Shorebirds exhibit niche partitioning on multiple dimensions at a small staging site on the Northumberland Strait, New Brunswick, Canada

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Abstract

Animal populations take advantage of environmental heterogeneity to partition themselves into microhabitat niches. Such partitioning plays an important role in regulating interspecific competition and community structure by allowing multiple species to coexist. Atlantic Canada has many small coastal staging sites that host southbound migrant shorebirds. However, most shorebird studies in the region have been focused on larger sites in the Bay of Fundy, resulting in limited knowledge about staging ecology at these small sites, which often host more diverse shorebird assemblages. We examined niche partitioning by shorebirds on the Northumberland Strait, New Brunswick, Canada, to better understand how small coastal staging sites support diverse shorebird populations. We found evidence of partitioning on three niche dimensions: space, foraging behaviour, and diet. Most species specialized in at least one dimension, with foraging constraints based on bill morphology and habitat access based on species size likely driving segregation. Environmental heterogeneity at sites on the Northumberland Strait created multiple dimensions for segregation and fulfilled the niche requirements of diverse shorebird species during migratory staging. These findings broaden our understanding of staging ecology of multispecies flocks and suggest that conservation of small coastal sites is important for success of migratory shorebirds in Atlantic Canada.

Key words: shorebirds, niche partitioning, foraging behaviour, staging ecology

Introduction

Niche partitioning is the process by which species compress their realized niche to limit overlap with potential competitors. Animal populations use environmental heterogeneity to partition themselves into microhabitat niches, and thus avoid competitive exclusion from resources (MacArthur 1958). Niche partitioning allows for the fulfillment of more functional roles in species-rich communities, thus increasing total resource consumption (Finke and Snyder 2008). Migratory shorebirds (order Charadriiformes) often forage in mixed-species flocks. These different species have a variety of morphological features that are adapted for different diets and foraging strategies (Chandler 2009), leading to enhanced resource partitioning and narrowing of niches (Bocher et al. 2014). Shorebirds undertaking costly long-distance migrations need to replenish fat stores by foraging at a restricted set of staging sites along their migration route (Schaub and Jenni 2000). Because high-quality staging areas are limited (Meyers et al. 1987; Fiala 2009), most host multiple species concurrently. Under these circumstances, niche partitioning by multispecies flocks during migratory staging may be an important mechanism for optimizing resource consumption unless resources are superabundant and competition is limited (Choi et al. 2017).

To coexist in a diverse community with limited space or resources, shorebirds should partition themselves on multiple niche dimensions, as interspecific competition is the main driver of niche segregation (Wiens 1992). Foraging behaviour, habitat, and diet are common and important dimensions for niche segregation in shorebirds (e.g., Burger et al. 1977; Davis and Smith 2001; Novcic 2016; Faria et al. 2018). However, these dimensions are rarely independent, and coexisting species likely exhibit varying degrees of overlap in more than one dimension (Schoener 1974). Therefore, a multidimensional approach is most effective for examining niche partitioning in diverse communities.

Shorebirds exhibit a range of foraging strategies, often varying with bill morphology (Barbosa and Moreno 1999; Dit Durell 2000; Norazlimi and Ramli 2015). This variation can facilitate resource segregation by limiting the accessible depth of buried prey (Bocher et al. 2014). Pecking, wherein shorebirds access prey on or near the sediment surface (Barbosa and Moreno 1999; Dit Durell 2000), is common in birds with short bills. Probing is facilitated by longer bills (Barbosa and Moreno 1999), which allows shorebirds to access prey buried deeper in the sediment (Dit Durell 2000). Skimming and grazing behaviours are used by several species of Calidrid sandpipers (Kuwae et al. 2008; MacDonald et al. 2012) to scrape

biofilm off the sediment surface with specialized spines on the tongue (Elner et al. 2005; Kuwae et al. 2012). Although foraging behaviour and bill morphology are commonly used proxies for resource consumption, they do not always predict diet partitioning (Kent and Sherry 2020), and there is considerable variability in the degree of diet partitioning among species (Bocher et al. 2014). Shorebirds often have broad diets and opportunistically forage on the most available prey at migratory stopover sites (Davis and Smith 2001; Andrei et al. 2009; MacDonald et al. 2012; Gerwing et al. 2016); therefore, many coexisting species consume similar prey taxa (Skagen 1997). In these circumstances, foraging strategies often cause segregation of size or depth of prey (Bocher et al. 2014).

Environmental factors can also influence resource segregation. Sediment characteristics affect the efficacy of foraging strategies (Van Dusen et al. 2012), as coarse, resistant sediments inhibit probing shorebirds from reaching buried prey (Finn et al. 2008). This reduces prey availability even if prey is abundant. The presence of standing water reduces prey availability for small shorebirds (Iola et al. 2000), creating spatial segregation between large and small shorebird species (Davis and Smith 2001; Novcic 2014). As a result, greater environmental heterogeneity within a stopover area increases species richness by fulfilling the niche requirements of more species (Danufsky and Colwell 2003) and can facilitate spatial segregation of shorebirds into microhabitats with suitable foraging conditions (Davis and Smith 2001).

Coastal areas of Atlantic Canada provide important staging habitat for shorebirds on southbound migration. The Bay of Fundy is well established as a critical staging site, especially for Semipalmated Sandpipers (*Calidris pusilla*) (Hicklin 1987; Neima et al. 2020, 2022). However, coastal sites outside the Bay also provide important habitat for a wide range of species (Atlantic Canada Shorebird Survey 2022). These smaller sites have received less attention, but recent and ongoing work suggest that they can support birds as they prepare for migration (Doiron 2021; Linhart et al. 2022, 2023). Coastal staging sites on the Northumberland Strait in New Brunswick, Canada, host a diverse shorebird community that, in late summer, includes Semipalmated Sandpipers, White-rumped Sandpipers (*Calidris fusicollis*), Semipalmated Plovers (*Charadrius semipalmatus*), Greater and Lesser Yellowlegs (*Tringa melanoleuca* and *Tringa flavipes*), Least Sandpipers (*Calidris minutilla*), and Short-billed Dowitchers (*Limnodromus griseus*) (Atlantic Canada Shorebird Survey 2022).

Shorebird populations have declined by an estimated 37% since the 1970s (Rosenberg et al. 2019). Long-distance migrants show even greater losses and tend to fall under higher conservation concern (Hope et al. 2019; NABCI 2019). Given the importance of shared stopover sites (Hutto 1998; Newton 2004; Anderson et al. 2019; McKellar et al. 2020), understanding niche partitioning at these sites will enhance our ability to implement appropriate conservation measures. We examined niche partitioning at two shorebird staging sites on the Northumberland Strait, New Brunswick, Canada. Our objective was to examine the various niche dimensions on which shorebirds may partition to better understand staging ecology of shorebirds at small coastal sites in the face of inter-

Fig. 1. Map of study sites on the Northumberland Strait in New Brunswick, Canada. Petit-Cap: 46.19°N, −64.15°W, ~80 ha; Cape Jourimain: 46.15°N, −63.85°W, ~20 ha. Made with Natural Earth. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.
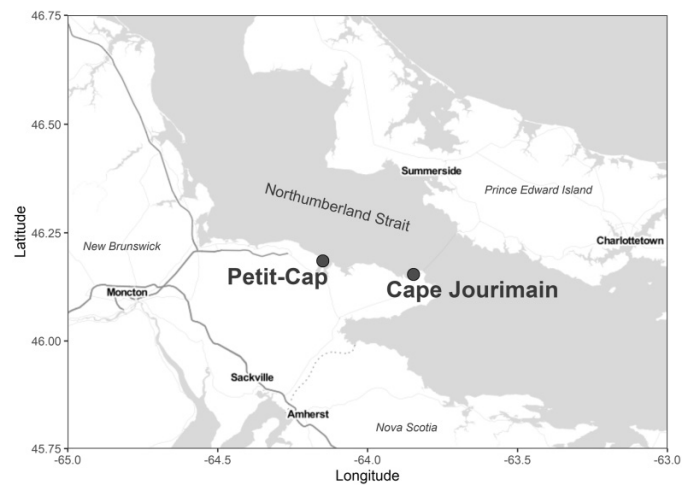
specific competition and population declines. Therefore, we are addressing the following research questions: (1) Is niche partitioning present in shorebird populations at coastal sites on the Northumberland Strait? and (2) On what niche dimensions do shorebird species partition themselves to reduce interspecific competition and increase resource consumption?

