# SEX-RELATED DIFFERENCES IN FEEDING BEHAVIOUR AND IMPLICATIONS FOR DIFFERENTIAL MIGRATION IN WESTERN SANDPIPERS (*CALIDRIS MAURI*)

by

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# ABSTRACT

I examined relationships between bill morphology, feeding behaviour and non-breeding distribution in a sexually dimorphic shorebird, the Western Sandpiper (*Calidris mauri*). The sexes are differentially distributed across the non-breeding range, with males, the shorter-billed sex, shifted north relative to females. Males are more reliant on pecking (surface feeding) during both migration and the non-breeding period while females do more probing (subsurface feeding). I tested whether differences in feeding mode result in sex-related differences in diet. Results of surficial food removal plots and stable isotope analyses were equivocal. I also tested the hypothesis that latitudinal gradients in the vertical distribution of food (invertebrates and biofilm) underlie differential migration in Western Sandpipers. Surface food predominated at northern sites, while subsurface food predominated at southern sites. This study is the first to relate latitudinal scale changes in the distribution of food to functional morphology and differential non-breeding distribution in a shorebird.

# DEDICATION

~I dedicate this thesis to my grandmother.~

# ACKNOWLEDGEMENTS

I have had the opportunity to work and interact with so many great people through the course of my degree at Simon Fraser University, and I am happy to have the chance to acknowledge them here.

I would like to start by thanking Ron Ydenberg, my senior supervisor. It was Ron whose charisma and enthusiasm first persuaded me to pursue a degree in biology, and I have never once regretted that decision. Ron provided me with great feedback and support throughout my degree, but also had enough confidence to allow me the freedom to develop this project as I saw fit. Thank you to Bob Elner, whom I worked most closely with throughout my degree, and who first reeled me in to the world of the Western Sandpiper by hiring me to study the "Canadian Sandpiper". Bob has been an amazing source of intellectual, financial and personal support throughout my degree, and I have great admiration for his academic integrity. I would also like to thank David Green who was the lone 'non-sandpiperologist' on my committee, and who helped me to see how my work fits into the broader picture. Terri Sutherland acted as public examiner at my defense, and provided many useful comments.

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# CHAPTER 1:

# GENERAL INTRODUCTION

## Background

Perhaps the best known examples of the functional significant of bill morphology are classic studies on the Galapagos Islands demonstrating the relationship between bill morphology, feeding behaviour and diet in ground finches (Boag and Grant 1981, Schluter 1981). However, the implications of bill morphology on feeding behaviour and diet have been studied in numerous avian groups (Durell 2000, Parchman and Benkman 2002, Radford and du Plessis 2003). Intra-specific variation in bill morphology is of particular interest because differences in feeding and diet among subsets of a population may result in differences in habitat selection criteria, vulnerability to predators, and susceptibility to interference (Durell 2000). In turn, these may have important demographic consequences and conservation implications.

In this thesis, I investigate the influence of bill morphology on inter-sexual differences in feeding mode in a sexually dimorphic shorebird, the Western Sandpiper (*Calidris mauri*). The implications of sex-related differences in feeding behaviour on diet and foraging plasticity are studied. Also, sex-related differences in feeding and diet are tested as a potential mechanisms underlying differential migration in this species.

## Study species: Western Sandpiper

The Western Sandpiper is a small calidrid shorebird with a global population of several million (Wilson 1994). Western Sandpipers breed in western Alaska and eastern Siberia in May and June. They spend the non-breeding season distributed primarily along

the west coast of the Americas, between California and Péru, and to a lesser extent are also found on the east coast of the Americas between New Jersey and Surinam (Wilson 1994). Western Sandpipers are differential migrants: males tend to winter north of females, and juveniles are under-represented in the centre of the non-breeding range (Nebel et al. 2002).

Western Sandpipers display two broad categories of feeding behaviour: surface and subsurface (Ashmole 1970, Sutherland et al. 2000). Surface feeding includes pecking and surface sewing (rapid multiple pecks), and is directed at prey on the sediment surface. Subsurface feeding includes probing and deep sewing (rapid multiple probes) and is directed at prey buried in the sediment column.

Western Sandpipers are sexually dimorphic. Males are circa 5% smaller than females with respect to most body measures, but 12% smaller with respect to bill length (Cartar 1984). Thus, given the associations between bill morphology and feeding mode observed in other shorebirds (Durell 2000), it seems likely that male and female Western Sandpipers will exhibit sex-related differences in feeding behaviour.

As a consequence of sexual dimorphism in bill length and partial sexual segregation on the non-breeding grounds, there is an overall pattern of increasing bill length from North to South in the non-breeding range. Furthermore, within each age and sex class, there is a trend towards increasing bill length at more southerly overwintering sites (O'Hara 2002). Therefore, latitudinal patterns in the abundance or distribution of food combined with sex-related differences in feeding and diet have been hypothesized to play a role in shaping the non-breeding distribution in Western Sandpipers (Elner and Seaman 2003).

## Study sites

Field work for this thesis was carried out at one major migratory stopover site, Roberts Bank (RB), in British Columbia (49°05'N, 123°12'W), and six non-breeding sites: Humboldt Bay (HB, N 40°50, W 124°05), Bodega Bay (BB, N 38°19, W 123°02),

and San Francisco Bay (SFB, N 37°30, W 122°06) in California, Punta Banda (PB, N 31°45', W 116°37') and La Paz (LP, N 24°06', W 110°22') in México, and Costa del Este (CE, N 09°00', W 79°27') in Panamá (Figure 1). These overwintering sites were selected because they span a broad range of latitudes.

## Visual sexing method

I attempted to sex individuals by eye whenever focal observations were made based on the high degree of bill dimorphism that exists between sexes. Page and Fearis (1971) established sexing criteria for this species 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, I classified long billed individuals as females and short-billed individuals as males. In order to avoid sex misclassification, individuals with intermediate bill lengths were termed "intermediate", and are excluded from all analyses presented in this thesis.

Given Page and Fearis's (1971) sexing criteria, 5% of Western Sandpipers should fall in the intermediate category. Over 30% of focal observations at each site were classified as intermediate, indicating that sexing by eye was likely conservative. Also, at one of the non-breeding sites sampled in this thesis, La Paz, México, I was able to take advantage of the presence of a large number of uniquely colour banded individuals in order to independently verify the accuracy of the visual sexing technique. Observations of colour banded birds confirmed that my visual sex assignments were conservative. The probabilities of incorrectly assigning an individual as 'male' or 'female' were 9.1% and 0%, respectively (Table 1-1).

## Thesis overview

This thesis consists of three independent research chapters that explore the implications of bill dimorphism on feeding behaviour, feeding plasticity, diet and differential migration in Western Sandpipers. Chapter 2 (published in the Canadian

Journal of Zoology, 2004) tests two non-exclusive hypotheses for an observed trend towards decreased surface feeding behaviour (pecking) during northward migration at a stopover site in British Columbia. Using shorebird exclosure cages and control plots, I tested whether changes in the distribution or abundance of prey, and/or changing sex ratios at the site combined with sex-related foraging specializations could account for the overall trend in feeding behaviour throughout the migratory period.

Chapter 3 investigates tidally-mediated behavioural interactions between Western Sandpipers, their invertebrate prey, and their predators, Peregrine Falcons (*Falco peregrinus*), at a non-breeding site in Panamá. The vertical distribution of invertebrates was quantified for rising and falling tide periods, and concurrent observations of Western Sandpiper feeding behaviour were made. Tide-related shifts in peregrine attack frequencies on flocks of Western Sandpipers were also recorded. A mechanism for prey selection in Western Sandpipers is postulated, and inter-sexual differences in feeding plasticity and vulnerability to predation are discussed.

Chapter 4 is the final research chapter of the thesis. This chapter tests the hypothesis that latitudinal patterns in the vertical distribution of prey in the sediment are a mechanism underlying the non-breeding distribution of Western Sandpipers. Western Sandpiper feeding behaviour and prey distributions were recorded at six non-breeding sites between California and Panamá, and resultant patterns are discussed in terms of optimal non-breeding site selection for birds of various bill lengths. I also used experimental manipulations and stable isotope analyses to determine the extent to which sex-related differences in feeding behaviour confer sex-related differences in diet.

Chapter 5 provides a general synthesis of the preceding chapters. The key findings of this thesis are highlighted and some additional data are presented to extend on ideas illuminated in Chapter 4. Finally, directions for future research are identified and the conservation implications of the major findings are discussed.

## Acknowledgements

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**Table 1-1:** Independent verification of sexing criteria based on visually assigned sexes to individually colour banded birds in LaPaz, México, whose actual sex based on Page and Fearis (1971) classification scheme was known. Values in parentheses indicate sample sizes.

| Actual Sex | Visually assigned sex | Probability of correct classification | Probability of false classification to this sex |
|---|---|---|---|
| Male | Male (21) | | |
| (24) | Intermediate (3) | 87.5% (21/24) | 9.1% (1/11) |
| | Female (0) | | |
| Indeterminate | Male (1) | | |
| (1) | Intermediate (0) | 0% (0/1) | 26.5% (9/34) |
| | Female (0) | | |
| Female | Male (0) | | |
| (10) | Intermediate (6) | 40% (4/10) | 0% (0/25) |
| | Female (4) | | |

Figure 1-1: Map of study sites. RB = Roberts Bank, British Columbia; HB= Humboldt Bay, California;  BB = Bodega Bay, California; SFB = San Francisco Bay, California; PB= Punta Banda, México; LP = La Paz, México; and CE = Costa del Este, Panamá..

# CHAPTER 2:

# EVIDENCE FOR SEXUAL PARTITIONING OF FORAGING MODE IN WESTERN SANDPIPERS (*CALIDRIS MAURI*) DURING MIGRATION

Kimberley J. Mathot and Robert W. Elner

# 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 three-month period bracketing the migration, we determined that neither seasonal nor shorebird induced changes in the relative availability of surface as compared to subsurface prey accounted for the decline in the prevalence of pecking feeding behaviour. However, strong peaks in both surface and subsurface 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 pecking 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 non-breeding range and sex-related differences in contaminant profiles are discussed.

# Introduction

Shorebirds may expend over half of their annual energy budget migrating thousands of kilometers between their breeding and non-breeding 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, Dierschke et al. 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-specific competition but also mechanisms responsible for differential distribution patterns over the non-breeding 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 non-breeding season distributed from California to Péru, and are partially segregated on the basis of sex with males predominating in the northern end of the non-breeding 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 feeding (pecking), sub-surface feeding (probing), and a form of surface tension feeding on suspended prey (Ashmole 1970, Rubega 1997, Sutherland et al. 2000, Davis and Smith 2001).

Observations of Western Sandpipers in the Fraser River delta, British Columbia, indicate that the predominant foraging mode shifts from pecking to probing 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 pecking to probing if the relative availability of surface as compared with subsurface prey declines over the migration period. A second, although not mutually exclusive, hypothesis for the decline in pecking 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 probing in other species of shorebirds (Puttick 1981, Summers et al. 1990, Durell et al. 1993, Pierre 1994, 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 pecking versus probing 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 surface versus subsurface prey.

## Methods

### 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. 2-1), 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 in order to quantify temporal changes in foraging behaviour. Observations were made using a spotting scope in the open amongst flocks of foraging sandpipers. Individuals were randomly selected for 1 minute 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 micro-cassette 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 $\leq 24.2$ mm and individuals with bills $\geq 24.8$ 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. In order to avoid sex misclassification, individuals with intermediate bill lengths were not assigned to either male or female sex categories, and are 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 are 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 in order 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 surface and subsurface food sources by erecting five $1m^2$ shorebird exclusion cages constructed with 4 metal stakes and a ceiling constructed from a 20 mm by 20 mm wire mesh attached 50 mm

above the sediment surface. In order to be able to test for shorebird induced changes in food distribution open 1m$^2$ control plots were defined 2 m from each exclosure using 4 metal stakes. Western Sandpipers were regularly observed feeding within control plots and there was no indication that the proximity of the exclosures affected either the presence or behaviour of the sandpipers within the controls. The exclosures 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, subsurface 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). Surface prey 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.

Subsurface prey samples were thawed and washed with distilled water through a 500 micron 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 40X magnification. We used the concentration of chlorophyll a as an index of surface food density. Chlorophyll a concentration 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 'pecking' foraging behaviour, while 'probes' and 'deep sews' were grouped into 'probing' foraging behaviour. A regression model with date and date$^2$ 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 surface and subsurface food between the 5 pairs of control and exclosure 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 date$^2$ 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 were 45.78 (range= 28 to 82) and 58.85 (range= 34 to 88) in 2001 and 2002 respectively. In 2001, we found a significant effect of both date ($F_{[5,38]}$, p<0.001) and date$^2$ ($F=_{[5,38]}$, p<0.001) on the percentage of pecking foraging behaviour through the migration. Percent pecking decreased from greater than 80% early in the migration to less than 50% late in the migration (Fig. 2-2). In 2002, there was a significant effect of sex on the percent of pecking ($F_{[2,101]}$=62.38, p<0.001), but neither date ($F_{[2,101]}$=0.094, p=0.76) nor the interaction term, date*sex ($F_{[3,100]}$=2.17, p=0.14), were significant (Fig. 2-3). The mean percentage of pecking foraging behaviours was 84.05% (range = 63.24 to 100%) for females and 96.33% (range= 85.45 to 100%) for males.

The invertebrate communities within the cores were dominated by polychaetes, nematodes and harpacticoid copepods, with cumaceans, ostracods, bivalves, tanaidacea, and foraminiferans occurring in relatively low frequencies (Fig. 2-4). Control and exclosure plots did not differ significantly in either subsurface (p=0.22) or surface (p=0.55) food densities at the onset of the experiment. In 2002, strong seasonal patterns in food density were observed. There were significant effects of both date and date$^2$ terms

in the models for subsurface ($F_{[1,61]}=8.71$, p=0.0045 and $F_{[1,61]}=9.16$, p=0.0036) and surface food densities ($F_{[1,58]}=6.90$, p=0.011 and $F_{[1,58]}=6.28$, p=0.015) reflecting the peaks in abundance which coincided with the arrival of the earliest migrants (Fig. 2-5). However, within the migration period, no significant effect of either date or date$^2$ was detected for either subsurface ($F_{[1,16]}=0.025$, p=0.88 and $F_{[1,16]}=0.029$, p=0.87) or surface prey samples ($F_{[1,13]}=2.59$, p=0.13 and $F_{[1,13]}=2.44$, p=0.14). Differences between exclosure and control plots did not vary significantly with respect to the date or date$^2$ terms in the model for either subsurface ($F_{[1,16]}=1.43$, p=0.25 and $F_{[1,16]}=1.43$, p=0.25) or surface ($F_{[1,13]}=6.11$, p=0.73 and $F_{[1,13]}=5.57$, p=0.75) food densities during the migration period (Fig. 2-6).

## Discussion

Focal observations of individual Western Sandpipers during the 2001 northward migration indicated a shift in foraging behaviour throughout the migration. Although a significant effect of date$^2$ was observed, reflecting a large decline in the percentage of pecking in the first 8 days of the migration followed by a smaller increase in the last 3 days, there was nonetheless an overall pattern of decline in the relative use of pecking across the migration. Assessing whether this trend reflects sex-related feeding specialization or prey switching is important to understanding both intra-specific competition and mechanisms responsible for differential distribution patterns over the non-breeding range (Elner and Seaman 2003).

