ECOLOGICAL FACTORS UNDERLYING THE NONBREEDING DISTRIBUTION OF WESTERN SANDPIPERS

by

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ABSTRACT

Avian species in which males and females migrate to different nonbreeding areas provide candidate systems to study ecological factors underlying distribution patterns. Western Sandpipers (*Calidris mauri*) are such 'differential migrants'. They breed mainly in Alaska and overwinter along the American Pacific and Caribbean coastlines. In this thesis, I document an increasing proportion of females at more southerly latitudes. I review existing explanatory hypotheses for differential migration, propose two novel hypotheses, and test these with data collected at four latitudes.

According to the feeding niche hypothesis, intertidal invertebrates are buried more deeply towards the south, possibly due to higher ambient temperature and/or desiccation. Longer bills enable probing (foraging on buried prey) to greater depths. Females have disproportionately long bills, and therefore can exploit a feeding niche at greater vertical depth. Bill length residuals, corrected for tarsus length, were predicted to increase towards the south. This was only found in males. No clear change of feeding mode with latitude was detected. Females probed more than males at all locations, even though aspects of the ultrastructure of female bills did not indicate greater specialisation for probing. At the one site where the relationship was measured, both sexes probed more with increasing sediment temperature.

According to the predation danger hypothesis, predator escape ability of males and females, indexed by wingloading, differs consistently across latitudes. Escape ability is generally reduced with higher wingloading. Individuals with poorer escape ability were therefore predicted to prefer southern sites, where less fat is required as insurance against environmental variability. Wingloading was higher overall for females. At one site I compared the sex ratio of carcasses, assessed molecularly, to that of free-living birds, but found no evidence for any sex-bias in predator-induced mortality. Wingloading increased with latitude in both sexes, but an index of predation danger remained constant across latitudes. Within latitudes, wingloading was lower at smaller, and presumably more dangerous, sites.

My results provide evidence for both hypotheses, while other hypotheses for differential migration were not supported. I suggest that both escape performance and feeding niche divergence are important factors in determining large-scale spatial distribution in Western Sandpipers.

DEDICATION

I dedicate this Dissertation to my parents.

'When one tugs at a single thing in nature, he finds it attached to the rest of the world.'

John Muir

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I. GENERAL INTRODUCTION

Background

The phenomenon of bird migration has captivated humans for centuries, if not millennia. Migratory birds have inspired poets, artists and researchers, who are trying to find proximate and ultimate explanations for these 'epic journeys'. Why do birds migrate in the first place? How do they decide where to go to? When should they depart and how do they find their way?

Even within species, individuals of different age or sex often show marked differences in the timing of migration or choice of nonbreeding area (Cristol et al. 1999). Differential migrants are a candidate system to study the ecological factors underlying distribution patterns, as costs and benefits of choosing a site may vary with sex- or age-specific characteristics, and can thereby help to identify the factors driving the spatial distribution.

Three main hypotheses have been proposed to explain sexual segregation of migratory birds on the nonbreeding grounds. The 'Dominance Hypothesis' predicts that asymmetrical interactions between males and females can produce geographical segregation (Gauthreaux 1978). Dominant individuals are thought to decrease costs associated with long-distance migration by monopolising areas close to the breeding grounds. Alternatively, body size differences between sexes may interact with local climate to produce differential distributional optima ('Body Size Hypothesis', Ketterson & Nolan 1976). Larger individuals can survive longer periods of fasting and are therefore thought to be better suited to survive the colder and less predictable climates at higher latitudes. Or, according to the 'Arrival Time Hypothesis', individuals benefiting more from earlier arrival on the breeding grounds will gain by wintering closer to the breeding grounds (Ketterson & Nolan 1976, Myers 1981). However, empirical evidence supporting these hypotheses remains inconclusive (Cristol et al. 1999). Here, I will propose and test two novel hypotheses to explain differential distribution, which will contribute to our knowledge of the evolution of bird migration, and broaden our understanding of animal distribution patterns in general.

Study species

The Western Sandpiper (*Calidris mauri*), family Scolopacidae, is the most abundant shorebird in the Pacific flyway of the Americas (Morrison et al. 2001). Western Sandpipers are long-distance migrants, which breed in the tundra of western Alaska and eastern Siberia. In contrast to the restricted breeding area, the range of the nonbreeding distribution is vast, extending over two hemispheres. They inhabit intertidal areas along the Pacific coast from British Columbia to Peru, and, to a lesser extent, from New Jersey to Surinam along the East coast of the Americas (Wilson 1994). Females have been documented to be more abundant towards the southern part of the nonbreeding area (Page et al. 1972, Harrington & Haase 1994, Naranjo et al. 1994, Buenrostro et al. 1999).

Only a decade has passed since the publication of the Western Sandpiper species account in the Birds of North America (Wilson 1994), but since then, the amount of data that has become available has increased substantially (see Nebel & Lank 2003). The Western Sandpiper therefore seems an appropriate candidate to develop and test hypotheses underlying differential migration patterns, drawing from what is known about its spatial distribution, its behaviour, ecology, and physiology. Study of distribution patterns in a species where males and females make different decisions regarding site choice avoids the problem of phylogenetic non-independence encountered in interspecific comparisons, while taking advantage of a broad range of intraspecific differences in behaviour.

Study areas

Data on Western Sandpipers morphometrics and behaviour were collected at four latitudes, aiming to sample individuals from a large part of the nonbreeding range (Fig. I-1). Study sites within the four regions were: Bodega Bay (38.2°N, 123.0°W), Tomales

Bay (39.2°N, 123.0°W), and San Francisco Bay, California, USA (37.5°N, 122.3°W); Bull Island, South Carolina, USA (32.8°N, 79.6°W); Bahía Santa María, Sinaloa, Mexico (24.0°N, 108.0°W); Chitré, Herrera, Panama (8.0°N, 80.5°W), Costa del Este, Rio Pacora and Rio Chico in the upper Bay of Panama, Republic of Panama (9.0°N, 79.2°W). San Francisco Bay, Bahía Santa María and the upper Bay of Panama sustain large numbers of Western Sandpipers, while the other sites are less extensive and used by a small number of individuals.