Methods

Study area

We examined staging ecology of shorebirds at Petit-Cap (PCAP) and Cape Jourimain (CJ) on the Northumberland Strait in New Brunswick, Canada (Fig. 1). Behavioural observations and habitat samples were taken at both sites, but shorebirds were captured only at PCAP.

We used a stratified random sampling design to sample the mud- and sandflats at PCAP and CJ to estimate prey availability. Transects were 300 m long, and ran perpendicular to shore, starting at the high tide line. At CJ, we placed three transects 100 m apart. At PCAP, we placed two transects facing the ocean on the open side of the barrier beach, 400 m apart, and three transects facing the interior flats, 100 m apart. We collected invertebrate and biofilm samples from two random points within each 100 m stratum, for a total of six samples per transect. We replicated transect sampling early (July 17–18, 2019) and late (September 6–12, 2019) in the season using different sets of random points.

We collected invertebrate samples with a 5.5 cm diameter sediment core, and sieved samples through 500 μm mesh to remove sediment. Retained invertebrates were stored in 95% ethanol until they could be sorted by taxon. Sorted invertebrates were dried at 90 °C for at least 24 h (40GC Gravity Convection Oven, Quincy Lab Inc., Chicago, IL) and then weighed. Following weighing, shelled invertebrates (phylum Mollusca) were ashed at 550 °C for 2 h (Isotemp Programmable

Muffle Furnace 650-750 Series, Fisher-Scientific, Waltham, MA) to burn off consumable biomass and reweighed. The difference between pre- and post-ashing mass (ash free dry mass) was used to estimate consumable biomass.

Foraging behaviour

We observed foraging behaviour of shorebirds between June 17th and October 9th, 2019 at PCAP and CJ. Behavioural observations took place throughout the day during periods when tidal flats were exposed. We observed foraging behaviour of flocks with more than five individuals and recorded whether the flock was foraging in a puddle. We used focal animal sampling (Altman 1974) to estimate pecking and probing rates of foraging shorebirds by recording the number of times an individual shorebird pecked or probed for a maximum of 1 min. Focal animal samples were taken on each bird in a flock, or until the flock flew away. We also simultaneously performed scan sampling (Altman 1974) on the same shorebird flocks to determine the average number of individuals of each species in the flock throughout the focal observation period. This method was used to account for individuals joining or leaving the flock throughout the sampling time.

After collecting behaviour observations, we took two invertebrate samples from the location at which each flock was seen foraging, following the methods described for transect sampling. Flocks were flushed to take samples, or in the case flocks flushed during observations due to disturbance or unknown reasons, we sampled invertebrates immediately after flushing to ensure the most accurate representation of the prey base being consumed. At each foraging location, we also measured the penetrability of sediments (Gerwing et al. 2020) and collected two sediment samples and four biofilm samples. Sediment samples were used to analyze sediment particle size and water content, and were collected using 3 cm diameter vials pressed approximately 8 cm into the sediment. We recorded the wet weight of a small, homogenized subsample of each sediment sample, then dried at 90 °C for at least 24 h and reweighed. We calculated the proportion water content in each sample as (wet mass − dry mass)/wet mass. We sieved the remaining sediment in each sample through a cascade of 850, 500, 250, 125, and 63 μm mesh sizes, and collected water and suspended sediment that flowed through all mesh sizes in a bucket under the finest sieve, termed the pan fraction. A particle size profile for each sample was calculated by drying and weighing material from each fraction, and calculating the proportional contribution of each fraction. Pan fraction sediment mass was estimated by collecting a 20 mL subsample from the well-mixed water and sediment suspension, drying and weighing that sediment, and scaling up the mass to reflect the total volume in the pan fraction.

Biofilm samples consist of the top 2 mm of sediment, collected using a modified 10 cc syringe following Coulthard and Hamilton (2011). We measured chlorophyll a (Chl a) concentration, a proxy for biofilm standing crop, from each sample. Sediments were freeze dried at −50 °C and 0.05 mBar (FreeZone one-liter benchtop freeze drier, Labconco Corporation, Kansas City, MO) for a minimum of 5 h. We extracted Chl a from a 0.2 g subsample of the sediments with 5 mL of

3:2 90% acetone to dimethyl sulfoxide for 30 min (Shoaf and Lium 1976). We centrifuged samples for 20 min at 2500 rpm (Thermo Fisher Scientific Model No. 225A, Waltham, MA; Hettick MIKRO 120, Beverly, MA) to separate the extracted Chl a solution before measuring Chl a concentration with fluorometric techniques (Welschmeyer 1994) (10 AU Chl a Fluorometer, Turner Designs, San Jose, CA). We converted Chl a concentration from relative fluorescence units (RFU) to μg/L using the calibration curve $y = 7.064x - 0.7656$, where $y =$ RFU and $x = $ μg/L. We then calculated concentration of Chl a per gram of sediment using the following formula:

$$\frac{[\text{Chl } a] \, (\mu g/L) * \text{Extraction volume (L)}}{\text{Mass of sediment (g)}} = \frac{\mu g \, \text{Chl } a}{g \, \text{sediment}}$$

Catching and sampling shorebirds

To collect blood plasma samples for analysis of stable isotopes of ^{15}N and ^{13}C, we captured Semipalmated Sandpipers, White-rumped Sandpipers, Semipalmated Plovers, Short-billed Dowitchers, and Least Sandpipers at PCAP between August 1st and September 13th, 2019. We set up mist nets in arrays across the intertidal zone and captured birds at night when tides were appropriate. Shorebirds were weighed upon capture, and we collected approximately 140 μL of blood from the brachial vein of those that met species-specific minimum weight requirements (Table 1). Shorebirds arrive at staging sites light and become heavier over time as they forage (Tsipoura and Burger 1999; Quinn and Hamilton 2012). Plasma isotope levels reflect diet in approximately the previous week (Hobson and Clark 1993). Therefore, restricting sampling to birds with moderate levels of body fat compared with lean mass estimates (Anderson et al. 2019) coupled with the rapid turnover of plasma helps to ensure plasma samples reflect diets of shorebirds during their stopover in the region. Following bleeding, we fitted shorebirds with aluminum USGS bands on the upper left leg and field-readable alphanumeric flags on the upper right leg and took morphometric measurements for ongoing shorebird banding initiatives, and then released the birds. Blood samples were stored on ice. After returning from the catching site, we centrifuged blood samples for 1 min at 6300g (mySPIN12 Mini Centrifuge, Thermo Scientific) to separate plasma and red blood cells (RBCs). Separated plasma and RBC samples were stored at −20 °C until further analyses. All methods of catching and sampling shorebirds were reviewed and approved by the Mount Allison University Animal Care Committee prior to commencement of the research and adhere to guidelines provided by the Canadian Council for Animal Care.

Diet analysis

We collected 139 blood plasma samples from shorebirds of various species at PCAP for analysis of stable isotopes of ^{13}C and ^{15}N. Briefly, δ^{13}C values reflect prey origin (e.g., terrestrial prey are more enriched than marine organisms), and δ^{15}N values reflect trophic level, with higher values found in organisms from higher trophic levels (Kelly 2000). While we did not also collect samples from birds at CJ, we know from previous work in the region that shorebirds make frequent, short

Table 1. Details of shorebird capture and blood sampling for stable isotope analysis at Petit-Cap, New Brunswick, Canada in 2019.

Species (common name)	Captured (N)	Minimum weight for stable isotope analysis (g)	Blood samples for analysis (N)
Semipalmated Sandpiper	229	30	82
White-rumped Sandpiper	57	45–48	20
Least Sandpiper	27	25	3
Semipalmated Plover	46	50	20
Short-billed Dowitcher	16	No minimum	15

movements between these and other sites in the Northumberland Strait (Doiron 2021; Linhart et al. 2023). This, coupled with the fact that the prey base does not differ significantly between PCAP and CJ (Linhart et al. 2022), suggests that plasma isotopes of shorebirds captured at PCAP likely reflect diets across a range of local foraging habitats.