We tested whether prey switching at the population level could account for the decline in the percentage of pecking observed during the 2001 migration by assessing changes in the relative abundance of surface food resources. A decline in the relative abundance of surface food resources was not observed within the time frame of the migration in either shorebird exclusion cages or on areas of the mudflat where Western Sandpipers were able to feed. Thus, neither seasonal nor shorebird induced changes in the relative abundance of surface food occurred within the migration period. Although spatial heterogeneity across the mudflat may make the detection of changes in the density of

invertebrates difficult due to 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 subsurface and surface food abundance. Declines of equal magnitude were observed as the migration tapered off. While 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 probing through the migration. We observed a consistent separation between male and female foraging behaviour throughout the migration, with males being more specialized at pecking feeding behaviours than females. However, the temporal decline in percent pecking 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 such that they

are more concentrated nearer the surface (Clifton et al. 1995). Therefore, the higher reliance of males on surface 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 surface versus subsurface prey but rather sex-related foraging specializations. Differential foraging mode specializations within a species are believed to be a mechanism through which intra-specific competition is reduced (Durell et al. 1993). Given that competition between male and female Western Sandpipers is already reduced on migration due to their partial temporal segregation, we suggest that sexual partitioning of foraging mode is a means of reducing intra-specific competition not on migration, but on the non-breeding grounds, by allowing Western Sandpipers to exploit a broader range of non-breeding 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 non-breeding 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 sediment profile (Fleeger et al. 1995, Kumar 1997, Sutherland et al. 2000). Observations at several non-breeding sites indicate that sexual partitioning of foraging mode is maintained on the non-breeding grounds (Chapter 4), however, no studies have yet considered how the Western Sandpiper prey base changes across non-breeding 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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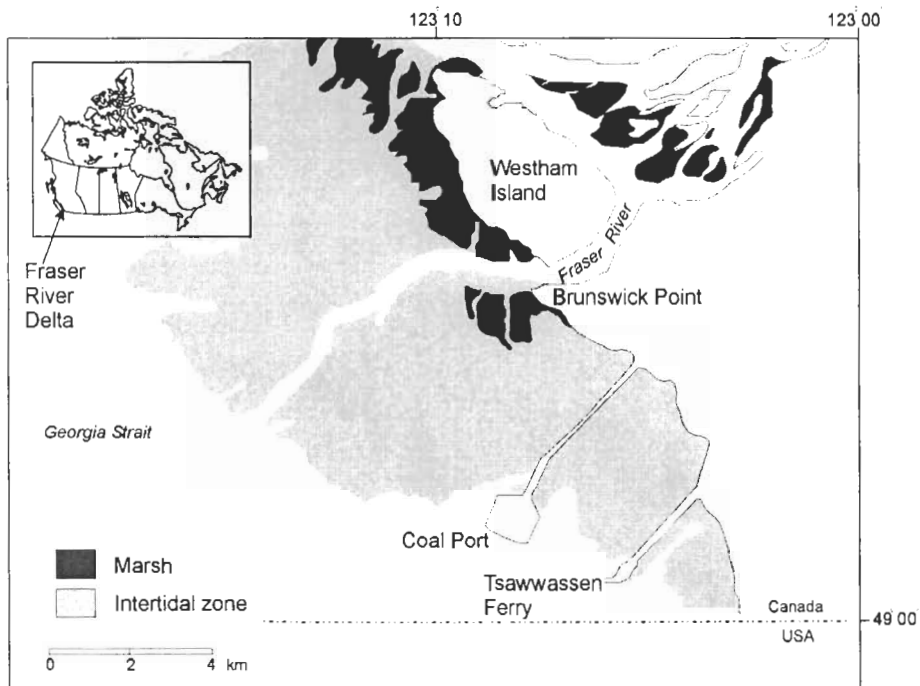
**Figure 2-1: Roberts Bank, Fraser River Delta, British Columbia, Canada.**
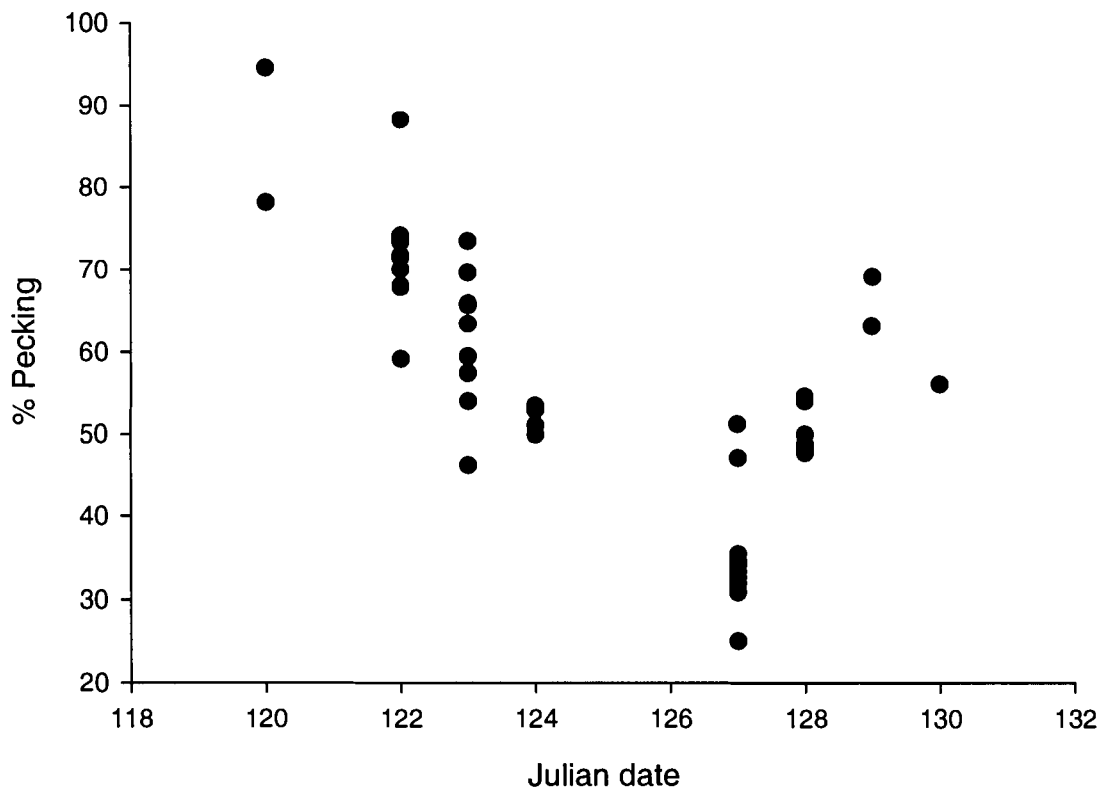
**Figure 2-2: Percent pecking versus julian date for the 2001 northward migration**
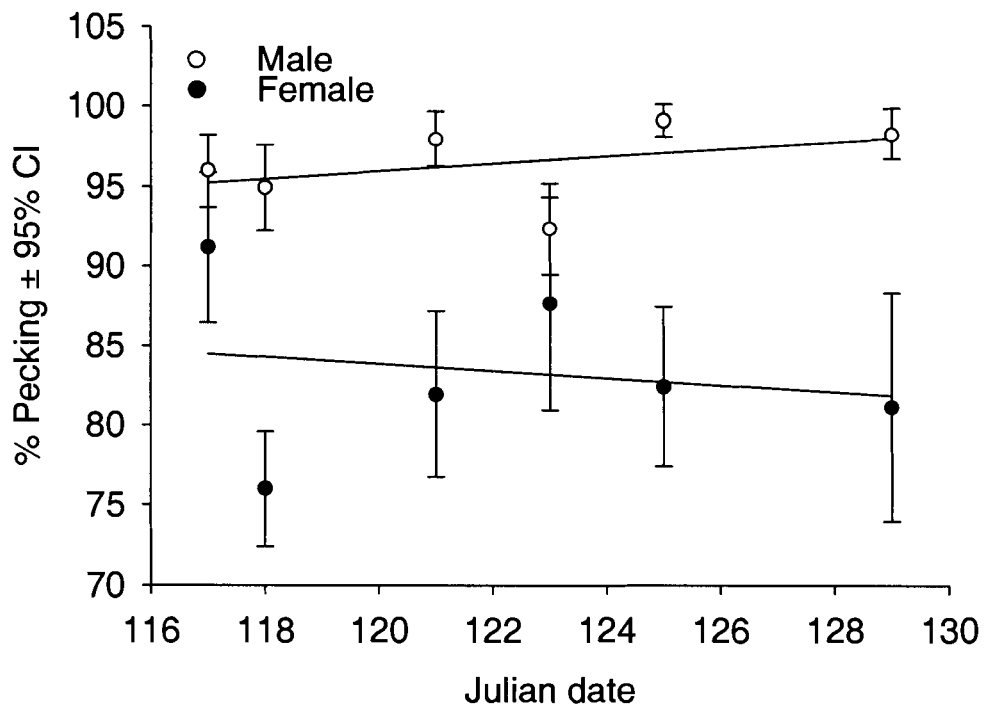
**Figure 2-3: Percent pecking versus julian date by sex class for the 2002 northward migration.**
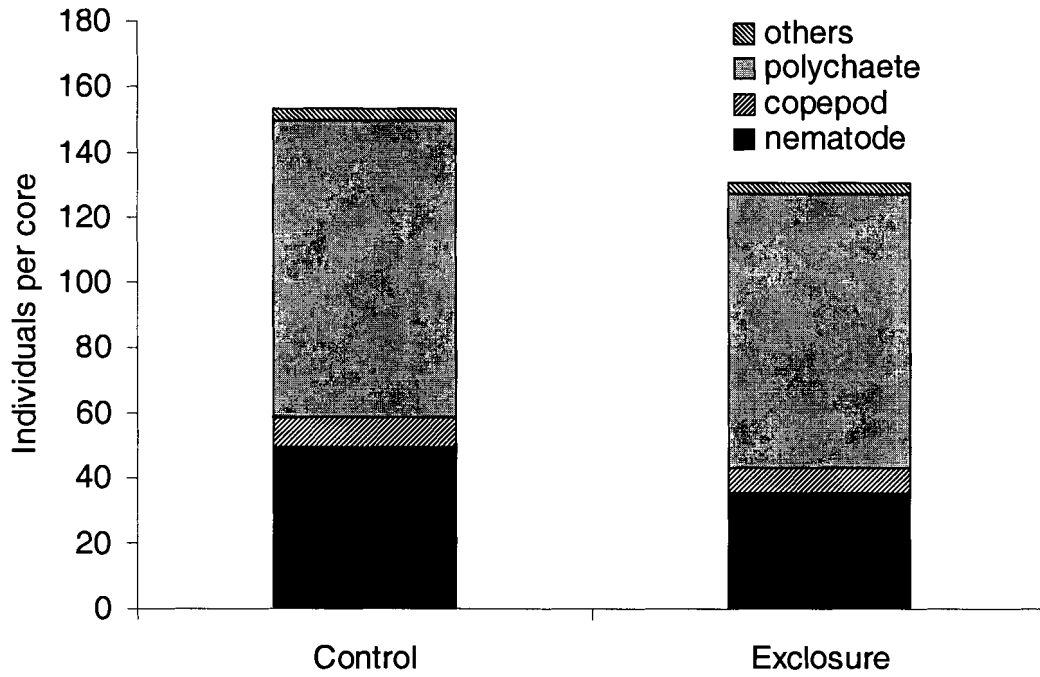
**Figure 2-4:** Invertebrate composition of control and exclosure subsurface prey cores. Foraminiferan, cumacean, tanaid, bivalve, insect larva and ostracod counts are pooled as 'others'.
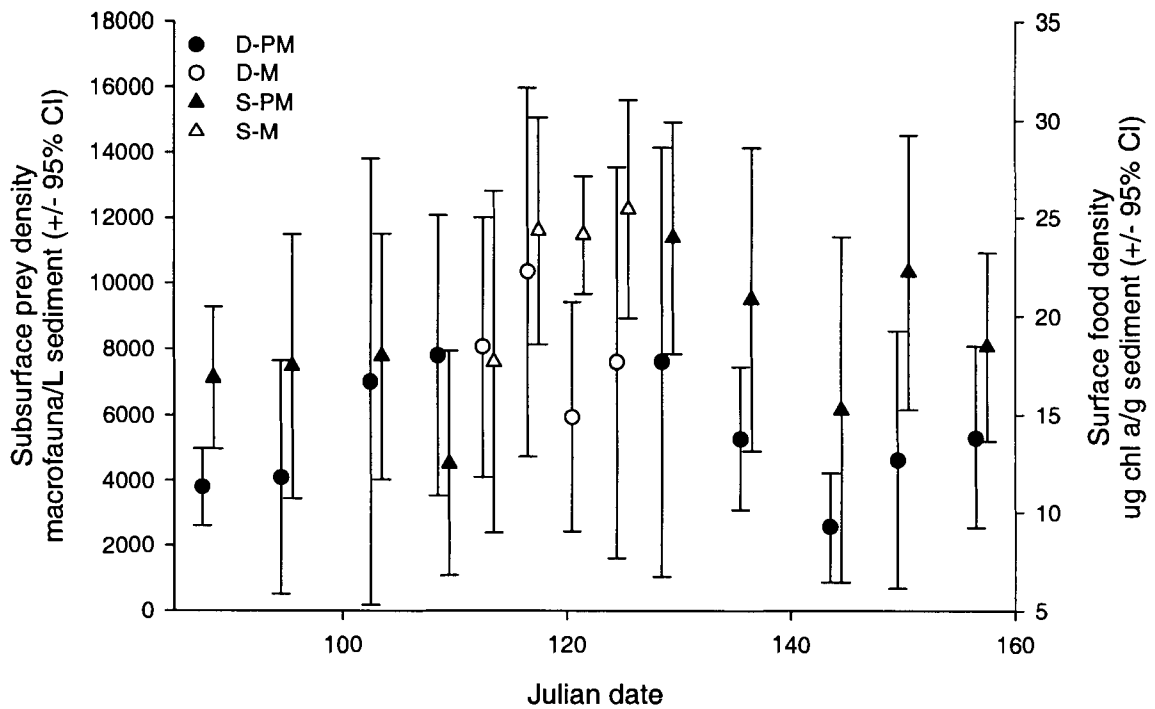
Figure 2-5: Subsurface and surface food densities versus julian date in exclosure
plots. Solid black circles show pre- and post-migration subsurface prey
abundance (D-PM), while hollow circles show subsurface prey
abundance during migration (D-M). Solid black triangles show pre-
and post-migration surface food densities (S-PM), while hollow
triangles show surface food abundance during migration (S-M).
Subsurface and surface data points are offset from one another for
clarity.
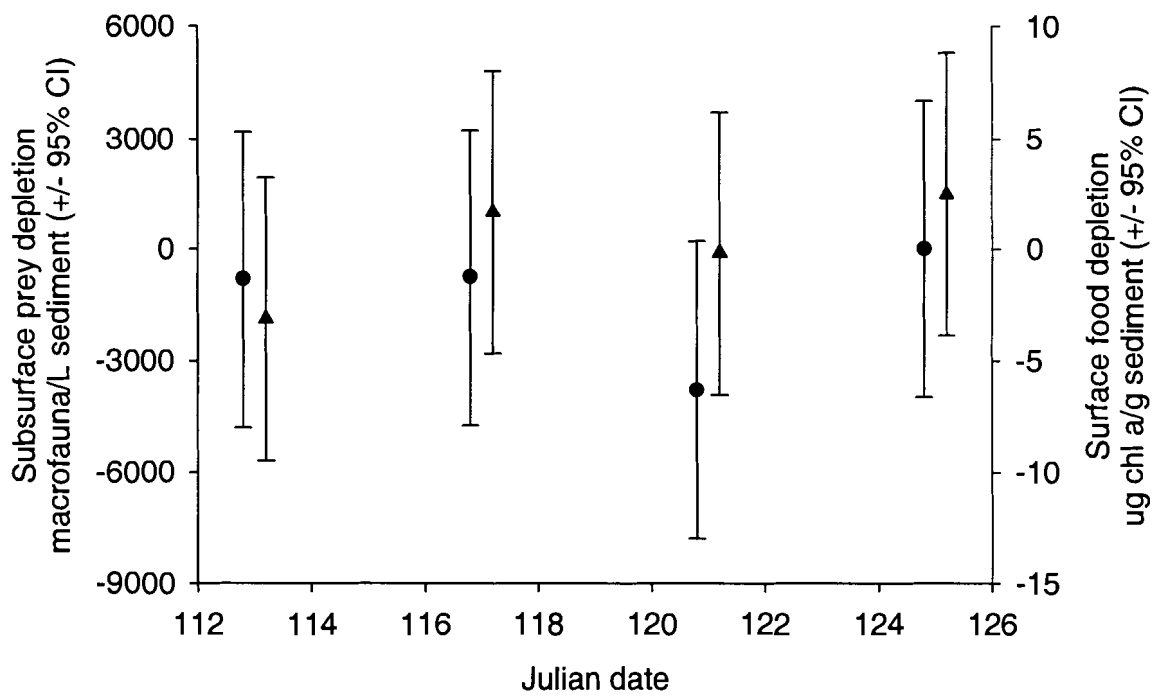
**Figure 2-6:** **Differences in surface and subsurface food densities between exclosure and control plots (E-C). Subsurface prey counts are shown with circles, surface food counts are shown with triangles. Subsurface and surface data points are offset from one another for clarity.**

