) \;-\; 1}{R_{(Standard)}}\right] * \; 1000$$

Where a = the heavier isotope, X = the element of interest (Nitrogen or Carbon), and R = the ratio of heavy to light isotope.

Behaviour

I observed behaviour of Lesser Yellowlegs using focal animal sampling. Pairs of observers watched individual birds for 2 - 5 minutes. At the start of the observation round, I used

a random number generator to generate a number between 1 and the total number of Lesser Yellowlegs in the observation flock. I then counted off Lesser Yellowlegs from the left side of the flock to the randomly generated number to find the first bird I would observe. At the start of the first observation period, my partner recorded the time and the total number of birds, the total number of Lesser Yellowlegs, and all species present in the flock, and repeated this again at the end of the observation period. I recorded all behaviours the focal bird exhibited into a hand-held voice recorder (Table 1). To obtain environmental data associated with each observation, I also used a Kestrel 3000 (Kestrel Instruments, SKU 0830#) to measure average and maximum wind speed, average air temperature, and average humidity over the duration of the observation. At the end of the observation period, I determined a cloud cover score from 1-10 by mentally splitting the sky into ten equal sections and then estimating how many of them were filled with clouds. I then repeated this process for half of the birds in the flock, or the entire flock if there were less than five Lesser Yellowlegs and I could visually keep track of which birds had already been observed, following the approach of Nol et al. (2014).

After I finished observing the flock, I collected sediment cores (8 cm diameter) from the location in which they were foraging. The cores were stratified to create sediment layers that were 0.5cm, 1.5cm, 3cm, and 5cm deep, which allowed me to look at whether invertebrate type and density varied with depth.

I sieved sediment samples from all locations with a 500 μm sieve and preserved them with 95% ethanol. Samples from Petit-Cap and the stormwater Retention Pond were dyed with Rose Bengal to make invertebrates easier to identify (Mason & Yevich, 1967). I sorted the invertebrates to the lowest identifiable taxon and size class into aluminum weigh boats. Molluscs and amphipods were measured in 2 mm size classes (range 0 - 12 mm), polychaetes and oligochaetes were measured as < 10, 10-20, 20-30, > 30 mm, and insect larvae were measured in 5 mm size classes (range 0 - 15 mm). Samples were dried at 90^{o}C for at least 24 hours before being weighed. Molluscs were then ashed for two hours in a muffle furnace (Isotemp Programmable Muffle Furnace 650-750 Series, Fisher-Scientific, Waltman, MA) at 550^{o}C to eliminate organic material. They were then re-weighed, and the consumable biomass was calculated as the difference between pre- and post-ash weights.

Table 1. Ethogram of measured Lesser Yellowlegs behaviours

Behaviour	Description
Peck	Quick, shallow insertion of the bill into the substrate or water
Probe	Long, deep insertion of the bill into the substrate or water
Sweep	While standing or walking, scythes bill back and forth just beneath the surface of the water
Catch	Catching insects out of the air or picking them off vegetation
Vigilance	Head and neck are stretched tall, may be looking around
Preen	Head is bent into the wings or back and the bill is going through the feathers, bathing in water by using the wings to splash water over the back
Walk	Bird is taking slow steps, not actively foraging
Run	Bird is taking quick steps, not actively foraging
Flying	Bird is in flight
Sleep	Bird is standing with head tucked into the back feathers, eyes are closed, may be standing on one leg
Stand	Bird is standing still, eyes are open, not actively foraging
Aggression	Record if focal bird is the aggressor or the victim, if it is an intraspecific or interspecific interaction, if it is interspecific record the other species (adapted from Recher & Recher, 1969)
1	Intentional movement towards another bird, victim is displaced from foraging spot, victim may display defensive behaviours
2	Displacement events followed by pursuit, displacement events where the victim is forced to fly, standoff displays
3	Fighting

Length of stay and movement

I caught Lesser Yellowlegs during the day and night between July 20 and October 11, 2022 using mist nets with a 38 mm mesh size. I used a playback of Lesser Yellowlegs calls and shorebird foraging calls to draw birds to the nets. During daytime catching at Petit-Cap, I also herded Lesser Yellowlegs into the nets. Upon capture, birds were weighed either by placing them in a cloth bird bag and using a Pesola (± 0.5 g) or by placing them head down into a metal cup that was placed on a scale (± 0.1 g). I also attached a field-readable alpha-numeric flag to their upper right leg and a USGS band on their upper left leg for individual identification. Then, I took a blood sample by pricking the brachial vein using a 27.5-gauge needle and filling three 70 µL capillary tubes to use for isotopic diet analysis. Bleeding was stopped by holding a small piece of paper towel to the site with firm pressure and holding the wing in its natural resting position. After the bleeding stopped, I measured bill length (culmen to tip), tarsus length, and flattened, straightened wing chord length (± 0.1 mm). I determined age (juvenile or adult) by examining the tertials, back, and breast feathers for buffness and wear following Pyle (1997). If the bird was a juvenile, I pulled or cut the sixth primary covert from the base. I also measured fat score by blowing on the breast to determine the fullness and colour of the furcular region (Meissner, 2009). Each bird also received a Motus nano tag with a 10 second burst rate (Lotek NTQB2-3-2-M), which I attached by cutting a small patch of feathers about two centimeters above the uropygial gland and attaching to the skin and feather stubble with cyanoacrylate glue. This facilitated tracking of the bird's movement throughout the region using the Motus Wildlife Tracking System (Taylor et al. 2017). If captured at night, after processing a bird I placed it in a burlap pen for approximately 10 min to readjust to darkness before being released using a red light setting on the headlamp. Birds handled during daylight were released directly.

After returning from the field, blood samples that were stored in a cooler on ice for ~ 6 h were centrifuged for one minute at 10,000 rpm (mySPIN12 Mini Centrifuge, Thermo Scientific) to separate red blood cells from plasma, which was then pipetted off into a separate Eppendorf tube. Both fractions were then frozen at -20º C for later analysis.

Statistical Analysis

All statistical analyses were performed in R version 4.2.2 (R Core Team 2022). Parametric assumptions were tested with a Levene's test for homogeneity of variance and Shapiro-Wilk test for normality. I applied transformations to data that did not meet assumptions and used non-parametric tests if transformations did not work. All plotting was done using R packages 'ggplot2' version 3.4.2 (Wickham, 2016) and 'simmr' version 0.5.0 (Parnell, 2019).

Diet

Stable isotope data failed normality and homogeneity of variance tests, so were analysed using PERMANCOVA. Blood plasma $\delta^{13}C$ and $\delta^{15}N$ levels were the dependent variables and age, tagging location, and fat mass were the independent variables. I calculated fat mass first by determining that structural size, as measured by tarsus length, did not differ between adults and juveniles (using a Welch 2-sample t-test: $t_{20.863} = 0.13$, $p = 0.90$), and then running a multiple regression of body weight against fat score and tarsus length with both age classes pooled. Using the regression intercept and slope, I estimated lean mass for each bird given their tarsus length and setting fat score to zero. I then subtracted lean body mass from the total body mass as a measure of mass attributable to fat (Owen & Moore, 2006). The PERMANCOVA was done using the R package 'vegan' version 2.6-4 (Oksanen et al., 2018). I used a Bray-Curtis dissimilarity matrix and 999 permutations. Multivariate dispersion was tested using the 'betadisper' function from 'vegan'.

I used a Bayesian mixing model to assess the relative proportion of different invertebrates in the diet using the R package 'simmr'. This method estimates the likely proportion of each prey item in the diet using the $\delta^{13}C$ and $\delta^{15}N$ levels from the blood plasma and comparing them to the average isotopic signatures of the sampled prey. Only abundant prey that were likely to be part of the diet were included in the model to reduce potential errors. Prey types that were included were coastal bivalves, inland chironomids, inland oligochaetes, coastal malacostraca, coastal polychaetes, and a grouped category of inland aquatic detritivores, which consisted of Plecoptera, Ephemeroptera, and Trichoptera larvae. A fractionation coefficient of 3.3 ± 0.3 (mean ± SD) for $\delta^{15}N$ signatures, and 0.5 ± 0.3 for $\delta^{13}C$ signatures was added to the model to account for the values changing as they got incorporated into the bird's tissue. The fractionation coefficient was calculated using a captive feeding study of Dunlin (*Calidris alpina*) (Ogden et

al., 2004). Dunlin are the only shorebird species in which diet-tissue fractionation coefficients have been directly calculated, and the similarity to the values for Lesser Yellowlegs is unknown, but it is the closest estimate available. I fit the model with flat priors because there are no data available on preferred prey for Atlantic populations of Lesser Yellowlegs to inform priors. No statistical analysis was done on the results, for example to compare coastal and inland bird diets, because uncertainty in the fractionation coefficient and the prey types assessed by the model could potentially lead to significant error in my interpretation. As such, the results from the mixing model are for qualitative comparison and to generate baseline information for future research.

