

Evidence for sexual partitioning of foraging mode in Western Sandpipers (*Calidris mauri*) during migration

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Abstract: Migrating Western Sandpipers, *Calidris mauri* (Cabanis, 1857), observed feeding at an intertidal stopover site on the Fraser River delta, British Columbia, shifted their foraging mode from surface-pecking to probing over a 3-week period in April and May. We tested possible mechanisms to account for the field observations. Using control and shorebird exclusion plots over a 3-month period bracketing the migration, we determined that neither seasonal nor shorebird-induced changes in the relative availability of epifaunal compared with infaunal prey accounted for the decline in the prevalence of epifaunal feeding behaviour. However, strong peaks in both epi- and in-faunal prey densities coincided with the migration period, suggesting that migratory timing may be linked with the productivity schedule of major stopover sites. Males, which precede females in the migration and have relatively shorter bills, were observed to engage in epifaunal feeding more frequently than females. Thus, while foraging behaviour of the Western Sandpiper at a population level appears “plastic”, the feeding repertoire of individuals is more specialized and results in sexual partitioning of prey resources. The implications of our findings for differential distribution patterns over the nonbreeding range and sex-related differences in contaminant profiles are discussed.

Résumé : Nous avons observé des bécasseaux d’Alaska, *Calidris mauri* (Cabanis, 1857), en migration, qui se nourrissaient à un site d’arrêt intercotidal dans le delta du Fraser, changer leur mode de recherche de nourriture de becquetages de surface à des sondages plus profonds au cours d’une période de trois semaines en avril et en mai. Nous évaluons divers mécanismes explicatifs de ces observations de terrain. Nous avons établi des parcelles témoins et de parcelles d’exclusion des oiseaux de rivage sur une période de 3 mois qui couvre et dépasse la durée de la migration; nous avons montré qu’aucun changement dans la disponibilité relative des proies de l’épifaune par rapport à celles de l’endobenthos ne peut expliquer le déclin de l’alimentation prédominante dans l’épifaune, que ces changements soient dus à la variation saisonnière ou à la présence des oiseaux de rivage. Il y a, cependant, de forts maximums d’abondance dans l’épifaune et de l’endobenthos qui coïncident avec la période de migration, ce qui laisse croire que le calendrier de la migration est lié avec celui de la productivité des principaux sites d’arrêt. Les mâles qui précèdent les femelles lors de la migration et qui ont des becs relativement plus courts peuvent être observés plus fréquemment que les femelles en train de se nourrir de l’épifaune. Ainsi, bien que le comportement de recherche de nourriture chez le bécasseau d’Alaska semble flexible au niveau de la population, les répertoires individuels sont plus spécialisés et ont comme résultat de partager les proies en fonction des sexes. Les conséquences de nos découvertes sur les différences de patterns de répartition des sexes hors de la saison de reproduction et sur les profils de contaminants distincts des deux sexes font l’objet d’une discussion.

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Introduction

Shorebirds may expend over half of their annual energy budget migrating thousands of kilometres between their breeding and nonbreeding grounds (Drent and Piersma 1990). Consequently, given the challenge of sustaining an adequate

energy intake, foraging behaviour has been a focus of numerous avian migration studies (Mouritsen 1994; Davis and Smith 1998; De Leon and Smith 1999; Dierschke et al. 1999a, 1999b; Davis and Smith 2001; Cole et al. 2002; Masero 2003). Although shorebird feeding behaviour is generally considered to be “plastic”, with individuals opportunistically switching foraging mode in response to changes in prey availability (Skagen and Oman 1996; Davis and Smith 2001), the degree to which the total plasticity seen at the species level corresponds to plasticity within individuals seems ambiguous, as many shorebird species also display sexual dimorphism in bill size that can result in functional distinctions in feeding behaviour (Puttick 1981; Summers et al. 1990; Pierre 1994; Lauro and Nol 1995; Rubega 1996; Zharikov and Skilleter 2002). Assessing the trade-off between feeding specialization and plasticity in individual shorebirds appears critical to not only understanding intra-