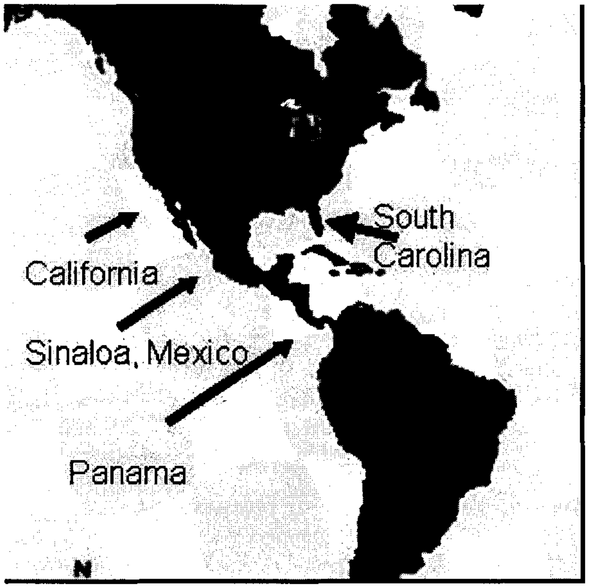

Fig. I-1. Study sites were distributed across four latitudes.

Dissertation outline

This dissertation consists of five independent research chapters, which form integral parts in attempting to identify the factors driving the differential distribution patterns of Western Sandpipers. In Chapter 2 (published in Auk 2002), I assembled existing data on age- and sex ratios to produce a detailed picture of the differential distribution during the nonbreeding season. The remaining four chapters develop and test two hypotheses aiming to explain the differential distribution of males and females, namely intraspecific feeding niche divergence (Chapter 3 and 4), and predation danger (Chapter 5 and 6). More specifically, in Chapter 3 (*in review*), I propose that the sexual segregation on the nonbreeding grounds is caused by intra-specific feeding niche divergence, which allows females to exploit feeding grounds further south than males. Chapter 4 relates gross bill morphology and micro-anatomy of Western Sandpipers to sex-specific feeding behaviour and compares bill shape with two close relatives. In Chapter 5, it is hypothesised that the sexual segegation is caused by site- and sex-specific differences in escape performance. In Chapter 6 (*in review*), we test whether males and females at a major nonbreeding site in Mexico suffer differences in predator-induced mortality. Chapter 7, the Synthesis, summarises the main results and gives directions for future research.

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II. WESTERN SANDPIPERS DURING THE NONBREEDING SEASON: SPATIAL SEGREGATION ON A HEMISPHERIC SCALE

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Silke Nebel, David B. Lank, Patrick D. O'Hara, Guillermo Fernández, Ben Haase, Francisco Delgado, Felipe A. Estela, Lesley J. Evans Ogden, Brian Harrington, Barbara E. Kus, James E. Lyons, Francine. Mercier, Brent Ortego, John Y. Takekawa, Nils Warnock, and Sarah E. Warnock

Abstract

The nonbreeding distribution of Western Sandpipers (*Calidris mauri*)was documented using 19 data sets from 13 sites along the Pacific and Atlantic coasts of the Americas. Western Sandpipers showed latitudinal segregation with regard to sex and age. Females wintered farther south than males. A ''U'' shaped pattern was found with respect to age, with juveniles occurring at higher proportions at both the northern and southern ends of the range. Distribution of sexes might be affected by differences in bill length and a latitudinal trend in depth distribution of prey. For age class distribution, two different life-history tactics of juveniles might exist that are related to the higher cost of feather wear for juveniles compared to adults. Most juveniles complete three long-distance migrations on one set of flight feathers whereas adults complete two. Juveniles may winter either far north, thereby reducing feather wear induced by ultraviolet light, migration, or both, or far south and spend the summer on the nonbreeding area.

Introduction

'Differential migration' refers to either differences in timing of migration or to spatial distribution of age or sex classes within a species during the nonbreeding season (Myers 1981a, Gauthreaux 1982, Ketterson & Nolan 1983, Hockey et al. 1989, Turpie 1994, Cristol et al. 1999). According to a recent review, this tactic occurs in the majority of migratory bird species (Cristol et al. 1999).

The Western Sandpiper (*Calidris mauri*) is well suited for the study of differential migration. It is one of the most common shorebirds in North America, with the latest estimate being 3.5 million (Bishop et al. 2000, Morrison et al. 2001). Most of the population breeds in western Alaska, while during the nonbreeding season, its range extends along the American Pacific coast from southern Canada to Peru, and, to a lesser extent, along the East coast of the Americas (Wilson 1994). During winter, the largest concentrations occur in western central Mexico and in Panama (Morrison and Ross 1989, Morrison et al. 1993, 1994, 1998, 2001). No subspecies are recognized (Wilson 1994).

Recently, a latitudinal difference in Western Sandpiper life-history tactics was discovered. Most juveniles wintering in California and western Mexico fatten up and migrate north in their first spring (Warnock & Fernández unpubl. data). In contrast, nearly all juvenile Western Sandpipers wintering at Chitré, Panama, do not undergo hyperphagia, prepare for northward migration, or molt into significant amounts of alternate plumage. Instead, they spend their yearling summer in predominantly basic plumage on the nonbreeding grounds (O'Hara et al. 2002). We assume that the difference between these sites reflects a latitudinal trend within Western Sandpipers, with higher propensity to oversummer the further south the birds overwinter. Across shorebird species, a higher propensity to oversummer occurs in those with longer migratory flights (Summers et al. 1995, Hockey et al. 1998).

Females are more abundant towards the southern part of the nonbreeding area (Page et al. 1972, Harrington & Haase 1994, Naranjo et al. 1994, Buenrostro et al. 1999), but no information on the distribution of age classes is documented. Here, we combine unpublished data from sites across the entire nonbreeding range, allowing us to present an account of the nonbreeding sex and age distribution and to suggest possible explanations for the observed patterns.

Methods and Study Sites

We used 19 data sets gathered from 13 different locations (Table 1). To restrict comparisons to residents, only birds caught between November and February were included in the analyses. All sandpipers were caught with mistnets, and we assumed capture did not produce a bias towards a sex or age class that would vary among sites. We assigned sex on the basis of bill length (Page & Fearis 1971). Given that Page & Fearis (1971) analyzed birds collected in California only, the method was verified by internally sexing over 250 Western Sandpipers from Panama and British Columbia, of which only one was misidentified using bill length (Guglielmo pers. comm.). Juveniles (birds in their first winter) were distinguished from adults on the basis of plumage (Prater et al. 1977) at all sites except Florida, which was not included in the age analysis. Second-winter birds, if recognized, were treated as adults. By comparing bill lengths of adults and juveniles on fall migration in the Fraser River Delta, British Columbia, we demonstrated that juvenile bill lengths were full adult length on southward migration (mean bill length of juvenile males: 22.65 mm, *n*=590, adult males: 22.55 mm, *n*=857, t=-1.02, df=1445, *P*=0.31; juvenile females: 26.75 mm, *n*=847, adult females: 26.80 mm, *n*=342, t=0.91, df=1187, *P*=0.36). This demonstrates that using bill length to assign sex in juveniles will not create a bias towards males. As a measure of migration distance, we calculated the Great Circle Route (km, program: http://www.indo.com/distance/index.html) from the breeding grounds, represented by Nome, Alaska (Wilson 1994), to the nonbreeding site.

