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Avian Behavior, Ecology, and Evolution

Habitat use and local movement of staging Lesser Yellowlegs (*Tringa flavipes*) differ between coastal and inland habitat in Atlantic Canada

El uso de hábitat y los movimientos locales del Pitotoy Chico (*Tringa flavipes*) en paradas migratorias difieren entre hábitats costeros e interiores en el Atlántico canadiense

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ABSTRACT. Staging sites provide essential resources for migratory birds to build the energy stores required to fuel long-distance travel between breeding and non-breeding sites. Atlantic Canada is an important staging region for many high-latitude breeding shorebirds during southbound migration. In this region, Lesser Yellowlegs (*Tringa flavipes*) is observed in both marine coastal and inland freshwater habitats; however, a lack of understanding of how these different habitats are used makes it difficult to make effective species and habitat conservation decisions. We characterized local movement, habitat use, and foraging behavior of Lesser Yellowlegs at marine coastal sites near the Northumberland Strait and freshwater inland sites near the Bay of Fundy using automated radiotelemetry, focal behavioral observations, prey availability samples, and citizen science eBird data. Daily distance moved and overall minimum length of stay did not differ between individuals tagged at marine coastal and freshwater inland sites and individuals were rarely detected moving between the Bay of Fundy and Northumberland Strait, indicating potentially different migratory subpopulations. Coastal sites were used mainly for foraging, whereas roosting behavior predominated at freshwater inland sites. Despite higher proportions of time spent foraging at coastal sites, mean foraging rates when actively searching were similar across all sites, varying only with environmental variables, like cloud cover. Stable isotope analysis of blood plasma suggests similar diets, dominated by marine-derived prey, for all individuals regardless of tagging location. Taken together, these results suggest that staging Lesser Yellowlegs are using both coastal and inland habitat within localized areas to access different critical resources (i.e., foraging vs. resting). The use of multiple sites suggests the potential for flexible staging behavior spread across habitat types that may provide some resilience to climate and land-use change. However, the different functional uses of these sites for access to habitat-specific resources highlights the importance of retaining multiple habitat types across the landscape. This study broadens our understanding of Lesser Yellowlegs staging ecology in a region with little-to-no prior data on this species. We highlight the need to understand functional reliance on different habitats and consider staging site heterogeneity in conservation.

RESUMEN. Los sitios de parada migratoria proporcionan recursos esenciales para que las aves que migran acumulen las reservas de energía necesarias para recorrer largas distancias entre las áreas reproductivas y las no reproductivas. El Atlántico canadiense es una región clave de parada para muchas aves playeras que se reproducen en latitudes altas durante la migración hacia el sur. En esta región, el Pitotoy Chico (*Tringa flavipes*) se observa tanto en hábitats marinos costeros como en hábitats de agua dulce interiores; sin embargo, la falta de conocimiento acerca de cómo se usan estos diferentes hábitats dificulta la toma de decisiones efectivas para la conservación de la especie y su hábitat. Caracterizamos el movimiento local, el uso del hábitat y el comportamiento de forrajeo del Pitotoy Chico en sitios marinos costeros cercanos al Estrecho de Northumberland y en sitios interiores de agua dulce cercanos a la Bahía de Fundy, utilizando radiotelemetría automática, observaciones focales de comportamiento, muestreos de disponibilidad de presas y datos de ciencia ciudadana de eBird. La distancia diaria recorrida y la duración mínima total de permanencia no difirió entre individuos marcados en sitios marinos costeros e interiores de agua dulce, y rara vez se detectaron movimientos de individuos entre la Bahía de Fundy y el Estrecho de Northumberland, lo que indica potencialmente diferentes subpoblaciones migratorias. Los sitios costeros se usaron principalmente para forrajear, mientras que el comportamiento de descanso predominó en los sitos interiores de agua dulce. A pesar de que en los sitios costeros se dedicó una mayor proporción de tiempo al forrajeo, las tasas medias de búsqueda activa fueron similares en todos los sitios, variando únicamente con variables ambientales como la cobertura de nubes. El análisis de isótopos estables en plasma sanguíneo sugiere dietas similares, dominadas por presas de origen marino, para todos los individuos independientemente del lugar de marcaje. En conjunto, estos resultados sugieren que los Pitotoy Chicos en parada migratoria utilizan tanto hábitats costeros como interiores dentro de áreas localizadas para acceder a diferentes recursos críticos (es decir, alimentación vs. descanso). El uso de múltiples sitios sugiere un comportamiento de parada flexible distribuido entre distintos tipos de hábitat, lo que podría conferir cierta resiliencia frente al cambio climático y los cambios en el uso del suelo. Sin embargo, los diferentes usos funcionales de estos sitios para acceder a recursos específicos del hábitat destacan la importancia de conservar múltiples tipos de hábitats en el paisaje. Este estudio amplía nuestro entendimiento de la ecología de paradas migratorias del Pitotoy Chico en una región con pocos o nulos datos previos sobre la especie. Resaltamos la necesidad de comprender la dependencia funcional de diferentes hábitats y considerar la heterogeneidad de los sitios de parada en la conservación.

Key Words: *foraging behavior; Maritime Canada; migration and movement ecology; Motus radiotelemetry; shorebirds; stopover dynamics*

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INTRODUCTION

Each year, millions of migratory shorebirds travel from high-latitude breeding sites to their non-breeding grounds. Species that make trans-oceanic flights migrate in a series of "jumps," stopping once or twice for extended periods at staging sites to rebuild energy (fat) stores (Warnock and Bishop 1998, Warnock 2010). High-quality staging sites are critical to migratory success and survival because efficient mass gain allows birds to refuel and continue migration quickly, minimizing risk in unfamiliar habitats (Warnock 2010). Beyond refueling, shorebirds also use staging habitat to rest and roost (Linscott and Senner 2021). Because it may not be possible to meet all needs at a single staging site, migrating individuals may use multiple smaller sites within a larger region (Linhart et al. 2023). Studies of habitat use can inform conservation decisions by offering a better understanding of site dependency (i.e., habitat generalists vs. specialists) and the relative importance of smaller sites for different functional uses (Linscott and Senner 2021).

Lesser Yellowlegs (*Tringa flavipes*) is a species of long-distance migratory shorebird that breeds in open boreal forests of North America and winters in Central and South America (hereafter non-breeding grounds; Clay et al. 2012). At staging sites during southward migration, Lesser Yellowlegs use coastal habitats such as salt marshes, mudflats, and beaches, as well as inland freshwater habitats (Nisbet 1959, Hicklin 1987). Lesser Yellowlegs are generalist foragers, feeding on a wide variety of invertebrate prey (Andrei et al. 2009, Bellefontaine and Hamilton 2023), meaning they may be able to exploit resources in varied habitats. For example, a large proportion of their coastal diet consists of crustaceans, nereid polychaetes, and oligochaetes (Michaud and Ferron 1990, Pérez-Vargas et al. 2016), whereas they frequently consume diptera, coleoptera, and ephemeroptera in freshwater environments (Rundle 1982, Smith et al. 2012).