Behaviour and habitat use

Before the behaviour data were analysed, I conducted a principal component analysis (PCA) on the continuous weather variables collected during my observation period (average wind speed, maximum wind speed, humidity, and air temperature) to reduce the number of independent variables in the models. I used the principal function from the 'psych' package version 2.3.3 (Revelle, 2023) and a varimax rotation, which left me with two useable principal components that explained 59% of the variance (Table 2). PC1 was positively associated with both wind speed measurements and humidity, while PC2 was positively associated with air temperature.

Table 2. Results of a Principal Component Analysis (PCA) on four measures of weather that occurred during each observation period.

Factor loadings	**PC1**	**PC2**	**PC3**	**PC4**
Average wind speed	0.61	0.08	0.25	0.75
Maximum wind speed	0.96	0.05	0.10	0.24
Humidity	0.11	0.01	0.98	0.14
Air temperature	0.05	1.00	0.01	0.05
Component importance	**PC1**	**PC2**	**PC3**	**PC4**
Proportion of variance	0.33	0.26	0.25	0.16
Cumulative proportion	0.33	0.59	0.84	1.00

Activity budgets were calculated for each site as the proportion of time spent foraging (all foraging behaviours and active searching) and proportion of time spent inactive (standing, sleeping, preening). Data were analysed using a PERMANCOVA, as described previously, with proportion of time spent of each activity as dependent variables and site, time of day, day of year, PC1, PC2, and cloud cover as independent variables. In the first analysis, I included all interactions with site, and then the least significant interaction was removed for each subsequent PERMANCOVA. I was left with an interaction between site and cloud cover, so I split my dataset by coastal and inland observations and re-ran a PERMANCOVA for each. Multivariate dispersion for significant categorical variables was tested using the 'betadisper' function in the 'vegan' R package, and similarity percentages between levels of each significant factor were calculated using the 'simper' function from the 'vegan' R package.

Foraging rates were calculated for pecking and probing as the number of actions per minute of foraging time and were again analysed using PERMANCOVA. Pecking and probing rate per minute of foraging time were the dependent variables and site, time of day, day of year, PC1, PC2, and cloud cover were the independent variables. The first PERMANCOVA included all interactions with site, that were then sequentially removed by the smallest effect size. Multivariate dispersion and simper tests were run as described above. Significant continuous variables were further examined with univariate linear regressions.

Prey availability

The relationships between prey availability and foraging rate were analysed with four ANCOVAs using type II sums of squares to account for unbalanced data (Langsrud, 2003). Peck rate was the dependent variable, and it was compared against site and invertebrate abundance in the top layer only, as well as in all layers of sediment. Probe rate was another dependent variable, and it was compared against site and invertebrate abundance in the bottom layer only, and again for all layers of sediment combined. The difference is because pecking only samples food resources from the surface, while probing reaches deeper sediment depths. Invertebrate abundance in each depth was calculated by averaging the number of each type of invertebrate between the two sediment cores I took from each foraging location. I then summed each average type within the location to get average abundance of all invertebrates in the top layer (0 - 0.5 cm), in the bottom layer (0.5 - 5 cm), and in all layers (0 - 5 cm). Post-hoc testing between

significant relationships was done using the 'emmeans' R package version 1.8.5 (Lenth, 2023). Residuals of all models passed assumptions.

Length of stay and movement

Data downloaded from the Motus website was cleaned to remove any false detections. Detections were removed if they were not possible based on the time period or travel time, or if they had fewer than three consecutive detections (Crewe et al. 2020). The density of towers is lower on the coast than inland, so to avoid bias based on different detectability, movement among areas was estimated by noting whether birds visited coastal or inland towers at any point in their stay, excluding the 24 h period before they were last detected (to avoid confounding habitat use with initiation of migration). Minimum length of stay was calculated as number of days between the first detection in the region and the last. This method has been found to provide reasonable estimates of the true length of stay in the region (Neima et al., 2022).

Results

Diet analysis

Based on stable isotope analyses, there is no evidence of a difference in diet for birds captured inland versus on the coast (Figure 1, Figure 2, Table 3). Similarly, diet appears to be unrelated to estimated fat mass of individuals, or age (adult versus juvenile; Table 3). Results of a Bayesian mixing model approach agreed, showing that the diets of birds captured inland and on the coast appear to be very similar (Figure 3).

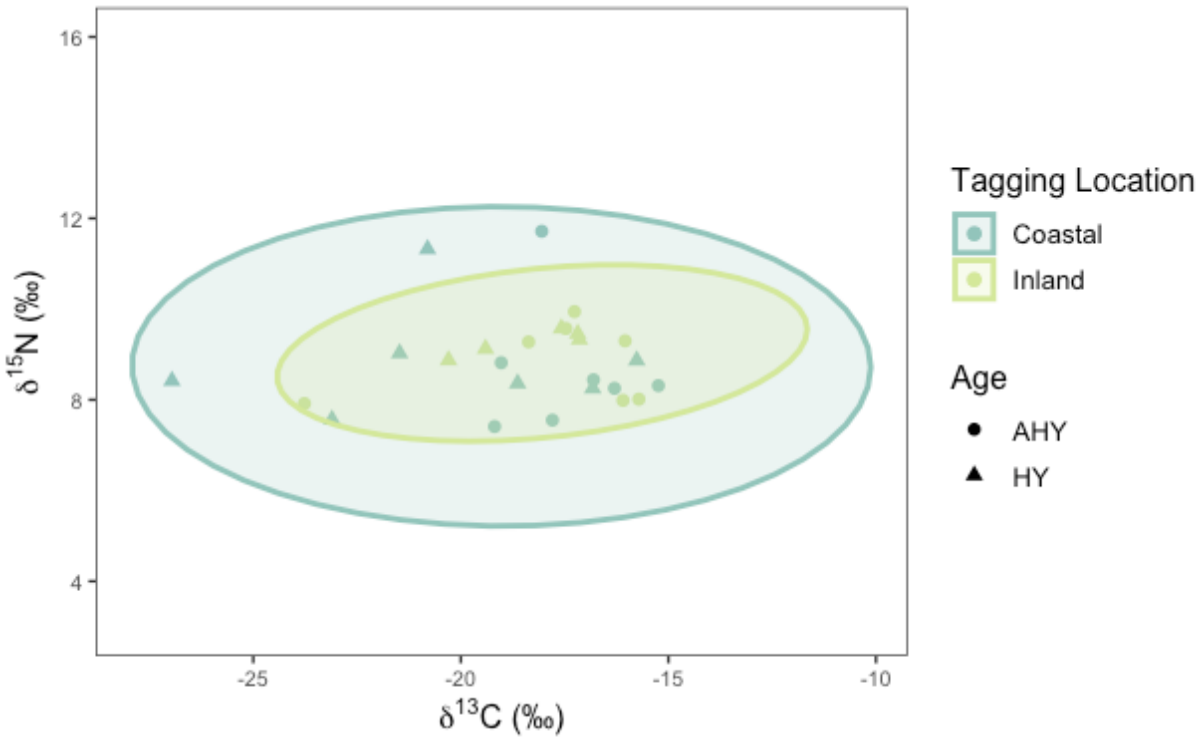

Figure 1. Estimates of the isotopic niches of Lesser Yellowlegs caught inland and on the coast, using blood plasma $\delta^{13}C$ and $\delta^{15}N$ levels. Each point represents one bird, coloured by tagging location (blue represents coastal and green represents inland) and by shape (circles represent adults, AHY, and triangles represent juveniles, HY).