Statistical analysis

We analyzed the relative proportions of each age and sex class as a function of distance from breeding grounds, using analysis of covariance (ANCOVA). Class frequencies were modeled as binomial probabilities, using a linear model with a logit link function. Preliminary analysis indicated overdispersion in the data (reflecting strong heterogeneity in sample size), so we used a quasi-likelihood adjustment by rescaling the parameter estimates using model deviance divided by the model degrees of freedom. The relative proportions of all age- and sex classes were arcsin transformed prior to analysis in order to stabilize variance. We performed analyses of variance using GENMOD, SAS, version 8.1 (SAS Institute, 2001).

Results

In the northwestern part of the wintering range (Canada, U.S. and Mexico) the proportion of males was higher than that of females, while south of Mexico it was vice versa (Table II-1). The proportion of females increased linearly with distance from Nome (Fig. II-1). The slope of this relationship did not differ between ages ($\chi^2=0.00$, $P=0.99$). However, between Mexico and Panama, sex ratios were more female skewed for juveniles than adults (Fig. II-2).

In contrast, we detected no differences in the slope of the proportion of adults and migration distance between males and females ($\chi^2=0.79$, num df=1, denom df=20, $P=0.383$), nor differences between intercepts $\chi^2=1.58$, num df=1, denom df=21, $P=0.209$). When we pooled sexes, there was no evidence of a simple linear trend in age-ratio with distance from the breeding grounds ($\chi^2=0.04$, num df=1, denom df=20, $P=0.85$). However, a model where age-ratio was a function of distance and distance-squared (accounting for the U-shape) was supported by the data (distance: $\chi^2=36.48$, $P<0.001$; distance^2: $\chi^2=37.05$, $P<0.001$). At sites relatively close and relatively distant from the breeding grounds, the proportion of adults in the sample was lower than observed at intermediate distances, resulting in a ‘U-shaped’ distribution (Fig. II-3).

In the north, the proportion of the population that were adult males increased with distance from Nome, peaking at an intermediate distance, and decreasing further south (Fig. II-4a). The proportion of adult females increased linearly with distance from the breeding grounds (Fig. II-4b). Proportions of juvenile males formed a U-shaped pattern with distance (Fig. II-4c). Juvenile females showed a linear increase in proportions with distance (Fig. II-4d); in contrast to adult females, proportions were somewhat higher at the northern end of the range. Results were not notably influenced by excluding data from the Atlantic Flyway.

Discussion

Western Sandpipers showed latitudinal segregation with regard to sex and age classes during the nonbreeding season. As in previous studies, females overwintered further south than males. We found a U-shaped pattern with respect to age: juveniles occurred at higher proportions at both the northern and southern ends of the range. This pattern could be produced by disproportionately high mortality of juveniles wintering in the center of the range, but this seems unlikely. Alternatively, some males may shift their wintering grounds further south as they age, whereas some females shift further north, despite substantial annual nonbreeding ground site fidelity (Fernández et al. unpubl. data, O'Hara 2002).

Given the relationship (r^2=0.92) between migration distance and latitude, we include both in our discussion despite small difference in statistical fit. Note however, that while the proportion of females in Puerto Rico seems high for its latitude, it fits well with other data points when plotted against migration distance.

There has been considerable effort put into explaining differential migration patterns, primarily by testing single-factor hypotheses (see Cristol et al. 1999). We suggest that a useful approach involves considering trade-offs between differential costs and benefits among classes of birds with respect to three aspects: (1) performance at the nonbreeding site, (2) intraspecific interactions, and (3) "cross-seasonal interactions" with the breeding season (Myers 1981b).

1) Performance at the nonbreeding site. – We suggest two ecological variables that could vary on a latitudinal gradient and might affect the distribution of shorebirds: climate and food.

Climate. - Body size differences may interact with local climate to produce differential distributional optima, principally by sex (Ketterson & Nolan 1976:690). This is based on a physiological argument: larger individuals can survive longer periods of fasting and are therefore thought to be better suited to survive colder or less predictable climates, typically found at higher latitudes. This prediction has not been supported with unequivocal empirical evidence for shorebirds (Myers 1981a, Shepherd et al. 2001) or any other bird species (see Cristol et al. 1999). In Western Sandpipers, members of the larger sex, females, winter further south. This hypothesis cannot account for the distribution we found.

Food. – Western Sandpipers feed on invertebrate prey items during the nonbreeding season (Wilson 1994). They use several different modes of feeding, but pecking, with the bill just touching the substrate surface, and probing, when the bill is more deeply inserted, is most common (Sutherland et al. 2000). Female Western Sandpipers have longer bills than males (on average, 12%), while other structural measurements differ only slightly (between 0 and 5%; Cartar 1984). The difference in bill length is likely related to habitat use and/or mode of feeding (Harrington 1982, Durrell 2000). A longer bill may be better suited for probing and probing may be a more profitable feeding mode further south. This could be caused by a latitudinal gradient in temperature affecting burying depth of invertebrates.

2) Intraspecific Interactions. - Asymmetrical interactions among age and sex classes can produce habitat segregation (Marra 2000), and might produce geographical segregation ("Dominance Hypothesis", Gauthreaux 1978:30). Dominant individuals may benefit by monopolizing areas closer to the breeding grounds, thereby lowering "migration costs". If we assume that the larger sex dominates the smaller sex, and that adults dominate juveniles (but see Komers & Komers 1992), we would expect to find higher proportions of females and adults at more northern sites, in contrast to the patterns we observed.

3) Cross-seasonal interactions. - Factors other than maximizing overwinter survivorship may influence nonbreeding distributions (Myers 1981b). In particular, a sex or age class that benefits more from earlier arrival on the breeding grounds will gain by wintering closer to the breeding grounds ("Arrival Time Hypothesis", Ketterson and Nolan 1976:690, Myers 1981a:1531). Since males are the primary territory holders in Western Sandpipers and arrive on the breeding grounds before the females (Holmes 1971, Warnock and Bishop 1998), this hypothesis predicts the general pattern we observed with respect to sex. However, Western Sandpipers wintering at Punta Banda, Mexico, initiate northward migration two to three weeks earlier than those in central California (Fernández et al. 2001), which could offset the longer distance. Similar differences occur in other shorebird species (Turpie 1994), which may make this effect less important.