Lesser Yellowlegs have been assessed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2020) and populations have declined by 60–80% since the 1970s (Andres et al. 2012, McDuffie et al. 2022a, Smith et al. 2023). They are considered highly vulnerable to climate change (Bateman et al. 2020), have been identified as a priority for conservation in Canada (Hope et al. 2019, McDuffie et al. 2022a), and are part of the Road to Recovery initiative in North America (Road to Recovery 2022). Regional variation in declines is driven by a variety of factors, including loss of staging habitat to agricultural and commercial development, exposure to agrochemicals, unregulated hunting, and climate change (Clay et al. 2012, COSEWIC 2020). At staging sites, climate change can result in sea level rise, which threatens tidal wetlands (Thorne et al. 2018) and thus may reduce available staging habitat. Climate change can also lead to a higher frequency of extreme tidal events, which can submerge the roosting sites and engage staging shorebirds in over ocean flocking, increasing energetic costs and leading to longer lengths of stay (Mann et al. 2017). As populations continue to decline, it becomes imperative to better understand the species' behavior and habitat needs to determine which sites and areas are most important for staging, and if they are affected differently by climate change. During migration, a detailed knowledge of movement, habitat use, and foraging behavior is critical to develop effective strategies to mitigate the loss of staging habitat and to ensure the availability of a variety of habitats.

Foraging behavior can broadly indicate habitat use and resource availability while staging. Lesser Yellowlegs exhibit multiple foraging behaviors, but most commonly employ pecking and probing tactics (Bellefontaine and Hamilton 2023). They share some of their foraging behaviors with other generalist shorebirds but may avoid inter-specific competition by foraging in deeper water, which smaller shorebirds typically do not access (Novcic 2016, Bellefontaine and Hamilton 2023). Individuals are commonly observed foraging in water depths between 2.5 cm and 16 cm, which allows them to feed at a wider range of tidal heights than some smaller shorebirds that are restricted to foraging on exposed substrate or in very shallow water (Rundle and Fredrickson 1981, Baldassarre and Fischer 1984, Weber and Haig 1996, Ramli and Norazlimi 2016). Lesser Yellowlegs staging in the Atlantic Flyway are believed to forage primarily in coastal habitats. However, those that migrate through the Central Flyway are known to use freshwater ponds, wetlands, and floodplains during stopover, while a large proportion of individuals spend the non-breeding period at inland sites in the Argentine Pampas (McDuffie et al. 2022b). Thus, it is not unexpected that Lesser Yellowlegs migrating through the Atlantic Flyway and staging in Atlantic Canada would also use freshwater habitat in addition to coastal habitat. However, we currently know very little about how populations of Lesser Yellowlegs in Atlantic Canada allocate foraging effort between marine and freshwater habitats, the functional uses of these habitats, or whether there are sub-populations with greater affinities for certain habitats. Dependence on either type of habitat could increase vulnerability to habitat degradation (Clay et al. 2012), while flexible habitat selection through an ability to use multiple sites could improve adaptability and resilience.

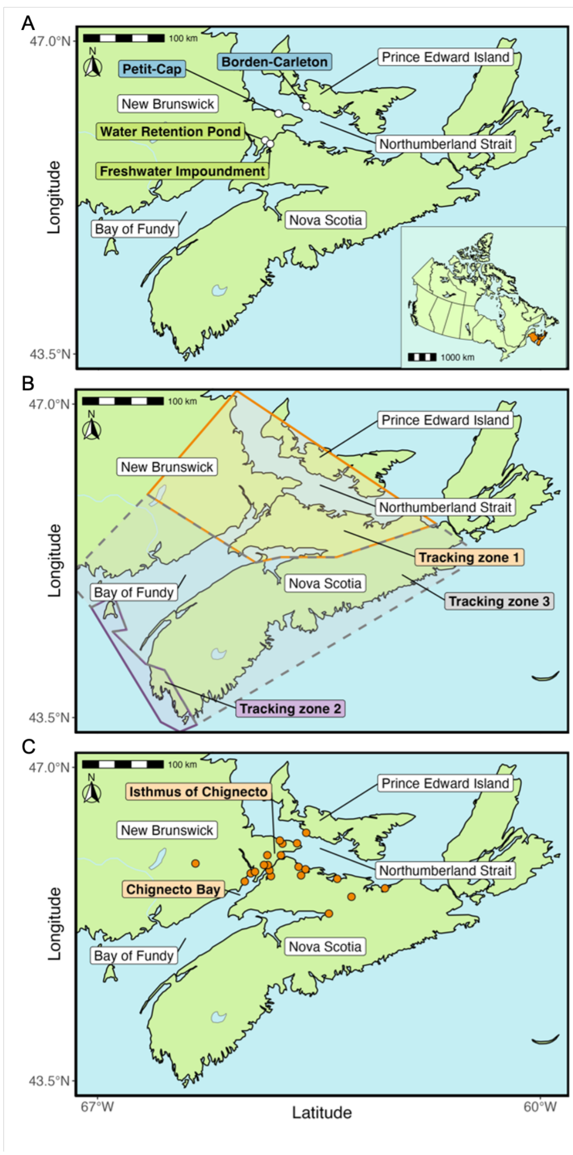
There are currently no studies on the importance of wetlands to Lesser Yellowlegs staging in Atlantic Canada, and in general staging ecology of this species is poorly understood. The objective of this study was to quantify local movement, habitat use, and foraging behavior of Lesser Yellowlegs staging at coastal and freshwater inland sites. At coastal and inland sites, we captured Lesser Yellowlegs and used the Motus Wildlife Tracking System to examine local movement. We also performed behavioral observations to better understand habitat use. We predicted that birds, regardless of tagging site, would use both coastal and inland habitats, but that coastal sites would be used primarily for foraging while inland sites would be used primarily for roosting. Other large shorebirds species, including members of the *Tringa* genus, exhibit this pattern of habitat use (Ramer 1985, Placyk and Harrington 2004). We also predicted that foraging rate would be higher on the coast due to our prediction that inland habitat would mainly be used for roosting. Given our prediction that all birds would use both types of habitat, we further expected overlap in dietary niches (reflecting similar prey trophic levels and marine versus freshwater influence), as well as similar movement patterns and length of stay because movement-related energy expenditure may affect time until departure (Mann et al. 2017, Linhart et al. 2023).

METHODS

Study sites

Our overall study region was the Canadian Maritimes, which we split into several subregions to aid the analysis and discussion of our habitat use and movement data. Specifically, we divided the region into three zones: (1) the central area around the Bay of Fundy and the Northumberland Strait, (2) southwest Nova Scotia, and (3) the area between these two regions (Fig. 1). The choice of these zones was based on previous research on shorebird movements in the region to delineate between staging relocation movements, which tend to occur within zones, versus departure flights that travel across zones and particularly along the Atlantic coast of Nova Scotia (Linhart et al. 2023). We further divided zone 1 into the northern area around the Northumberland Strait and the southern area around the upper Bay of Fundy. Within these two subdivided areas, we hereafter refer to sampling locations as sites.