We dried plasma samples at 70 °C for at least 24 h. The target weight for analysis of both $\delta^{13}C$ and $\delta^{15}N$ from blood plasma was 0.800 mg. We subsampled dried plasma samples using a Mettler-Toledo MX5 microbalance with readability to 0.001 mg, and subsamples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ signatures at the Environmental Analytics and Stable Isotope Laboratory at Mount Allison University in Sackville, New Brunswick, Canada, using an Elementar PyroCube Elemental Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) and an Isoprime Precision Isotope Ratio Mass Spectrometer (Elementar UK Ltd, Cheadle, UK). Delta values of isotope signatures are a relative isotope ratio of the sample to international standards based on the following formula:

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

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

Statistical analyses

Analyses were performed using R (version 4.0.3) with RStudio interface. Nonparametric methods were used as data failed to meet parametric assumptions. Dissimilarity matrices were created using the Bray–Curtis method unless otherwise specified. Data were plotted using the "ggplot2" package (Wickham 2016). Test statistics were compared with an alpha of 0.05. We adjusted the alpha level with the Holm's sequential Bonferroni procedure (Holm 1979; Abdi 2010) for multiple comparisons within datasets.

We fourth root transformed the abundance of shorebird species in each observed flock to improve consideration of rare species. We used a permutational multivariate analysis of variance (PERMANOVA) in the R package "vegan" (Oksanen et al. 2020) to compare species composition between flocks foraging in and out of tide pools (permutations = 999). We then performed a similarity percentage (SIMPER) analysis to compare the contributions of each species to the dissimilarity in species composition. Using untransformed abundance

data, we calculated the mean and standard error of the abundance of each species in and out of tide pools.

We examined spatial variation in prey availability on the Northumberland Strait using data collected from transects at PCAP and CJ. We grouped prey into the following taxonomic groups: amphipods, bivalves, decapods, gastropods, polychaetes, and meiofauna. Shelled prey >12 mm long were excluded as they are too large to be consumed by most shorebirds in our study (Kober and Bairlein 2006). We performed a nested PERMANOVA (R package BiodiversityR; Kindt and Coe 2005) with transect nested in site to examine spatial variation in prey availability (permutations = 9999). We used a Mantel test (R package vegan; Oksanen et al. 2020) to test for a relationship between flock species composition (based on average number of individuals of each species in the flock during scans of that flock) and the available prey community where the flock was observed foraging (permutations = 99 999; correlation method = Spearman's coefficient). This was performed with a Bray–Curtis dissimilarity matrix of shorebird species abundances in each flock, and a Euclidean distance matrix of biomasses of prey taxa collected from the location each flock was foraging.

We analyzed foraging strategies of seven shorebird species; however, Greater Yellowlegs and Lesser Yellowlegs were pooled together as "Yellowlegs". Pecking and probing rates were calculated in actions per minute. We used a permutational multivariate analysis of covariance (PERMANCOVA) to examine differences among species in foraging rates while controlling for habitat covariates (permutations = 9999). The full model tested pecking and probing rates against species and nine covariates: availability of six prey taxa, Chl a concentration, and two components extracted from a principal component analysis of sediment characteristics. Species composition of the flock was also considered as a covariate, but was nonsignificant (Table S1), so it is not included in the main model to improve sample size (one flock lacked composition data). The first component primarily reflected sediment water content and the second sediment particle size. We removed nonsignificant covariates and reran the model. We compared the multivariate dispersions of foraging strategies between species using the permutest function (vegan package; permutations = 9999; Oksanen et al. 2020). Data were square root transformed prior to plotting to improve visualization of results. We performed 15 pairwise PERMANCOVAs using the covariates from the reduced model to compare foraging strategies between each species (permutations = 9999), with critical alpha levels corrected for multiple comparisons.

Table 2. Results of SIMPER analysis to determine contributions of species to differences in flock composition detected by PERMANOVA.

Species	Tide pool		Not tide pool		Diss./SD	Contribution (%)
	Mean	SD	Mean	SD		
Semipalmated Sandpiper	8	9.7	18	10.8	1.14	20.7
Short-billed Dowitcher	12	21.1	1	3.0	1.03	19.1
Semipalmated Plover	3	3.8	10	9.6	1.22	18.6
Yellowlegs spp.	9	9.6	10	14.4	1.08	17.8
White-rumped Sandpiper	2	4.0	2	3.5	1.09	12.5
Least Sandpiper	3	5.8	0.3	0.5	1.08	11.3

Note: Data were fourth root transformed prior to analysis. Mean and standard deviation (SD) are calculated from untransformed abundance data ($N = 20$). Diss./SD is the average contribution of a given species to between-group dissimilarity divided by its SD of the contribution. Values exceeding 1 represent a meaningful contribution.

Isotopic values of δ^{13}C and δ^{15}N were measured from Semipalmated Sandpiper, White-rumped Sandpiper, Least Sandpiper, Semipalmated Plover, and Short-billed Dowitcher plasma (Table 1). Too few Least Sandpipers were sampled to be included in analyses, and one Semipalmated Sandpiper sample was excluded as the height of its N_2 mass spectrometry peak fell below quality assurance limits. We visually inspected plasma isotope data to ensure individual birds' isotope signatures did not vary with bird mass, which might have suggested influence of prey from elsewhere in the range (Catry et al. 2022). We used a PERMANOVA to test δ^{13}C and δ^{15}N against species (permutations = 9999) and a permutest (permutations = 9999; Oksanen et al. 2020) to compare multivariate dispersions of δ^{13}C and δ^{15}N among species. We plotted the isotopic diet niches using ggplot2, following the methods of stable isotope Bayesian ellipses in R (R package SIBER; Jackson et al. 2011).

Results

Habitat segregation

Species composition of flocks of foraging shorebirds varied between areas with and without available tide pools (PERMANOVA, $F_{1,19} = 4.76$, $p = 0.02$). Semipalmated Sandpipers and Semipalmated Plovers were most abundant outside of tide pools, while Short-billed Dowitchers were most abundant in tide pools (Table 2). The remaining species had similar abundances in both habitats (Table 2). SIMPER analysis showed that the contribution to dissimilarity in species composition between flocks observed in and out of tide pools was similar among species except that White-rumped Sandpipers and Least Sandpipers, which were less abundant overall, contribute slightly less than other species (Table 2). Non-metric multidimensional scaling (NMDS) ordination separates flocks with a high abundance of Short-billed Dowitchers and Yellowlegs (both long-legged birds) from those with a high abundance of the smaller Semipalmated Plovers and Calidrid sandpipers (Semipalmated, Least, and White-rumped Sandpipers) (Fig. S2).

There was considerable spatial variation in the availability of invertebrate prey within coastal sites on the Northumberland Strait. Prey availability, measured as the biomass of six different prey taxa, did not vary significantly between PCAP and CJ (nested permutational MANOVA, $F_{1,83} = 2.43$, $p = 0.087$); however, prey availability did vary among transects nested in site ($F_{6,83} = 2.13$, $p < 0.001$), suggesting there is significant within-site variation. Flock species composition was correlated with the assemblage of available invertebrate prey (Mantel test, $r = 0.22$, $p = 0.047$).