# CHAPTER 3:

# TIDALLY MEDIATED SHIFTS IN WESTERN SANDPIPER FORAGING BEHAVIOUR AND PEREGRINE FALCON ATTACK RATES

Kimberley J. Mathot

# Abstract

Changes in allocation to pecking (surface) and probing (subsurface) feeding modes by Western Sandpipers (*Caldris mauri*) in response to tidally-mediated changes in the distribution of their prey were investigated. The absolute density of both surface and subsurface prey remained constant over the tidal cycle, but the density of non-prey changed, causing the proportion of invertebrate items that were classed as prey to change. Prey proportions decreased in surface layers, and increased in subsurface layers from falling to rising tide. At the same time, Western Sandpipers increased their allocation to probing feeding modes. Subsurface feeding reduces an individual's ability to detect approaching predators and Peregrine Falcons (*Falco peregrinus*) increased their attack rate on Western Sandpipers 6 fold during the rising tide period. Western Sandpipers did not increase their scanning rates in response to the higher attack frequency on the rising tide, likely due to high dilution effects. This study suggests that increasing the abundance of non-prey relative to prey may reduce intake rate. A possible mechanism is that Western Sandpipers require involvement time with encountered invertebrates to discriminate prey from non-prey. Similar phenomena may exist in other biological systems, and may have implications for how habitat quality, giving up densities, and patch depletion are assessed.

# Introduction

The need for foragers to balance the benefits of feeding against the risk of mortality due to predation has received a great deal of attention in both theoretical and empirical studies (Lima and Dill 1990, Houston et al. 1993, Lima 1998). The trade-off between food and safety is often considered on a spatial scale, where individuals must choose between sites that differ in the level of food and safety offered (Lima and Dill 1990, Lima 1998). Alternatively, the trade-off between food and safety can be measured on a temporal scale, where feeding and anti-predator behaviours are mutually exclusive, and individuals must determine how to allocate their time to each of these activities (Lima and Dill 1990). However, many foragers exhibit multiple feeding modes and/or diet specializations, which may differ in foraging profitability and probability of mortality due to predation (Lima and Dill 1990, Lima 1998, Durell 2000). Therefore, another level at which the optimization between food and safety may be studied is the allocation of time to different feeding modes in response to changes in the distribution and abundance of prey, and resultant changes in the risk of mortality due to predation.

The Western Sandpiper (*Calidris mauri*) is an ideal study species for this type of investigation because it displays two distinct feeding modes: surface (pecking) and subsurface (probing) (Sutherland et al. 2000). The foraging benefit of pecking versus probing feeding modes varies as a function of both how prey are distributed in the sediment and bill morphology. All else being equal, distributions biased towards the sediment surface will tend to favour pecking, while distributions biased towards deeper sediment will tend to favour probing. Therefore, because many intertidal invertebrates shift their vertical distribution in the sediment column over the tidal cycle (Boaden and Platt 1971, Steyaert et al. 2001), we can expect Western Sandpipers to show coincident shifts in their allocation to pecking and probing feeding modes.

Empirical studies on other species of birds have shown that "head-down" feeding behaviours such as probing reduce an individual's ability to detect approaching predators relative to "head-up" feeding behaviours such as pecking (Barbosa 1995, Lima and

Bednekoff 1999). Predators should concentrate their attack efforts when the probability of success is greatest. Therefore, we can expect Peregrine Falcons (*Falco peregrinus*), the primary predator of Western Sandpipers (Wilson 1994), to concentrate their attack efforts during the tidal period when Western Sandpipers have the highest use of probing feeding behaviours. Western Sandpipers may counteract the increased danger associated with probing by increasing their allocation to anti-predator vigilance or by foraging in less dangerous habitats.

Here, the Western Sandpiper is used as a model system to investigate changes in time allocation to different feeding modes in response to tidally-mediated changes in the distribution of their prey. The effect of changes in feeding mode on an individual's probability of mortality due to predation, inferred by Peregrine Falcon attack rates, was also recorded. Finally, the ability of Western Sandpipers to compensate for increased danger associated with particular feeding modes was studied by investigating changes in their time allocation to scanning versus feeding behaviours.

## Methods

### Study site

This study was conducted between 14 October 2003 and 27 November 2003 at Costa del Este (9°00'40" N, 79°27'31" W), located on the eastern edge of Panamá City, Republic of Panamá. Costa del Este is a large (3 km long) intertidal mudflat that supports over 200,000 sandpipers during the non-breeding season, October through February (Morrison et al. 1998). The western boundary of Costa del Este is defined by the Río Matías Hernández and the eastern side is flanked by mangroves.

### Behavioural observations

Focal observations were made of foraging individuals on both rising and falling tide periods. "Falling tide" was defined as the 3 hour period following the high tide, and "rising tide" was defined as the 3 hour period preceding the high tide. On all sampling days, falling tides preceded rising tides during daylight hours. Observations were made using a spotting scope in the open from the upper intertidal. Individuals were randomly

selected for 1-min observations in which the occurrence of each of the following foraging behaviours was recorded: peck, surface sew, probe, deep sew, and scan. 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. Scanning was defined as "head up" behaviour where the bill was parallel to the horizon or higher. All observations were recorded onto micro-cassette tapes and later transcribed. Because males and females are known to exhibit differences in feeding behaviour (Mathot and Elner 2004), the sex of focal individuals was noted at the onset of a focal observation. Western Sandpipers are sexually dimorphic: males are circa 5% smaller with respect to most body measures, but 12% smaller with respect to bill length (Cartar 1984). Thus, short-billed males and long-billed females can easily be distinguished by eye, with a large proportion of birds with intermediate bill lengths remaining unsexed and being excluded from the analyses. A single observer (KJM) made all focal observations. Feeding behaviour was analyzed by grouping pecks and sews together as "pecking" feeding behaviours and probes and deep sews as "probing" feeding behaviours. "Percent pecking" was used as an index of feeding technique.

I also recorded the frequency of Peregrine Falcon attacks on flocks of Western Sandpipers during both rising (n = 8) and falling tide (n = 7) periods. Flocks of Western Sandpipers respond to peregrine attacks with a characteristic flushing behaviour (Nebel 2003) and observation of this behaviour was used to identify recent peregrine attacks. In many cases, I was able to directly observe the peregrine that had mounted the attack. Although attack rates are known to change as a function of prey flock size (Whitfield 2003), attack rates presented here are not corrected for flock size. The reasons for this are twofold: 1) the scale at which Whitfield (2003) observed changes in attack rate (flock sizes from 0 to >50) is markedly different from the typical flock sizes observed at Costa del Este (>500, personal observation), and 2) many attacks were observed from distances exceeding 1 km, and precise flock sizes could not be estimated.

## Invertebrate sampling

I collected 14 cores during falling tides and 15 during rising tides over four days (14 and 22 October, and 12 and 26 November) using a modified syringe with a 26 mm internal diameter to a depth of 40 mm. These core dimensions have been used previously to sample Western Sandpiper prey (Sutherland et al. 2000, Wolf 2001, Mathot and Elner 2004). Cores were collected haphazardly in the upper intertidal area to correspond with the area where focal observations were made, approximately 25 meters from the shoreline.

Immediately following collection, each core was sliced at 5 mm intervals and each fraction was stored in individually labelled plastic bags, placed in a cooler, and later preserved in 10% formalin in sea water. Invertebrate samples were washed with filtered sea water through a 500 $\mu$m sieve to separate the macrofaunal fraction of invertebrates. The fauna retained on the sieve were then identified and enumerated on a scored petri dish under a binocular microscope at 40X magnification.

Calidrid shorebirds rely heavily on non-visual cues to locate prey when feeding on mudflats (Gerritsen and van Heezik 1985) and may incur a time cost in order to discriminate between prey and non-prey invertebrates (see Discussion). Therefore, I distinguished prey and non-prey when measuring Western Sandpiper food abundance. Western Sandpipers feed on a wide variety of invertebrates within the size range of 0.1 to 5 mm (Davis and Smith 2001). However, nematodes, have been demonstrated to be absent from stomach contents (Reeder 1951, Recher 1966, Senner 1979, Baldassarre and Fischer 1984, Quammen 1984, Senner et al. 1989, Davis and Smith 2001) and fecal droppings (Quammen 1984, Wolf 2001, Seaman 2003). Furthermore, exclosure experiments that have detected the depletion of several invertebrate taxa following periods of high intensity foraging by Western Sandpipers have failed to detect any depletion of nematodes (Sutherland et al. 2000). Thus, it appears that nematodes are excluded from Western Sandpiper diet, possibly because some species are endoparasites (see Wilson 1994 and references therein) and/or due the low digestibility of their extensive cuticle. Therefore, all invertebrates excluding nematodes were classified as "prey", while nematodes were classified as "non-prey" for Western Sandpipers.

**Statistical analysis**

I tested for changes in prey and non-prey densities as well as prey proportions in surface and subsurface layers of sediment between tidal periods using ANOVAs or Welch ANOVA F-tests if variances differed between tidal periods. Surface prey densities were obtained from the top 5 mm core slices. Subsurface prey densities were obtained by summing the abundances for each of the slices from 5 to 40 mm depth from each core.

An ANOVA with 'sex' and 'tide state' as factors was used to test for changes in the relative use of pecking between rising and falling tides. I tested whether Peregrine Falcons adjusted their attack effort (as indicated by attack rate) in response to tide-related changes in the intrinsic vigilance level of their prey (Western Sandpipers). I also tested the effects of 'sex' and 'tide state' on Western Sandpiper scanning rates using the PROC GENMOD platform specifying a Poisson distribution in SAS® 9.1. For each analysis, non-significant interaction terms were dropped from the models.

# Results

The invertebrate community at Costa del Este was numerically dominated by nematodes, polychaetes, and copepods. Ostracods, foraminiferans, gastropods, arthropods, bivalves and cumaceans occurred in lower frequencies (Fig. 3-1). Copepods were more abundant in surface than in subsurface layers. In contrast, polychaetes predominated in subsurface layers.

There were no significant changes in the density of either prey ($F_{[1,27]} = 0.00$, p = 0.99) or non-prey ($F_{[1,27]} = 0.42$, p = 0.52) in the surface layer of sediment between falling and rising tide, although the mean density of non-prey recorded was higher on the rising tide. There was a tendency for the proportion of invertebrates classed as prey to decrease in the surface layer during the rising tides, however, this change was only marginally significant ($F_{[1,27]} = 3.48$, p = 0.07). Subsurface prey density did not change between falling and rising tide ($F_{[1,27]} = 0.14$, p = 0.71), but there was a significant decline in the density of non-prey ($F_{[1,27]} = 9.60$, p = 0.0045). Consequently, there was a

significant increase in the proportion of subsurface items classed as prey ($F_{[1,27]} = 13.58$, p=0.0010) (Table 3-1).

Both sex and tidal state were significant factors affecting the percent pecking in Western Sandpipers. Males used pecking feeding modes more so than females ($F_{[1,118]} = 22.67$, p < 0.0001), and there was greater use of probing behaviours on rising tides compared with falling tides ($F_{[1,118]} = 21.92$, p < 0.0001) (Fig. 3-2).

Peregrine attack rates on Western Sandpipers were significantly higher on rising than on falling tides (t = -4.72, df =13, p<0.001). The mean attack rate on falling tides was 0.25 attacks per hour, compared with 1.5 attacks per hour on the rising tides, a 6 fold increase in attack rate (Fig. 3-3). Sex was a significant factor affecting Western Sandpiper scanning rates ($\chi^2 = 13.64$, p = 0.0002), males had higher vigilance rates than females on both rising and falling tides (Fig. 3-4). Vigilance rates did not differ significantly between tidal periods ($\chi^2 = 0.08$, p = 0.77).

## Discussion

This study investigated tidally mediated shifts in Western Sandpiper foraging behaviour and Peregrine Falcon attack rates. No changes in the vertical distribution of prey were recorded over the tidal cycle. However, the vertical distribution of non-prey changed resulting in higher prey proportions in subsurface layers and lower prey proportions in surface layers during the rising tide period. Coincident with these shifts in prey proportions, Western Sandpipers increased their level of probing from falling to rising tide while Peregrine Falcons showed a 6-fold increase in attack rates. Western Sandpipers did not increase scanning rates in response to the increased attack rates on rising tides.

Although no significant tide-related changes in the distribution of prey were observed in this study, changes in non-prey distribution resulted in changes in the proportion of prey in surface and subsurface layers between tidal periods. The proportion of prey decreased in surface layers by 33% (from 0.35 to 0.21), and increased in

subsurface layers by 65% (from 0.32 to 0.53) from falling to rising tide. Invertebrates generally undergo net downward vertical migrations during tidal exposure (Boaden and Platt 1971). However, nematodes exhibit species specific vertical migration patterns (Steyaert et al. 2001). At this study site, the species assemblage of nematodes appears to be such that there is a net upward migration of nematodes resulting in a trend towards lower prey proportions in surface layers and significantly higher prey proportions in subsurface layers during rising tides.

Western Sandpipers decreased their percentage of pecking on the rising tide, from 99.2 to 96.2% in males and from 90.6 to 81.0% in females. The shift towards decreased pecking coincided with decreasing prey proportions in surface layers and increasing prey proportions in subsurface layers. If Western Sandpipers are assumed to require involvement time to recognize prey types, decreasing the proportion of prey may reduce intake rate as more of the total time available for foraging will be spent assessing invertebrates that are ultimately rejected, thereby reducing the rate at which prey are consumed.

Calidrid shorebirds are known to use four cue types to locate prey: visual, tactile direct, tactile indirect, and chemical (van Heezik et al. 1983, Gerritsen and van Heezik 1985, Gerritsen and Meiboom 1986). On mudflats, where prey are likely to be covered by sediment, the use of visual cues may be limited (Gerritsen and van Heezik 1985) and prey are more commonly located using tactile or chemical cues. Western Sandpipers forage on mudflats where mean grain size is typically less than 0.2 mm (Quammen 1982) in order to locate prey between 0.1 and 5 mm in size (Davis and Smith 2001). Median macroinvertebrate densities are on the scale of 1000s of individuals/m$^2$ (Ysebaert et al. 2003) and prey do not differ from non-prey in their specific gravities (Price et al. 1977). Thus, although the mechanisms by which Western Sandpiper locate and recognize prey are not well understood, it seems possible that they may not be able to discern prey from non-prey remotely using tactile or chemical cues and that involvement time may be required to evaluate invertebrates once located. Therefore, the shift from pecking to probing may reflect a response of Western Sandpipers to decreased intake rates using

pecking feeding modes and/or increased intake rates using probing feeding modes during the rising tide.