Fig. 1. Map depicting our study sites and the relevant Motus towers within the region. (A) Coastal sites at which we captured and observed Lesser Yellowlegs (*Tringa flavipes*) are depicted in blue and inland sites in green. (B) Motus tracking zones used in the movement analysis. (C) Orange dots show Motus towers on which our birds were detected in the Isthmus of Chignecto and within the Bay of Fundy/Northumberland Strait zone.



We studied the behavior and habitat use of Lesser Yellowlegs at two marine coastal and two freshwater inland sites (Fig. 1A). The coastal sites were along the Northumberland Strait at Petit-Cap beach, New Brunswick (46° 11′ 06″ N, 64° 08′ 54″ W) and Borden-Carleton, Prince Edward Island (46° 16′ 27.1″ N, 63° 42′ 23.8″ W), representing tidal sand flats that were approximately 36 km apart and about 0.33 km² and 0.8 km² in size, respectively. The inland sites were near the upper reaches of the Bay of Fundy. These included a constructed wetland acting as a water retention pond in Sackville, NB (45° 53′ 35.9″ N, 64° 21′ 52.9″ W) and a drawn down freshwater impoundment near Aulac, NB (45° 51′ 00.0″ N, 64°16′ 48.0″ W), which were approximately 8 km apart and about 0.04 km² and 0.16 km² in size, respectively. Both inland freshwater sites were located within 5 km of the upper Bay of Fundy mudflats (Chignecto Bay) and within 25 km of the Northumberland Strait (Baie Verte) across the Isthmus of Chignecto. The two inland sites were also approximately 37 km and 63 km from the Petit-Cap and Borden-Carleton coastal sites, respectively. We caught Lesser Yellowlegs at all four sites, but behavioral observations were restricted to one coastal site (Petit-Cap) and one inland site (the inland retention pond), which are hereafter referred to as the coastal and inland sites, respectively. Both sites are consistently used by large numbers of Lesser Yellowlegs during the staging period, offering a good comparison of behavior and habitat use. Environmental characteristics of both sites are summarized in Appendix 1, Table A1.3.

Local movement

We captured Lesser Yellowlegs in 2022 between July 20 and October 11 using mist nets (38 mm mesh size) with playback and corralling. Birds were caught at the coastal sites (Petit-Cap and Borden-Carleton) between August 12 and October 11. Catching at the inland sites occurred between July 20 and August 24. Upon capture, birds were weighed either using a Pesola (± 0.5 g) or a digital scale (± 0.1 g). A field-readable alpha-numeric flag was attached to their upper right leg and a USGS band on their upper left leg for individual identification. We took blood samples by brachial venipuncture (27.5-gauge needle) and filled three 70 µL capillary tubes per bird to use for isotopic diet analysis. We measured bill length, tarsus length, and flattened, straightened wing chord length (± 0.1 mm). Birds were aged (juvenile or adult) by examining the tertials, back, and breast feathers for buffness and wear following Pyle (1997). We also measured fat score by blowing on the breast to determine the fullness and color of the furcular region on a scale from 0–7 (Meissner 2009).

Each bird also received a radiotelemetry tag with a 10.1 s burst rate (Lotek NTQB2-3-2- M) and a mass of 0.68 g, which was less than 0.82% of the average mass of birds caught (mean ± sd = 83.63 g ± 11.93 g). Tags were attached by cutting a small patch of feathers about two centimeters above the uropygial gland and adhering to the feather stubble with cyanoacrylate glue, allowing us to track individual movements throughout the region using the Motus Wildlife Tracking System (Taylor et al. 2017, Motus Wildlife Tracking System 2022). Motus towers in this region consist either of simple omnidirectional antennas, which have short detection radii (1 km) or more complex Yagi antennas with longer detection radii (20 km; Taylor et al. 2017). Detections represent presence of birds but cannot assess absences due to the signal strength being heavily influenced by bird activity, position relative to the horizontal axis of the tower antennae, and signal interference from vegetation. Therefore, we are unable to include variation in signal strength in our analysis and we consider all movement metrics as relative proxies of true movement behavior. Although there is evidence that tags can influence movement and migratory behavior, a review by Geldart et al. (2022) found that effects of dorsal glue-mounted radio tags were generally absent. Further, given the low proportional body mass of these tags in our study and the fact that they tuck fully under the feathers preventing aerodynamic issues, we are confident that the data generated reflect typical movements.

After returning from the field, blood samples that were stored in a cooler on ice 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 into a separate Eppendorf tube. Both fractions were then frozen at -20 °C for later analysis.

Foraging behavior and habitat use

We conducted standardized behavioral observations during the day (8:30–17:00) using focal sampling (Altmann 1974) at the coastal site (Petit-Cap) and the inland site (inland retention pond) between July 22, 2022 and September 19, 2022. Pairs of observers watched randomly selected individual birds for 2–5 minutes and recorded all behaviors on a hand-held voice recorder (Appendix 1, Table A1.1). None of the observations included previously tagged birds. This process was repeated for half of the birds in the flock, or the entire flock if fewer than five birds and we could confidently track which birds had already been observed, following Nol et al (2014). To obtain environmental data, we used a Kestrel 3000 (Kestrel Instruments, Boothwyn, USA) to measure average air temperature and humidity over the duration of the observation. After observations, we scored cloud cover from 1–10 by visually splitting the sky into 10 equal sections and then estimating the proportion covered by clouds. The sample size for focal behavioral observations was 20 birds at the coastal site and 36 at the inland site.

After we finished observing a flock, we collected sediment cores (8 cm diameter) from the location in which they were foraging. The cores were stratified to create sediment layers that were 0.5 cm, 1.5 cm, 3 cm, and 5 cm deep, allowing us to assess invertebrate type and density across depths. We sieved sediment samples from all locations with a 500 µm sieve and preserved retained material with 95% ethanol and Rose Bengal dye to more easily identify invertebrates (Mason and Yevich 1967). We counted and sorted invertebrates to the lowest identifiable taxon and calculated total abundance of invertebrates in each layer by summing counts of all taxa together. This method was used because Lesser Yellowlegs are thought to be diet generalists (Andrei et al. 2009, Bellefontaine and Hamilton 2023).

We pipetted 15 µl of blood plasma into pre-weighed aluminum capsules, which were then dried at 70 °C for at least 24 hours to meet the target mass of 0.800 0 mg (Mettler-Toledo MX5 microbalance; ± 0.001 mg). 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:

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

where a = the heavier isotope, X = the element of interest (nitrogen or carbon), and R = the ratio of heavy to light isotope.

Statistical analysis

All statistical analyses were performed in R version 4.3.2 (R Core Team 2023). We applied transformations to data that did not meet assumptions and used non-parametric tests if assumptions were still not met. All plotting was done using the R package ggplot2, version 3.5.0 (Wickham 2016).