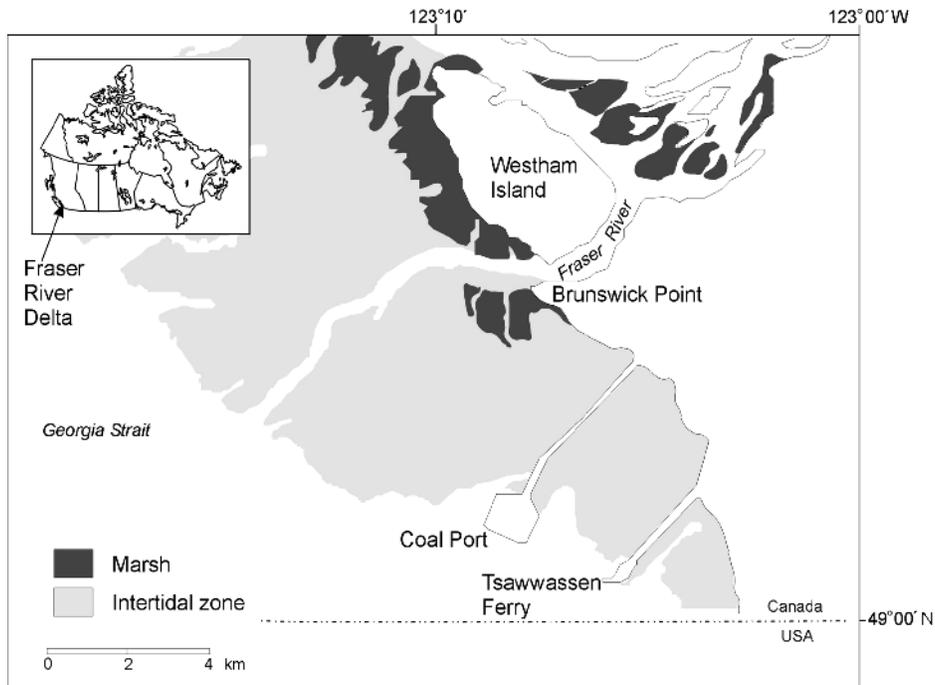
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Fig. 1. Roberts Bank located on the Fraser River Delta, British Columbia, Canada.



specific competition but also mechanisms responsible for differential distribution patterns over the nonbreeding range (Elner and Seaman 2003).

The Western Sandpiper, *Calidris mauri* (Cabanis, 1857), is an ideal study candidate to extend understanding of shorebird foraging strategies given their long-distance migrations, abundance, repertoire of feeding modes, and sexual dimorphism. Western Sandpipers spend the nonbreeding season distributed from California to Peru, and are partially segregated on the basis of sex with males predominating in the northern end of the nonbreeding range (Nebel et al. 2002). They migrate to breeding sites in Alaska and Siberia in April and May (Wilson 1994). Western Sandpipers forage primarily on intertidal mudflats and display three distinctive foraging modes: surface (hereinafter referred to as epifaunal) feeding, subsurface (hereinafter referred to as infaunal) feeding, and a form of surface-tension feeding on suspended prey (Ashmole 1970; Rubega 1996; Sutherland et al. 2000; Davis and Smith 2001).

Observations of Western Sandpipers in the Fraser River delta, British Columbia, indicated that the predominant foraging mode shifted from epifaunal to infaunal feedings over the course of the spring migration (R.W. Elner, personal observations). Although the phenomenon itself has not previously been quantified, two possible underlying mechanisms can be hypothesized. First, if high plasticity in foraging behaviour is expressed at the level of the individual, shorebirds may adjust their foraging mode from epifaunal to infaunal feedings if the relative availability of epifaunal compared with infaunal preys declines over the migration period. A second, although not mutually exclusive, hypothesis for the decline in epifaunal feeding invokes sexual partitioning of foraging mode. Female Western Sandpipers have culmens (bills) that are, on average, 13% longer than their male conspecifics (Page and Fearis 1971), and longer culmens have

been associated with specialization for infaunal feeding in other species of shorebirds (Puttick 1981; Summers et al. 1990; Pierre 1994; Durell et al. 1993; Lauro and Nol 1995; Durell 2000; Zharikov and Skilleter 2002). Therefore, since male Western Sandpipers precede females on migration (Butler et al. 1987), the apparent shift in foraging mode may be attributable to the shifting sex ratio on the stopover site and sex-related foraging specialization.