A multifactor hypothesis. - None of these single-factor hypotheses completely accounts for the patterns we have seen in Western Sandpipers (see Cristol et al. 1999). The pattern of males wintering further north and females further south might relate to bill length differences, which allow females to better exploit resources at greater depths. Ambient temperature increases closer to the equator which might affect burying depth of intertidal invertebrates. Females might prefer southern latitudes due to higher predictability of environmental conditions (Ketterson & Nolan 1976, Lovvorn 1994).

For the U-shaped pattern in the distribution of juveniles, we suggest an explanation based on work by O'Hara et al. (2002). Molt tactic and feather wear might account for the latitudinal differences in juvenile migration behavior through their influence on migratory flight performance. Adult Western Sandpipers molt flight feathers following each southward migration, and then perform northward and southward migration on these feathers. Juveniles, on the other hand, retain flight feathers grown in June of their hatching year until late summer of their second year of life (Prater et al. 1977). Juveniles that migrate thus make three migratory flights on this set of feathers.

We propose that juveniles wintering further north benefit by avoiding additional primary wear associated with longer migration distances and/or induced by higher intensity of ultraviolet light closer to the equator. For juveniles wintering further south, feather wear is less of a consideration, since they oversummer and will have molted new primaries prior to their first northward migration in their second spring. Additionally or alternatively, intraspecific competition might play a role, with adults excluding juveniles from the nonbreeding site in the center of the distribution.

We suggest that latitudinal trends in environmental variability, ultraviolet light intensity and temperature affecting burying depth of invertebrates interact with body size and bill length differences as well as age-specific molting schedules, creating different optima in nonbreeding distribution depending on age and sex of individual Western Sandpipers (Fig. 4). Whatever the causes, our findings have important implications for the conservation of the species as well as for the study of survivorship. When creating protected areas for a population of conservation concern, it is important to know whether both sexes occur in similar numbers in these areas, as otherwise the effective population size will be smaller than the actual one (Ridley 1996).

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Table II-1. Sample locations, distance from Nome, Alaska (km), sample sizes and proportions of female and juvenile Western Sandpipers at 13 locations.

Location	Distance from Nome (km)[1]	No. of birds	% females	% juveniles	Source
British Columbia, Fraser River Delta[17]	3037	32	0.19	0.91	2, 3,
California, different locations[18]	4149	407	0.28	0.56	3, 4, 5, 6
Mexico, Punta Banda[19]	4942	582	0.17	0.57	7
Mexico, Bahia Santa Maria[20]	5965	1383	0.28	0.16	8
Texas, different locations[21]	6185	112	0.17	0.07	3, 9
South Carolina, Georgetown[22]	6532	67	0.55	0.55	10
Florida, Marco Island[23]	7133	66	0.24		11
Costa Rica, central Pacific coast[24]	8556	143	0.58	0.32	3
Puerto Rico, Cabo Rojo Saltflats[25]	8613	42	0.95	0.50	12
Panama, Chitré[26]	8986	4945	0.59	0.33	13
Venezuela, Araya Peninsula[27]	9490	584	0.58	0.37	14
Colombia, Punta Soldado[28]	9547	35	0.69	0.48	3, 15
Ecuador, Santa Elena Peninsula[29]	9965	512	0.81	0.75	16

[1]=distance measured as Great Circle Route

sources: [2]=L.J. Evans Ogden, [3]=Banding Office, [4]=B.E. Kus, [5]=S. Nebel, [6]=J.Y. Takekawa and S. Warnock,
[7]=G. Fernández, H. de la Cueva and N. Warnock, [8]=G. Fernández, [9]=B. Ortego, [10]=J. Lyons, [11]=T. Below,
[12]=B. Harrington, [13]=P.D. O'Hara and F. Delgado, [14]=F. Mercier, [15]=F.A. Estela, [16]=B. Haase
years of data collection: [17]='78-79,'98,'00; [18]='57-58,'68-93,'00; [19]='93-98; [20]='99-01; [21]='72, '81-84, '95-00;
[22]='91-93; [23]='86-89; [24]='74-80,'85-88; [25]='89-94; [26]='95-98; [27]='84-86; [28]='84-96; [29]='91-99.

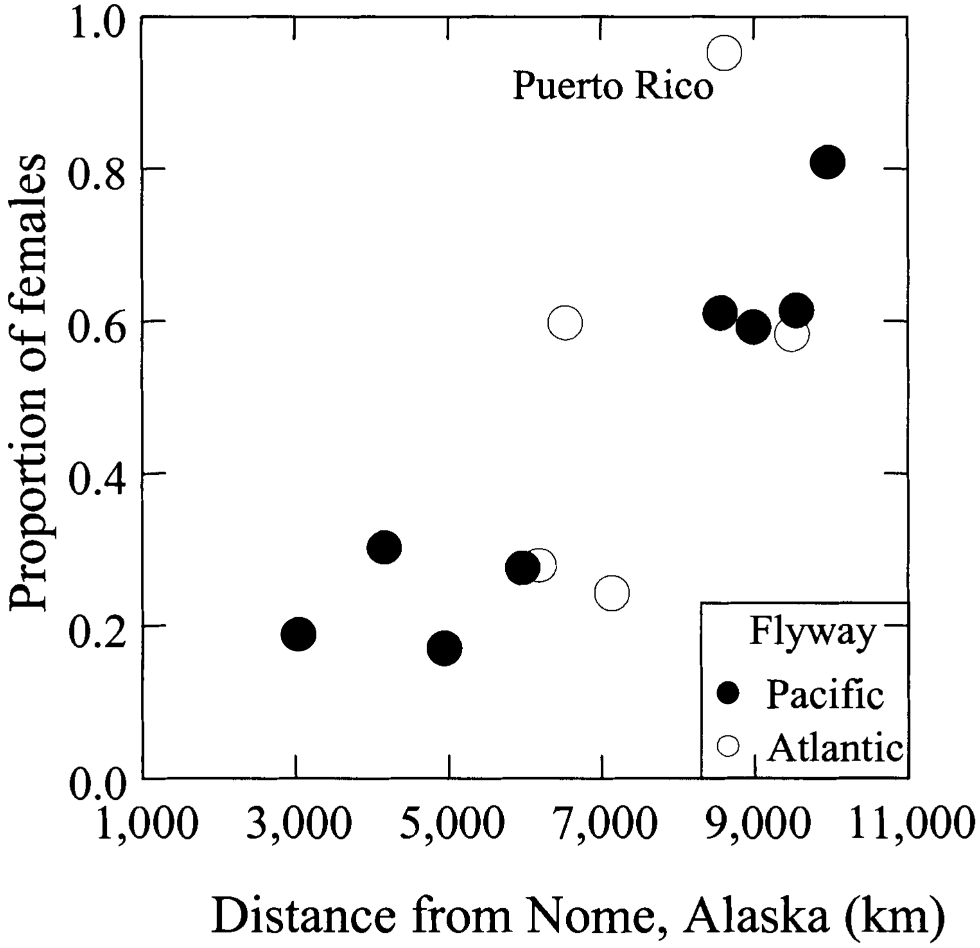

Fig. II-1. The proportion of female Western Sandpipers increased linearly with distance from the breeding grounds, centered at Nome, Alaska ($\chi2$=128.42, num df=1, denom df=21, P<0.001).