### Foraging strategy segregation

Between July 24 and October 9, 2019, we observed foraging rates of 625 individual shorebirds. Foraging strategies, measured by pecking and probing rates, varied with species when controlled for significant ($p < 0.05$) covariates (Table 3; Fig. 2). The foraging strategies of Short-billed Dowitchers and Semipalmated Plovers differed from all other species, and the foraging strategy of Yellowlegs differed from all but White-rumped Sandpipers (Table 4; Fig. 2; Table S2). Semipalmated Sandpipers, White-rumped Sandpipers, and Least Sandpipers did not use significantly different foraging strategies (Table 4; Fig. 2). SIMPER analysis showed that these differences in foraging strategy were often largely driven by variation in pecking rates (Table S3). Semipalmated Plovers mostly pecked, but had a low mean pecking rate (11 actions per min), while Short-billed Dowitchers mostly probed with the highest mean foraging rate of all species (71 actions per min) (Fig. 2; Table S3). The Calidrid sandpipers used a combination pecking and probing strategy, but all had higher mean pecking rates than probing rates (Fig. 2; Table S3). Yellowlegs also used a combination of pecking and probing, but their mean pecking and probing rates were similar and relatively low (Fig. 2; Table S3). Dispersion of pecking and probing rates varied significantly among species (Permutest, $F_{6,619} = 5.94$, $p = 0.001$), and pairwise comparisons revealed that this was driven by Semipalmated Plovers and Yellowlegs, which had foraging niche breadths significantly different from other species (Table 5). Although not a significant covariate in the model of foraging rates among species (Table 3), sediment water content was positively correlated with probing rate (Pearson's correlation; $r_{(623)} = 0.33$, $p < 0.001$) and negatively correlated with pecking rate (Pearson's correlation; $r_{(623)} = -0.09$, $p = 0.03$).

Table 3. Results of PERMANCOVA testing differences in foraging strategies among shorebird species controlling for habitat covariates.

Comparison	Source of variation	Df	MS	F	p
Full model	Species	5	2.32	132.92	**0.001**
	Sediment water content	1	0.01	0.61	0.541
	Sediment particle size	1	0.10	5.46	**0.006**
	Amphipod	1	0.14	7.94	**0.001**
	Bivalve	1	<0.01	0.20	0.835
	Gastropod	1	0.09	5.28	**0.007**
	Decapod	1	0.02	1.35	0.247
	Polychaete	1	0.04	2.20	0.108
	Meiofauna	1	0.24	13.51	**0.001**
	Chlorophyll a concentration	1	0.04	2.52	0.081
	Residuals	610	0.02		
	Total	624			
Reduced model	Species	5	2.32	131.26	**0.001**
	Sediment particle size	1	0.10	5.45	**0.006**
	Amphipod	1	0.14	7.83	**0.002**
	Meiofauna	1	0.21	11.69	**0.001**
	Residuals	616	0.02		
	Total	624			

Note: The full model was run with all covariates, and nonsignificant covariates were removed from succeeding PERMANCOVAs to create the reduced model. Significant p values ($p < 0.05$) are in bold.

Fig. 2. Biplot of foraging behaviour of six shorebird species at coastal staging sites Petit-Cap and Cape Jourimain NB. Size, shape, and location of ellipses within the plot represent foraging behaviour. Ellipses stretched in the direction of an axis represent a foraging strategy that utilizes that behaviour. Data were square root transformed prior to plotting, but axes are back-transformed for presentation. SESA = Semipalmated Sandpiper ($n = 209$), WRSA = White-rumped Sandpiper ($n = 14$), SEPL = Semipalmated Plover ($n = 132$), SBDO = Short-billed Dowitcher ($n = 116$), LESA = Least Sandpiper ($n = 32$), YELL = Yellowlegs ($n = 122$).
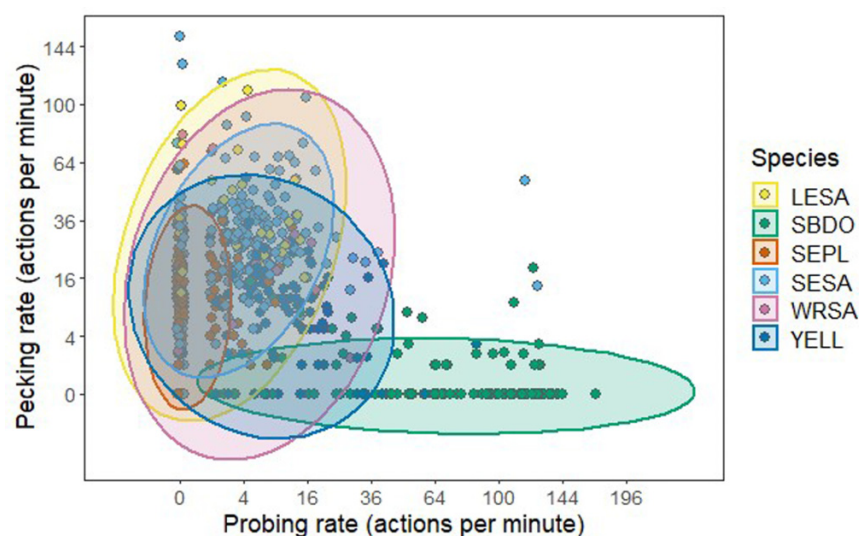
Diet segregation

Blood plasma signatures for $\delta^{15}N$ and $\delta^{13}C$, reflecting dietary differences, varied significantly among shorebird species (PERMANOVA, $F_{3,80} = 13.65$, $p = 0.001$). However, these differences were driven primarily by differences in dispersion among species (Permutest, $F_{3,80} = 7.37$, $p = 0.001$).

Thus, while there was substantial overlap in dietary niche for all species (Fig. 3), diet niche breadth differed among species (Table 6). Semipalmated Plovers and Short-billed Dowitchers had the broadest niches, followed by Semipalmated Sandpipers and finally White-rumped Sandpipers with the narrowest diet niche (Fig. 3).

Table 4. p values of pairwise PERMANCOVAs testing differences among species in foraging strategies (pecking and probing rates), controlled for significant habitat covariates.

	SESA	WRSA	SEPL	SBDO	LESA
SESA					
WRSA	0.272				
SEPL	**<0.001**	**<0.001**			
SBDO	**<0.001**	**<0.001**	**<0.001**		
LESA	0.542	0.208	**<0.001**	**<0.001**	
YELL	**<0.001**	0.086	**<0.001**	**<0.001**	**<0.001**

Note: Alpha level was corrected for 15 tests with Holm's sequential Bonferroni procedure. Significant p values are bolded. See Table S2 for full table of results. Species codes are as described in Fig. 2.

Table 5. Permuted p values of pairwise comparisons of multivariate dispersions of foraging strategy breadth.

	SESA	WRSA	SEPL	SBDO	LESA
SESA					
WRSA	0.098				
SEPL	0.010	0.004			
SBDO	0.119	0.521	**<0.001**		
LESA	0.158	0.593	**0.002**	0.820	
YELL	**0.001**	0.720	**<0.001**	0.327	0.652

Note: Alpha level was corrected for 15 tests with Holm's sequential Bonferroni procedure. Significant p values are bolded.

Fig. 3. Isotopic diet niches of shorebirds captured at Petit-Cap, estimated using $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of blood plasma in parts per thousand. $N_{SESA} = 29$, $N_{WRSA} = 20$, $N_{SEPL} = 20$, $N_{SBDO} = 15$.
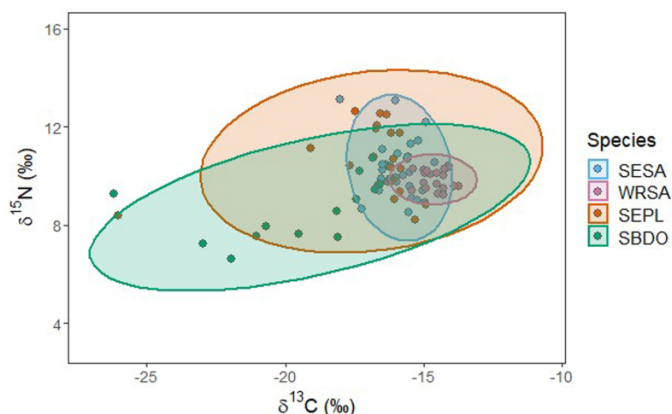
Table 6. Permuted p values of pairwise comparisons of multivariate dispersions of isotopic diet niche breadth estimated using $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of blood plasma in parts per thousand.