An alternative explanation for the shift from pecking to probing between rising and falling tide periods is that evaporation of water from the mudflat surface over the low tide period reduces the ability of sandpipers to feed on surface prey types. This could occur if sandpipers rely on surface water for either surface tension transport (Rubega 1997) or because water increases the activity and therefore the availability of invertebrates (Yates et al. 1993). However, two lines of evidence suggest that this possibility is not likely. First, because the mudflat surface at Costa del Este is very uneven, standing water remains on a substantial proportion (>30%, personal observation) of the mudflat surface through the entire low tide period. Second, if evaporation of water off the sediment was significant, we should expect invertebrates to retreat from the surface in order to avoid desiccation (Ravenscroft and Beardall 2003). No such retraction into the sediment was observed as the densities of surface invertebrates remained constant between falling and rising tidal periods.

Nonetheless, the relationship between foraging mode and the relative abundance of prey observed in this study is correlative. Experimental manipulation of prey densities and prey:non-prey ratios are called for in order to unequivocally establish the proportion of prey as a factor underlying shifts in feeding behaviour. While experimental manipulation of prey densities and relative densities may not be feasible for shorebird species such as Western Sandpipers which feed on very small prey, it can be done for larger species such as Red Knots (*C. canutus*) which feed primarily on bivalves (Piersma et al. 1998).

Male and female Western Sandpipers differed in the magnitude of their shifts in feeding behaviour. Males decreased their percent pecking by 3 % (from 99% to 96%) while females decreased their percent pecking by 10% (from 92% to 82%) between the falling and rising tide period. Females have been proposed to be able to exploit a broader range of prey burial depths due to their having longer bills (Nebel 2003). The observation

of a larger shift in feeding behaviour among females is consistent with the hypothesis that females have greater foraging plasticity than males.

Although the magnitude of the shifts in feeding behaviour appear relatively small, it is important to note that the relationship between recorded feeding behaviours and intake rates is not known. Therefore, an individual using 90% pecking is not necessarily obtaining 90% of its prey intake from the surface, but may be obtaining a substantially smaller proportion of its diet from the surface if many of the surface feeding behaviours recorded reflect tactile prey locating mechanisms rather than prey ingestion events. Unfortunately the mechanisms by which Western Sandpipers locate and ingest prey are poorly understood and the actual effect of the recorded shifts in feeding behaviour on the proportion of prey obtained from the surface versus the subsurface is unclear.

Coincident with the shift by both males and females to greater use of probing on the rising tide was a 6 fold increase in mean Peregrine Falcon attack rates. Many studies have documented an apparent avoidance by predators towards attacking relatively more vigilant prey (Lima 1998). "Head-down" (probing) feeding behaviours have been shown to reduce an individual's ability to detect approaching predators relative to "head-up" (pecking) feeding behaviours in other birds (Barbosa 1995, Lima and Bednekoff 1999). Thus, it appears that Peregrine Falcons are able to assess the vigilance level of their prey, and concentrate their attack efforts during the tidal period when they have the greatest probability of success for a given attack.

An alternative explanation for the increased attack rate during rising tides is that mass gain over the foraging period, from falling to rising tide, reduces the escape performance of individuals thereby increasing the probability of a successful attack. Inter-individual differences in wing loading (mass per unit area of wing) are correlated with escape performance such that individuals with higher wing loading have poorer escape ability (Burns and Ydenberg 2002). However, within an individual Western Sandpiper, relatively large changes in mass (5 grams = 20% of body mass) have small effects on the probability of a successful escape (A.C. Pomeroy, unpublished data). Therefore, mass gain over the foraging period during tidal exposure of mudflats, is

unlikely to have an appreciable effect on an individual's escape performance, and I advocate that reduced ability to detect approaching predators remains the most likely mechanism mediating the increased attack rate on rising tides.

If higher peregrine attack rates are perceived by Western Sandpipers as greater predation danger, Western Sandpipers should compensate for the increased danger by increasing their scanning rates on rising tides. No change in scanning rates between falling and rising tides was recorded. However, this study site is used by circa 200,000 sandpipers (Morrison et al. 1998). Therefore, the effect of increased attack success or increased attack rates by Peregrine Falcons during the rising tide on an individual sandpiper's probability of predation may be small due to dilution effects.

Although neither sex altered their scanning rates between tidal periods, sex-related differences in scanning rates were observed. Males scanned at approximately 4 times higher rates than females. These differences may be associated with sex-related differences in vulnerability to predation, with the more vulnerable sex investing more heavily in anti-predator behaviours. In a study of escape performance in Western Sandpipers, Burns and Ydenberg (2002) recorded no sex-related differences in take-off speed, and small but significant differences in take-off angle (female: $8.1^{\circ}$, male: $5.7^{\circ}$). Given their lesser take-off angle, males appear more vulnerable than females. However, the biological significance of such a small difference in take-off performance is questionable. Alternatively, the observed differences in scanning rate in this study may reflect sex-related differences in feeding. Individuals that use pecking as opposed to probing behaviours rely more heavily on visual cues and may exhibit more 'head up' behaviour because they scan the mudflat for prey (Gerritsen and van Heezik 1985). Therefore, some of the scanning behaviour recorded for males may reflect prey searching behaviours rather than anti-predator behaviours.

**Conclusions**

This study recorded tidally-mediated shifts in the distribution of invertebrates over the tidal cycle. The vertical distribution of prey did not change, however, non-prey showed a net upward vertical migration resulting in lower prey proportions in the surface

layer and higher prey proportions in the subsurface layer during the rising tide. Western Sandpipers appear to be sensitive to changes in prey proportions, as they exhibited coincident shifts towards increased probing on the rising tide. Peregrines concentrated their attack effort during the rising tide, when Western Sandpipers had higher use of probing feeding behaviours and therefore had a reduced ability to detect approaching predators. The increased attack rate on rising tides did not cause Western Sandpipers to increase their scanning rates, presumably due to dilution effects. The suggestion that intake rates may be negatively influenced by the presence of non-prey is novel and merits further investigation. If foraging decisions are indeed mediated by relative prey abundances, then how we assess habitat quality, giving up densities, and patch depletion may need to be modified to incorporate possible interference by non-prey.

## Acknowledgements

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**Table 3-1:** Surface and subsurface prey and non-prey densities (individuals/L sediment) ± 1 se and prey proportions (prey/ (prey + non-prey)) ± 1 se for rising and falling tidal periods.

| Prey depth | Tidal state | Prey | Non-prey | Prey proportion |
|---|---|---|---|---|
| Surface | Falling | 3069 ± 762 | 9853 ± 2803 | 0.35 ± 0.06 |
| Surface | Rising | 3065 ± 736 | 12387 ± 2708 | 0.21 ± 0.05 |
| Subsurface | Falling | 1119 ± 183 | 2677 ± 373 | 0.32 ± 0.04 |
| Subsurface | Rising | 1213 ± 177 | 1070 ± 360 | 0.53 ± 0.04 |
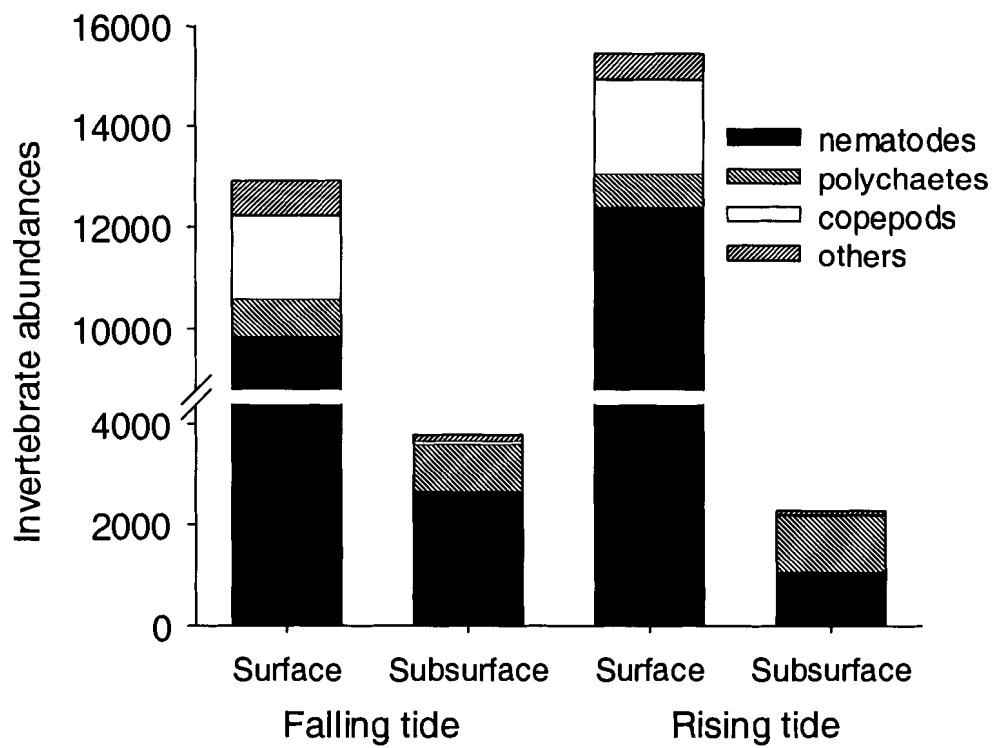
Figure 3-1:  Mean surface and subsurface invertebrate abundances (individuals/L)
by tidal state.  Note that the y-axis is not continuous
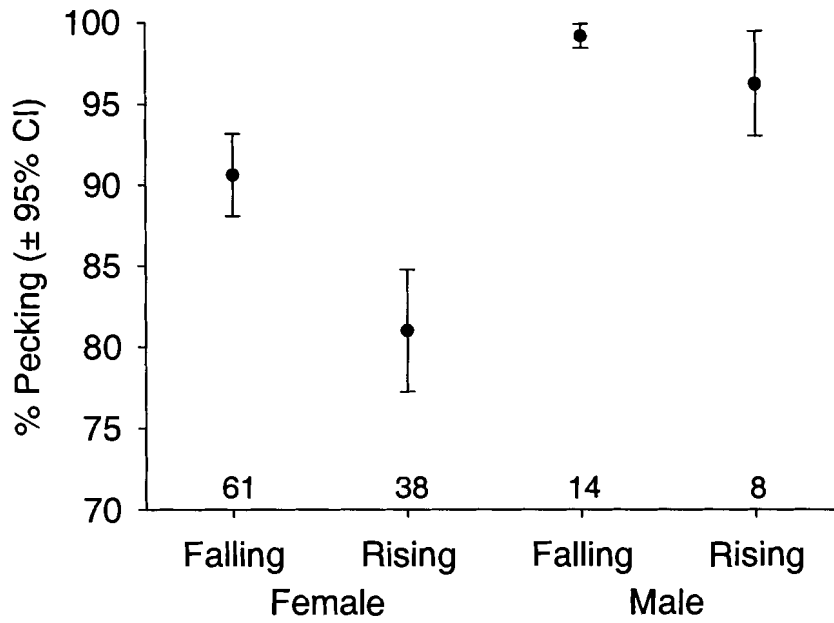
**Figure 3-2**  **Percent pecking by sex and tidal state. Values above x-axis indicate sample sizes.**
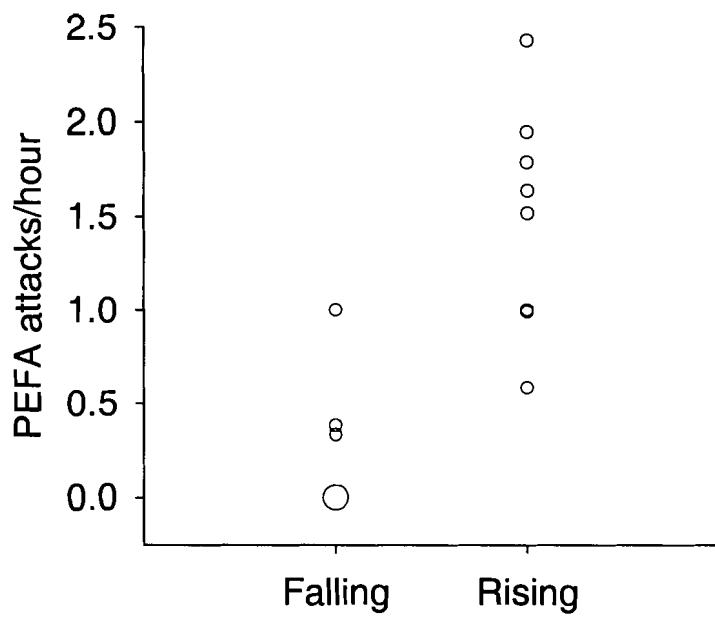
**Figure 3-3** Peregrine Falcon (PEFA) attack rate versus tidal state. Large circle denotes 4 overlaid data points.
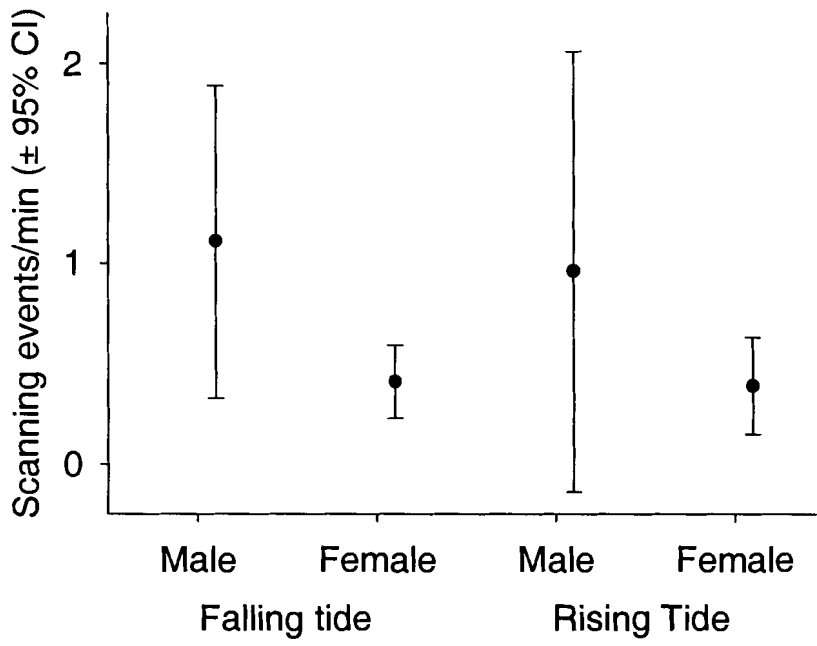
**Figure 3-4: Scanning rates by sex and tidal state.**

# CHAPTER 4:
# A TEST OF THE 'FORAGE SELECTION' HYPOTHESIS FOR DIFFERENTIAL MIGRATION IN A SHOREBIRD

Kimberley J. Mathot and Robert W. Elner

# Abstract

Sexual segregation outside of the breeding season occurs in many vertebrate taxa and several hypotheses have been proposed to explain the phenomenon. In this study, we test the 'forage selection' hypothesis as a mechanism to explain differential migration in a shorebird, the Western Sandpiper (*Calidris mauri*), based on inter-sexual differences in the ability to exploit different food types. In Western Sandpipers, the sexes are differentially distributed across the non-breeding range, with males shifted north relative to females (termed 'differential migration'). Also, males use a higher percentage of pecking (surface) feeding modes compared to females which use a higher percentage of probing (subsurface) feeding modes. Therefore, the 'forage selection' hypothesis predicts that northern (male-biased) non-breeding sites should have surface-biased food distributions, while southern (female-biased) non-breeding sites should have subsurface-biased food distributions. We measured the vertical distribution of both macrofaunal invertebrates and biofilm densities across the non-breeding range. Surface invertebrates dominated at northern sites, while subsurface invertebrates dominated at southern sites. No latitudinal trend was observed for biofilm. However, variability in biofilm densities was higher in more northerly sites, indicating the presence of more high density biofilm patches at these sites compared with southern sites. Thus, latitudinal patterns of food distribution were consistent with predictions derived from the 'forage selection' hypothesis. We also attempted to verify the use of biofilm as a food source by Western Sandpipers, however, the results of surficial food removal plots (biofilm and surface invertebrates) and stable isotope analysis were equivocal. This study is the first to relate broad scale changes in the distribution of food to the non-breeding distribution of a shorebird. Our results support the hypothesis that males and females segregate during the non-breeding season in response to latitudinal variation in the abundance of surface and subsurface food types and inter-sexual differences in the ability to exploit those food resources.