Data downloaded from the Motus website were cleaned to remove any false detections. Detections were removed if deemed impossible (false) based on timing and distance moved, or if there were fewer than three consecutive detections (Crewe et al. 2020). We defined three Motus tracking zones, as described above (Fig. 1B): (1) the upper Bay of Fundy, Northumberland Strait, and the area between them (including the Isthmus of Chignecto; Fig. 1C), (2) southwestern Nova Scotia, and (3) all Motus towers between these zones. Previous tracking studies using the Motus network have found that some shorebird species either depart zone 1 via the eastern shore of Nova Scotia after staging, or reposition during staging to southwestern Nova Scotia, and resume staging there until final departure (Linhart et al. 2023; D. Hamilton and J. Paquet, *unpublished data*). Dividing Atlantic Canada into these tracking zones allowed us to examine only the daily distance moved within the upper Bay of Fundy and Northumberland Strait without including the long repositioning flights to southwestern Nova Scotia.

We calculated daily distance moved within the upper Bay of Fundy/Northumberland Strait zone as the relative distance traveled between towers per day, excluding the 24 hours prior to the onset of migration or repositioning to avoid confounding local and longer-distance movements. Each tower was considered the centroid of a small detection region, so daily distance moved is a relative measure of distance traveled for comparison among the studied population, not the absolute distance, and uncertainty around estimated distance values should be consistent among individuals. Detections were binned per minute and smoothed to avoid spurious back and forth movements between adjacent towers due to simultaneous detections. If birds were detected on two towers within the same one-min interval, a central point between the two towers was used in the relative distance calculation. Minimum length of stay was calculated for the upper Bay of Fundy/Northumberland Strait zone as number of days between the first detection and the last, excluding the last 24 hours. Most birds were first detected within three days of the day they were tagged. This minimum length of stay calculation method provides reasonable estimates of the true length of stay (Neima et al. 2022) and most birds showed clear signs of departure (movement into the Eastern shore of Nova Scotia and detections on Sable Island). We used a generalized linear mixed model (GLMM) with a Poisson error distribution in package lme4 (Bates et al. 2015) to test differences in daily distance moved between birds caught on the coast and inland. Before testing for differences in minimum length of stay, we removed birds detected after Hurricane Fiona (n = 4) to avoid a confounding storm effect (Fraser et al. 2025). Differences in minimum length of stay between birds tagged on the coast and inland were tested with a Wilcoxon rank sum test (R Core Team 2023). Age and date of capture were not significantly related to minimum length of stay and were therefore omitted from the model (Danyk 2023).

Activity budgets were calculated for each bird as the proportion of time spent foraging (all foraging behaviors and active searching), proportion of time spent inactive (standing, sleeping, and preening), and proportion of time spent active (walking, running, flying). Proportion of time spent foraging and inactive accounted for most of the time, so only foraging behavior was used for the analysis because inactive behavior essentially represented the inverse. Foraging rates were calculated as the number of pecks and probes per minute of foraging time. Pecking accounted for 72% of foraging behaviors (Danyk 2023), so only pecking rate was used for the analysis. We then ran multiple regressions for both proportion of time foraging and pecking rate as dependent variables, and site, time of day, air temperature, humidity, cloud cover (pooled as < ½ and > ½), time of behavioral observation from high tide, and invertebrate abundance in the top layer of sediment as predictors. We first checked for correlations between all predictors (all were < 0.71) and multicollinearity among time of day and the weather variables (all had variance inflation factors < 3.11), then we proceeded with an all subsets analysis of remaining variables. We used Akaike information criterion model selection with a correction for small sample sizes (AICc) and model averaging of models with a Δ AICc < 3 to determine a suite of predictors (Bartoń 2023).

Diets were compared between birds captured on the coast versus inland by visually assessing isotopic niche plots created with the SIBER package (Jackson et al. 2011) and then plotted in ggplot2 using the stat_ellispse function (Wickham 2016). Diet was also formally assessed with a PERMANCOVA of δ^{13}C and δ^{15}N against calculated fat mass, site type, and age as independent variables. We calculated fat mass by first 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 mass against fat score and tarsus length with both age classes pooled. Using the regression intercept and slope, we estimated lean mass for each bird given their tarsus length and setting fat score to zero. We then subtracted lean body mass from the total body mass as a measure of mass attributable to fat (Owen and Moore 2006, de Zwaan et al. 2022).

Effect of habitat type on Lesser Yellowlegs use

To understand broader scale patterns potentially driving Lesser Yellowlegs use of coastal versus inland habitats, we tested the influence of tidal height on relative abundance at our coastal and inland sites. Raw count data for each site were extracted from eBird using "auk" (eBird 2023, Strimas-Mackey et al. 2023). Data were filtered to retain only counts from July through September. Checklists were between 5 and 120 minutes long and distance traveled less than 2 km. Due to the recent construction of the inland retention pond, data were only available from 2020–2022. We considered 2021 and 2022 because only 6 checklists were submitted for 2020, compared to ~90 per year in subsequent years. Tidal height (meters) was extracted from the Canadian Tides and Water Levels Data Archive (Government of Canada 2023), using the closest station with hourly data. For the coastal site, we used the Cap Pelé station (46° 14′ 09.6″ N, 64° 15′ 39.6″ W) in the Northumberland Strait (~10 km distance) and for the inland site, the Pecks Point station (45° 44′ 31.2″ N, 64° 28′ 48.0″ W) in the Bay of Fundy (~18 km). Tidal height and abundance data were combined by hourly interval.

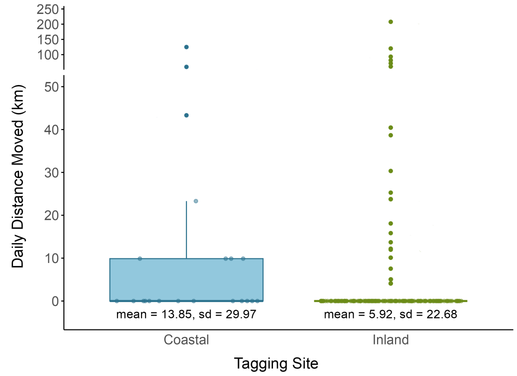
For coastal and inland sites separately, we fit a generalized linear model with a Poisson error distribution. Observed count was the response variable, tide height the predictor, and both ordinal date and year were covariates. Tide height was tested as both a linear and quadratic variable, and the best fit was determined using AICc.

RESULTS

Local movement

We obtained radio tracking data from 11 Lesser Yellowlegs tagged on the coast (5 adults and 6 juveniles) and 10 tagged inland (6 adults and 4 juveniles) between July 20 and October 11, 2022. Within the upper Bay of Fundy/Northumberland Strait zone, daily distance moved did not differ statistically between Lesser Yellowlegs tagged at the coastal (mean ± sd = 13.85 km ± 29.97 km) and inland sites (mean ± sd = 5.92 km ± 22.68 km); β = -1.12, $p = 0.11$; Fig. 2), despite average distances moved being nearly twice as large for coastal birds. A summary of detections by each tower can be found in Appendix 1, Table A1.2. All 11 birds tagged along the coast were detected in coastal habitats, while only two were detected in inland habitats for approximately 1 day. Of the 10 tagged inland birds, all 10 were detected in inland habitats and 4 were detected in coastal habitats around the Northumberland Strait for approximately 1 day. Only one juvenile individual that was originally caught on the coast repositioned to the southwestern Nova Scotia tracking zone. In the upper Bay of Fundy/Northumberland Strait tracking zone, it was detected for one day and moved less than one km. It was also only detected for 1 day in southwestern Nova Scotia (excluding the 24 hours before the final detection) and it moved just over 72 km.