	SESA	WRSA	SEPL
SESA			
WRSA	**0.002**		
SEPL	0.118	**0.015**	
SBDO	**<0.001**	**<0.001**	0.152

Note: Alpha level was corrected for six tests with Holm's sequential Bonferroni procedure. Significant p values are bolded. Species codes are provided in Fig. 2.

Discussion

We found clear evidence of niche partitioning on multiple dimensions within shorebird species assemblages at small coastal sites in New Brunswick, Canada, during migratory staging. Environmental heterogeneity at coastal staging sites, coupled with differences among species in morphology and foraging behaviour, creates opportunities for partitioning of resources and allows a diverse shorebird assemblage to coexist.

Spatial segregation

Foraging microhabitat is an important dimension for segregation among coexisting species (Burger et al. 1977; Pöysä 1983; Davis and Smith 2001; Kent and Sherry 2020) as habitat influences the type and availability of prey (VanDusen et al. 2012) as well as the efficacy of foraging behaviours (Finn et al. 2008). The most prominent foraging microhabitats on the tidal flats at PCAP and CJ are tide pools, which created clear spatial boundaries between species that are and are not tall enough to forage in standing water (Burger et al. 1977). Although tide pools in the Northumberland Strait often attracted multispecies flocks of shorebirds, this size division of available habitat was evident. Short-billed Dowitchers and Yellowlegs could access prey in deeper water due to their greater bill and tarsal lengths (Baker 1979) and were more abundant in tide pools than the smaller species. Yellowlegs took advantage of their broad range of exploitable water depths by foraging both in and out of tide pools, whereas Short-billed Dowitchers almost exclusively foraged in tide pools. This is likely due to softer substrates in tide pools (VanDusen et al. 2012), which make prey more accessible for tactile foragers such as the Short-billed Dowitcher (Mouritsen and Jensen 1992; Finn et al. 2008). Tide pools may be especially attractive for tactile foragers at coastal sites as sediments are often sandy and dense (Davis 2019). Standing water also prolongs surface activity of invertebrates (VanDusen et al. 2012), which may explain why all shorebirds in this study used tide pools to a certain extent. Semipalmated Sandpipers and Semipalmated Plovers were too small to forage in deep water (Novcic 2016) and were clearly more abundant outside of tide pools. However, even they were attracted to the edges of tide pools where the water was shallow, perhaps because of increased invertebrate surface activity (VanDunsen et al. 2012). Least and White-rumped Sandpipers were not abundant enough for analysis of their microhabitat preference; however, given their size, it is likely that they foraged more frequently outside of tide pools like Semipalmated Sandpipers and Semipalmated Plovers.

Spatial segregation between wet and dry microhabitats has been observed at other migratory stopover areas (e.g., Davis and Smith 2001) but is less prominent at sites with limited habitat diversity (Novcic 2016). Therefore, heterogeneity of structural habitat, such as the presence and absence of tide pools, facilitates spatial partitioning of different shorebird species into microhabitat niches. We found evidence of significant spatial heterogeneity of prey availability within coastal sites, and there is a correlation between species composition of foraging flocks and the available prey community where

they foraged. As such, if shorebird species target different prey items, prey heterogeneity may contribute to spatial segregation at coastal sites. However, given that some species that overlap in foraging microhabitat had significantly different diet niches (e.g., Semipalmated Sandpipers and Semipalmated Plovers), there is little evidence to suggest that shorebirds target microhabitats within a site based on prey availability or that spatial segregation is driving variation in diet niches. Morphology and foraging behaviour are more likely facilitators of diet variation, as has been suggested for similar species at different stopover sites (Davis and Smith 2001).

Behaviour and diet segregation

Foraging behaviour is a widely studied niche dimension in birds (e.g., Baker and Baker 1973; Davis and Smith 2001; Novcic 2014, 2016; Choi et al. 2017). However, unless prey are distributed in a way that restricts their availability to particular foraging behaviours, it may not reflect prey taxon-level resource partitioning, as large behavioural differences often translate to only small differences in diet (Kent and Sherry 2020). The main difference between pecking and probing foraging behaviours is the depth of consumed prey (Dit Durell 2000), which largely depends on bill morphology, as birds with longer bills can access a wider range of probing depths. Therefore, shorebird species foraging at different sediment depths target spatially segregated prey items, though the prey taxa in their diets may overlap unless these taxa are segregated by depth. For example, gastropod species typically dwell on or near the sediment surface (Huxham et al. 1995; Chandrashkara and Frid 1998), while other invertebrate taxa, including bivalves and polychaete worms, can be found at a range of sediment depths (Henriksen et al. 1983; Zwarts and Wanink 1989; Touhami et al. 2018). Within the taxonomic levels to which we classified burrowing invertebrates for diet niche models in this study, individuals can be found at a wide range of depths, sometimes spanning 0 to over 10 cm (Zwarts and Wanink 1989; Davey 1994). Larger prey also tend to burrow deeper in muddy or sandy intertidal sites (Zwarts and Wanink 1989; Coulthard and Hamilton 2011; Touhami et al. 2018). Thus, long-billed shorebird species, which in our study were larger than the short-billed plovers and small Calidrids (and therefore could consume larger prey items), may have had access to prey items that their smaller competitors could not have consumed. Variation in foraging behaviour therefore reveals a potential for niche partitioning via foraging depth that could not be detected by diet examination alone. As such, it is important to pair behavioural observations with diet analyses when attempting to explain resource partitioning.

We found significant differences in the foraging behaviours and diets of shorebird species during staging in the Northumberland Strait. Short-billed Dowitchers had very high probing rates and low pecking rates, resulting in little behavioural overlap with other species in this study. Long bills, such as that of the Short-billed Dowitcher, are adapted for probing deep into the sediment (Barbosa and Moreno 1999), and thus, pecking behaviours are rarely observed (Baker and Baker 1973; Novcic 2016). This specialized foraging behaviour has

been observed in Dowitchers across their migratory range (Baker 1979; Davis and Smith 2001; Novcic 2016), and likely is necessary to reach prey buried in the sediment under standing water. At our site, this behaviour would have provided these birds with access to prey that most other species could not reach. Analyses of plasma isotopes suggested that Short-billed Dowitchers consumed a broad diet, and their lower range of δ^{15}N values suggests they consumed prey from lower trophic levels than the other species. The diet niche of Short-billed Dowitchers had some overlap with other species; however, their behavioural specialization and limited foraging microhabitat likely result in a realized niche that has little competitive overlap with the other shorebird species on the Northumberland Strait.

Semipalmated Plovers also had unique foraging behaviour. They pecked more than probed, and overall, their foraging rates were low compared with other species. Semipalmated Plovers are visual foragers that spend more time moving and looking for prey items than making foraging attempts (Nol 1986; Ouellette 2021), which results in lower foraging rates than species that peck or probe steadily while walking (Baker and Baker 1973). MacKellar (2018) found that Semipalmated Plovers at similar coastal sites in northeastern New Brunswick had lower foraging rates than Semipalmated Sandpipers feeding in the same area. Given their short bills and pecking behaviour, the dietary niche of Semipalmated Plovers is likely limited to invertebrates dwelling on or near the sediment surface (Dit Durell 2000). Rose et al. (2016) found that Semipalmated Plovers foraged opportunistically and consumed a broad range of invertebrate prey items across various foraging sites on the nonbreeding grounds. This dietary opportunism was reflected in a broad isotopic niche and likely balances their limited range of accessible prey depth. Semipalmated Plovers likely experienced substantive competitive overlap only with the Calidrid sandpipers in the Northumberland Strait due to their similarity in foraging microhabitat. Further, Semipalmated Plovers at Petit-Cap concentrate feeding during daylight hours, while sandpipers continue to forage nocturnally (Ouellette 2021), suggesting an additional level of temporal segregation that would reduce resource competition among these species. As such, Semipalmated Plovers' broad diets and narrow range of foraging behaviours combined with diurnal foraging trends may allow them to coexist with sandpipers to the extent observed in the Northumberland Strait.