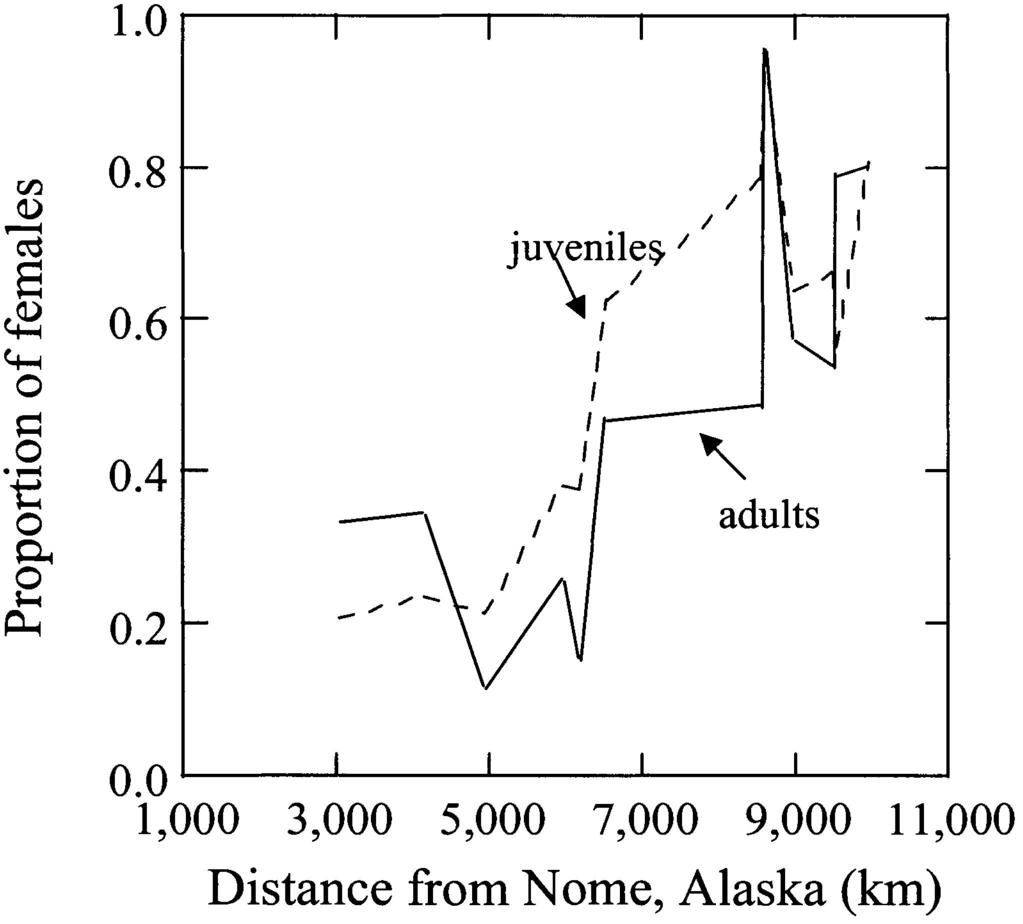

Fig. II-2. The proportion of female Western Sandpipers was greater among juveniles than among adults for a given distance (χ^2=8.18, num df=1, denom df=21, *P*=0.004).