Fig. 2. Boxplots depicting daily distance moved for the 17 Lesser Yellowlegs (*Tringa flavipes*) caught and tracked in coastal and inland sites. The horizontal lines represent the median daily distance moved, and the box extent represents the 25th and 75th quantiles. Each point represents a measure of distance moved on each day birds were detected; points are offset for clearer representation of data. Y axis is broken from 50–60 using the ggbreak package for easier visualization of the distribution (Xu et al. 2021).



Minimum length of stay in the upper Bay of Fundy/ Northumberland Strait zone for Lesser Yellowlegs was similar between coastal (mean ± sd = 14.26 ± 11.70) and inland (mean ± sd = 18.75 ± 4.54) tagging sites (Wilcoxon rank sum test: W = 26, p = 0.37), though there was more variability among coastal birds (Fig. 3).

Foraging behavior and habitat use

The AIC model selection identified seven models with reasonable support (AICc < 3) predicting the proportion of time spent foraging (Table 1). After model averaging, coefficients suggested that Lesser Yellowlegs decreased foraging effort as humidity increased at both coastal and inland sites (t = -3.26, p < 0.01; Fig. 4A), but coastal birds spent more time foraging (t = -4.45, p < 0.0001; Fig. 4B; Table 2). On the coast, mean proportion of time spent foraging was 0.47 ± 0.33 (mean ± sd), compared to 0.20 ± 0.32 inland.

For analysis of pecking rate, AICc model selection resulted in five models with reasonable support (Table 3), and following model averaging we found that air temperature, cloud cover, and humidity predicted pecking rate, but that site (inland versus coastal) was not a significant predictor (Table 4). Lesser Yellowlegs decreased their pecking rate per minute of foraging time as air temperature increased on the coast, but not inland (t = -3.81, p < 0.001; Fig. 5A). Across sites, pecking rate increased with humidity (t = 4.07, p < 0.001; Fig. 5B). When cloud cover was less than 50%, Lesser Yellowlegs had a higher pecking rate at the inland site compared to the coastal site, but lower on the coast when the cloud cover exceeded 50% (t = -2.46, p = 0.02; Fig. 5C). Coastal pecking rate was on average 17.07 ± 5.80 per min (mean ± sd), compared to 15.04 ± 6.91 inland.

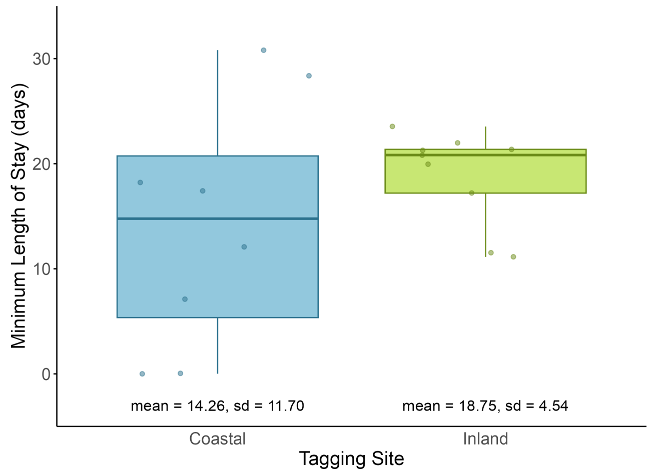
Based on stable isotope analyses, there was no evidence of a difference in diet for Lesser Yellowlegs captured on the coast versus those captured inland (F = 0.787, p = 0.427). Most birds from both coastal and inland sites had $\delta^{13}C$ levels between -20 and -16 (Fig. 6), suggesting prey of mostly marine origin. Similarly, there was little variation in $\delta^{15}N$, with most birds narrowly clustered in the 8 to 10 range.

After controlling for day of year, abundance of Lesser Yellowlegs was associated with tidal height at both the coastal and inland site. At the coastal site, the relationship was linear, indicating a decrease in abundance with higher tides in the Northumberland Strait (β = -0.92, p = 0.003; Fig. 7A). Inland, there was a quadratic relationship between relative abundance and tide height in the adjacent Bay of Fundy, with abundance increasing after a certain threshold (β = 1.50, p < 0.001; Fig. 7B).

DISCUSSION

Our results show that Lesser Yellowlegs tagged at two geographically distinct staging areas in the Bay of Fundy and Northumberland Strait exhibited localized movement and remained separated. In both staging areas, birds had similar foraging strategies and used both coastal and inland habitats. Results from foraging behavior observations suggested that birds in the two staging areas visited both types of habitats, but for different functions and to access different resources.

Fig. 3. Boxplots depicting minimum length of stay of Lesser Yellowlegs (*Tringa flavipes*) caught on the coast and inland, n = 17 birds. The horizontal lines represent the median minimum length of stay and boxes represent the 25th and 75th quantiles. Each point represents minimum length of stay for an individual bird; points are offset for clearer representation of data.



Habitat use

Our tracking data show that within the upper Bay of Fundy/ Northumberland Strait zone, birds caught on the Northumberland Strait coast and those caught inland near the upper Bay of Fundy moved similar distances per day. The tracking data also suggest that birds caught at coastal sites near the Northumberland Strait stayed in coastal habitat while birds caught at inland sites near the upper Bay of Fundy used inland habitat in the area. Because the diet and behavior data suggest that both groups of tagged birds foraged mainly on the coast, we believe that this tracking result is an artifact of gaps in coverage in the tracking array or missing detections due to variations in antenna length and signal strength. Further, although daily distances moved were not statistically different between both groups, the coastal birds moved nearly twice as much as the inland birds. This result is also likely an artifact of gaps in tower coverage and our low sample size. The Motus array on the Isthmus of Chignecto, between the upper Bay of Fundy and the Northumberland Strait coast, is extensive. Thus, we are confident that birds tagged at inland sites near the upper Bay of Fundy were not traveling across the Isthmus of Chignecto to use coastal habitat on the Northumberland Strait. However, Motus coverage along the upper Bay of Fundy tidal rivers, saltmarshes, and mudflats closest to our inland catch sites at the head of Chignecto Bay is limited, making it unlikely that birds using this stretch of the inner Bay of Fundy coastline would have been detected while there. This is further supported by anecdotal observations that suggest that Lesser Yellowlegs tagged at the inland sites near the Bay of Fundy did use closer coastal habitat along the upper Bay of Fundy (D. Hamilton, *personal observation*). Future studies should incorporate manual telemetry with a handheld receiver to better characterize movements between coastal and inland habitat and eliminate this gap.