Unlike Short-billed Dowitchers and Semipalmated Plovers, Yellowlegs pecked and probed at similar rates while foraging. This resulted in foraging behaviour that differed from all but the White-rumped Sandpiper. Yellowlegs are tall shorebirds and often forage in standing water (Danufsky and Colwell 2003). Yellowlegs in the Northumberland Strait foraged both in and out of tide pools. Sediment coarseness affected pecking and probing rates of foraging shorebirds, with coarser sediment inhibiting foraging efficiency, as has been seen in other studies (Danufsky and Colwell 2003). These coarser sediments tended to be drier, while wetter and more penetrable sediments supported more probing behaviours. Therefore, Yellowlegs may adjust their foraging behaviour for the sediment conditions they encounter in

different microhabitats, resulting in similar mean pecking and probing rates. Yellowlegs' broad habitat use likely resulted in competitive overlap with both Short-billed Dowitchers and the smaller sandpipers and plovers. We did not estimate diet of Yellowlegs; however, Andrei et al. (2009) found that Yellowlegs consumed broad diets at stopover sites in the southern United States. Niche complementarity predicts that Yellowlegs should exhibit niche specialization on some dimension to compensate for competitive overlap (Schoener 1974). However, it is possible that Yellowlegs forego foraging specialization and instead use a generalist staging strategy to exploit the full range of available resources at coastal sites.

Semipalmated Sandpipers, Least Sandpipers, and White-rumped Sandpipers did not have significantly different foraging behaviour. These species are congeners and are morphologically similar (Thomas et al. 2004), which likely plays a part in their similar behaviour (Barbosa and Moreno 1999; Dit Durell 2000; Norazlimi and Ramli 2015). All three sandpiper species used both pecking and probing behaviours but had higher pecking rates than probing rates. Resource competition is likely high among the sandpiper species; however, differences in diet breadth may have compensated for spatial and behavioural overlap. The diet of White-rumped Sandpipers was considerably narrower than that of Semipalmated Sandpipers. On their wintering grounds, White-rumped Sandpipers consume high proportions of the most abundant prey items (de los Angeles Hernandez and Bala 2007), which suggests they modify their diet to maximize foraging efficiency at different sites across their migratory range. The diet niche of Semipalmated Sandpipers in our study was also narrow compared with niches of Short-billed Dowitchers and Semipalmated Plovers; however, Semipalmated Sandpipers are considered generalist foragers (Gerwing et al. 2016) and have been found to opportunistically target the most available prey when more favourable prey items are unabundant (MacDonald et al. 2012). The heterogeneity of habitat and prey assemblages in the Northumberland Strait likely allows Semipalmated and White-rumped Sandpipers to opportunistically target the specific prey taxa that they can consume most efficiently, thus limiting dietary overlap with Dowitchers and Plovers.

Conclusion

Overall, migratory shorebirds staging in the Northumberland Strait during southbound migration exhibited partitioning on three niche dimensions: microhabitat space, foraging behaviour, and diet. All species, with the exception of Yellowlegs, used a staging strategy that was specialized in at least one niche dimension, which would alleviate interspecific competition. Staging sites with diverse habitat and resources can host richer species assemblages and higher populations of individual species by meeting the unique niche requirements of more species (Recher 1966; Danufsky and Colwell 2003; Elliott et al. 2020); therefore, environmental heterogeneity likely makes the Northumberland Strait an attractive staging area for a species-rich and morphologically diverse shorebird assemblage.

Traditional approaches to directing conservation efforts in vulnerable habitats are aimed at protecting the greatest biodiversity in the smallest land area (Kareiva and Marvier 2003), rather than taking steps to preserve a diversity of habitats across a larger land area. When considering the ecological importance of staging habitats, it may be easy to overlook small sites such as the ones we studied (~20–80 ha, Fig. 1) when much larger ones (e.g., the vast Bay of Fundy mudflats) are nearby. However, it is crucial to recognize the role these sites play during shorebird migration (Fuller 2003; Van Brederode and Roersma 2020). The results of this study add to the growing pool of research suggesting small coastal staging sites are important for the success of migratory shorebirds in Atlantic Canada (Doiron 2021; Linhart et al. 2022, 2023), and calling for recognition of a combination of these small sites within the region (McKellar et al. 2020). The Northumberland Strait is geographically close to the Bay of Fundy, a site of hemispheric importance to migratory shorebirds (WHSRN 2019), but these staging locations are structurally very different (Bellefontaine 2020; Linhart et al. 2022). It is possible these structural and environmental differences allow the Northumberland Strait to host more diverse shorebird communities than the Bay of Fundy, where the shorebird population is dominated by Semipalmated Sandpipers (Hicklin 1987; Bellefontaine 2020). Given the widespread declines in shorebird populations, it is critical to consider the importance of staging sites that exhibit habitat and prey heterogeneity as they support a great diversity of migratory shorebirds. Studying whole shorebird communities and their interactions with habitat conditions may be an important step to understanding how we can preserve staging habitats for shorebirds.

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Article information

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Data availability

Data generated or analyzed during this study are available in the Borealis repository (https://doi.org/10.5683/SP3/BTKNRR).

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Competing interests

The authors declare that there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/facets-2022-0230.

References

Abdi, H. 2010. Holm's sequential Bonferroni procedure. *In* Encyclopedia of research design. *Edited by*. N Salkind. Sage, Thousand Oaks, CA. pp. 1–8.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour, **49**: 227–267. doi:10.1163/156853974X00534. PMID: 4597405.

Anderson, A.M., Duijns, S., Smith, P.A., Friis, C., and Nol, E. 2019. Migration distance and body composition influence shorebird migration strategies and stopover decisions during southbound migration. Frontiers in Ecology and Evolution, **7**: 251. doi:10.3389/fevo.2019.00251.

Andrei, A.E., Smith, L.M., Haukos, D.A., Surles, J.G., and Johnson, W.P. 2009. Foraging ecology of migrant shorebirds in saline lakes of the Southern Great Plains. Waterbirds: The International Journal of Waterbird Biology, **32**(1): 138–148. doi:10.1675/063.032.0117.

Atlantic Canada Shorebird Survey. 2022. Environment and Climate Change Canada [online]. Available from https://naturecounts.ca/nc/default/datasets.jsp?code=PRISM-ACSS.

Baker, M.C. 1979. Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). Oikos, **33**(1): 121–126. doi:10.2307/3544520.

Baker, M.C., and Baker, A.E.M. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecological Monographs, **43**: 193–212. doi:10.2307/1942194.

Barbosa, A., and Moreno, E. 1999. Evolution of foraging strategies in shorebirds: an ecomorphological approach. The Auk, **116**(3): 712–725.

Bellefontaine, S. 2020. Niche partitioning and behaviour of migratory shorebirds in the Northumberland Strait and Bay of Fundy. B.Sc. Hons. thesis, Mount Allison University, New Brunswick.

Bocher, P., Robin, F., Kojadinovic, J., Delaporte, P., Rousseau, P., Dupuy, C., and Bustamante, P. 2014. Trophic resource partitioning within a shorebird community feeding on intertidal mudflat habitats. Journal of Sea Research, **92**: 115–124. doi:10.1016/j.seares.2014.02.011.

Burger, J., Howe, M.A., Caldwell Hahn, D., and Chase, J. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migratory shorebirds. The Auk, **94**(4): 743–758. doi:10.2307/4085271.

Catry, T., Granadeiro, J.P., Gutiérrez, J.S., and Correia, E. 2022. Stopover use of a large estuarine wetland by dunlins during spring and autumn migrations: linking local refuelling conditions to migratory strategies. PLoS ONE, **17**(1): e0263031. doi:10.1371/journal.pone.0263031. PMID: 35077514.

Chandler, RJ. 2009. Shorebirds of North America, Europe, and Asia. Princeton University Press. p. 480.

Chandrasekara, W.U., and Frid, CLJ. 1998. A laboratory assessment of the survival and vertical movement of two epibenthic gastropod species, *Hydrobia ulvae* (Pennant) and *Littorina littorea* (Linnaeus), after burial in sediment. Journal of Experimental Marine Biology and Ecology, **221**(2): 191–207. doi:10.1016/S0022-0981(97)00123-8.