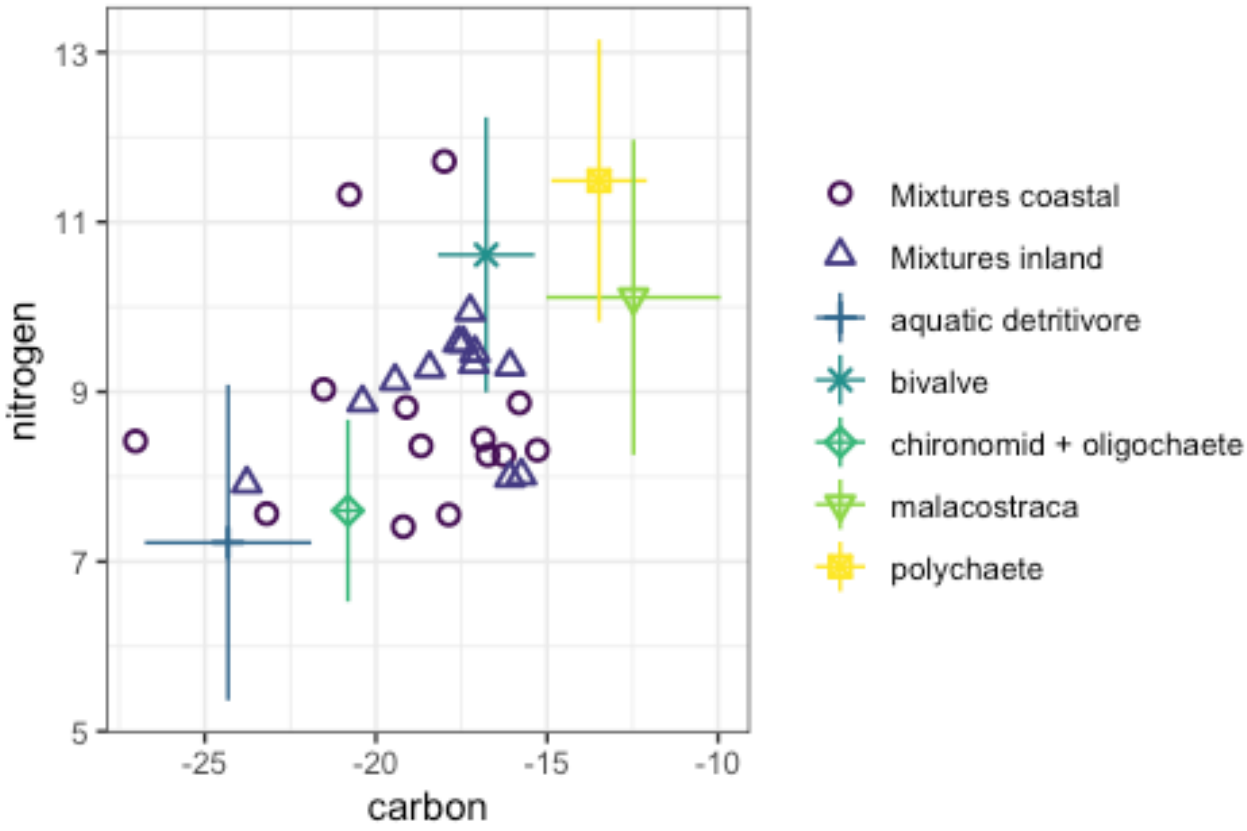

Figure 2. Trace plot that shows the blood plasma isotope values in relation to invertebrate isotope levels. Open circles show plasma isotope signatures of birds caught on the coast and open triangles show plasma isotope signature of birds caught inland. Aquatic detritivore and chironomid + oligochaete were inland prey sources, and bivalve, malacostraca, and polychaete were coastal prey sources.

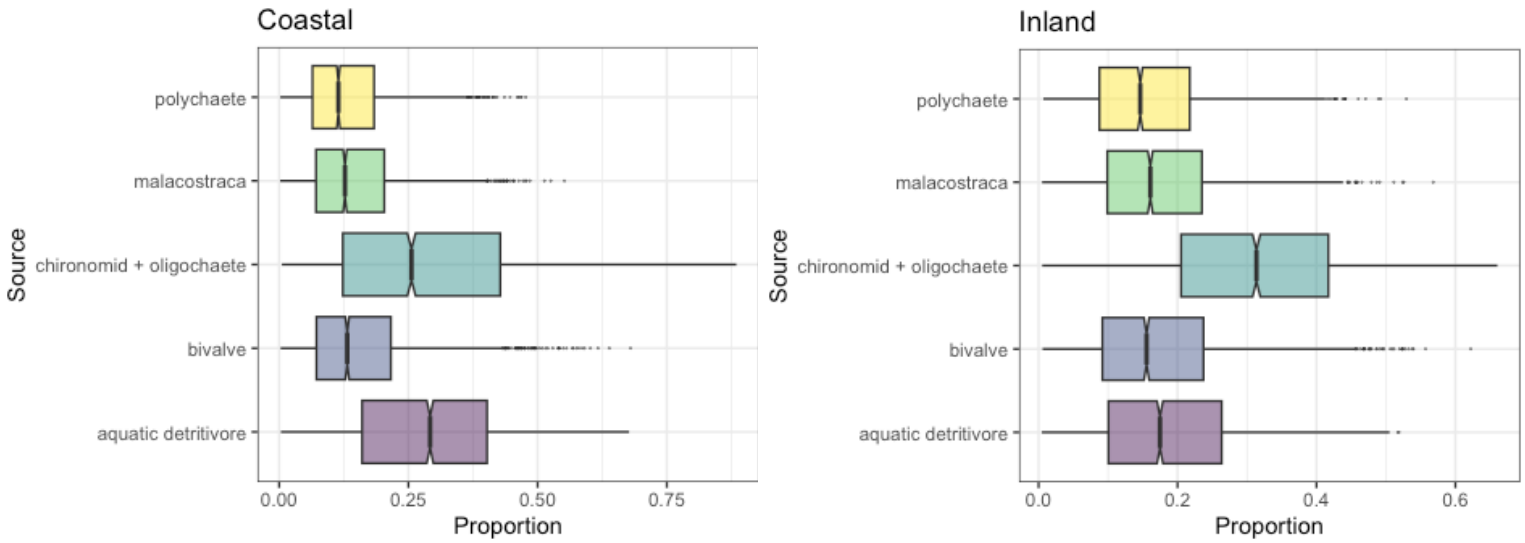

Figure 3. Diet estimate of Lesser Yellowlegs caught on the coast (left) and inland (right) using flat priors. Estimates were made by comparing blood plasma $\delta^{13}C$ and $\delta^{15}N$ levels to coastal and inland $\delta^{13}C$ and $\delta^{15}N$ levels using Bayesian mixing models. Boxes represent the proportion of each prey source that is likely to be in the diet.

Table 3. Results of a PERMANCOVA (Bray-Curtis dissimilarity matrix, 999 permutations) of $\delta^{13}C$ and $\delta^{15}N$ levels against calculated fat mass, tagging site type (coastal or inland), and age. Columns, from left to right, represent degrees of freedom, mean squares, f statistic, r^2, and p value.

	Df	**MS**	**F**	**r^2**	**p**
Fat mass	1	0.002	0.14	0.006	0.87
Site type	1	0.009	0.79	0.03	0.47
Age	1	0.03	2.57	0.10	0.10
Fat mass:Site type	1	0.009	0.79	0.0	0.43
Fat mass:Age	1	0.004	0.34	0.014	0.73
Residuals	20	0.01	0.81		
Total	25	1			

Behaviour

I combined environmental variables into two components that explained 59% of the variability in the data and were subsequently used as covariates in foraging models. PC1 explained 33% of the variation and PC2 explained 26% of the variation. PC1 was positively associated with average wind speed (0.61), maximum wind speed (0.96), and humidity (0.11), while PC2 was positively associated with air temperature (1.00).

Activity Budget

Borden-Carleton had a mean proportion of time spent foraging of 0.85 ± 0.08 (mean ± SD) and a mean proportion of time spent inactive of 0.06 ± 0.07. At Petit-Cap, the mean proportion of time spent foraging was 0.47 ± 0.33 and the mean proportion of time spent inactive was 0.39 ± 0.38. The Retention Pond had a mean proportion of time spent foraging or inactive of 0.20 ± 0.32 and 0.66 ± 0.35, respectively.

Proportion of time spent foraging and inactive varied with time of day (Table 4). Proportion of time spent foraging was highest at mid-day and proportion of time spent inactive was highest in the morning and afternoon (Figure 5). There were also differences between salt and freshwater habitats, including a significant interaction between site and cloud cover. When models were run separately for the two levels of cloud cover, I found that foraging and inactive times still varied by site at both less than half cloud cover ($F_{2, 31} = 6.37$, $p = 0.003$) and more than half cloud cover ($F_{2, 27} = 54.27$, $p = 0.0001$). However, multivariate dispersion also differed among sites for both levels of cloud cover (low cloud – $F_{2, 36} = 12.67$, $p = 0.001$; high cloud – $F_{2, 36} = 7.11$, $p = 0.002$), suggesting that the overall significant result may be a combination of differences in centroids and dispersion. Borden-Carleton appeared to have the least variability in proportion of time spent foraging and inactive due to cloud cover, while Petit-Cap and the Retention Pond had a relatively high amount of variability in proportion of time spent foraging and inactive driven by differences in cloud cover (Figure 4).