Table 1. Results of multiple regressions of proportion of time spent foraging versus a suite of predictors. Models with Δ AICc smaller than three are presented. The full model contained proportion of time foraging against site, time of day, air temperature, humidity, cloud cover, invertebrate abundance in the top 0.5 cm of sediment, and time from high tide. Invert refers to invertebrate abundance and tide refers to time from high tide. Values to the left of the df column represent the estimated effect on proportion of time foraging of one unit of increase in the given continuous variable. A "+" indicates that the given categorical variable was included in the model.

Air temp	Cloud cover	Humidity	Site	Invert	Time	Tide	df	logLik	AICc	Δ	weight
		-0.009	+				4	-10.09	29.0	0.00	0.31
	+	-0.011	+				5	-9.65	30.5	1.55	0.14
		-0.009	+	-0.002			5	-9.71	30.6	1.66	0.13
-0.008		-0.009	+				5	-9.79	30.8	1.81	0.12
		-0.009	+			-0.003	5	-9.88	31.0	2.00	0.11
		-0.007	+		+		6	-8.70	31.1	2.16	0.10
-0.013		-0.009	+	-0.004			6	-8.93	31.6	2.63	0.08

Fig. 4. Plots depicting the relationship of humidity (A) and site (B) with proportion of time Lesser Yellowlegs (*Tringa flavipes*) observed at coastal and inland sites spent foraging, n = 56 birds. In plot A, the lines represent a linear trendline and shaded areas represent 95% confidence intervals. In plot B, the horizontal lines represent the median proportion of time spent foraging and boxes represent the 25th and 75th quantiles. Results of statistical comparisons are provided in the text. Each point represents a measure of proportion of time foraging; points are offset in B for clearer representation of data.

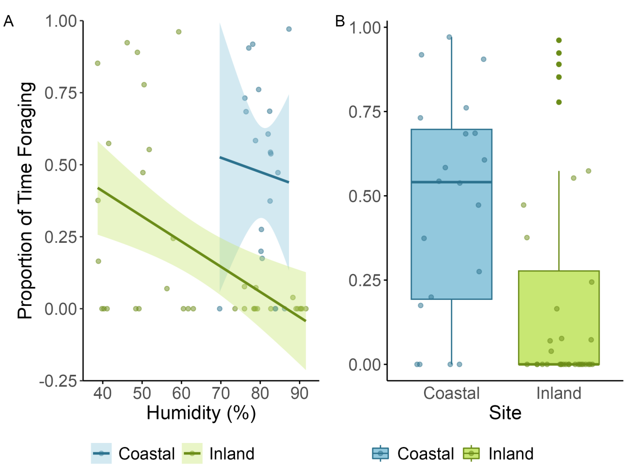


Table 2. Coefficients from conditional model averaging of a multiple regression containing proportion of time spent foraging against air temperature, humidity, site, cloud cover, invertebrate abundance in the top 0.5 cm of sediment, time from high tide, and time of day.

	Estimate	SE	z value	Pr(> |z|)
(Intercept)	1.26	0.30	4.10	< 0.001
Humidity	-0.01	0.003	2.86	0.004
Site (inland)	-0.44	0.10	4.31	< 0.001
Cloud cover (> ½)	0.10	0.11	0.88	0.380
Invert abundance (top 0.5 cm)	-0.003	0.003	0.96	0.339
Air temperature	-0.01	0.01	0.89	0.376
Time from high tide	-0.003	0.01	0.61	0.545
Time of day (mid-day)	0.05	0.11	0.47	0.635
Time of day (morning)	-0.12	0.12	0.94	0.348

Similarly, we are confident that birds tagged on the Northumberland Strait were not visiting inland habitat near the Bay of Fundy because they would have been detected while moving though the isthmus. Recent data from Lesser Yellowlegs tagged with Argos satellite transmitters at our coastal site on the Northumberland Strait shows that birds made local movements to other inland habitats closer to the tagging location, along the Northumberland Strait (up to approximately 4 km; D. Hamilton and J. Paquet, *unpublished data*).

Our results suggest that Lesser Yellowlegs staging at our field sites potentially represented at least two geographically distinct groups: (1) individuals who use coastal and inland habitat along the Northumberland Strait and rarely move into the Bay of Fundy, and (2) individuals who use coastal and inland habitat along the upper Bay of Fundy and rarely move into the Northumberland Strait. Although our findings are not conclusive, the relatively low daily distance moved by both birds tagged on the coast and birds tagged inland suggests segregation between the two groups. These results are consistent with Linhart et al. (2023), who found that some Semipalmated Sandpipers (*Calidris pusilla*) used staging habitat almost exclusively in the Bay of Fundy, while others used sites outside the bay and rarely traveled into the bay.

Dietary niche data further support our suggestion that birds tagged at coastal sites and those tagged inland used both marine and freshwater habitats. Plasma isotope analyses integrate dietary isotope signatures over roughly the week prior to sample collection (Hobson and Clark 1993). Isotope $\delta^{13}C$ levels are indicative of terrestrial/marine prey sources, with more enriched levels indicating a marine origin, and $\delta^{15}N$ levels are associated with trophic level, with higher values associated with a higher trophic origin of prey (Michener and Lajtha 2007). There were no notable differences in the blood plasma $\delta^{13}C$ and $\delta^{15}N$ levels between birds tagged on the coast and birds tagged inland, between juveniles and adults, and there was no relationship with fat mass (which suggests diets were not changing consistently as birds progressed through their staging period). The majority of $\delta^{13}C$ levels for birds tagged on the coast and inland fell between -20 and -16. This suggests a primarily marine diet with a small amount of freshwater influence because other shorebird species

Table 3. Results of multiple regressions of pecking rate versus a suite of predictors. Models with Δ AICc smaller than three are presented. The full model contained pecking rate per minute of foraging time against site, time of day, air temperature, humidity, cloud cover, invertebrate abundance in the top 0.5 cm of sediment, time from high tide, and an interaction between cloud cover and site. Invert refers to invertebrate abundance and tide refers to time from high tide. Values to the left of the df column represent the estimated effect on pecking rate of one unit of increase in the given continuous variable. A "+" indicates that the given categorical variable was included in the model.

Air temp	Cloud cover	Humidity	Site	Invert	Tide	df	logLik	AICc	Δ	weight
-0.828	+	0.270				5	-90.79	194.0	0.00	0.43
-0.787	+	0.354	+			6	-89.85	195.2	1.22	0.23
-0.768	+	0.257			0.110	6	-90.41	196.3	2.34	0.13
-0.889	+	0.291		-0.034		6	-90.60	196.7	2.72	0.11
-0.593		0.179			0.223	5	-92.26	196.9	2.94	0.10

Table 4. Coefficients from conditional model averaging of a multiple regression containing pecking rate per minute of foraging time against site, time of day, air temperature, humidity, cloud cover, invertebrate abundance in the top 0.5 cm of sediment, time from high tide, and an interaction between cloud cover and site.