# Introduction

Segregation of the sexes outside of the breeding season is common in many vertebrates. In birds the phenomenon is also known as differential migration (Cristol et al. 1999). Understanding the mechanisms responsible for differing patterns of habitat occupancy between sexes can have important implications for effective conservation and habitat management (Durell 2000, Elner and Seaman 2003, Bowyer 2004).

In avian systems, studies of differential migration have dealt almost exclusively with one or more of the following three hypotheses (see Cristol et al. 1999 for review). The 'arrival time' hypothesis states that the sex that stands to gain the most from early arrival to the breeding grounds will be selected to spend the non-breeding season closest to the breeding grounds. The 'body-size' hypothesis proposes that size-related differences in physiological tolerance allow the larger sex to survive harsher climates. Finally, the 'dominance hypothesis' states that the dominant sex excludes the subordinate sex from the preferred regions of non-breeding range. The level of empirical support for these hypotheses varies among species (Cristol et al. 1999)

A separate set of hypotheses have been proposed for sexual segregation in ungulates (see Bonenfant et al. 2004 and references therein). The 'activity budget' hypothesis proposes that sex-related differences in activity patterns lead to habitat segregation. The 'predation risk' hypothesis states that inter-sexual differences in vulnerability to predators cause the more vulnerable sex to seek safer habitats. Finally, the 'forage selection' hypothesis proposes that inter-sexual differences in nutritional requirements resulting from sexual dimorphism in body size, cause males and females to prefer different habitats.

The distinction between hypotheses to explain sexual segregation in ungulates versus birds is artificial, as many of the above hypotheses could reasonably be applied to either system. For example, many species of birds show sexual dimorphism in bill features which results in inter-sexual differences in feeding specializations (Durell 2000).

Thus, while male and female birds may not differ in their nutritional requirements, as is postulated for ungulates (Bonenfant et al. 2004), they often differ in the types of food resources they are able to exploit (Durell 2000). Therefore, the 'forage selection' hypothesis may provide a mechanism to explain the phenomenon of differential migration in birds (see Elner and Seaman 2003).

In this study, we use the Western Sandpiper (*Calidris mauri*) as a model organism to test the 'forage selection' hypothesis for differential migration in a shorebird. Western Sandpipers spend the non-breeding season distributed between California and Péru (Wilson 1994) and are partially segregated on the basis of age, sex and morphology. Males tend to winter north of females, juveniles are overrepresented in the northernmost and southernmost extremes of the non-breeding range (Nebel et al. 2002), and there is a pattern of increasing bill length with decreasing latitude within each age and sex class (O'Hara 2002). Western Sandpipers are sexually dimorphic, with females being on average 5% larger than males for most body measurements, but 12% larger than males with respect to bill length (Cartar 1984). This sexual dimorphism in bill length is associated with inter-sexual differences in feeding technique, with males tending to use pecking (surface) feeding modes more so than females, which use more probing (sub-surface) feeding modes (Mathot and Elner 2004).

The 'forage selection' hypothesis predicts that northern (male-biased) non-breeding sites should have food distributions biased towards the surface, while the vertical distribution of food at southern (female-biased) sites should be more biased towards the subsurface. In this study, we observed Western Sandpiper feeding behaviour at 6 non-breeding sites in order to verify that sex-related differences in feeding observed at a migratory stopover site (Mathot and Elner 2004) are maintained across the non-breeding range. We also measured the distribution of food, both macrofaunal (> 0.5 mm) invertebrates and biofilm, across the non-breeding range. Biofilm was measured as a potential food source because a recent study suggests that biofilm may comprise a component of Western Sandpiper diets, particularly males (Elner et al. 2005). Biofilm, which consists of diatoms, bacteria and muco-polysaccharides (Cognie et al. 2001) covers the surfaces of the intertidal mudflats on which Western Sandpipers forage, and is

rich in carbohydrates and proteins (Decho and Lopez 1993). We also used surficial food removal plots and stable isotope analysis to test the hypothesis that biofilm is ingested and assimilated by Western Sandpipers.

## Methods

### Study sites

This work was carried out at six Western Sandpiper non-breeding sites. Humboldt Bay (N 40°50, W 124°05), Bodega Bay (N 38°19, W 123°02), and San Francisco Bay (N 37°30, W 122°06) in California were sampled in January and February 2003. Punta Banda (N 31°45', W 116°37') and La Paz (N 24°06', W 110°22') in México were sampled in January 2004, and Costa del Este (N 09°00', W 79°27') in Panamá was sampled between September and December 2003 (Fig. 4-1). These sites were selected because they represent a broad range of latitudes. Western Sandpipers were collected by shotgun at Roberts Bank in British Columbia (49°05'N, 123°12'W) during their northward migration in April 2003 under a permit to R.W. Elner as part of a study by the Canadian Wildlife Service (Scientific permit # 59-03-0398 and permit # 59-03-0398 amendment #1 issued by Environment Canada). Tissues collected from that project were used in this study for stable isotope analysis.

### Feeding behaviour

Observations were made using a spotting scope in the open amongst flocks of foraging sandpipers. Individuals were randomly selected for 1 minute observations in which we recorded the occurrence of each of the following foraging behaviours: peck, surface sew, probe, and deep sew. 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. Pecks and sews were classified as 'pecking' feeding behaviour and probes and deep sews were classified as 'probing' feeding behaviour. Percent pecking was used as an index of feeding mode. All observations were recorded onto micro-cassette tapes and later transcribed. Because the

sexes are highly dimorphic (Page and Fearis 1971), we were able to classify individuals as male or female by eye (see Mathot and Elner 2004). Intermediate sized individuals were not assigned to a sex and are excluded from the analyses. Observations were made of a total of 506 individuals, 75% were classified as male and 25% were classified as female. Sample sizes per site are presented in Table 4-1. A single observer (KJM) made all focal observations.

**Invertebrate and biofilm sampling**

Cores were collected using a haphazard sampling design immediately following tidal exposure. We used a modified syringe with a 26 mm internal diameter and sampled to a depth of 40 mm to collect cores in the upper intertidal area where focal observations were made, approximately 25 meters from the shoreline. These core dimensions were used because they allowed comparability with other studies (Sutherland et al. 2000, Wolf 2001, Seaman 2003, Mathot and Elner 2004) and because the depth is appropriate for sampling prey accessible to Western Sandpipers. Although the deepest prey sampled exceed the length of the longest Western Sandpiper bills by approximately 10 mm, they likely represent prey that would be accessible to the longest-billed Western Sandpipers prior to retraction into the sediment during sampling (Wolf 2001, Seaman 2003). Thus, depth intervals for sampled prey do not correspond directly to bill length, but increasing prey depth corresponds to prey accessible to increasingly longer-billed individuals. Sample sizes per site are presented in Table 4-1.

Immediately following collection, each core for invertebrate estimates was sliced at 5 mm intervals and each fraction stored in individually labelled plastic bags, placed in a cooler, and later preserved in 10% formalin in sea water. Invertebrate samples were washed with filtered sea water through a 500 $\mu$m sieve to separate the macrofaunal fraction of invertebrates. The fauna retained on the sieve were then identified and enumerated on a scored petri dish under a binocular microscope at 40X magnification. Nematodes were excluded from prey counts as they are not a component of Western Sandpiper diets (Reeder 1951, Recher 1966, Senner 1979, Baldassarre and Fischer 1984, Quammen 1984, Senner et al. 1989, Davis and Smith 2001).

Because the biomass of individuals may differ markedly across broad latitudinal scales, biomass rather than numerical abundance may be the biologically meaningful variable to measure when comparing food abundances across latitudes (Piersma et al. 1993). However, the numerical abundance of prey may also be meaningful, as it will affect encounter rates and consequently, intake rates (Begon et al. 1996). Therefore, we compare both the vertical distribution of biomass (ash free dry weight or AFDW) across latitudes and the vertical distribution of individuals. Mean AFDWs were determined by subtracting the mass of all individuals of a given taxa from a given site after being combusted at 575°C for 24hours, from their dry mass obtained after 72 hours in a drying oven at 25°C. The resultant mass was divided by the total number of individuals to obtain average AFDW per individual of a given taxa for each site.

Haphazardly collected core samples were also used for biofilm estimates (sample sizes per site are presented in Table 4-1). Biofilm cores were frozen immediately following collection, and the top 2 mm were sliced off the frozen core. Biofilm abundance drops off dramatically below this depth (Sutherland et al. 1998a) and biofilm is likely to be targeted only by surface feeding modes (Elner et al. 2005). Chlorophyll concentration was used as an index of biofilm abundance and was determined fluorometrically according to the method outlined in Sutherland et al. (1998b).

**Diet assessment**

Surficial removal plots were used as a means of determining whether male and female Western Sandpipers differed in the extent of their use of biofilm. This experiment was conducted at only one of the non-breeding sites, Costa del Este in Panamá, because high bird densities made observations of birds in marked plots feasible. Focal observations were made of individuals foraging in 1 X 1m plots marked with wooden stakes. Control plots were left unaltered while experimental plots had the top 5 mm of sediment removed with a squeegee in order to remove biofilm, which can only grow on or near the surface due to limited penetration of UV rays into fine sediments (Ahrens and Hickey 2002). Therefore, both biofilm and surface invertebrates were absent from surficial removal plots. The time spent in each plot was recorded for each individual, and individuals that displayed no feeding behaviours in a plot were excluded from analyses.

We predicted that if males rely on biofilm to a greater extent than females, they should show a greater reduction in time spent foraging in surficial removal plots compared with control plots than would females. Observations of feeding behaviour and feeding rates in marked plots are not presented because spurious results may arise due to the short observation times associated with birds in marked plots (range: 1-20 seconds).

Stable isotope analysis was used as an additional means of assessing the prevalence of biofilm in the diet of Western Sandpipers. Specifically, the ratio of $^{15}$N to $^{14}$N was compared between males and females to infer differences in the trophic level of their diet. Both $^{15}$N and $^{14}$N are naturally occurring stable isotopes of nitrogen and are therefore both present in the tissues of organisms. However, during excretion, amination and deamination processes, there is preferential loss of the lighter nitrogen isotope, $^{14}$N (Peterson and Fry 1987), which results in a stepwise enrichment of $^{15}$N between trophic levels (Hobson et al. 1994). Therefore, biofilm, which is the product of a primary producer, will be less enriched in $^{15}$N compared with invertebrates, which are consumer species. Consequently, if male Western Sandpipers consume more biofilm than females, they should show relatively less enriched $^{15}$N values than females.

We performed stable isotope analysis on liver samples from 30 males and 31 females collected at Roberts Bank in British Columbia. Liver samples were frozen immediately upon collection. Laboratory analysis was performed at Kansas State University, Kansas. Prior to analysis, samples were freeze-dried and ground in an analytical mill. Stable nitrogen isotope assays were performed on 1 mg subsamples of homogenized materials. Samples were then combusted at 1800°C in a CE 1110 elemental analyzer for solid sample combustion with a Conflo II interface and the resultant gas was analyzed in a Thermo Finnigan Delta Plus mass spectrometer. Stable isotope ratios are expressed in $\delta$ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta^{15}N = [((^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{standard})-1]*1000,$$

where the $^{15}$N/$^{14}$N$_{standard}$ is obtained from atmospheric $N_2$ (air). Thus, a lower $\delta^{15}$N value indicates consumption of lower trophic level food items.

## Statistical analyses

Latitudinal patterns in feeding mode were studied for each sex using a regression. A model with sex and latitude as factors was not used, because no females were observed at the 2 northernmost non-breeding sites, therefore we could not test for a sex*latitude interaction. Latitudinal trends in the vertical distribution of macrofaunal invertebrates, both numerical densities and biomass, were compared with latitude and depth interval as fixed factors. Prior to analysis, summed biomass and invertebrate counts per core were brought to unity and the proportion of biomass or individuals at a given depth was used in order to control for differences between cores in the total biomass or total number of individuals. Depth interval refers to the sampling depth such as 0 – 5 mm, 5 – 10 mm, etc. and was treated as an ordinal variable. Latitudinal trends in biofilm abundance were analyzed with latitude as a fixed factor.

For the surficial removal experiment, plot residency times were analyzed for each sex with treatment as a factor. We did not use a model with sex and treatment as factors, because we had low power to detect an interaction due to a low sample of females on surficial removal plots. Because repeated observations on the same plots were made on a given day, means per sex were calculated for each plot, and analysis was performed on these means. In total, 16 plots were observed with males (6 control plots, 10 surficial removal plots), and 8 plots were observed with females (5 control plots, 3 surficial removal plots).

For all tests, significance was determined at p = 0.05 for main effects, and p = 0.10 for interactions. All non-significant interaction terms were removed from the models.

# Results

## Feeding behaviour

Males used a higher percentage of pecking feeding behaviours than females ($F_{[1,499]} = 173.35$, $p < 0.0001$), and there was no effect of latitude on feeding behaviour

within females ($F_{[1,119]} = 0.5291$, p = 0.4684) (Fig 4-2). There was a small (from 99.8% to 98.1% pecking) but significant decrease in the percent pecking in males with decreasing latitude ($F_{[1,379]} = 5.010$, p = 0.0189). Feeding rate did not differ between males and females ($F_{[1,499]} = 0.8259$, p = 0.3639), however, there was a strong latitudinal trend towards decreasing feeding rate with increasing latitude within each sex ($F_{[1,499]} = 85.01$, p < 0.0001) (Fig 4-3).

## Latitudinal patterns in the vertical distribution of food

The latitude*depth interaction was significant ($F_{[7,768]} = 9.71$, p<0.0001) in explaining variation in the proportion of invertebrate biomass at various depths between sites. The proportion of prey biomass increased with increasing latitude in surface layers of the sediment, but decreased with increasing latitude at increasing burial depths (Fig. 4-4). Similarly, the latitude*depth interaction was also significant in explaining variation in the proportion of prey at different depths between sites ($F_{[7,768]} = 9.71$, p<0.0001). The proportion of prey increased with increasing latitude in surface layers of the sediment, but decreased with increasing latitude at increasing burial depths (Fig. 4-5).

There was no linear effect of latitude on biofilm abundance across the non-breeding distribution of Western Sandpipers ($F_{[1,102]} = 0.52$, p = 0.47, $r^2 = 0.005$, Fig. 4-6), however biofilm density estimates were more variable at northern non-breeding sites.