A simper analysis of site revealed that a difference in the proportion of time spent foraging was driving the difference between Petit-Cap and the Retention Pond ($p = 0.015$), where they spent, on average, a little over double the proportion of time foraging at Petit-Cap. A difference in both the proportion of time spent foraging ($p = 0.001$) and inactive ($p = 0.001$) was driving the difference between Borden-Carleton and the Retention Pond (Table 5). There was a

higher proportion of time spent foraging at Borden-Carleton and a higher proportion of time spent inactive at the Retention Pond.

Significant differences among times of day were not related to variation in dispersion ($F_{2, 71} = 0.86$, $p = 0.45$). Differences in the proportion of time spent foraging drove the difference between morning and mid-day ($p = 0.006$) and between mid-day and afternoon ($p = 0.05$) (Table 6). In the morning, the average proportion of time they spent foraging was 0.33 ± 0.36, and at mid-day they spent an average proportion of time they spent foraging was 0.56 ± 0.35

Table 4. Results of a PERMANCOVA (Bray-Curtis dissimilarity matrix, 9999 permutations) with proportion of time foraging and inactive as dependent variables, and site, day of year, the two weather principal components, time of day, and cloud cover as predictors. Columns, from left to right, represent degrees of freedom, mean squares, f statistic, r^2, and p value. Significant and interpretable results are in bold.

	Df	**MS**	**F**	**r^2**	**p**
Site	2	2.97	31.15	0.42	**0.0001**
Day of year	1	0.079	0.83	0.006	0.37
PC1	1	0.09	0.97	0.007	0.32
PC2	1	0.13	1.36	0.009	0.25
Time of day	2	0.34	3.57	0.05	**0.03**
Cloud cover	1	0.004	0.04	0.0003	0.93
Site:cloud cover	2	0.65	6.79	0.09	**0.002**
Residuals	63	0.10	0.425		
Total	73	1			

Table 5. Results of a simper analysis to identify behavioural drivers of differences between sites. The average column depicts the average dissimilarity between the proportions and the ratio column shows the ratio of the average dissimilarity to the standard deviation. Ratios > 1 imply meaningful results.

Contrast: Petit-Cap_Retention Pond				
	Average	**SD**	**Ratio**	**p**
Proportion of time spent foraging	0.28	0.19	1.42	0.02
Proportion of time spent inactive	0.26	0.18	1.44	0.15
Contrast: Petit-Cap_Borden-Carleton				
	Average	**SD**	**Ratio**	**p**
Proportion of time spent foraging	0.23	0.16	1.43	0.10
Proportion of time spent inactive	0.20	0.18	1.13	1
Contrast: Retention Pond_Borden-Carleton				
	Average	**SD**	**Ratio**	**p**
Proportion of time spent foraging	0.38	0.17	2.24	0.001
Proportion of time spent inactive	0.34	0.18	1.91	0.001

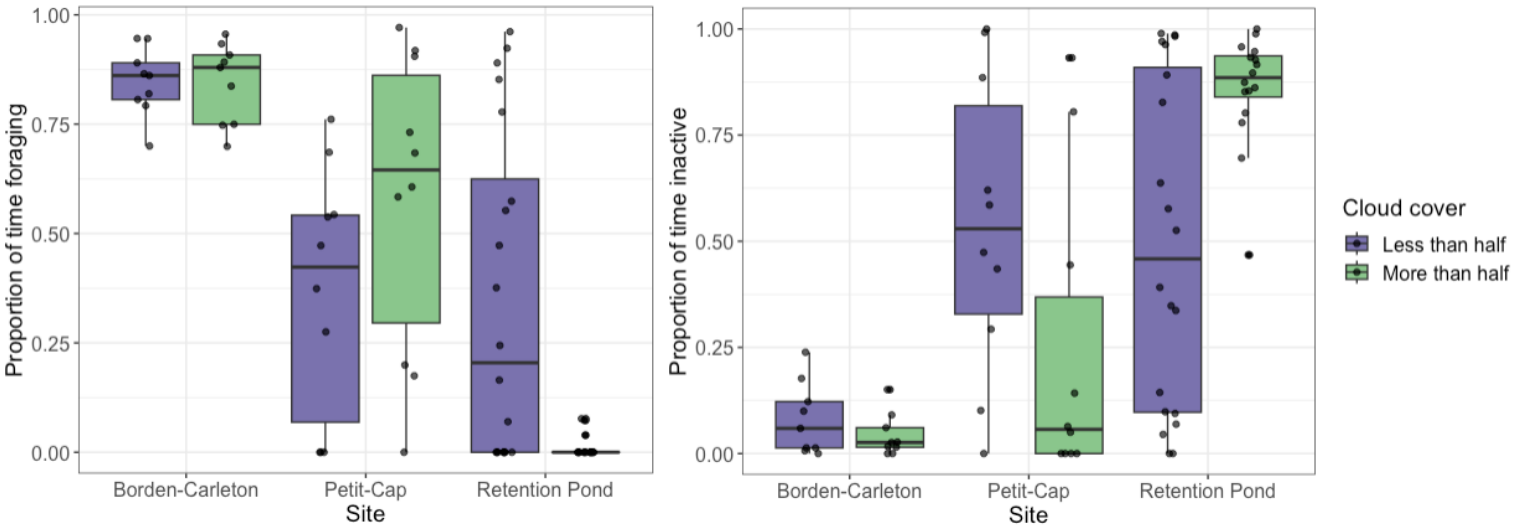

Figure 4. Boxplots depicting the variability in proportion of time spent foraging (left) and inactive (right) at less than half cloud cover (purple) and more than half cloud cover (green). Black, horizontal bars represent the median proportion of time and boxes represent the 25th and 75th quantiles. Results of statistical comparisons are provided in the text.

Table 6. Results of a simper analysis to identify behavioural drivers of differences among times of day. The average column depicts the average dissimilarity between the proportions and the ratio column shows the ratio of the average dissimilarity to the standard deviation. Ratios > 1 imply meaningful results.

Contrast: Morning_Mid-day				
	Average	**SD**	**Ratio**	**p**
Proportion of time spent foraging	0.28	0.20	1.42	0.006
Proportion of time spent inactive	0.26	0.19	1.42	0.17
Contrast: Morning_Afternoon				
	Average	**SD**	**Ratio**	**p**
Proportion of time spent foraging	0.25	0.20	1.29	0.86
Proportion of time spent inactive	0.24	0.20	1.22	0.92
Contrast: Mid-day_Afternoon				
	Average	**SD**	**Ratio**	**p**
Proportion of time spent foraging	0.27	0.20	1.38	0.05
Proportion of time spent inactive	0.27	0.20	1.31	0.16

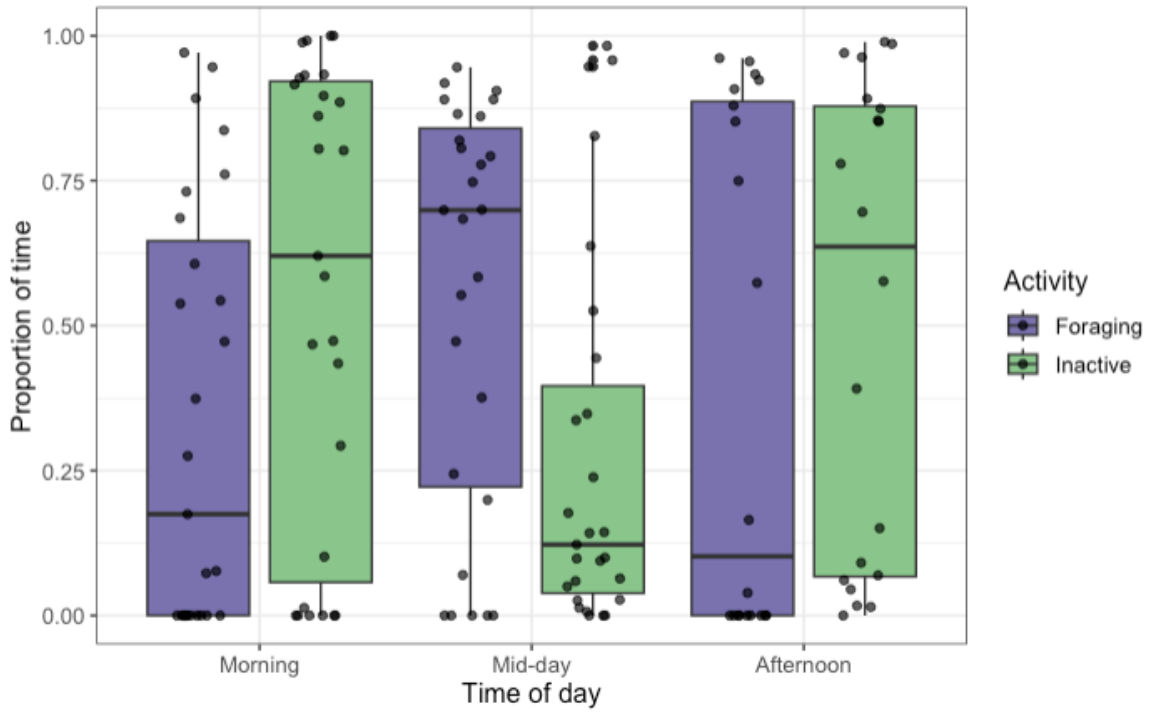

Figure 5. Boxplot depicting the proportion of time spent foraging (purple) and inactive (green) at each time of day. Black, horizontal bars represent the median proportion of time and boxes represent the 25th and 75th quantiles. Results of statistical comparisons are provided in the text.