In this study, we assessed the nature of feeding plasticity in Western Sandpipers by comparing temporal patterns in epifaunal versus infaunal foraging behaviours against concurrent sex ratios and relative food availability at a stopover site. Using shorebird exclusion cages, we were able to test for both seasonal and shorebird-induced declines in the relative abundance of epifaunal versus infaunal preys.

Methods and materials

Study site

During the northward migration, more than 1 million Western Sandpipers pass through the Fraser River delta in British Columbia en route to breeding grounds in the Arctic (Butler et al. 1987). Our study was conducted at Roberts Bank (49°05'N, 123°12'W; Fig. 1), a 6000-ha intertidal mudflat in the Fraser River delta, during the northward migration in both 2001 and 2002. All work was carried out in the upper intertidal.

Behavioural observations

In April and May 2001 and 2002, focal observations were made of individuals throughout the migration to quantify temporal changes in foraging behaviour. Observations were made using a spotting scope in the open among flocks of foraging sandpipers. Individuals were randomly selected for 1-min observations in which we recorded the occurrence of

each of the following foraging behaviours: peck, surface sew, probe, and deep sew. We were careful to avoid repeated observations of the same individuals. A peck was defined as a single contact of the bill to the sediment surface. Probes were defined as insertion of the bill more than 1/3 its length into the sediment. Surface sews and deep sews were multiple pecks and probes, respectively, occurring too rapidly to count individual events. All observations were recorded onto microcassette tapes and later transcribed. Because the sexes are highly dimorphic, we were able to sex individuals by eye during the 2002 season. Page and Fearis (1971) established sexing criteria based on bill length, whereby individuals with bills ≤ 24.2 mm and individuals with bills ≥ 24.8 mm could be classified as males and females, respectively, with an accuracy of 95%. Therefore, we classified long-billed individuals as females and short-billed individuals as males. To avoid gender misclassification, individuals with intermediate bill lengths were not assigned to either male or female sex categories, and were excluded from the analyses. Given Page and Fearis's (1971) sexing criteria, 5% of Western Sandpipers should fall in the intermediate category. Given that over 30% of our focal observations were classified as intermediate, we were confident that males and females were indeed classified accurately. Furthermore, a single observer (K.J. Mathot) made all focal observations. Protocol for focal observations in 2002 was the same as during the 2001 migration, with the exception that in 2002 focal individuals were purposely selected to obtain approximately equal counts of males and females on each sampling day, notwithstanding changing sex ratios throughout the migration.

Invertebrate sampling

In 2002, we monitored seasonal changes in the density of epifaunal and infaunal food sources by erecting five 1-m² shorebird exclusion cages constructed with four metal stakes and a ceiling constructed from a 20 mm \times 20 mm wire mesh attached 50 mm above the sediment surface. To be able to test for shorebird-induced changes in food distribution, open 1-m² control plots were defined 2 m from each enclosure using four metal stakes. Western Sandpipers were regularly observed feeding within control plots and there was no indication that the proximity of the enclosures affected either the presence or the behaviour of the sandpipers within the controls. The enclosures and controls were sampled once every 7 days for 1 month prior to the migration and 1 month following the migration and every 4 days during the migration (13 sampling days from 29 March 2002 to 6 June 2002). On sampling days, cores were collected using a modified syringe with a 26-mm internal diameter to a depth of 40 mm. The same core dimensions have been used previously to sample Western Sandpiper prey (Sutherland et al. 2000; Wolf 2001), which range in size from 0.1 to 5 mm (Davis and Smith 2001). Epifaunal samples were collected by slicing the upper 5 mm of sediment with a modified spatula. Samples were placed in a cooler with ice immediately following collection until they could be frozen.