## Diet

Males spent significantly less time in plots where surficial food types had been removed compared with those where it had not ($F_{[1,14]} = 17.87$, p < 0.001, Fig. 4-7). The effect of surficial food removal on plot residency times was not significant for females ($F_{[1,7]} = 3.26$, p = 0.12, Fig. 4-7), however, females also showed a trend towards decreased plot occupancy times when surficial food types were removed. The lack of a significant effect in females may reflect a low power to detect such an effect as there were only three surficial removal plots on which observations of female feeding behaviour was made.

$\delta^{15}N$ values did not differ by sex ($F_{[1,59]} = 0.38$, p = 0.54, Fig 4-8). However, the measured values were quite variable ($\text{range}_{female} = 10 -16.1\%o$, $\text{range}_{male} = 9.1 -14.3\%o$)

indicating consumption of prey of varying trophic levels. Within sexes, there was no relationship between $\delta^{15}N$ values and culmen length (female: $r^2 < 0.001$, $F_{[1,29]} = 0.019$, p = 0.97, male: $r^2 = 0.008$, $F_{[1,28]} = 0.23$, p = 0.64).

## Discussion

Sexual segregation outside of the breeding season occurs in many vertebrate taxa. In birds, where males and females may occupy different geographic regions outside of the breeding season, this phenomenon is also known as differential migration. The mechanisms underlying differential migration in birds remain poorly understood (Cristol et al. 1999). In this study, we tested the 'forage selection' hypothesis, originally formulated to explain sexual segregation in ungulates (Bonenfant et al. 2004), as a potential mechanism underlying differential migration in Western Sandpipers.

Male and female Western Sandpipers showed consistent differences in their feeding behaviour across six non-breeding sites spanning over 30° of latitude. The percentage of pecking was greater than 95% for males, and between 80 and 90% for females. These levels of pecking are similar to the levels recorded at a migratory stopover site in British Columbia (Mathot and Elner 2004). There were no substantial shifts in feeding behaviour across latitudes within either sex, suggesting that intra-sexual variation in bill length which exists across broad latitudinal ranges (O'Hara 2002) has little effect on the relative use of pecking versus probing feeding behaviours. This study observed significant shifts in prey regimes exist across latitudes. Therefore, the lack of shifts in feeding mode within either sex may indicate that plasticity in the feeding behaviour of individuals is more restricted than is conventionally thought for shorebirds (Skagan and Oman 1996, Davis and Smith 2001).

Although the relative use of pecking and probing feeding modes did not differ within sexes across latitudes, both males and females showed a circa 50% increase in feeding rate, from 39 to 55 feeding events/minute in males, and from 35 to 52 feeding events/minutes in females, between the southernmost site (Costa del Este, Panamá) to the northernmost site (Humboldt Bay, California: males, and San Francisco Bay, California:

females). Unfortunately, intake rates cannot be estimated when making focal observations of individuals because most consumed prey are not large enough to be visible to the observer. Consequently the relationship between feeding rate and intake rate is unclear. However, if feeding rate and intake rate are correlated, this result may indicate that Western Sandpipers must work harder to meet their metabolic demands at more northerly latitudes either due to higher costs of thermoregulation (Castro et al. 1992) or reduced time available for foraging in the north during the winter due to shorter day lengths. Alternatively, predation danger may increase with decreasing latitude causing Western Sandpipers at more southerly wintering sites to invest more time on anti-predator vigilance thereby reducing their foraging rate. Data on predation danger, as indexed by flight time in Western Sandpipers following Peregrine Falcon (*Falco peregrinus*) attacks, support this hypothesis (Nebel 2003). Flight duration per attack increased with decreasing latitude. Also, data on vigilance behaviour collected in this study show increasing vigilance rates with decreasing latitude in males, but no trend in females (unpublished data). Elucidating the mechanisms mediating the latitudinal trend in feeding rate is an avenue for future research and will require a better understanding of the relationship between feeding rate and intake rate.

We tested the 'forage selection' hypothesis as a potential mechanism underlying the non-breeding distribution of Western Sandpipers. This hypothesis states that males and females select different non-breeding sites as a result of inter-sexual differences in feeding behaviour, resulting from sexual dimorphism in bill features. Based on the known inter-sexual differences in feeding behaviour (Mathot and Elner 2004), males tending to have higher use of pecking than females, we predicted that the distribution of food across the non-breeding range would shift such that surface food types predominate in the northern (male-biased) part of the non-breeding range, while subsurface food types predominate in the southern (female-biased) part of the non-breeding range. The vertical distribution of prey, both in terms of biomass and numerical density, did differ across latitudes. In the uppermost layer of sediment, 0 – 5 mm, the proportion of biomass increased significantly with increasing latitude. In contrast, the two deepest layers of sediment sampled, 30 – 35 mm and 35 – 40 mm showed the opposite pattern, with the proportion of biomass decreasing with increasing latitude. Intermediate prey depths (5 –

30 mm) showed no latitudinal trends in biomass proportions. Similar results were observed when the proportion of prey was analyzed at various burial depths across latitudes. Thus, surface prey predominate in northern (male-biased) non-breeding sites, and subsurface prey predominate in southern (female-biased) non-breeding sites, as predicted by the 'forage selection' hypothesis.

Of the three hypotheses commonly evoked to explain differential migration in birds (the dominance hypothesis, the body size hypothesis, the arrival time hypothesis), only the arrival time hypothesis has received empirical support for the Western Sandpiper (see Cristol et al. 1999, Nebel et al. 2002). However, while the arrival time hypothesis accurately predicts the sex that should overwinter closest to the breeding grounds, it does not make any predictions regarding morphological trends within sexes across the non-breeding range. In contrast, the 'forage selection' hypothesis predicts not only that females, due to their having longer bills, should overwinter south of males, but also that within each sex, longer-billed individuals should tend to winter further south. Given that this prediction matches with the observed distribution of Western Sandpipers, there is strong evidence that latitudinal gradients in the distribution of food are closely tied to patterns of differential migration in this species.

We also assessed latitudinal gradients in the distribution of biofilm and tested the hypothesis that biofilm constitutes a component of Western Sandpiper diets. Mean biofilm abundance did not change across latitudes. However, there was greater variance associated with the biofilm density estimates in the more northerly non-breeding sites. Therefore, the number of patches with high biofilm densities was greater at male-biased non-breeding sites and, if biofilm is a predominantly male-exploited food resource, these results may also support the 'forage selection' hypothesis.

We tested the hypothesis that males ingest and assimilate biofilm more than females (Elner et al. 2005) using both experimental and laboratory techniques. Male Western Sandpipers, but not females, spent less time foraging on experimental plots where surficial food types had been removed compared with those where surficial food types were left intact. However, we were only able to observe 3 surficial removal plots

with females, and therefore had low power to detect any changes in female plot occupancy times. Nonetheless, trends towards such sex-related differences in the effect of treatment indicate that males and females may differ in their response to biofilm removal: males reduced their plot occupancy times by approximately 80%, from 14 to 4 seconds, while females reduced their plot occupancy time by only 50%, from 11 to 6 seconds. These results are consistent with the hypothesis that males, as the sex with the shorter bill, should rely more heavily on biofilm than females (Elner et al. 2005).

The reduced foraging time on surfical removal plots may result from either biofilm removal or removal of the surface invertebrates, therefore, we used stable isotope analysis to determine whether biofilm is assimilated into Western Sandpiper body tissue. We did not detect any significant differences in the stable nitrogen isotope ratios between males and females. However, a more direct means of assessing whether biofilm is used as a food resource by Western Sandpipers may be to determine whether they possess the enzymes required to digest carbohydrate materials. Although this study is unable to demonstrate unequivocally that biofilm is a major food source for male Western Sandpipers, our surficial removal plot data indicates that this remains a possibility, and further investigation is warranted.

**Conclusions**

Western Sandpipers showed significant and consistent sex-related differences in feeding behaviour across their non-breeding range and males used pecking more than females. Based on differences in feeding mode and bill and tongue ultrastructure, Elner et al. (2005) proposed that male Western Sandpipers ingest biofilm to a greater extent than females. Our results, based on experimental removal of biofilm and stable isotope analysis, neither confirm nor negate this hypothesis.

We also investigated latitudinal patterns in the distribution of food as a potential mechanism underlying the non-breeding distribution of Western Sandpipers. Consistent with predictions from the 'forage selection' hypothesis, we recorded surface-biased prey distributions at northerly (male-biased) non-breeding sites and subsurface-biased prey distributions at southerly (female-biased) sites. Furthermore, the continuous latitudinal

trends towards more subsurface biased food distributions with decreasing latitude illuminate a potential mechanism underlying the pattern of increasing bill length within age and sex classes from north to south (O'Hara 2000) across the non-breeding range, a pattern that had thus far not been addressed by any other hypotheses for differential migration.

Although the results presented here add to our understanding of the processes underlying differential migration in Western Sandpipers, we do not propose that latitudinal gradients in the distribution of prey alone are the mechanism underlying differential migration in this species. Rather, latitudinal gradients in the distribution of prey are likely one mechanism among many that contribute to the non-breeding distribution of Western Sandpipers, including the "arrival time hypothesis", which has received empirical support in the literature (Cristol et al. 1999). Nonetheless, the findings of this study are significant in that, to our knowledge, it is the first to demonstrate a relationship between patterns of differential non-breeding distributions and food availability in any shorebird species.

## Acknowledgements

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**Table 4-1:** Sample sizes per site for foraging observations, macrofaunal cores, and biofilm cores.