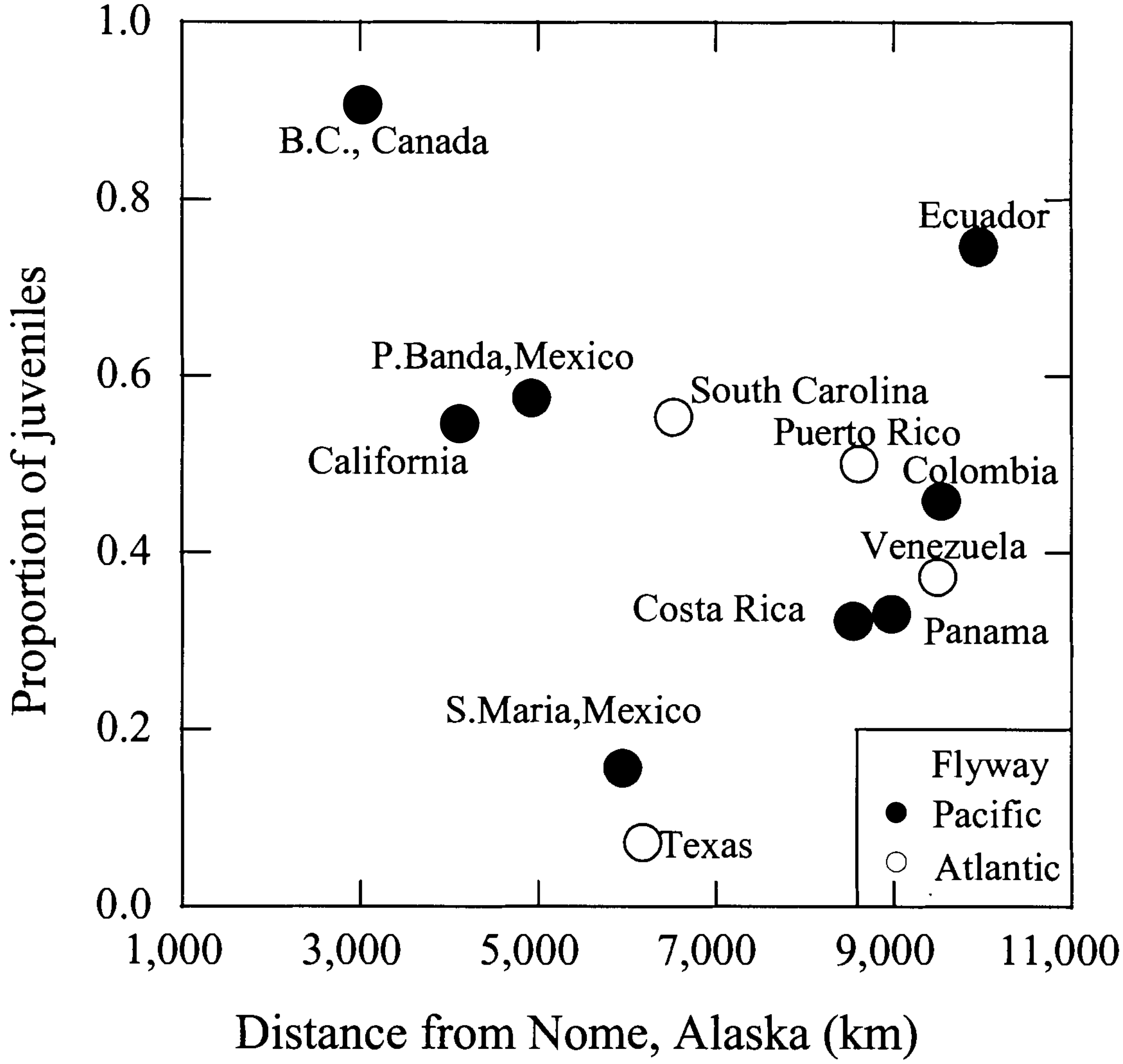

Figure II-3. Age ratio of Western Sandpipers captured at 12 locations.

The proportion of juveniles vs. migration distance described a U-shaped pattern ($F_{1,22}$=5.08, P<0.005).

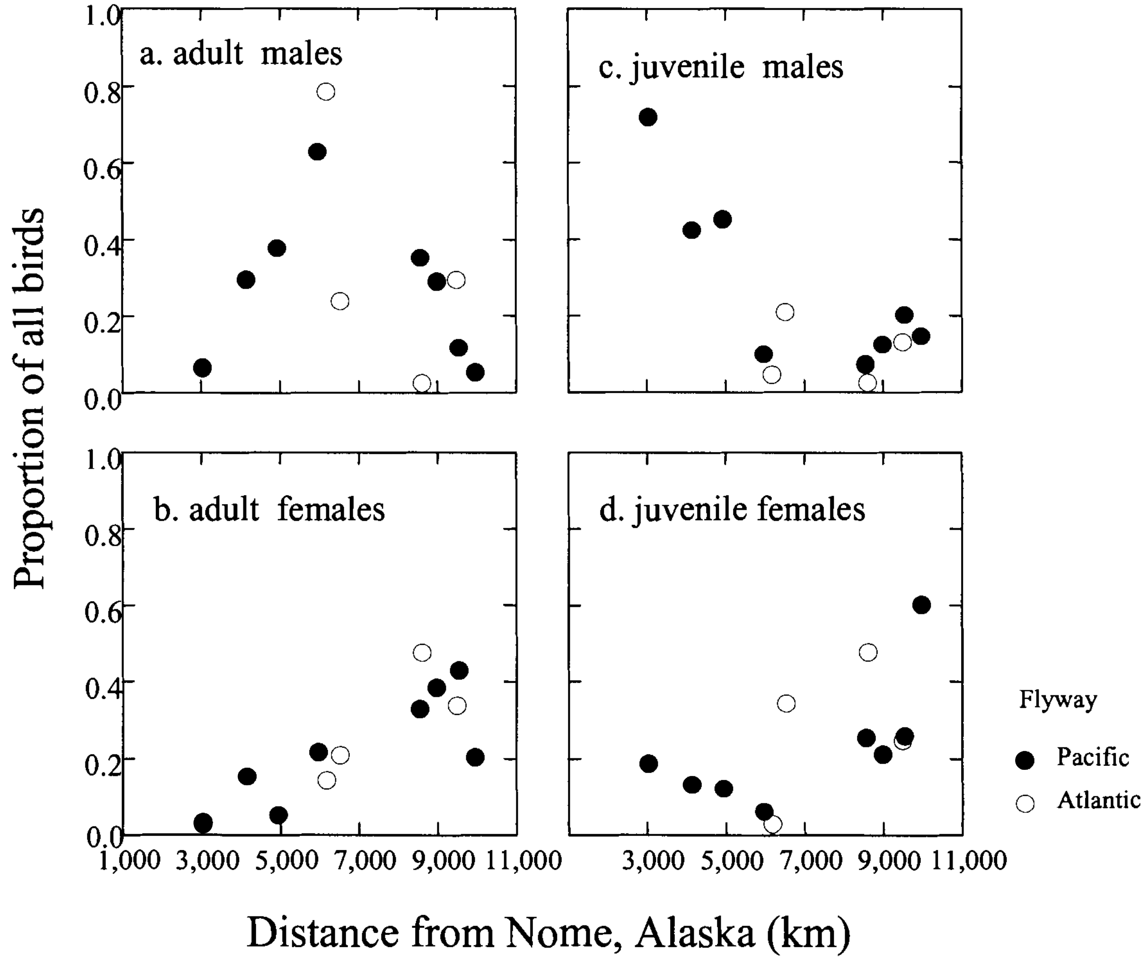

Figure II-4. Distribution for the four age and sex classes of Western Sandpipers.

For each site, the proportions of the four graphs add up to one. a - proportions of adult males peaked at intermediate distance from Nome (quadratic model: $P=0.043$, $r^2=0.50$, F change from adding a quadratic term: $P=0.02$), b - proportions of adult females increased with distance from Nome (linear model: $P=0.002$, $r^2=0.64$), c - proportions of juvenile males decreased with distance from Nome (quadratic model: $P<0.001$, $r^2=0.90$, F change from adding a quadratic term: $P<0.001$), d - proportions of juvenile females increased with distance from Nome (linear model: $P=0.044$, $r^2=0.35$).

III. INTRASPECIFIC FEEDING NICHE DIVERGENCE AND A LATITUDINAL CLINE IN SEX RATIO IN A MIGRATORY SHOREBIRD

Manuscript in review

Silke Nebel

Abstract

Avian species in which males and females migrate to different nonbreeding areas are candidate systems to study the ecological factors underlying distribution patterns. Western Sandpipers (*Calidris mauri*) are such 'differential migrants'. They mainly breed in Alaska and overwinter along the American Pacific and Caribbean coasts. Females migrate further south than males, creating a latitudinal bias in sex ratio. Here, I propose that intraspecific feeding niche divergence underlies this pattern. I hypothesised that intertidal invertebrates are buried more deeply towards the south, possibly due to higher ambient temperature and/or desiccation. Longer bills enable probing (foraging on buried prey) to greater depths. Females have disproportionately long bills, and can therefore exploit a feeding niche at greater vertical depth. Females probed more than males at all locations. Bill length residuals, corrected for tarsus length, were predicted to be larger at southern sites. This was only found in males. No clear change of feeding mode with latitude was detected. At the one site where the relationship was measured, both sexes probed more with increasing sediment temperature. The effect of intraspecific feeding niche divergence on large-scale spatial distribution patterns has not been documented previously in birds and offers an exciting avenue for future research.