Infaunal samples were thawed and washed with distilled water through a 500- μ m sieve to separate the macrofauna fraction of invertebrates. The fauna retained on the sieve were then stored in vials with 85% ethanol. Invertebrate taxa

present were identified and enumerated on a scored petri dish under an AUS Jenna 452000 dissecting microscope at 40 \times magnification. We used epipellic diatoms as an index of epifaunal food density, given the strong correlation between the concentration of diatoms and the biomass of chlorophyll and deposit-feeding organisms (Barnes and de Villiers 2000). The concentration of diatoms in the top 5 mm of sediment was determined fluorometrically using the method outlined in Sutherland et al. (1998).

Statistical analyses

Trends in foraging behaviour were studied by grouping "pecks" and "surface sews" into epifaunal foraging behaviour, whereas "probes" and "deep sews" were grouped into infaunal foraging behaviour. A regression model with date and date² as fixed factors was used to test for temporal trends in foraging mode in 2001. Tests for temporal and sex-related differences in foraging behaviour in 2002 were carried out using an ANCOVA with date as a fixed factor and sex as a random factor.

We tested for differences in the densities of epi- and infaunal foods between the five pairs of control and enclosure plots at the onset of the experiment using a paired *t* test on the mean densities obtained for each sampling station from 4 sampling days prior to the migration period. Hypotheses related to temporal patterns in food density and distributions were tested using mixed-model multiple regressions with date and date² as fixed factors and sampling station as a random factor. The data were analyzed both for long-term patterns as well as patterns within the migration period alone, where the migration period was defined as dates with >30 000 Western Sandpipers using Robert's Bank.

Results

Focal observations were made of 46 individuals over 7 days across the migration in 2001, and 48 females and 56 males were observed over 6 days through the migration period in 2002. The mean number of foraging events recorded per minute was 45.78 (range 28–82) and 58.85 (range 34–88) in 2001 and 2002, respectively. In 2001, we found a significant effect of both date ($F_{[5,38]} = 31.83$, $p < 0.001$) and date² ($F_{[5,38]} = 31.07$, $p < 0.001$) on the percentage of epifaunal foraging behaviour through the migration. Percentage of epifaunal foraging decreased from >80% early in the migration to <50% late in the migration (Fig. 2). In 2002, there was a significant effect of sex on the percentage of epifaunal foraging ($F_{[2,101]} = 62.38$, $p < 0.001$), but neither date ($F_{[2,101]} = 0.094$, $p = 0.76$) nor the interaction term date \times sex ($F_{[3,100]} = 2.17$, $p = 0.14$) were significant (Fig. 3). The mean percentage of epifaunal foraging behaviours was 84.05% (range 63.24%–100%) for females and 96.33% (range 85.45%–100%) for males.

The invertebrate communities within the cores were dominated by polychaetes, nematodes, and harpacticoid copepods, with cumaceans, ostracods, bivalves, tanaids, and foraminiferans occurring in relatively low frequencies (Fig. 4). Control and enclosure plots did not differ significantly in either infaunal ($p = 0.22$) or epifaunal ($p = 0.55$) food densities at the onset of the experiment. In 2002, strong seasonal patterns in food density were observed. There were signifi-

Fig. 2. Percentage of epifaunal foraging behaviours versus julian date for the 2001 northward migration of Western Sandpipers, *Calidris mauri*.