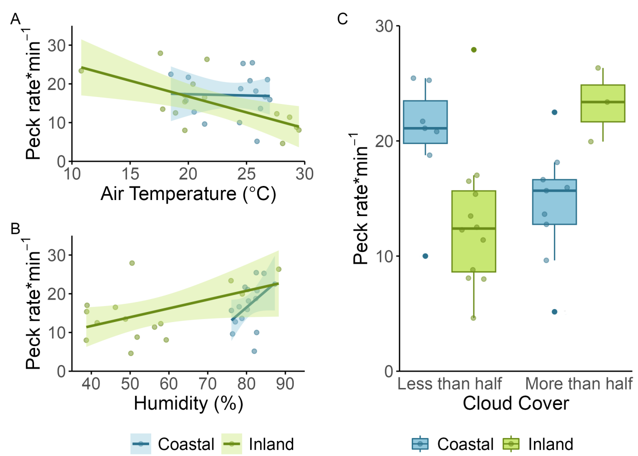
	Estimate	SE	z value	Pr(> |z|)
(Intercept)	16.88	7.40	2.20	0.028
Air temperature	-0.79	0.23	3.24	0.001
Cloud cover (> ½)	-5.61	2.40	2.24	0.025
Humidity	0.28	0.09	3.07	0.002
Site (inland)	3.55	2.78	1.22	0.224
Time from high tide	0.16	0.14	1.05	0.292
Invert abundance (top 0.5 cm)	-0.03	0.06	0.54	0.589

thought to have an entirely marine diet that were sampled at our coastal site previously clustered tightly between -16 and -15 (Linhart et al. 2022, Bellefontaine and Hamilton 2023). Short-billed Dowitchers (*Limnodromus griseus*), which are thought to have a more varied diet with both marine and freshwater influences have a $\delta^{13}C$ range between -25 and -16 (Bellefontaine and Hamilton 2023).

Minimum length of stay also did not differ between Lesser Yellowlegs tagged on the coast and those tagged inland. In both cases, birds remained in the Bay of Fundy/Northumberland Strait zone for an average of about 16 days after capture. However, minimum length of stay was more variable for birds tagged at coastal sites than for those tagged inland. Variation in mass on capture may have affected our measure of minimum length of stay because birds that have a higher fat mass may have arrived earlier and thus have been closer to departure. Our relatively small sample size prevented us from controlling for this statistically (as no relationships were detected), but it should be considered in future studies.

If we are correct that Lesser Yellowlegs tagged in this study represent two geographically distinct groups within the larger staging population (Northumberland Strait versus upper Bay of Fundy), the lack of difference in minimum length of stay suggests that these birds can successfully stage in multiple areas throughout the region. Furthermore, coastal habitats on the Northumberland Strait and in the Bay of Fundy likely provide similarly adequate resources for timely mass gain. Linhart et al. (2023) found that

Fig. 5. Plots depicting the relationship of air temperature (A), humidity (B), and cloud cover (C) with the pecking rate per minute of foraging time of Lesser Yellowlegs (*Tringa flavipes*) observed at coastal and inland sites, n = 31 birds. In plots A and B, the lines represent a linear trendline and the shaded areas represent 95% confidence intervals. In plot C, the horizontal lines represent the median pecking rate per minute of foraging time and boxes represent the 25th and 75th quantiles. Results of statistical comparisons are provided in the text. Each point represents a measure of pecking rate per minute of foraging time; points are offset in C for clearer representation of data.

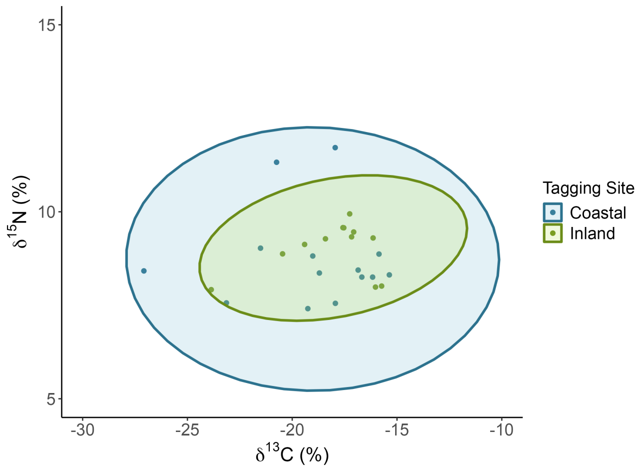


Semipalmated Sandpipers could gain mass effectively in both the upper Bay of Fundy and the Northumberland Strait, although birds staging in the Bay of Fundy remained in the region longer than those on the Northumberland Strait.

Foraging behavior

Lesser Yellowlegs spent a higher proportion of time foraging at the coastal site than they did at the inland site, suggesting that inland habitat may only be used as supplemental foraging habitat during high tide. Indeed, we found that bird abundance was greater at our inland site during high tide, while at the coastal site, Lesser Yellowlegs were generally absent at very low or high tide. These patterns are consistent with birds moving inland when

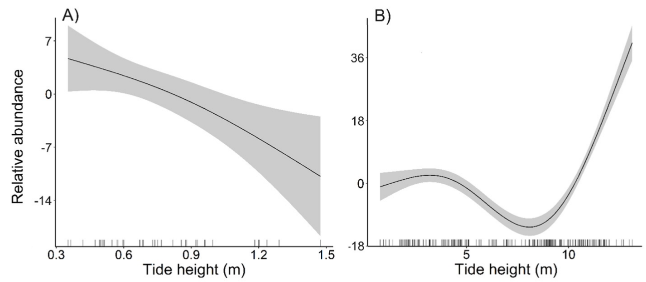
Fig. 6. Estimates of the isotopic niches of Lesser Yellowlegs (*Tringa flavipes*) caught at coastal and inland locations, using blood plasma δ^{13}C and δ^{15}N levels, n = 26 birds. Each point represents one bird, colored by tagging location, and the ellipses represent 95% confidence intervals of isotopic niches for each group.



water levels were not optimal for foraging. These results agree with previous work, in which multiple species of shorebirds, including other members of the *Tringa* genus, foraged more in coastal mudflats than the freshwater marsh habitat, which was primarily used for roosting (Putra et al. 2017). Common Redshank (*Tringa totanus*), which is closely related to Lesser Yellowlegs, has been found to switch between locations in estuaries, roosting inland at high tide and foraging on the coast at low tide (Greenstreet 1986). Strategies that allow birds to forage all day, regardless of tide height, would be beneficial for staging because the main goal is to gain fat stores in a short time-period (Burger et al. 1997).