Foraging Rates

The average pecking rate was 16.08 ± 6.35 per minute (mean ± SD) of foraging time and the average probe rate was 2.24 ± 2.29 per minute of foraging time. Pecking and probing rates varied significantly with composite weather variables PC1 (average wind speed, maximum wind speed, and humidity) and PC2 (air temperature) (Table 7). Time of day was also significant (Table 7) and variation in pecking and probing rates among times of day was not due to differences in dispersion ($F_{2, 34} = 2.13$, $p = 0.15$) (Figure 6). Difference in pecking rate between morning and afternoon was driving the overall multivariate effect (Table 8). In the morning the average peck rate was 20.36 ± 4.84 and in the afternoon it was 14.24 ± 6.80 (Figure 6).

Table 7. Results of a PERMANCOVA (Bray-Curtis dissimilarity matrix, 9999 permutations) run on dependent variables pecking and probing rate per minute of foraging time, with predictors of site, time of day, weather components, cloud cover and day of year. Columns, from left to right, represent degrees of freedom, mean squares, f statistic, r^2, and p value. Significant and interpretable results are in bold.

	DF	**MS**	**F**	**r^2**	**p**
Site	2	0.04	1.12	0.05	0.33
Day of year	1	0.08	2.22	0.05	0.12
Time of day	2	0.10	2.68	0.11	**0.05**
PC1	1	0.15	3.94	0.08	**0.03**
PC2	1	0.16	4.24	0.09	**0.03**
Cloud cover	1	0.02	0.58	0.01	0.57
Residuals	28	0.04	0.60		
Total	36	1			

Table 8. The results of a simper analysis to determine whether the rate of pecking or probing is driving the difference in time of day. The average column depicts the average dissimilarity between the proportions and the ratio column shows the ratio of the average dissimilarity to the standard deviation. Ratios > 1 imply meaningful differences.

Contrast: Mid-day_Afternoon				
	Average	**SD**	**Ratio**	**p**
Peck rate per minute of foraging time	0.19	0.14	1.42	0.67
Probe rate per minute of foraging time	0.08	0.06	1.30	0.13
Contrast: Mid-day_Morning				
	Average	**SD**	**Ratio**	**p**
Peck rate per minute of foraging time	0.23	0.15	1.46	0.07
Probe rate per minute of foraging time	0.06	0.05	1.03	0.97
Contrast : Afternoon_Morning				
	Average	**SD**	**Ratio**	**p**
Peck rate per minute of foraging time	0.23	0.14	1.58	0.21
Probe rate per minute of foraging time	0.06	0.04	1.42	0.75

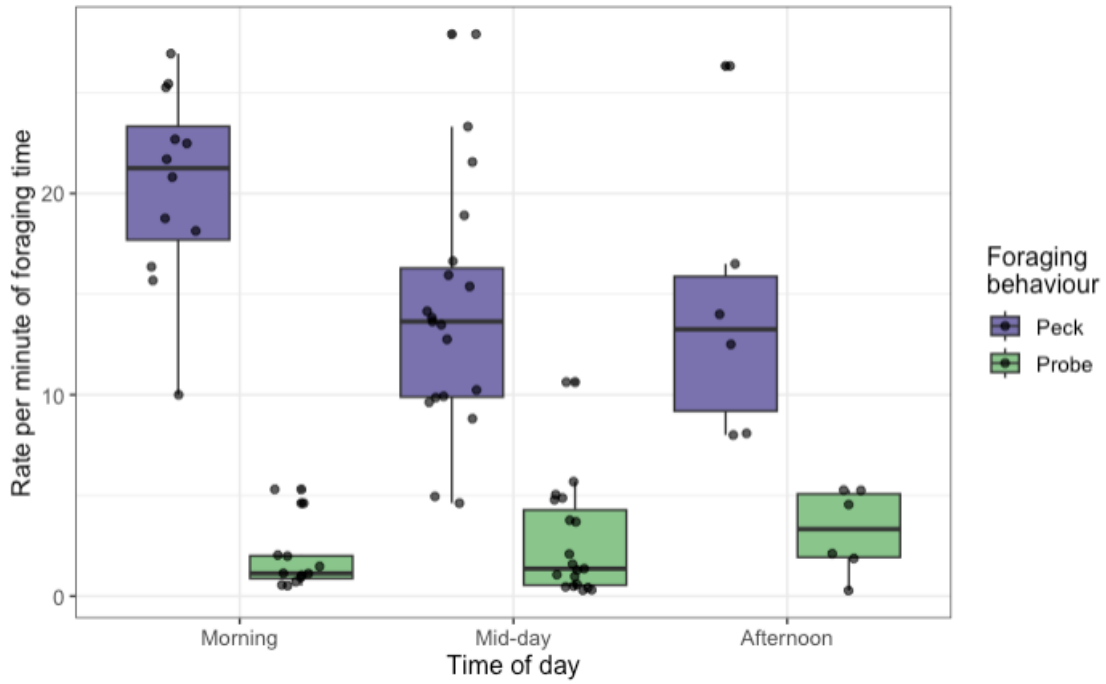

Figure 6. Boxplot depicting the pecking (purple) and probing (green) rates at each time of day. Black, horizontal bars represent the median foraging rate and boxes represent the 25th and 75th quantiles. Results of statistical comparisons are provided in the text.

I used univariate linear regressions to determine which foraging mode was driving the multivariate relationship with the two weather principal components. Pecking rate increased (p = 0.047) as wind speed and humidity increased (PC1), but there was no effect on probing rate (p = 0.224). Pecking rate decreased (p = 0.046) and probing rate increased (p = 0.011) as air temperature (PC2) increased.

Invertebrate availability

Pecking rate per minute of foraging time was positively correlated with both an increase in invertebrate abundance in the top 0.5 cm of sediment (Table 9, Figure 7), and an increase in abundance in the top 5 cm of sediment (Table 11, Figure 7). Both site and invertebrate abundance in the top layer had a significant, or close to significant, effect on pecking rate per minute of foraging time (Table 9, Table 11). Post-hoc testing revealed that when controlling for invertebrate abundance in the top 5 cm of sediment, Borden-Carleton had higher pecking rate than the Retention Pond (Table 12). When controlling for invertebrate abundance in the top 0.5

cm of sediment, the difference in pecking rate between Borden-Carleton and the Retention Pond was approaching significant (Table 10). There was no relationship between invertebrate availability in the bottom 0.5 - 5cm of sediment or the top 5cm of sediment and probing rate (Table 13).

Table 9. Results of an ANCOVA (type II sums of squares) of pecking rate per minute of foraging time against site and invertebrate abundance in the top 0.5 cm of sediment. The site x abundance interaction was tested and found to be non-significant ($p = 0.24$). Columns, from left to right, represent sums of squares, degrees of freedom, f statistic, and p value. Significant and interpretable results are in bold.

	SS	**Df**	**F**	**p**
Site	201.65	2	3.31	0.06
Abundance (0.5 cm)	169.34	1	5.55	**0.03**
Residuals	640.34	21		

Table 10. Post-hoc differences among sites (calculated using least squares means) of pecking rate per minute of foraging time, controlling for invertebrate abundance in the top 0.5 cm of sediment. Columns from left to right depict the sites that are compared, an estimate of the difference between least squares means of the pecking rate in each site, standard error of the estimate, degrees of freedom, t statistic, and p value. Significant and interpretable results are in bold.