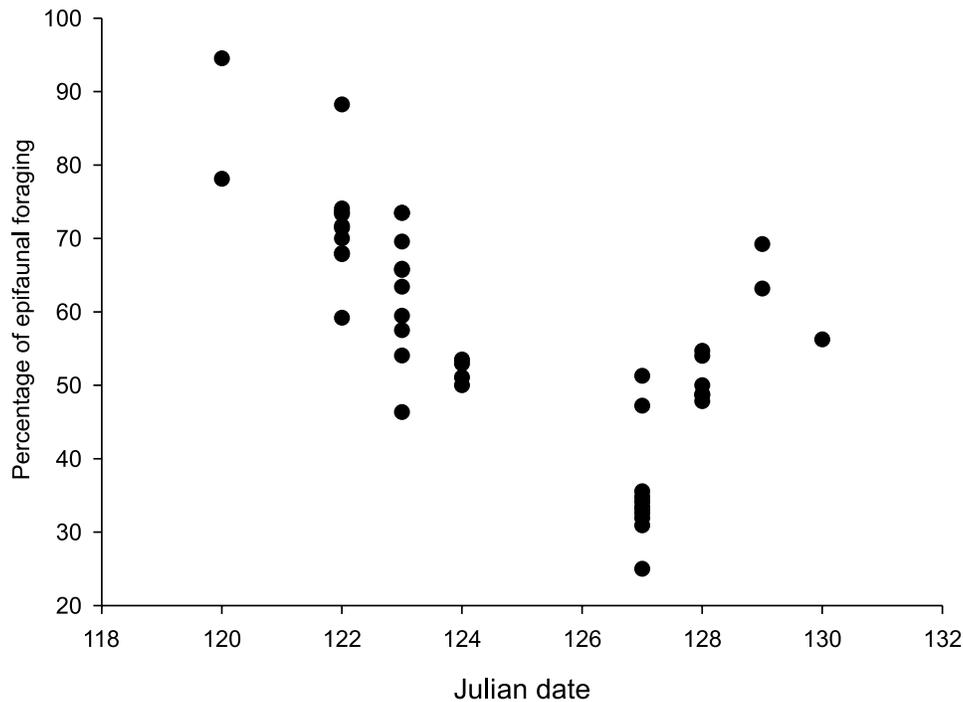
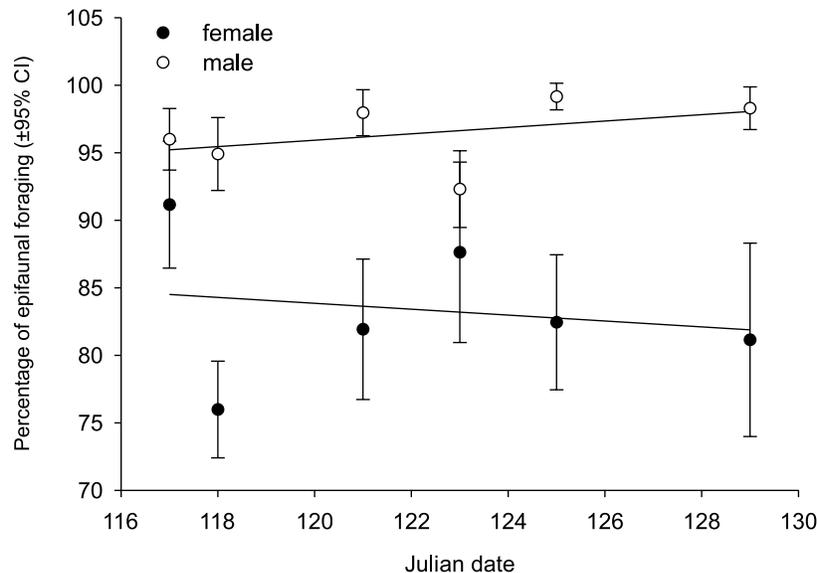


Fig. 3. Percentage of epifaunal foraging behaviours versus julian date by sex class for the 2002 northward migration of Western Sandpipers.



cant effects of both date and date² terms in the models for infaunal ($F_{[1,61]} = 8.71$, $p = 0.0045$ and $F_{[1,61]} = 9.16$, $p = 0.0036$) and epifaunal ($F_{[1,58]} = 6.90$, $p = 0.011$ and $F_{[1,58]} = 6.28$, $p = 0.015$) food densities, reflecting the peaks in abundance which coincided with the arrival of the earliest migrants (Fig. 5). However, within the migration period, no significant effect of either date or date² was detected for either infaunal ($F_{[1,16]} = 0.025$, $p = 0.88$ and $F_{[1,16]} = 0.029$, $p = 0.87$) or epifaunal ($F_{[1,13]} = 2.59$, $p = 0.13$ and $F_{[1,13]} = 2.44$, $p = 0.14$) samples. Differences between enclosure and

control plots did not vary significantly with respect to the date or date² terms in the model for either infaunal ($F_{[1,16]} = 1.43$, $p = 0.25$ and $F_{[1,16]} = 1.43$, $p = 0.25$) or epifaunal ($F_{[1,13]} = 6.11$, $p = 0.073$ and $F_{[1,13]} = 5.57$, $p = 0.075$) food densities during the migration period (Fig. 6).