Choi, C.-Y., Battley, P.F., Potter, M.A., Ma, Z., Melville, D.M., and Sukkaewmanee, P. 2017. How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. The Auk Ornithological Advances, **134**: 76–91.

Coulthard, M.E., and Hamilton, D.J. 2011. Effects of *Ilyanassa obsolete* (Say) on the abundance and vertical distribution of *Corophium volutator* (Pallas) on mudflats of the upper Bay of Fundy. Journal of Experimental Marine Biology and Ecology, **397**(2): 161–172. doi:10.1016/j.jembe.2010.12.001.

Danufsky, T., and Colwell, M.A. 2003. Winter shorebird communities and tidal flat characteristic at Humbolt Bay, California. The Condor, **105**(1): 117–129. doi:10.1093/condor/105.1.117.

Davey, J.T. 1994. The architecture of the burrow of *Nereis diversicolor* and its quantification in relation to sediment-water exchange. Journal of Experimental Marine Biology and Ecology, **179**(1): 115–129. doi:10.1016/0022-0981(94)90020-5.

Davis, C.A., and Smith, L.M. 2001. Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the southern Great Plains. The Auk, **118**(2): 484–495. doi:10.1093/auk/118.2.484.

Davis, S. 2019. Migratory stopover comparison of adult and juvenile Semipalmated Sandpipers (Calidris pusilla) in the Bay of Fundy and on the Northumberland Strait. B.Sc. Hons. thesis, Mount Allison University, New Brunswick.

de los, A., Hernandez, M., and Bala, LO. 2007. Prey selection and foraging patterns of the white-rumped sandpiper (*Calidris fuscicollis*) at Peninsula Valdes, Patagonia, Argentina. Ornitología Neotropical, **18**(1): 37–46.

Dit Durell, S.E.A. Le V. 2000. Individual feeding specialization in shorebirds: population consequences and conservation implications. Biological Reviews, **75**: 503–518. doi:10.1111/j.1469-185X.2000.tb00053.x. PMID: 11117199.

Doiron, P. 2021. Differences in use of Northumberland Strait habitat and fattening rates among migratory shorebird species. B.Sc. Hons. thesis, Mount Allison University, New Brunswick.

Elliott, L.H., Igl, L.D., and Johnson, D.H. 2020. The relative importance of wetland area versus habitat heterogeneity for promoting species richness and abundance of wetland birds in the Prairie Pothole Region, USA. The Condor Ornithological Applications, **122**: 1–21.

Elner, R.W., Beninger, P.G., Jackson, D.L., and Potter, T.M. 2005. Evidence of a new feeding mode in western sandpiper (*Calidris mauri*) and dunlin (*Calidris alpina*) based on bill and tongue morphology and ultrastructure. Marine Biology, **146**: 1223–1234. doi:10.1007/s00227-004-1521-5.

Faria, F.A., Faria Albertoni, E., and Bugoni, L. 2018. Trophic niches and feeding relationships of shorebirds in southern Brazil. Aquatic Ecology, **52**: 281–296. doi:10.1007/s10452-018-9663-6.

Fiala, J. 2009. An examination of the fueling strategies and energy sources utilized by Nearctic-neotropic migrants. Eukaryon, **5**: 15.

Finke, D.L., and Snyder, WE. 2008. Niche partitioning increases resource exploitation by diverse communities. Science, **321**: 1488–1489. doi:10.1126/science.1160854. PMID: 18787167.

Finn, P.G., Catterall, C.P., and Driscoll, PV. 2008. Prey versus substrate as determinants of habitat choice in a feeding shorebird. Estuarine, Coastal and Shelf Science, **80**: 381–390. doi:10.1016/j.ecss.2008.09.001.

Fuller, RA. 2003. Factors influencing foraging decisions in ruddy turnstones Arenaria interpres (L.). Ph.D. thesis, Durham University, England.

Gerwing, T.G., Barbeau, M.A., Hamilton, D.J., Allen Gerwing, A.M., Sinclair, J., Campbell, L., et al. 2020. Assessment of sediment penetrability as an integrated in situ measure of intertidal soft-sediment conditions. Marine Ecology Progress Series, **648**: 67–78. doi:10.3354/meps13428.

Gerwing, T.G., Kim, J., Hamilton, D.J., Barbeau, M.A., and Addison, J.A. 2016. Diet reconstruction using next-generation sequencing increases the known ecosystem usage by a shorebird. The Auk, **133**(2): 168–177. doi:10.1642/AUK-15-176.1.

Henriksen, K., Ramussen, M.B., and Jensen, A. 1983. Effect of bioturbation on microbial nitrogen transformations in the sediment and fluxes of ammonium and nitrate to the overlaying water. Ecological Bulletins, **35**: 193–205.

Hicklin, PW. 1987. The migration of shorebirds in the Bay of Fundy. The Wilson Bulletin, **99**(4): 540–570.

Hobson, K.A., and Clark, R.G. 1993. Turnover of ¹³C in cellular plasma fractions of blood: Implications for nondestructive sampling of avian dietary studies. The Auk, **110**(3): 638–641. doi:10.2307/4088430.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics, **6**(2): 65–70.

Hope, D.D., Petarik, C., Drever, M.C., Smith, P.A., Gratto-Trevor, C., Paquet, J., et al. 2019. Shorebirds of conservation concern in Canada – 2019. Wader Study, **126**(2): 88–100. doi:10.18194/ws.00148.

Hutto, RL. 1998. On the importance of stopover sites to migrating birds. The Auk, **115**(4): 823–825. doi:10.2307/4089500.

Huxham, M., Raffaelli, D., and Pike, AW. 1995. The effect of larval trematodes on the growth and burrowing behaviour of Hydrobia ulvae (gastropoda:prosobranchiata) in the Ythan estuary, north-east Scotland. Journal of Experimental Marine Biology and Ecology, **185**(1): 1–17. doi:10.1016/0022-0981(94)00119-X.

Isola, C.R., Colwell, M.A., Taft, O.W., and Safran, R.F. 2000. Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Joaquin Valley. Waterbirds: The International Journal of Waterbird Biology, **23**(2): 196–203.

Jackson, A.L., Parnell, A.C., Inger, R., and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER – stable isotope Bayesian ellipses in R. Journal of Animal Ecology, **80**(3): 595–602. doi:10.1111/j.1365-2656.2011.01806.x. PMID: 21401589.

Kareiva, P., and Marvier, M. 2003. Conserving biodiversity coldspots: recent calls to direct conservation funding to the world's biodiversity hotspots may be bad investment advice. American Scientist, **91**(4): 344–351. doi:10.1511/2003.4.344.

Kelly, JF. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology, **78**: 1–27. doi:10.1139/z99-165.

Kent, C.M., and Sherry, T.W. 2020. Behavioural niche partitioning reexamined: do behavioural differences predict dietary differences in warblers? Ecology, **101**(8): e03077. doi:10.1002/ecy.3077. PMID: 32304223.

Kindt, R., and Coe, R. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF). ISBN 92-9059-179-X. http://www.worldagroforestry.org/output/tree-diversity-analysis.

Kober, K., and Bairlein, F. 2006. Shorebirds of the Bragantinian Peninsula II. Diet and foraging strategies of shorebirds at a tropical site in northern Brazil. Ornitología Neotropical, **17**: 549–562.

Kuwae, T., Miyoshi, E., Hosokawa, S., Ichimi, K., Hosoya, J., Moriya, T., et al. 2012. Variable and complex food web structure revealed by exploring missing trophic links between birds and biofilm. Ecology Letters, **15**(4): 347–356. doi:10.1111/j.1461-0248.2012.01744.x. PMID: 22304245.

Kuwae, T., Neninger, P.G., Decottignies, P., Mathot, K.J., Lund, D.R., and Elner, R.W. 2008. Biofilm grazing in a higher vertebrate: the West-

ern Sandpiper, Calidris mauri. Ecology, **89**(3): 599–606. doi:10.1890/07-1442.1. PMID: 18459323.