Contrast	**Estimate**	**SE**	**Df**	**T**	**p**
Borden-Carleton_Petit-Cap	2.15	2.93	21	0.74	0.75
Borden-Carleton_Retention Pond	6.93	2.85	21	2.43	0.06
Petit-Cap_Retention Pond	4.77	2.63	21	1.82	0.19

Table 11. Results of an ANCOVA (type II sums of squares) on pecking rate per minute of foraging time against site and invertebrate abundance in the top 5 cm of sediment. The site x abundance interaction was tested and found to be non-significant ($p = 0.97$). Columns, from left to right, represent sums of squares, degrees of freedom, f statistic, and p value. Significant and interpretable results are in bold.

	SS	Df	F	p
Site	263.03	2	5.42	**0.01**
Abundance (5 cm)	192.2	1	7.92	**0.01**
Residuals	509.94	21		

Table 12. Post-hoc differences among sites (calculated using least squares means) of pecking rate per minute of foraging time, controlling for invertebrate abundance in the top 5 cm of sediment. Columns from left to right depict the sites that are compared, an estimate of the difference between least squares means of the pecking rate in each site, standard error of the estimate, degrees of freedom, t statistic, and p value. Significant and interpretable results are in bold.

Contrast	Estimate	SE	DF	T	P
Borden-Carleton_Petit-Cap	2.49	2.58	21	0.96	0.61
Borden-Carleton_Retention Pond	7.89	2.52	21	3.13	**0.01**
Petit-Cap_Retention Pond	5.41	2.35	21	2.30	0.08

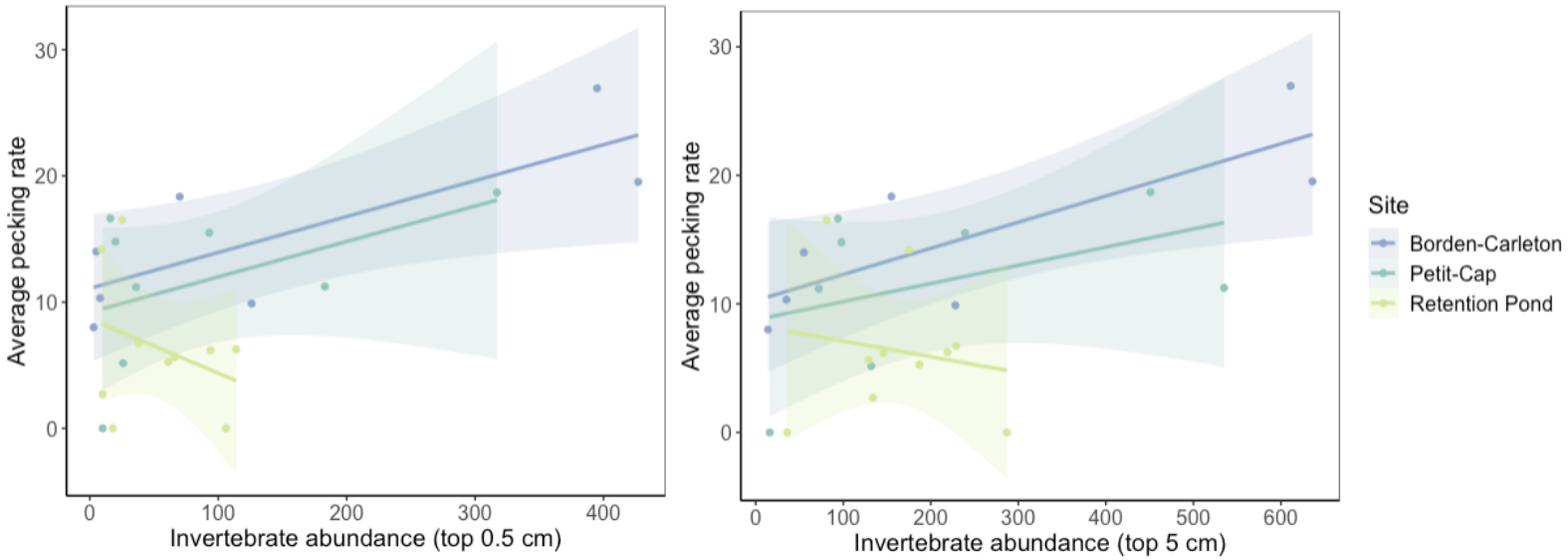

Figure 7. Plot depicting the change in pecking rate per minute of foraging time with invertebrate abundance in the top 0.5 cm of sediment (left) and the top 5 cm of sediment (right). Results of statistical comparisons are provided in the text.

Table 13. Results of ANCOVAs (type II sums of squares) on probing rate per minute of foraging time against site and invertebrate abundance in the bottom 0.5 – 5 cm of sediment (top) and in top 5 cm of sediment (bottom). The site x abundance interaction was tested and found to be non-significant, both for the bottom layer ($p = 0.87$) and in the top 5 cm ($p = 0.98$). Columns, from left to right, are sums of squares, degrees of freedom, f statistic, and p value. Significant and interpretable results are in bold.

		SS	**Df**	**F**	**p**
Bottom layer (0.5 – 5cm)	Site	0.25	2	1.96	0.17
	Abundance (0.5-5cm)	0.0004	1	0.007	0.94
	Residuals	1.35	21		
All layers (0-5cm)	Site	0.28	2	2.2	0.14
	Abundance (0-5cm)	0.03	1	0.41	0.53
	Residuals	1.32	21		

Length of stay and movement

I obtained radio tracking data from 11 coastal and 10 inland Lesser Yellowlegs. The mean minimum length of stay for coastal and inland birds was 14.3 ± 11.7 days (mean ± SD) and 21.7 ± 2.6 days, respectively. The mean minimum length of stay for adults (n=12) was 16.19 ± 8.40 days and 17.45 ± 9.97 days for juveniles (n=9). Minimum length of stay for Lesser Yellowlegs did not differ between coastal and inland tagging locations (Wilcoxon rank sum test: $W = 26$, $p = 0.37$), though there was more variability among coastal birds (Figure 8). Minimum length of stay also did not differ between juvenile and adult birds (Two-sample t-test: $t_{15} = -0.277$, $p = 0.79$) (Figure 9). Birds that were tagged on the coast appeared to use mainly coastal habitats, while birds that were tagged inland appeared to use a mix of both coastal and inland habitat (Table 14).

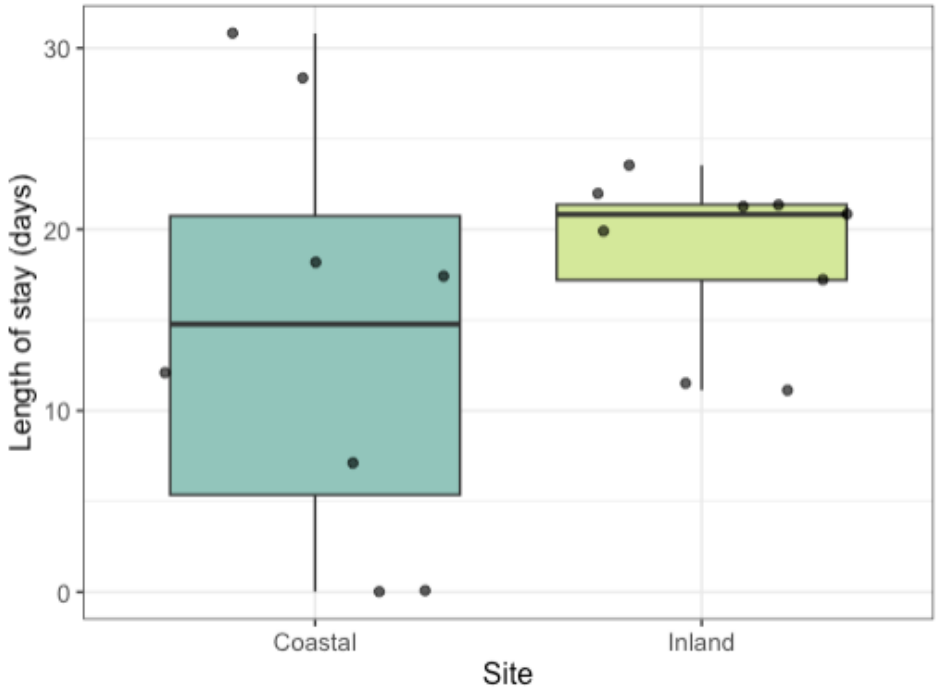

Figure 8. Boxplot depicting the minimum lengths of stay (in days) in Maritime Canada of Lesser Yellowlegs that were tagged on the coast or tagged inland. The horizontal black line represents the median length of stay and boxes represent the 25th and 75th quantiles. Results of statistical comparisons are provided in the text.