Discussion

Focal observations of individual Western Sandpipers during the 2001 northward migration indicated a shift in foraging

Fig. 4. Invertebrate composition of control and exclusion infaunal cores (mean number of individuals per core). Foraminiferan, cumacean, tanaid, bivalve, insect larva, and ostracod counts are pooled as “others”.

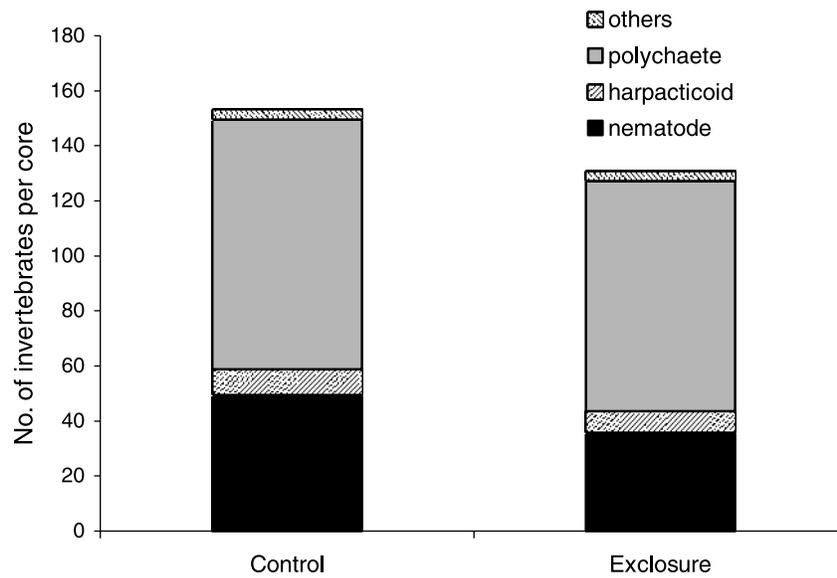
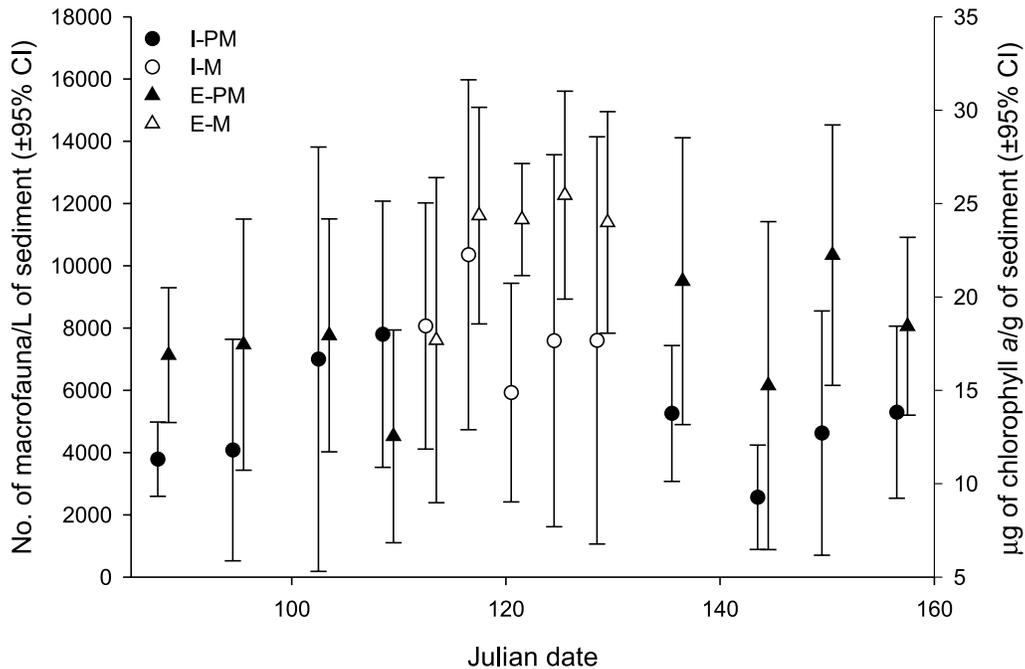