Linhart, R.C., Hamilton, D.J., Paquet, J., and Gratto-Trevor, C.L. 2023. Evidence of differing staging strategies between adult and juvenile semipalmated Sandpipers highlights the importance of small staging sites in Atlantic Canada. Ornithology, **140**: 1–14. doi:10.1093/ornithology/ukac056.

Linhart, R.C., Hamilton, D.J., Paquet, J., Bellefontaine, S.C., Davis, S.S., Doiron, P.B., and CL, G.-.T. 2022. Variation in resource use between adult and juvenile Semipalmated Sandpipers (Calidris pusilla) and use of physiological indicators for movement decisions highlights the importance of small staging sites during southbound migration in Atlantic Canada. Frontiers in Ecology and Evolution, **10**: 1059005. doi:10.3389/fevo.2022.1059005.

MacArthur, RH. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology, **39**(4): 599–619. doi:10.2307/1931600.

MacDonald, E.C., Ginn, M.G., and Hamilton, D.J. 2012. Variability in foraging behaviour and implications for diet breadth among semipalmated Sandpipers staging in the Upper Bay of Fundy. The Condor, **114**: 135–144.

MacKellar, H. 2018. Foraging habits and fattening rates of Semipalmated Sandpipers (Calidris pusilla) and Semipalmated Plovers (Charadrius semipalmatus) in the Acadian Peninsula. B.Sc. Hons. thesis, Mount Allison University, New Brunswick.

McKellar, A.E., Aubry, Y., Drever, M.C., Friis, C.A., Gratto-Trevor, C.L., Paquet, J., et al. 2020. Potential Western Hemisphere Shorebird Reserve Network sites in Canada: 2020 update. Wader Study, **127**(2): 11. doi:10.18194/ws.00190.

Meyers, J.P., Morrison, R.I.G., Antas, P.Z., Harrington, B.A., Lovejoy, T.E., Sallaberry, M., et al. 1987. Conservation strategy for migratory species. American Scientist, **75**(1): 18–26.

Mouritsen, K.N., and Jensen, KT. 1992. Choice of microhabitat in tactile foraging dunlins Calidris alpina: the importance of sediment penetrability. Marine Ecology Progress Series, **85**(1/2): 1–8. doi:10.3354/meps085001.

Neima, S.G., Hamilton, D.J., Gratto-Trevor, C.L., and Paquet, J. 2020. Intra- and interannual regional fidelity of Semipalmated Sandpipers (Calidris pusilla) during migratory stopover in the upper Bay of Fundy, Canada. Avian Conservation and Ecology, **15**(1): 14. doi:10.5751/ACE-01561-150114.

Neima, S.G., Linhart, R.C., Hamilton, D.J., Gratto-Trevor, C.L., and Paquet, J. 2022. Length of stay and departure strategies of semipalmated Sandpipers (Calidris pusilla) during post-breeding migration in the upper Bay of Fundy, Canada. Frontiers in Ecology and Evolution, **10**:897197. doi:10.3389/fevo.2022.897197.

Newton, I. 2004. Population limitation in migrants. Ibis, **146**: 197–226. doi:10.1111/j.1474-919X.2004.00293.x.

Nol, E. 1986. Incubation period and foraging technique in shorebirds. The American Naturalist, **128**(1): 115–119. doi:10.1086/284543.

Norazlimi, N.A., and Ramli, R. 2015. The relationship between morphological characteristics and foraging behaviour in four selected species of shorebirds and water birds utilizing tropical mudflats. The Scientific World Journal, **2015**: 105296. doi:10.1155/2015/105296. PMID: 26345324.

North American Bird Conservation Initiative Canada. 2019. The state of Canada's birds. Environment and Climate Change Canada, Ottawa, Canada.

Novcic, I. 2014. Foraging ecology of shorebirds at a stopover site: niche dynamics, aggression and resource use in Delaware Bay. Ph.D. thesis, The City University of New York, New York.

Novcic, I. 2016. Niche dynamics of shorebirds in Delaware Bay: foraging behaviour, habitat choice and migration timing. Acta Oecologica, **75**: 68–76. doi:10.1016/j.actao.2016.07.002.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. 2020. vegan: Community Ecology Package. R package version 2.5-6. Available from https://CRAN.R-project.org/package=vegan.

Ouellette, V. 2021. Nocturnal and diurnal feeding behaviour of migratory shorebirds at a Northumberland Strait stopover site. B.Sc. Hons. thesis, Mount Allison University, New Brunswick.

Pöysä, H. 1983. Resource utilization pattern and guild structure in a waterfowl community. Oikos, **40**(2): 295–307. doi:10.2307/3544594.

Quinn, J.T., and Hamilton, D.J. 2012. Variation in diet of semipalmated Sandpipers (Calidris pusilla) during stopover in the upper Bay of Fundy,

Canada. Canadian Journal of Zoology, **90**: 1181–1190. doi:10.1139/z2012-086.

Recher, H.F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology, **47**(3): 393–407. doi:10.2307/1932979.

Rose, M., Pollock, L., and Nol, E. 2016. Diet and prey size selectivity of Semipalmated Plovers (*Charadrius semipalmatus*) in coastal Georgia. Canadian Journal of Zoology, **94**: 727–732. doi:10.1139/cjz-2016-0039.

Rosenberg, K.V., Dokter, A.M., Blancher, O.J., Sauer, J.R., Smith, A.C., Smith, P.A., et al. 2019. Decline of the North American avifauna. Science, **366**: 120–124. doi:10.1126/science.aaw1313. PMID: 31604313.

Schaub, M., and Jenni, L. 2000. Fuel deposition of three passerine bird species along the migration route. Oecologia, **122**: 306–317. doi:10.1007/s004420050036. PMID: 28308281.

Schoener, TW. 1974. Resource partitioning in ecological communities. American Association for the Advancement of Science, **185**(4145): 27–39. doi:10.1126/science.185.4145.27.

Shoaf, W.T., and Lium, B.W. 1976. Improved extraction of chlorophyll a and b from algae using dimethyl sulfoxide. Limnology and Oceanography, **21**(6): 926–928. doi:10.4319/lo.1976.21.6.0926.

Skagen, S.K. 1997. Stopover ecology of transitory populations: the case of migrant shorebirds. Ecological Studies, **125**: 244–269. doi:10.1007/978-1-4757-2703-6_10.

Thomas, G.H., Wills, M.A., and Székely, T. 2004. A supertree approach to shorebird phylogeny. BMC Evolutionary Biology, **4**: 28. doi:10.1186/1471-2148-4-28. PMID: 15329156.

Touhami, F., Bazairi, H., Badaoui, B., and Benhoussa, A. 2018. Vertical distribution of benthic macrofauna in intertidal habitats frequented by shorebirds at Merja Zerga lagoon. Thalassas: An International Journal of Marine Sciences, **34**: 225–265. doi:10.1007/s41208-017-0059-5.

Tsipoura, N., and Burger, J. 1999. Shorebird diet during spring migration stopover on Delaware Bay. The Condor, **101**(3): 635–644. doi:10.2307/1370193.

Van Brederode, N.E., and Roersma, H.J. 2020. Turnover, passage population size and flight range of juvenile Ruddy Turnstones at a non-estuarine staging site in the Netherlands. Ardea, **108**(2): 213–222. doi:10.5253/arde.v108i2.a9.

VanDusen, B.M., Fegley, S.R., and Peterson, C.H. 2012. Prey distribution, physical habitat features, and guild traits interact to produce contrasting shorebird assemblages among foraging patches. PLoS ONE, **7**: e52694. doi:10.1371/journal.pone.0052694. PMID: 23285153.

Welschmeyer, NA. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography, **39**(8): 1985–1992. doi:10.4319/lo.1994.39.8.1985.

Western Hemisphere Shorebird Reserve Network. 2019. Western hemisphere shorebird reserve network sites [online]. Available from https://whsrn.org/whsrn-sites/.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York.

Wiens, JA. 1992. The ecology of bird communities. Vol. 1. Foundations and patterns. Cambridge University Press, Cambridge. p. 539.

Zwarts, L., and Wannink, J. 1989. Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. Marine Biology, **100**: 227–240. doi:10.1007/BF00391963.