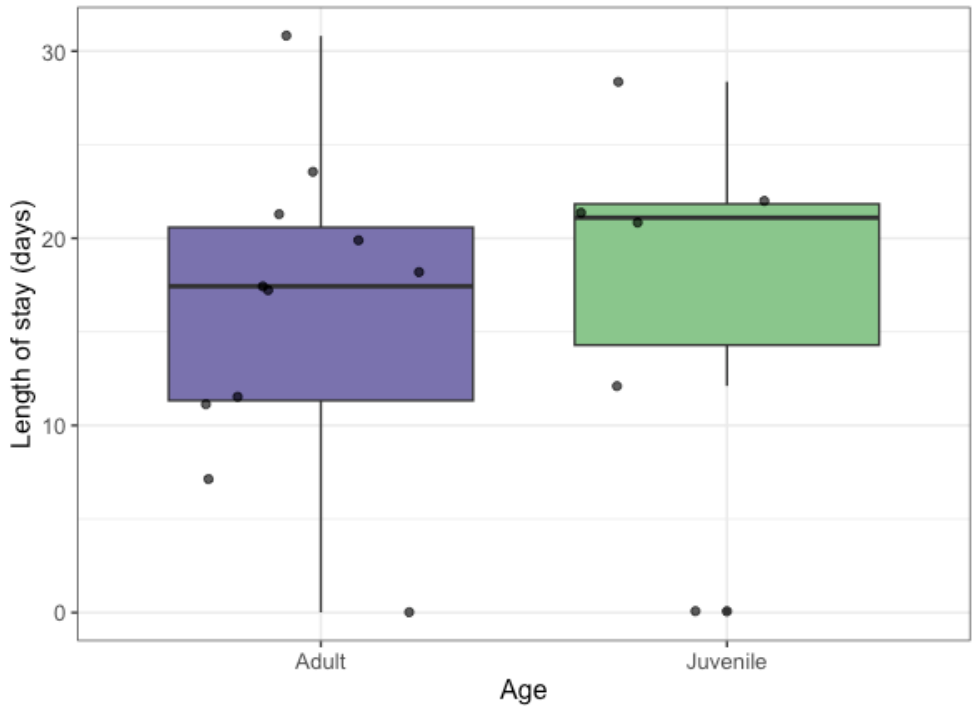

Figure 9. Boxplot depicting the minimum lengths of stay (in days) in Maritime Canada of adult and juvenile Lesser Yellowlegs. The horizontal black line represents the median length of stay and boxes represent the 25th and 75th quantiles. Results of statistical comparisons are provided in the text.

Table 14. Movement of Lesser Yellowlegs tagged inland and on the coast. For each tagging location, number tagged, as well as the number of birds from each location detected in each area is provided. The number of birds detected inland and coastal does not add up to the number tagged because an individual bird may be detected in both types of habitat.

Tagging location	Number tagged	Number detected inland	Number detected coastal
Inland	10	10	4
Coastal	11	2	11

Discussion

Lesser Yellowlegs populations are in decline, in part due to loss of staging habitat. High quality staging habitat is critical to survival during migration, but we know very little about their staging ecology, making it hard to develop effective conservation strategies. The objective of my study was to determine if Lesser Yellowlegs were moving between coastal and inland sites, and if so, whether their movement behaviour affected length of stay in the region. I also assessed whether there were differences in habitat use and foraging behaviour between coastal and inland sites, and if there was a correlation between prey availability and foraging rate.

Diet analysis

Isotopic niches

There were no notable differences in the blood plasma $\delta^{13}C$ and $\delta^{15}N$ levels between birds caught on the coast and those caught inland. The majority of $\delta^{13}C$ levels for both coastal and inland birds fell within the range observed in shorebirds that forage exclusively in a marine habitat (Quinn & Hamilton, 2012; Bellefontaine, 2020). This suggest that Lesser Yellowlegs also primarily forage in marine environments, although there were a few birds that appeared to have a mix of freshwater and marine influence in their diet as some of their $\delta^{13}C$ levels were very low (Guiry, 2019). This provides further support for the idea that inland birds are likely using coastal habitats more than what was detected using the Motus towers and that inland habitat alone may not be enough to support Lesser Yellowlegs while staging. However, the few birds that appear to forage primarily in inland areas suggest that there is some variation in diet among individuals, which could be linked to their body condition, carry-over effects from the breeding grounds, or responses to stopover conditions (Baker et al., 2004). From a population level perspective, variation among individuals is important because a population may be more resilient to habitat loss if there are birds within the population that are more flexible in their habitat use (Beever et al., 2017).

I also found no differences in the $\delta^{13}C$ and $\delta^{15}N$ levels between adult and juvenile birds or a relationship with fat mass. This indicates that adult and juvenile Lesser Yellowlegs have similar diets while staging, which is important information for conservation. No relationship between fat mass and $\delta^{13}C$ and $\delta^{15}N$ indicates that birds relied on similar food resources throughout their staging duration, as fat mass can be used as a proxy for how long they have

been in the region (Neima et al., 2022). No relationship also means that we can be sure we are not seeing isotope signatures carry-over from dietary influences on the boreal breeding grounds. Plasma $\delta^{13}C$ levels have a half-life of 2.9 days, which suggests they can estimate a bird's diet from about the past week (Hobson & Clark, 1993).

Mixing models

Mixing models integrate $\delta^{13}C$ and $\delta^{15}N$ values from the blood plasma and from the available prey to determine likely proportions of each prey type in the diet. In contrast to the isotopic niche estimate using blood plasma, results of the mixing model appears to show a relatively high proportion of the diet of birds captured at both inland and coastal sites consisting of inland sources like chironomids and oligochaetes. In other parts of their migratory range, where they use mainly freshwater staging sites, chironomids have been identified as an important source of food (Rundle, 1982). Oligochaetes, on the other hand, are not considered an important food source and sometimes Lesser Yellowlegs will avoid them entirely (Rundle, 1982; Andrei et al., 2009).

It is possible that the mixing model disagrees with the isotopic niche estimates and the movement data because we are missing important parts of their diet from the model. In other parts of their range, seeds have been identified in the diet of staging birds and therefore plant material is a possible food resource in Atlantic Canada that I did not address (Rundle, 1982). If primary production is not included as a potential food source, diets would be assigned erroneously to the next lowest trophic source (based on $\delta^{15}N$ signature), which in my model happened to be freshwater invertebrates. Alternatively, diet was highly variable among birds, with some having very low $\delta^{13}C$ values, indicating that much of their diet may have come from terrestrial or freshwater sources. There are no existing studies assessing individual variation in diets within the Atlantic Canada region. Given that I know isotopic signatures were not influenced by breeding site carry-over effects (see above), if a few birds were relying heavily on freshwater prey, the overall model considering the diet across all birds may be disproportionately weighted to freshwater prey. Incorporating priors in the model based on pre-existing knowledge linked to prey availability and foraging behaviours, such as time spent foraging in each location or the relative abundance of all possible food types, would likely produce more accurate estimates of diet. Future research should therefore include informative priors as well as train the

models on a wider variety of food sources from freshwater and terrestrial sources to improve our understanding of Lesser Yellowlegs diet in the region and variation among individuals.

Behaviour

Activity budget

The relative proportion of time that Lesser Yellowlegs spent foraging and inactive varied greatly among sites, and variation within sites was influenced by cloud cover. At Borden-Carleton, Lesser Yellowlegs consistently spent most of their time foraging and cloud cover had very little effect. Activities at Petit-Cap were more variable, but overall, they spent most of their time foraging, especially when there was a high amount of cloud cover. At the Retention Pond, birds were consistently more inactive but would sometimes spend more time foraging when there was a low amount of cloud cover.

Previous work suggests that cloud cover does not affect the activity of shorebirds on tidal flats (Burger, 1984), possibly because the response to the changing tide could mask the effect of cloud cover (Kasner, 1999). This conclusion is consistent with my results for Borden-Carleton but not Petit-Cap. It is possible differences between Petit-Cap and Borden Carleton in how the habitat responded to a falling tide were driving the effect of cloud cover in one site but not the other. It is also possible that they are foraging more with high cloud cover due to a trade-off between weather and predation risk. Other studies have found that Redshanks (*Tringa totanus*) spend a larger proportion of time foraging when it is cloudy because they need more food to thermoregulate (Hilton et al., 1999). However, foraging in the open can also put birds at risk from predators, particularly with cloudy skies when visibility is reduced (Hilton et al., 1999). It is therefore possible that Lesser Yellowlegs are foraging more in cloudy conditions at Petit-Cap but maintain consistent foraging rates at Borden-Carleton regardless of cloud cover due to differences in predation risk between the two sites. Future studies should investigate vigilance behaviour among sites to disentangle this potential interaction.