Fig. 5. Infaunal and epifaunal food densities versus julian date in exclusion plots. Solid black circles show pre- and post-migration infaunal abundance (I-PM), whereas open circles show infaunal abundance during migration (I-M). Solid black triangles show pre- and post-migration epifaunal densities (E-PM), whereas open triangles show epifaunal food abundance during migration (E-M). Infaunal and epifaunal datum points are offset from one another for clarity.

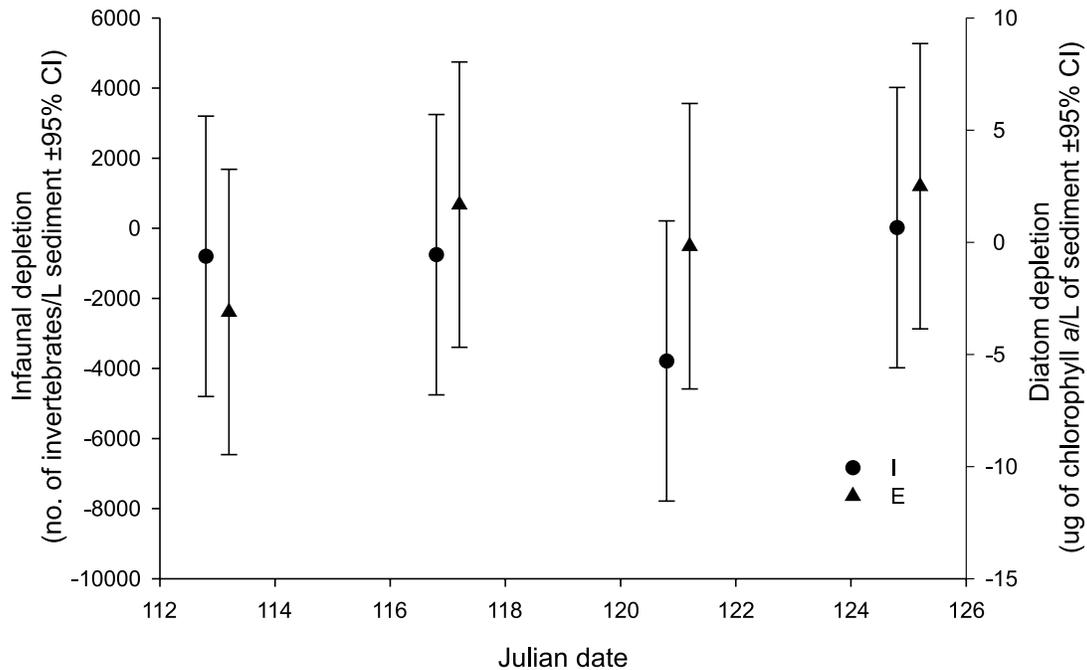


ing behaviour throughout the migration. Although a significant effect of date² was observed, reflecting a large decline in epifaunal foraging behaviour in the first 8 days of the migration followed by a smaller increase in the last 3 days, there was nevertheless an overall pattern of decline in epifaunal feeding across the migration. Assessing whether this trend reflects sex-related feeding specialization or prey-switching is important to understanding both intraspecific competition and mechanisms responsible for differential dis-

tribution patterns over the nonbreeding range (Elnor and Seaman 2003).