| Latitude | Site | Foraging observations | | Macrofauna cores | Biofilm Cores |
|---|---|---|---|---|---|
| | | Male | Female | | |
| 8°N | Costa del Este, Panamá | 22 | 107 | 14 | 15 |
| 24°N | La Paz, México | 68 | 2 | 15 | 15 |
| 31°N | Punta Banda, México | 65 | 7 | 15 | 15 |
| 37°N | San Francisco Bay, California | 110 | 8 | 19 | 20 |
| 38°N | Bodega Bay, California | 52 | 0 | 20 | 20 |
| 40°N | Humboldt Bay, California | 65 | 0 | 20 | 19 |
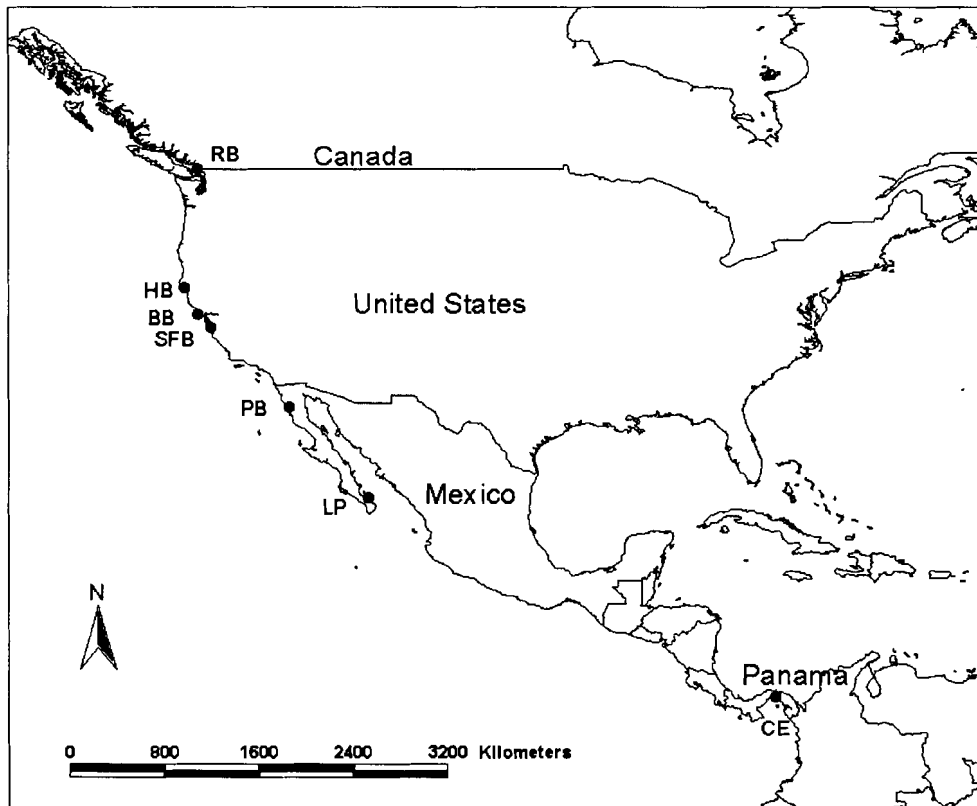
Figure 4-1: Map showing the latitudinal separation of study sites. HB= Humboldt
Bay, California; BB = Bodega Bay, California; SFB = San Fransisco
Bay, California; PB= Punta Banda, México; LP = La Paz, México; and
CE = Costa del Este, Panamá. RB = Roberts Bank, British Columbia,
the site were Western Sandpiper tissue samples were collected for
stable isotope analysis.
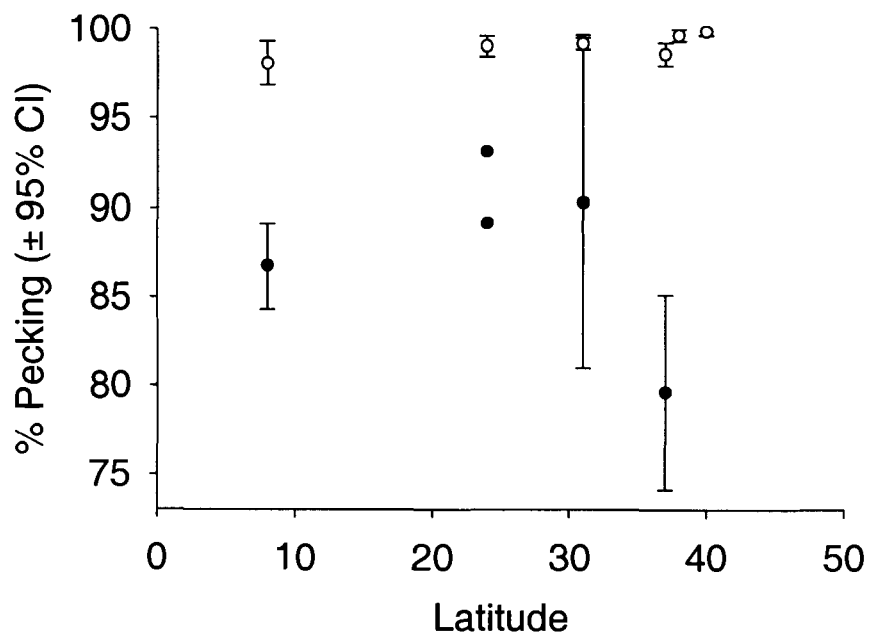
Figure 4-2: Latitudinal trends in feeding mode by sex. Hollow circles denote males, solid circles denote females. Error bars for females at La Paz, México (latitude= 24°N), are not presented because only 2 observations of females were made; raw data are presented instead.
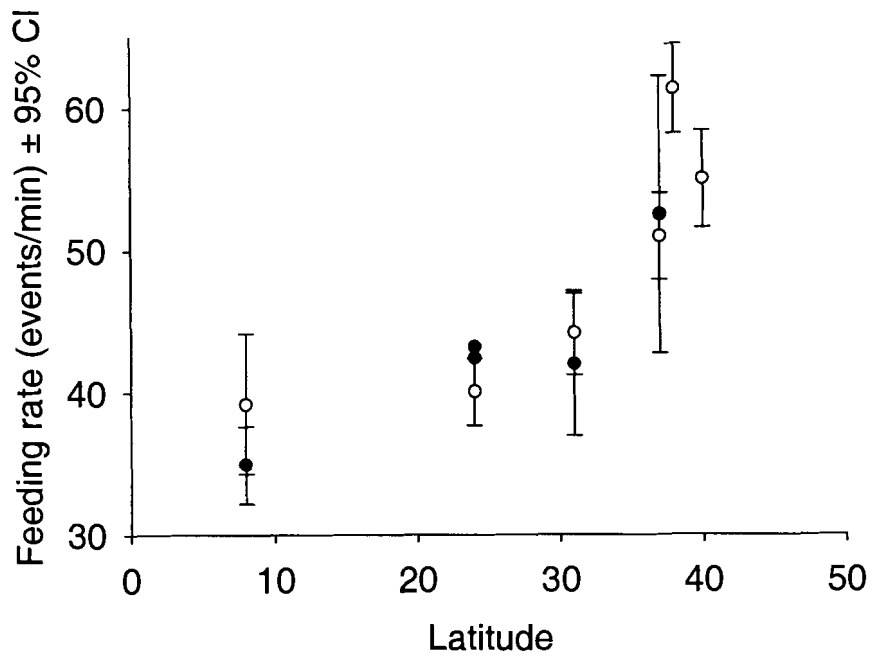
**Figure 4-3:** **Latitudinal trends in feeding rate by sex. Hollow circles denote males, solid circles denote females. Error bars for females at La Paz, México (latitude= 24°N), are not presented because only 2 observations of females were made; raw data are presented instead.**
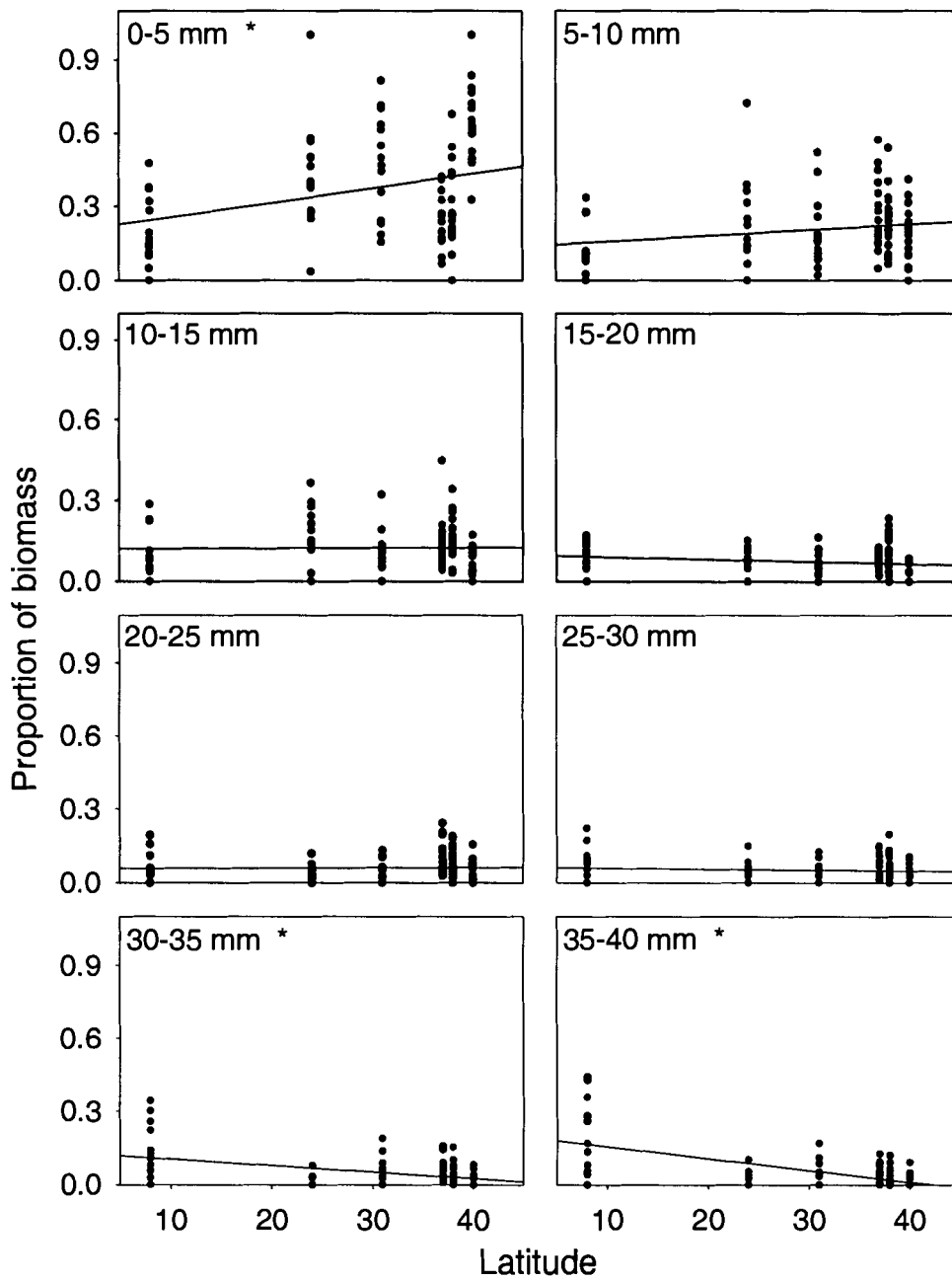
Figure 4-4: Latitudinal patterns in the vertical distribution of prey biomass. Asterisks denote slopes that differ significantly from 0.
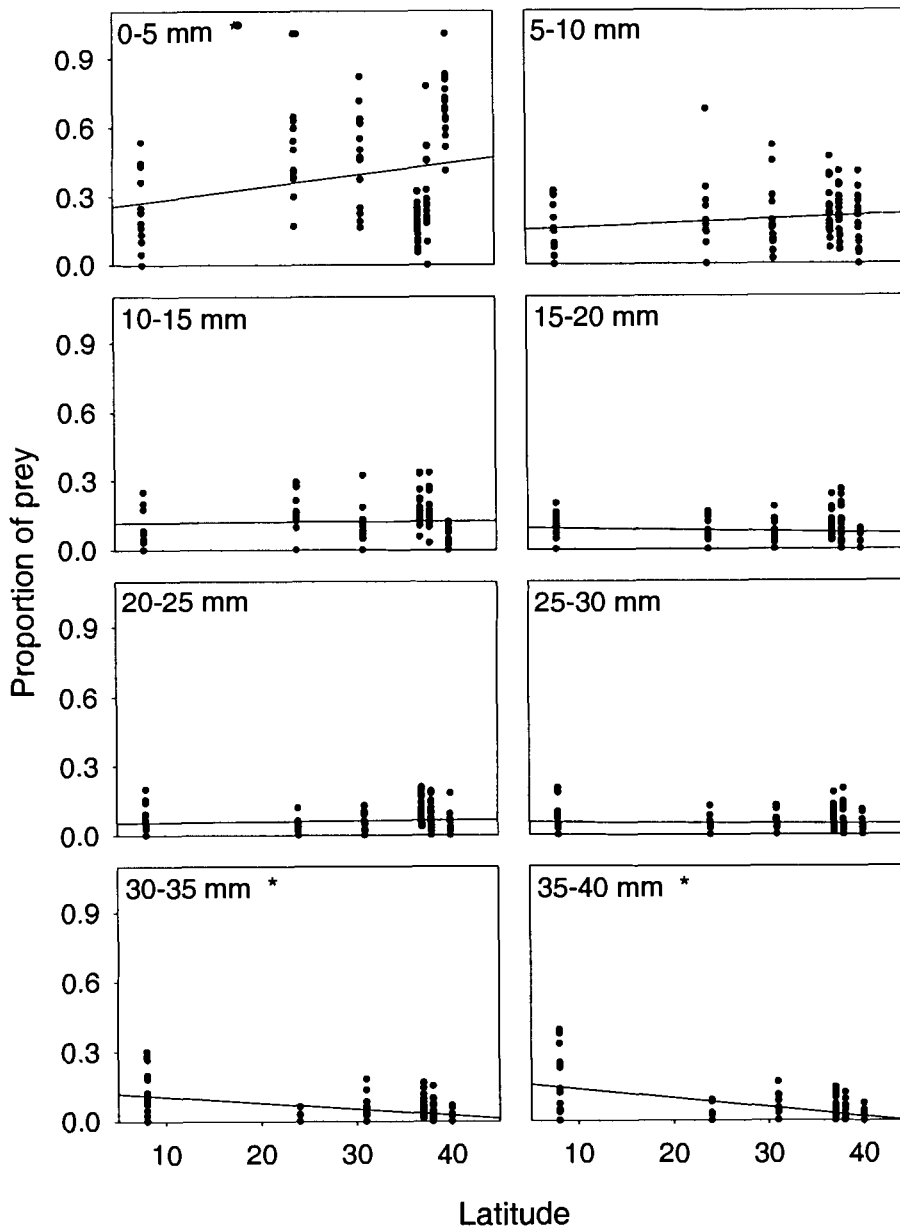
Figure 4-5: Latitudinal patterns in the vertical distribution of prey (numerical density). Asterisks denote slopes that differ significantly from 0.
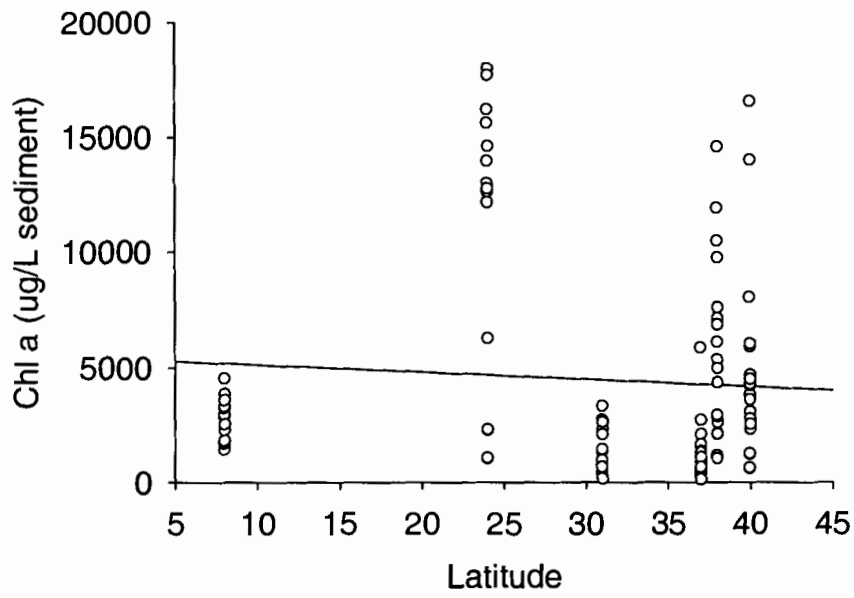
**Figure 4-6: Latitudinal trends in the abundance of biofilm in the top 5 mm of sediment.**
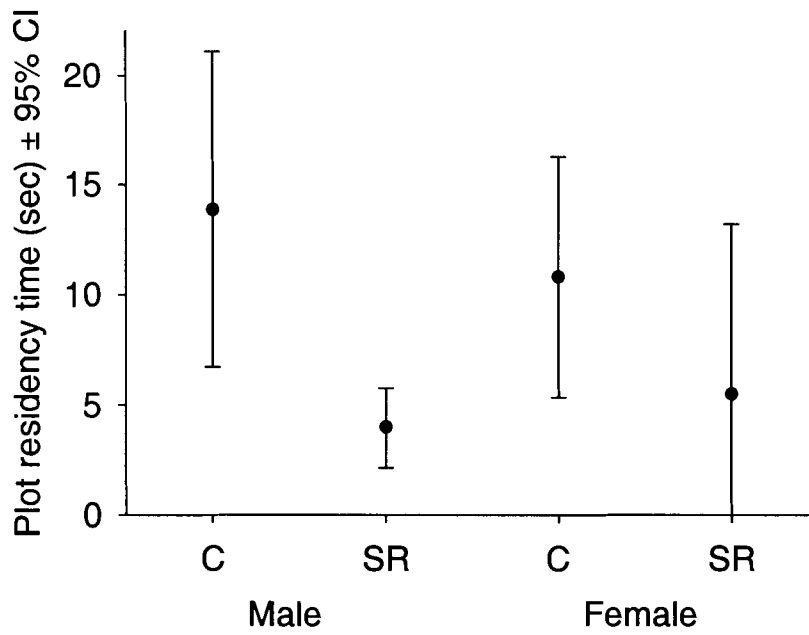
Figure 4-7: The effect of surficial food removal (SR) on plot residency times for males and females. Control plots (C) did not have surficial food types removed.
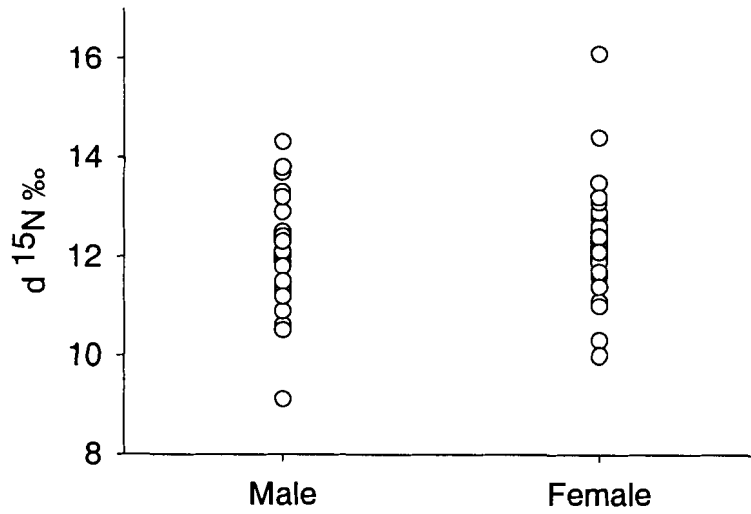
**Figure 4-8: Nitrogen stable isotope values for male and female Western Sandpipers.**

# CHAPTER 5: SYNTHESIS

## General synthesis

Differences in feeding behaviour among subsets of a population can result in differences in diet, vulnerability to predation, and habitat usage patterns. Such differences can have major implications for conservation strategies and may dramatically influence population demographics (Durell 2000, Bowyer 2004). Intra-specific variation in feeding behaviour in birds generally arises through intra-specific variation in bill morphology (Durell 2000, Parchman and Benkman 2002, Radford and du Plessis 2003). Therefore, species with marked variation in bill morphology provide good systems in which to examine the implications of intra-specific differences in feeding behaviour for different subsets of a population.

Western Sandpipers (*Calidris mauri*) are a highly sexually dimorphic shorebird. Males are on average 5% smaller than females with respect to most body measures, but 12% shorter billed (Cartar 1984). Although Western Sandpiper feeding behaviour has been observed in other studies (Ashmole 1970, Senner 1989, Sutherland et al. 2000, Wolf 2001, Nebel 2003, Seaman 2003), this thesis presents the first study to test two (non-exclusive) hypotheses for observed sex-related differences in feeding behaviour (Chapter 2). Males precede females during northward migration (Butler et al. 1987) and there is a trend towards increased probing across the two migration periods. Differences in the abundance of surface versus subsurface prey between male and female migration periods could not account for observed differences in feeding behaviour between those migrations. We found that in the absence of any changes in prey distribution, males used pecking more than females, which used more probing. This study provides the first conclusive evidence that the dimorphism in bill length present in Western Sandpipers is associated with sex-related differences in feeding behaviour.