Although pecking rate during periods when birds were foraging did not differ between coastal and inland sites, it appeared to be affected by cloud cover. When mostly sunny, pecking rates at the coastal site were higher than at the freshwater inland site, but when mostly cloudy the reverse was true. This difference could be driven by a trade-off between weather and predation risk. Foraging in the open, like on the coast, puts birds at risk from aerial predators, particularly with cloudy skies when visibility is reduced (Hilton et al. 1999). It is therefore possible that birds reduced their foraging rate and spent more time being vigilant on the coast to compensate for the lack of cover. Conversely, at our inland site, which has extensive shoreline vegetation, vulnerability may have been reduced as protective cover was nearby, so it remained safer to forage when cloudy. Most observations of foraging at our inland site saw Lesser Yellowlegs in close association with vegetation like cattails, which allowed them to quickly dart into cover in comparison to coastal sites where vegetative cover was often far away (K. Danyk, *personal observation*). Hilton et al. (1999) found that Redshanks spent a larger proportion of time foraging when it was cloudy because they needed more food to thermoregulate. As such, it is also

Fig. 7. The associations between relative abundance, derived from citizen science eBird observations, and tide height at the (A) coastal and (B) inland site. A relative abundance of zero is the average across all observations. Dashes along the X-axis represent observation samples. The shaded band is the 95% confidence interval of the partial residuals after controlling for day of year. Tide height represents measurements from the closest monitoring station, and thus differences in magnitude between the two sites are due to the inland site being closest to the megatidal Bay of Fundy and the coastal site closest to the Northumberland Strait, which has a much smaller tidal range.



possible that in our study, increased vegetative cover coupled with increased thermoregulatory demand from cloud cover (which was correlated with lower temperatures) caused the increased pecking rate at the inland site.

CONCLUSION

Lesser Yellowlegs populations are in decline, likely due to a combination of hunting in South America and loss of staging habitat (Clay et al. 2012). High quality staging habitat is critical to survival during migration (Baker et al. 2004), and it is important to have a detailed understanding of their staging ecology in this region to inform habitat conservation and buffer the effects of hunting. Our findings suggest that Lesser Yellowlegs rely on multiple habitat types for different functional uses during staging in the Canadian Maritimes. We found evidence of geographically distinct groups of staging Lesser Yellowlegs in the upper Bay of Fundy (Chignecto Bay) and on the Northumberland Strait. Furthermore, we found that both groups use coastal and inland habitat during their stay. Diet analysis revealed that most birds had a diet containing primarily marine sources, with some freshwater influence. The ability to successfully stage in multiple distinct areas throughout the region suggests that Lesser Yellowlegs may be more resilient to large-scale habitat loss while staging. However, the apparent dependence on both coastal and inland habitat for staging could leave them vulnerable to smaller-scale losses as coastal and inland habitats continue to be lost throughout the region. The scope of this study was not broad enough to determine if birds using habitat in the upper Bay of Fundy or the Northumberland Strait were part of different staging sub-populations, warranting future work with a larger sample size and more study sites.

Together, movement and diet observations suggest that coastal or inland habitats alone are not enough to support staging Lesser Yellowlegs. Instead, we highlight the predominant use of inland sites for roosting and coastal habitats for foraging, both of which are likely required to refuel and recuperate to continue migration. In support of this, individuals spent more time foraging at coastal sites compared to roosting or inactive at inland sites, indicating different functional uses. Additionally, at the population level, citizen science eBird data indicated that abundance inland increased with high tide at nearby coastal sites. This study improves our understanding of Lesser Yellowlegs staging ecology in the Canadian Maritimes, but due to the low sample size presented here, we recommend future studies to identify key sites and important habitats in this region. The Sackville retention pond, completed in 2020, supported large numbers of roosting individuals, suggesting that constructed wetlands can supplement natural wetlands, but an assessment of whether there are differences in site quality between natural and semi-natural habitat, as well as between different types of inland habitat, is needed.

Author Contributions:

The study was conceived jointly by all authors; KD led data collection, assisted by all other authors; KD and DRD designed and conducted the analysis, with contribution from DJH; KD led writing of the manuscript; all authors contributed to writing the manuscript, revising the drafts, and gave final publication approval.

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Data Availability:

Data and code are available at https://doi.org/10.5683/SP3/KKWVBG

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Appendix 1. Supplementary Information.

Table A1.1. Ethogram of Lesser Yellowlegs behaviors.

Behavior	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 and Recher 1969)
1	Intentional movement towards another bird, victim is displaced from foraging spot, victim may display defensive behaviors
2	Displacement events followed by pursuit, displacement events where the victim is forced to fly, standoff displays
3	Fighting

Table A1.2. Summary table of the number of detections per tower for birds tagged on the coast and inland. Tower region refers to whether the tower is associated with the Bay of Fundy (BoF) or Northumberland Strait (NuS). Tower name is the unique ID of each tower within the Northumberland Strait/Bay of Fundy zone. Inland represents the number of detections on each tower from birds who were tagged at the inland sites, and coastal represents the number of detections on each tower from birds who were tagged at the coastal sites.

Tower area	Tower name	Inland	Coastal
BoF	Amherst Point Migratory Bird Sanctuary	319	0
BoF	Atlantic Wildlife Institute	39	8
BoF	Beaubassin	144	0
BoF	Estabrooks	39	0
BoF	Hopewell2	13	0
BoF	Johnson's Mills	1	0
BoF	Mary's Point	6	0
BoF	Perry Settlement	16	0
BoF	Tantramar School	1 812	6
BoF	Truro	20	0
NuS	Allison (Johnston Point II)	0	131
NuS	Baie Verte2	34	184
NuS	Big Island	12	26
NuS	Borden-Carleton	0	6
NuS	Brule Point	14	66
NuS	Cape Jourimain	14	40
NuS	Johnstons Point	3	162
NuS	Kolbec	4	0
NuS	Linden2	5	50
NuS	Mount Thom	0	17
NuS	Pugwash	112	4

Table A1.3. Table of environmental characteristics at the coastal and inland behavior sites. Weather variables are averaged over the sampling period. The abundance and available biomass of the most common invertebrate groups are calculated as an average per m^2 of the four vertical core layers combined over the sampling period. Polychaete mass was provided by Angelozzi et al. unpublished data.

		Coastal (mean ± sd)	Inland (mean ± sd)
Weather	Temperature (°C)	23.77 ± 2.85	22.05 ± 4.55
	Humidity (%)	80.74 ± 4.03	64.30 ± 18.74
	Cloud cover	5.70 ± 2.60	6.00 ± 3.21
Invert abundance (number/m^2)	Bivalve	14 658 ± 19 509	298 ± 281
	Gastropod	166 ± 115	174 ± 95
	Polychaete	1 724 ± 2284	0.00 ± 0.00
	Oligochaete	0.00 ± 0.00	6 977 ± 3 364
	Chironomid	0.00 ± 0.00	3 011 ± 3 831
Invert available biomass (g/m^2)	Bivalve	24.48 ± 31.33	0.00 ± 0.00
	Gastropod	0.00 ± 0.00	1.03 ± 0.49
	Polychaete	0.50 ± 0.87	0.00 ± 0.00
	Oligochaete	0.00 ± 0.00	0.78 ± 0.36
	Chironomid	0.00 ± 0.00	0.97 ± 1.32

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