We tested whether prey-switching at the population level could account for the decline in epifaunal foraging behaviour observed during the 2001 migration by assessing changes in the relative abundance of epifaunal food resources. A decline in the relative abundance of epifaunal food resources was not observed within the time frame of the migration in either shorebird exclusion cages or on areas

Fig. 6. Differences in infaunal and epifaunal food densities between enclosure and control plots. Infaunal counts (I) are shown with circles and epifaunal counts (E) are shown with triangles. Infaunal and epifaunal datum points are offset from one another for clarity.



of the mudflat where Western Sandpipers were able to feed. Thus, neither seasonal nor shorebird-induced changes in the relative abundance of epifaunal food occurred within the migration period. Although spatial heterogeneity across the mudflat may make the detection of changes in the density of invertebrates difficult as a result of high variability (Sewell 1996), no temporal trend in foraging mode within sexes was observed during the migration as would be expected if prey-switching were the underlying mechanism for population-level shifts in foraging behaviour. Therefore, we infer that prey-switching is not the principle mechanism driving the temporal change in foraging mode in Western Sandpipers.

Although we did not observe significant changes in food abundance during the migration period, seasonal changes in food abundance were observed across a broader time scale than that of the migration. Coincident with the arrival of the earliest migrant Western Sandpipers were peaks in both infaunal and epifaunal food abundances. Declines of equal magnitude were observed as the migration tapered off. Although it has been speculated in the literature that migratory timing is scheduled to coincide with peaks in productivity at stopover sites (Lack 1960), data supporting this theory are scarce (Schneider and Harrington 1981). Our study provides strong empirical evidence that the timing of the northward migration in Western Sandpipers is linked with the productivity schedule of at least one of their major stopover sites.

Given the high degree of bill dimorphism in Western Sandpipers (Page and Fearis 1971) and partial temporal segregation of the sexes during migration (Butler et al. 1987), sexual partitioning of foraging modes may be the principal mechanism underlying increased infaunal feeding through the migration. We observed a consistent separation between male and female foraging behaviours throughout the migration, with males being more specialized at epifaunal feeding behaviours than females. However, the temporal decline in

epifaunal foraging in 2001 (30%) exceeded the sex-related differences observed in 2002 (20%), which suggests that while culmen length can account for a large proportion of the variation in foraging mode, foraging behaviour may also be influenced by other extrinsic factors.

Our finding also provides insight into possible mechanisms underlying sex-related differences in contaminant patterns previously observed in Western Sandpipers, with adult males having higher accumulations of cadmium in the liver and kidneys than females (McFarland et al. 2002). Contaminants accumulate in the sediment so that they are more concentrated nearer the surface (Clifton et al. 1995). Therefore, the higher reliance of males on epifaunal food sources, as indicated in this study, may make males more susceptible to environmental contaminant loading.

Differences in foraging behaviour exhibited by male and female Western Sandpipers on migration do not reflect changes in the relative abundance of epi- versus in-faunal preys but rather sex-related foraging specializations. Differential foraging-mode specializations within a species are believed to be a mechanism through which intraspecific competition is reduced (Durell et al. 1993). Given that competition between male and female Western Sandpipers is already reduced on migration owing to their partial temporal segregation, we suggest that sexual partitioning of foraging mode is a means of reducing intraspecific competition not on migration, but on the nonbreeding grounds, by allowing Western Sandpipers to exploit a broader range of nonbreeding sites. Elner and Seaman (2003) postulate that sex-related differences in foraging and diet could be an underlying mechanism explaining partial latitudinal segregation of male and female Western Sandpipers over the nonbreeding grounds. Sexual partitioning of foraging mode likely leads to sexual partitioning of food resources since specific taxa of prey tend to have distinctive vertical distributions within the sedi-

ment profile (Fleeger et al. 1995; Kumar 1997; Sutherland et al. 2000). Observations at several nonbreeding sites indicate that sexual partitioning of foraging mode is maintained on the nonbreeding grounds (K.J. Mathot, unpublished data); however, no studies have yet considered how the Western Sandpiper prey base changes across nonbreeding sites. Determining how the vertical distribution of prey varies across latitudes is a critical next step in elucidating the mechanisms underlying differential migration and distribution patterns in Western Sandpipers.

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