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Given that male and female Western Sandpipers differ in their relative use of pecking and probing, I investigated how specialization on different feeding modes influences the ability of individuals to adjust their feeding behaviour in response to changes in the vertical distribution of prey (Chapter 3). At a non-breeding site in Panamá, Costa del Este, shifts in the vertical distribution of invertebrates occur from falling to rising tide such that prey proportion declines in the surface layers of sediment, and increases in the subsurface layers. Coincident with these shifts in prey proportions, both males and females increased their use of probing during the rising tide period. These results suggest that increasing proportions of non-prey interferes with feeding in Western Sandpipers, perhaps through reduced intake rates. Females showed larger shifts in feeding behaviour than did males, suggesting that their feeding repertoire may be more plastic than that of males, as postulated by Nebel (2003) based on females having longer culmens and therefore presumable broader feeding niches. I also observed a 6 fold increase in Peregrine Falcon (*Falco peregrinus*) attack rates on Western Sandpipers during the rising tide, when sandpipers had higher use of probing feeding modes. This result is consistent with other studies demonstrating that "head-down" feeding behaviours tend to reduce the ability of foragers to detect approaching predators (Barbosa 1995, Lima and Bednekoff 1999), and that predators preferentially attack less vigilant prey (Lima 1998).

Finally, possible implications of sex-related differences in feeding on known differential migration patterns in Western Sandpipers were studied in Chapter 4. We tested the 'forage selection' hypothesis, originally proposed to explain differential habitat selection in ungulates, as a potential mechanism to explain differential migration in the Western Sandpiper. Inter-sexual differences in feeding behaviour previously observed during migration were maintained across the non-breeding range, males having higher use of pecking and females having higher use of probing feeding behaviours. Therefore, the 'forage selection' hypothesis predicts that northern (male-biased) non-breeding sites should have surface-biased food distributions, while southern (female-biased) non-breeding sites should have subsurface-biased food distributions. We observed that surface invertebrates predominated at northern sites, while subsurface invertebrates predominated at southern sites. No latitudinal trends were observed for biofilm, however, variability in

biofilm densities was higher in more northerly sites, indicating the presence of more high density biofilm patches at these sites compared with southern sites. Our results support the hypothesis that males and females segregate during the non-breeding season in response to latitudinal variation in the abundance of surface and subsurface food types and inter-sexual differences in the ability to exploit those food resources.

## Implications and future directions

Understanding the mechanisms underlying habitat selection is a major theme in ecology (Heglund 2002). This study recorded that latitudinal clines in the vertical distribution of macrofaunal invertebrate prey mirror the overlying clines in Western Sandpiper bill length across the non-breeding range. While these results provide strong support for the hypothesis that latitudinal clines in prey availability combined with inter-sexual differences in feeding behaviour underlie the non-breeding distribution of Western Sandpipers, additional information will be valuable in further substantiating this postulated mechanism. Although it appears intuitive that longer-billed individuals should be better able to exploit subsurface prey than shorter-billed individuals, quantifying the feeding advantage gained by longer-billed individuals that migrate further south will be critical to evaluating the extent to which non-breeding site selection is mediated by local prey distributions. Up to this point, an understanding of the relationship between feeding behaviour and intake rate has been missing in studies of Western Sandpiper feeding ecology. However, the use of high speed digital video recorders may provide a useful tool with which to begin to address this knowledge gap.

High speed digital video recordings may also aid in assessing whether different feeding modes reflect prey searching behaviours or prey ingestion behaviours, as well as if different feeding modes are used to target different prey types. In this study, we recorded the vertical distribution of macrofaunal (>500 $\mu$m) invertebrates. However, many surface feeding behaviours may also target meiofaunal (0.62 $\mu$m-500 $\mu$m) invertebrates (Sutherland et al. 2000) and it may therefore be valuable to record changes in the distribution of meiofauna across the non-breeding range. Although some analyses

of meiofaunal invertebrate samples were conducted in the course of this study (Appendix 1), the number of samples analyzed was too few to draw any conclusions regarding latitudinal patterns of meiofauna abundance.

Despite the need for further studies linking bill morphology to feeding mode and intake rates, this study represents a major advancement to our understanding of potential mechanisms mediating differential migration in birds. The findings of this study suggest that Western Sandpipers may select non-breeding sites with the optimal vertical distribution of prey for their bill length, which may have several management implications. First, in order to maintain the spectrum of morphological diversity present in this species, habitats across the entire non-breeding range must be conserved (Elner and Seaman 2003). Also, identifying the processes that act to generate and maintain local patterns in the vertical distribution of invertebrates will be important if habitat management efforts hope to conserve the site characteristics that render a site suitable for a particular subset of birds.

This thesis did not deal explicitly with identifying the mechanisms driving latitudinal gradients in the vertical distribution of prey, however, two non-exclusive mechanisms have previously been hypothesized: 1. Increasing temperatures with decreasing latitude cause invertebrates to bury themselves more deeply at southerly non-breeding sites, (Nebel et al. 2002) or 2. increasing intertidal crab densities in the tropics result in depletion of surface food resources (Elner and Seaman 2003). While it is clear that mean ambient temperature does increase from temperate to tropical regions, and that within a site, increasing temperature may result in deeper invertebrate burial depths (Barter 1988), the effects of inter-site differences in temperature on invertebrate burial depths are less clear because invertebrates may be adapted to local temperature regimes (Nebel 2003). Tests of this hypothesis will require experimental manipulation of temperature and concurrent measurements of the vertical profiles of invertebrates.

Counts of intertidal crab densities carried out through the course of this study indicate that crab densities do increase with decreasing latitude (Appendix 2). These results are consistent with the hypothesis that depletion of surface food resources by

crabs is driving latitudinal gradients in the vertical distribution of prey, however, these results are also preliminary in that they do not take into account the size or diet of crabs. Therefore, the recorded increase in intertidal crab densities with decreasing latitude may not correlate with increasing depletion of surface food by crabs. Intertidal crab exclosure plots should be used at several sites to measure the magnitude of depletion of surface food types that can be attributed to crabs.

Latitudinal gradients in the vertical distribution of food recorded in this study may also provide insight into mechanisms underlying the alternative life history strategies that exist within Western Sandpipers. Migration distance is correlated with likelihood of summer residency in yearling birds in numerous shorebirds including Western Sandpipers (Summers et al. 1995, O'Hara et al. in press). In Western Sandpipers, male and female juveniles tend to winter at the northernmost and southernmost ends of the non-breeding range respectively. Therefore, females have a higher propensity to over summer as yearlings, and forego reproduction. Longevity and body size are strongly correlated among shorebird species, so that the effect of deferred northward migration on lifetime reproductive success in small species such as Western Sandpipers is great (Summers et al. 1995, Fernández et al. 2004). Given the high costs associated with the decision of female juveniles to over winter at the most southerly extremes of the non-breeding range, we expect to find significant benefits to such behavioural decisions. The results of this thesis illuminate one potential benefit incurred by juvenile females migrating further south - better feeding conditions for their particular bill morphology (long-billed), which may result in increased survival. Testing this hypothesis requires not only that survivorship of juvenile females wintering at different latitudes be compared, but also that differences in survivorship for individuals of particular bill lengths be readily linked to differences in the vertical distribution of prey.

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# APPENDICES

# APPENDIX 1: LATITUDINAL PATTERNS OF MEIOFAUNA ABUNDANCE

Meiofauna samples were collected from the same non-breeding sites over the same time periods as described in Chapter 4. Cores were collected by the same methods as those outlined in Chapter 4 for macrofauna, except that meiofauna are invertebrates that washed through a 500 $\mu$m sieve but were retained on a 62 $\mu$m sieve. The number of samples processed for each site are as follows: Costa del Este (8°N), N=4; La Paz (24°N), N=5; Punta Banda (31°N), N=3, San Francisco Bay (37°N), N=9; Bodega Bay (38°N), N=10; and Humboldt Bay (40°N), N=5. Because the sample sizes for meiofauna estimates are small, data presented here are meant to show preliminary qualitative patterns, and no statistical analyses were performed. The two most abundant taxa of meiofaunal invertebrates were copepods and foraminiferans, followed by ostracods, polychaetes and unidentified individuals. Nematodes were also very abundant, but were excluded from prey counts (see Chapter 3). Figure A1-1 shows the vertical profile of meiofauna, presented as proportion of individuals, across the non-breeding range. However, because meiofauna are likely to be ingested only by surface feeding modes (Sutherland et al. 2000), Figure A1-2 shows latitudinal patterns in the density of meiofauna in the top 5 mm of sediments.

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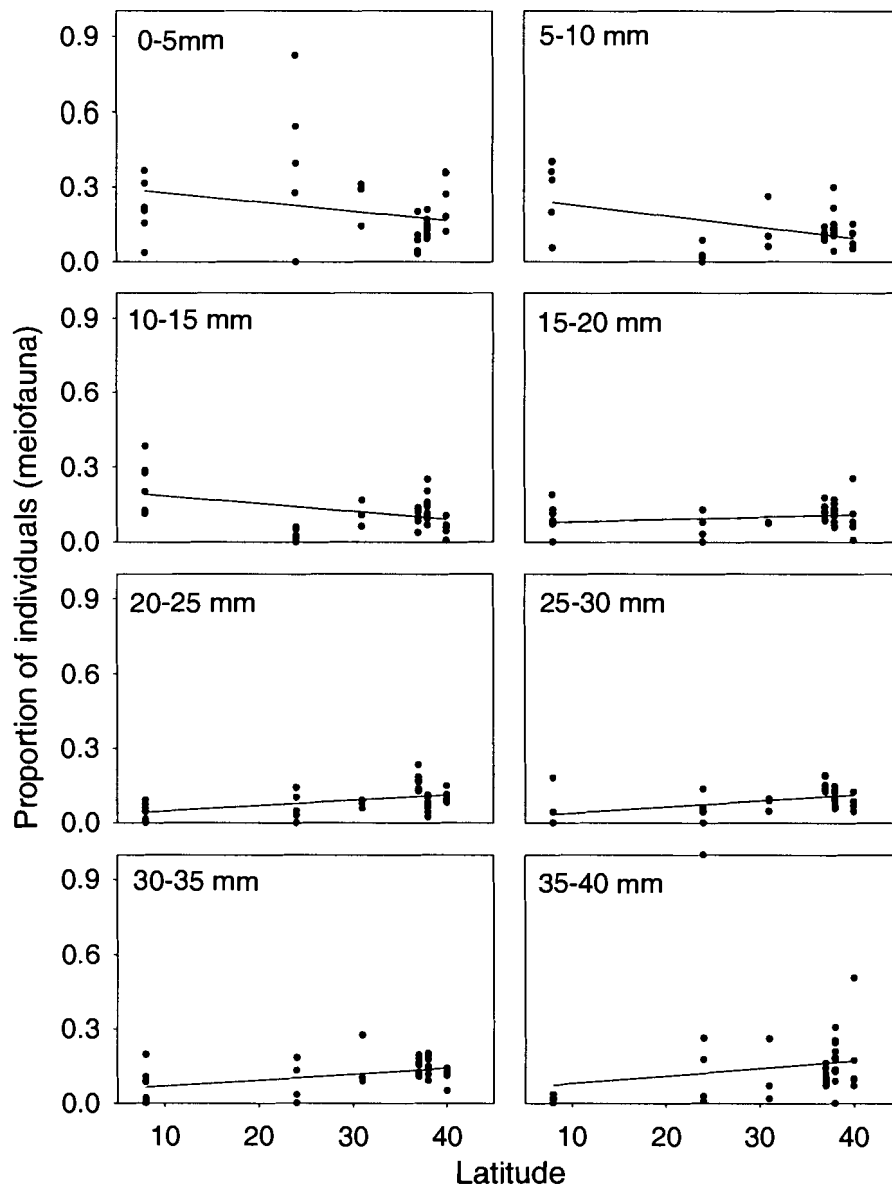
**Figure A1-1: Latitudinal patterns in the vertical distribution of meiofauna.**
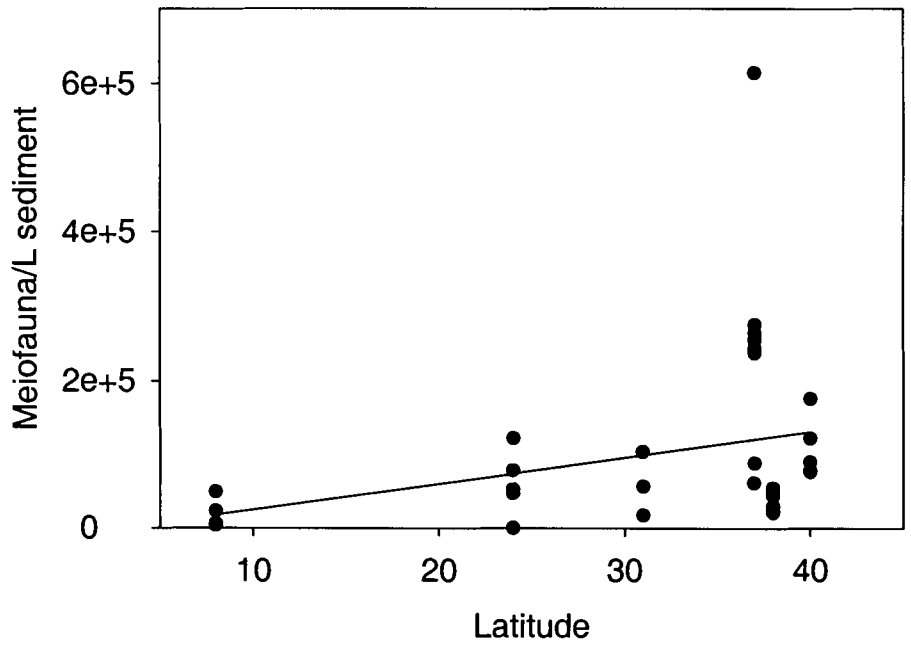
**Figure A1-2: Latitudinal patterns in meiofaunal invertebrate densities in the top 5 mm of sediment.**

# APPENDIX 2: LATITUDINAL GRADIENTS IN INTERTIDAL CRAB DENSITIES

Crab density estimates were taken at the same non-breeding sites as described in Chapter 4, over the same time period. Intertidal crab densities were estimated by counting either the number of crabs or crab burrows in a grid of a given size. Grid sizes varied between sites according to the local size and densities of crabs. Sample sizes and grid sizes for each site, as well as mean intertidal crab densities ± 95% confidence intervals are reported in Table A2-1. Crab densities reported here do not take into account the size of crabs observed, although crabs in Panamá were several fold larger than those seen in either of the two sites in México (personal observation).

**Table A2-1: Intertidal crab density estimates from 6 non-breeding sites. Asterisks under the sample size column for the three northernmost sites (San Francisco Bay, Bodega Bay and Humboldt Bay) indicate that no grid estimates of crab densities were conducted because no crabs or crab burrows were seen anywhere on the mudflat during low tide exposure.**

| Latitude | Site | Sample size | Grid size (m$^2$) | Range Crabs/m$^2$ | Mean Crabs/m$^2$ $\pm$ 95% CI |
|---|---|---|---|---|---|
| 8°N | Costa del Este, Panamá | 13 | 15 | 0 – 4.8 | 1.69 ± 0.85 |
| 24°N | La Paz, México | 20 | 1 | 0 -4 | 0.35 ± 0.51 |
| 31°N | Punta Banda, México | 20 | 1 | 0 – 2 | 0.15 ± 0.23 |
| 37°N | San Francisco Bay, California | * | N/A | 0 | 0 |
| 38°N | Bodega Bay, California | * | N/A | 0 | 0 |
| 40°N | Humboldt Bay, California | * | N/A | 0 | 0 |

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