Introduction

One of the major goals in ecology is to understand the factors that determine animal distribution patterns (Heglund 2002). Detailed knowledge of the ecological factors underlying animal movements over smaller time spans will broaden our understanding of the selective forces shaping animal distributions over evolutionary time. It will also help us to predict the ecological consequences of human-caused changes in the environment and of global climate change (Goodchild 2002).

A candidate system to study these factors is avian species in which males and females migrate to different nonbreeding latitudes. Costs and benefits of choosing a site can be attributed to sex-specific characteristics, and can thereby help to identify the factors driving the spatial distribution. So far, three main hypotheses have been proposed to explain sexual segregation in migratory birds (Berthold 1996). The 'Dominance Hypothesis' assumes that behavioural interactions between males and females produce geographical segregation (Gauthreaux 1978), because individuals of the dominant sex monopolise nonbreeding areas close to the breeding sites, thereby minimising flight costs. A second hypothesis suggests that body size differences between sexes interact with local climate to produce different optimal distributions (Ketterson & Nolan 1976). Larger individuals can survive longer periods of fasting and are therefore thought to be better suited to survive the colder and less predictable climates at higher latitudes. Finally, according to the 'Arrival Time Hypothesis', individuals benefiting more from earlier arrival on the breeding grounds will gain by wintering closer to the breeding grounds (Ketterson & Nolan 1976, Myers 1981). However, empirical evidence supporting these hypotheses remains equivocal (Cristol et al. 1999).

Western Sandpipers (*Calidris mauri*) are migratory shorebirds, which breed in western Alaska and eastern Siberia, but during the nonbreeding season inhabit intertidal areas along the Pacific coast from southern Canada to Peru, and, to a lesser extent, along the East coast of the Americas (Wilson 1994, Nebel et al. 2002). Males and females show latitudinal segregation, as the proportion of females increases towards the south, creating a latitudinal cline in sex ratio (Nebel et al. 2002). Here, I propose a novel explanation for this differential distribution pattern. I suggest that intraspecific feeding niche divergence leads to spatial segregation of males and females on a hemispheric scale. Intraspecific feeding niche divergence can result from differences in body size (Wilson 1975), in bill length (e.g. Suhonen & Kuitunen 1991, Temeles et al. 2000), or in feeding behaviour (Baker & Baker 1973). In Western Sandpipers, females are slightly larger than males, but have disproportionately longer bills (Cartar 1984). Moreover, Western Sandpipers employ several modes of feeding, including probing (bill deeply inserted), and pecking (Sutherland et al. 2000). Intraspecific feeding niche divergence is therefore assumed to occur.

The location of an animal's niche can be defined as the 'average position on the resource axis of a population', and can be inferred from the mean value of the character used to exploit the resource (Roughgarden 1972). During the nonbreeding season, Western Sandpipers feed on intertidal invertebrates, which tend to bury in the sediment (Wilson 1994); the location of an individual's feeding niche can thus be deduced from the length of its bill. Temperature and sediment desiccation affect distribution of intertidal invertebrates (Hutchins 1947, Brown 1960, Vader 1964, Meadows & Reid 1966, Wolcott 1973, Donn & Croker 1986). It has been suggested that high temperatures may force intertidal invertebrates to bury at greater depth, so as to avoid desiccation (Barter 1988), but to my knowledge, this has never been tested (Constable 1999).

In order to explain the cline in sex ratio in nonbreeding Western Sandpipers, the following hypothesis is put forward. The location of the feeding niche of Western Sandpipers, determined by invertebrate burying depth, decreases vertically (i.e. increases in depth) from the northern to the southern end of their nonbreeding range. This is possibly caused by a latitudinal increase in ambient temperature. Females, given their longer bills, exploit a feeding niche at greater vertical depth than males. Consequently, individuals distribute themselves such that the sex-specific feeding niche is at the same vertical depth as the local feeding niche, resulting in females overwintering further south (Fig. III-1).

I will test four predictions that follow from the hypothesis:

1. Within each sex, bill length increases from north to south.

As the location of the feeding niche increases in depth towards the south, bill length within both males and females should increase accordingly. An increase in bill length that is more pronounced than an increase in body size would serve as a stronger indicator that bill length, rather than overall body size, is the factor underlying the spatial distribution.

2. Both males and females probe more towards the south.

As the location of the feeding niche increases in depth towards the south, birds should adjust their feeding behaviour to a higher proportion of probing.

3. At a given site, females probe more than males.

Since feeding niche location of females is at a greater depth than that of males, the difference should be reflected in the sex-specific feeding behaviour, such that females employ their longer bill by probing more than males.

4. At a given site, individuals probe more with increasing temperature of the sediment surface.

As invertebrates increase burying depth with temperature, both males and females should probe more with increasing sediment temperature.

Methods

Study sites

Data were collected at nine locations distributed across four latitudes: (1) November-December 2000 at Tomales Bay (39.2°N, 123.00°W), Bodega Bay (38.3°N, 123.0°W), and San Francisco Bay, California, USA (38.1°N, 122.3°W); (2) December 2001 on Bull Island, South Carolina, USA (32.8°N, 79.6°W); (3) January-February 2000 in Bahía Santa María, Sinaloa, Mexico (24.0°N, 108.0°W); and (4) January-February 2002 at Costa del Este, Rio Pacora, and Rio Chico, in the upper Bay of Panama (9.0°N, 79.3°W), and February 2002 in Chitré, Herrera (8.1°N, 80.4°W), Republic of Panama.

Data on feeding behaviour were collected in California, South Carolina, and Panama; morphometric data were from California, Mexico, and Panama (Upper Bay of Panama only).

Body size measurements

Birds were caught with mist-nets. Length of bill and tarsus were measured with calipers to the nearest 0.1 mm. Individuals with an exposed bill of <24.3 mm were classified as males, and >24.7 mm as females (Page & Fearis 1971). Juveniles have reached adult bill length by the time they migrate south (Nebel et al. 2002), therefore adults and first-year birds were pooled in the analysis.