My finding that Lesser Yellowlegs foraged more when there was low cloud cover inland is supported by the findings of Kasner (1999), who studied inland wintering Least Sandpipers (*Calidris minutilla*) and found that they increased their use of water-covered sediment to forage when there were clear skies. At the Retention Pond, the water was quite cloudy, and sediment was stirred up very easily while walking (personal observation, 2022). It is possible that clear

skies made it easier for the birds to see their prey through the cloudy water than on days where the cloud cover was high, resulting in an increase in the time spent foraging.

I also found differences in the amount of time spent on each activity throughout the day. In the morning (8-11 am) and afternoon (2-5 pm), Lesser Yellowlegs spent more time inactive, but during the middle of the day (11 am-2 pm) they spent more time foraging. Other studies have found species-specific results for when shorebirds spend the most time actively foraging or inactive (Burger et al., 1997; Maron & Myers, 1985; McCarty et al., 2009; Ramli & Norazlimi, 2016). For example, Sanderlings (*Calidris alba*) were more inactive in mid-afternoon, and Buff-breasted sandpipers (*Tryngites subruficollis*) foraged more in the morning and evening relative to the afternoon (Maron & Myers, 1985; McCarty et al., 2009). Species-specific patterns suggest potential links to ecological traits, such as nocturnal behaviour.. Lesser Yellowlegs forage with similar frequencies during the day and night (Robert et al., 1989), potentially meaning individuals need to forage less in the morning and evening if they concentrate efforts around mid-day (this study) and at night. Variation in time spent foraging may also be linked to tide height, as many shorebirds exhibit a stronger association between foraging activity and tide height than time of day (Dodd & Colwell, 1998; Ramli & Norazlimi, 2016). However, since I did not include tide height in my analysis, due to the Retention Pond not experiencing tidal fluctuations, this is only speculative. Anecdotally, there were more Lesser Yellowlegs at the Retention Pond when there was a high tide on the coast, suggesting potential correlations between inland use and high tide. Overall, future work should incorporate nocturnal behaviour and associations with tide height, as well as investigate whether Lesser Yellowlegs use the Retention Pond when coastal tides are high for a more accurate picture of habitat use.

Foraging rates

I found no differences in foraging rates (when birds were actively foraging) between coastal and inland sites but noted that pecking rate was highest in the morning. Hence, while morning was not the period of highest foraging time, birds may have compensated for this by feeding faster during this time. Lesser Yellowlegs are mainly visual foragers during the day, but they do have some methods of tactile foraging, like probing and sweeping, that have been observed at low frequencies during the day (Nol et al., 2014). I also noted that overall, pecking rate was much higher than probing rate. This result contradicts findings by Bellefontaine (2020)

at Petit-Cap, who found that Lesser Yellowlegs peck and probe at similar rates. A reason for this discrepancy could be that they calculated pecking and probing rates per minute of observation time, whereas I calculated my rates per minute of time spent foraging to get an understanding of the intensity of foraging. My findings are supported, however, by the results of Nol et al. (2014), who also found that Lesser Yellowlegs have a much higher pecking than probing rate.

I also found relationships between pecking and probing rates and weather characteristics. I found that pecking rate increased as wind speed and humidity increased, but there was no effect on probing rate. One study also found an increase in pecking rate as wind increased, while another found no effect of wind on foraging activities in coastal areas (Burger, 1984; Beauchamp, 2006). Increased wind is associated with increased thermal demands and birds may respond by increasing their foraging rate (Beauchamp, 2006). I also found that pecking rate decreased, but probing rate increased as temperature increased. These results are supported by other studies that also found pecking rate decreases and probing rate increases as temperature rises (Nebel & Thompson, 2005; Beauchamp, 2006). The decrease in pecking rate and increase in probing rate may be in response to vertical migration of invertebrates through the sediment, as increasing sediment temperatures have been shown to cause invertebrates to bury deeper in the sediment (Hilton et al., 1999; Nebel & Thompson, 2005). The relationship with humidity is harder to explain, and there is no available literature on the subject, although it is possible that an interaction between air temperature, wind speed, and humidity affected the result.

Invertebrate availability

I found a positive relationship between pecking rates and total invertebrate availability, both in the top 0.5 cm layer of sediment and the total sediment column, at Petit-Cap and Borden Carleton, but at the Retention Pond there appeared to be no relationship. My results are consistent with work of Beauchamp (2009), who found an increase in foraging rate of Semipalmated Sandpipers (*Calidris pusilla*) as prey availability increased. Probing was not related to invertebrate abundance in either the bottom layer or all layers of the sediment. These results contradict a study by Wilson Jr. & Vogel (1997) who found that probing rate increased with invertebrate availability. Lesser Yellowlegs most commonly forage by pecking, using probing behaviours much less frequently (Nol et al., 2014), so it is possible that probing rate may not be affected by prey availability as clearly as pecking rate. Further, Lesser Yellowlegs also

have other foraging behaviours (sweeping, catching, and skimming) to target free-swimming invertebrates, flying insects and biofilm (Nol et al., 2014; Bellefontaine, 2020) that were not observed or part of this analysis. Further analysis should be done on these behaviours to see if they exhibit the same correlation with prey availability or site that pecking and probing do.

The correlation between pecking rate and prey availability at Petit-Cap and Borden-Carleton, but not at the Retention Pond, supports my previous findings that Lesser Yellowlegs primarily forage on the coast. Taken with the isotopic niche estimate, it provides a relatively clear picture of coastal habitat primarily being used for foraging and inland habitat primarily being used for resting.

Length of stay and movement

I found no differences in the lengths of stay between Lesser Yellowlegs that were caught on the coast and those caught inland. In both areas, birds remained in the region after capture for an average of about 16 days. It should be noted that this may underestimate the true staging duration of Lesser Yellowlegs in the region because birds were not necessarily captured immediately upon arrival. However, Neima et al. (2022) found that true length of stay of Semipalmated Sandpipers, another shorebird that stages in the region, is well represented by minimum length of stay estimates as presented here. Coastal birds appeared to have a more variable length of stay than inland birds. Variation in weight on capture may affect our measure of length of stay, as birds that have a higher fat mass may have arrived earlier and thus be closer to departure. With a relatively small sample size this is difficult to address but should be considered in future studies. Length of stay may also vary with the extent of movement while in the region, as a lot of movement between sites has been shown to increase length of stay in other species (Linhart et al., 2023).

Even though there were no differences in lengths of stay, the coastal and inland birds appeared to move around the region differently. Coastal birds primarily remained on the coast, while inland birds appeared to move between coastal and inland habitats. It appears that inland birds do not rely exclusively on inland habitats, but that coastal birds may rely heavily on coastal habitat. These results should be interpreted with caution, though, as the tower coverage in the region is lower on the coast than it is inland, so it is possible that inland birds use the coast more and we just failed to detect them. Similar lengths of stay between coastal and inland birds

suggest that different staging strategies can lead to similar staging times. This finding is in contrast to my prediction that birds that used inland sites would have longer lengths of stay but lends some support to the idea that these birds are using multiple sites while here, potentially for different staging needs.

Conclusion

Lesser Yellowlegs appear to move around the region is two main ways; one strategy uses habitat mostly on the coast and another strategy uses both coastal and inland habitat, but both strategies have similar lengths of stay. There are also no apparent differences in diet among the coastal and the inland birds and the isotope signatures suggest a mainly marine diet for most birds. The movement and diet data suggest that inland habitats alone are not enough to support these birds during staging, and they need coastal areas to meet the main goal of staging- gaining fat. These ideas are further supported by my results of behaviour and habitat use, where I found that although a lot of variation exists between sites due to cloud cover, overall, Lesser Yellowlegs spend more time foraging at the coastal sites and more time inactive at the Retention Pond. I found no difference in foraging rates among the sites but did find that Lesser Yellowlegs appear to be mostly visual foragers and have a much higher pecking rate than probing rate. I also found a relationship between invertebrate abundance and pecking rate, but not probing rate. This, and the results of the Bayesian mixing model could suggest that we are missing a part of their diet, and figuring out what is missing could provide a clearer picture between foraging rates and prey availability.

My results help to develop our understanding Lesser Yellowlegs' staging ecology in this region. We now know that there are two main strategies for movement around the region, and that they both help accomplish the goals of staging. We also know that they use coastal areas primarily for foraging and inland areas primarily for roosting. The Retention Pond was able to support large numbers of them while roosting, suggesting that constructed wetlands can supplement their use of natural wetlands, which could have important conservation implications.

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