Observation of feeding behaviour

Foraging Western Sandpipers were assigned a sex by estimating bill length using a spotting scope. To determine the accuracy of this technique, 11 observations were made on 9 individuals that were caught, colour banded by a second observer, and placed in a meshed tent on the mudflat, and subsequently sexed using a spotting scope. In 10 out of 11 observations, sex was determined accurately. While this does constitute a potential source of error, it is unlikely to bias the results, given that is a random rather than a systematic error.

Foraging behaviour was classified as 'peck', when less than half of the bill was inserted into the sediment, and as 'probe', when it was inserted for more than half (after Sutherland et al. 2000). Given that birds tended to feed either off the surface, or inserted the bill rather deeply, this usually allowed a clear distinction between the two foraging modes. Feeding mode was expressed as the proportion of probes (no. of probes/(no. of pecks + no. of probes)). The proportion was arcsine transformed prior to analysis to stabilise variance.

Temperature measurements of the sediment

Sediment temperature was measured at one study site only, at Costa del Este, Upper Panama Bay. Between January 25 to February 25, 2002, recordings took place between 7 am and 7 pm with a "Yellow Springs Instrument" temperature recorder, which was calibrated against a standard laboratory thermometer. Twelve probes were inserted into the sediment, with four probes each at three depths (0, 1, 3 cm), which encompasses the depth range Western Sandpipers can exploit. The recorder was placed approximately where feeding Western Sandpipers had been observed.

Results

Body size measurements

Bill length differed among sites for males (F=19.41, p<0.001), but not for females (F=0.13, p=0.90; Fig. III-2). Bills of males in California were shorter than those in Mexico and in Panama. Length of tarsus also differed among sites in males (F=3.19, p=0.043), but not in females (F=0.19, p=0.82; Fig. III-3). Males in California had shorter tarsi than those in Mexico. Bill length residuals corrected for length of tarsus differed among sites in males (F=4.47, p=0.012), where residuals were smaller in California than in Mexico. In females, no difference was detected (F=0.09, p=0.92; Fig. 4, Table III-1).

Feeding mode: effect of area and sex

The proportion of probes varied with 'sex', 'area' and their interaction term (females>males: F=6.45, p=0.012; area: F=5.24, p=0.006; area*sex: F=3.31, p=0.038; Fig. III-5, Table III-1). Therefore, each sex were analysed separately. In males, no difference in feeding mode was detected among areas (F=1.10, p=0.31), while females showed a significantly higher proportion of probes in South Carolina than in Panama (F=4.67, p=0.011). Pooling all sites, females had higher variance in feeding mode than males (Bartlett's Test: F=29.05, p<0.001; (Zar 1999)).

Feeding mode: effect of temperature

Mean sediment temperature at Costa del Este, Upper Panama Bay, was significantly higher on the surface and at 1 cm depth than at 3 cm depth (F=12.08, p=0.001; Table III-2). Both females and males increased the proportion of probes with temperature of the sediment surface (females: n=153, F=10.64, p=0.001; males: n=59, F=4.45, p=0.039; Fig. III-6).

Discussion

I proposed and tested a novel hypothesis to explain a latitudinal cline in sex ratio in nonbreeding Western Sandpipers. Namely, intraspecific feeding niche divergence and a latitudinal increase in depth of feeding niche location create different distributional optima for males and females. Are the predictions of the hypothesis supported by the data collected?

1. Within each sex, bill length increases from north to south.

Males in California had shorter bills than those in Mexico and Panama, even when correcting for length of tarsus. This suggests that bill length, rather than overall body size, underlies the spatial distribution. No pattern, however, was detected in females. This lack of detection might in part be attributable to the geographical range of sites sampled in this study, as no data were available from the southern end of the nonbreeding area. Indeed, a comparison of Western Sandpipers wintering in Mexico, Panama and Ecuador showed that within each age and sex class, length of bill and of wing increased towards the south. Moreover, the difference in bill length between northern and southern sites was larger in males than in females (O'Hara 2002). The limited sample size in this study might be able to detect the trend in males, but not in females, where it appears to be less strong. Data from both studies suggest that males, when wintering further south, where the location of the feeding niche is thought to be at a greater vertical depth, are under stronger selective pressure to increase bill length than females.

Two more arguments support the idea that the spatial distribution can be attributed to length of bill rather than to overall body size. First, the increase in body size from north to south is inconsistent with the idea that a larger body conveys an advantage in colder regions, as bigger animals have relatively smaller surface areas for heat loss (James 1970). And second, the size difference in structural variables between male and female Western Sandpipers is most pronounced with regard to bill length (ca. 10%), while body size differs only about 3% (Cartar 1984).

2. Both males and females probe more towards the south.

Contrary to the prediction, no difference was detected in foraging mode in males between sites. It is possible that, regardless of the burying depth of their prey, pecking is the most profitable foraging mode for the short-billed males. However, this seems to contradict the observation that males increase their bill length relative to tarsus length from a northern to two southern sites. In females, the pattern observed also does not follow the prediction, as females probe more in South Carolina than in Panama. While females probe the least at the most northern site, the sample size in California (n=1) is too small to allow detection of a significant trend. It seems that the variance in feeding mode is too high to allow a conclusion as to whether Western Sandpipers adjust their feeding behaviour with latitude, given the sample size available.

3. At a given site, females probe more than males.

Females do not only probe more than males, they also show more variability in their feeding behaviour, suggesting that they are better suited to exploit both shallow and more deeply buried prey items.

4. At a given site, individuals probe more with increasing temperature of the sediment surface.

Both males and females probed more with increasing sediment temperature at Costa del Este, Panama. While data from additional sites are called for, the relationship between temperature and feeding mode does suggests that intertidal invertebrates increase burying depth with high temperature, resulting in a decrease of the vertical feeding niche location of their avian predators.

In summary of the main findings, I provided evidence for intraspecific niche divergence in Western Sandpipers, as males and females not only had bills of different length, but also employed different feeding behaviour. The morphometric data suggested a vertical increase in location of feeding niche from north to south, but data from more sites is needed to establish this relationship. The data on feeding behaviour was likely too variable to be used to infer a shift in niche location with a small sample size. An increase of invertebrate burying depth with temperature was supported by the data.

These findings raise three questions:

1. Are there other factors that might cause a change in feeding niche location?

2. What other factors might affect Western Sandpipers nonbreeding distribution?

3. Does intraspecific feeding niche divergence during the nonbreeding season underlie the sexual bill dimorphism?

1. Are there other factors that might cause a change in feeding niche location?

If invertebrates at southern latitudes are adapted to high temperatures, they might not increase burying depth as much as a response to excessive heat. Locally, interspecific differences in temperature tolerance have been shown in a number of intertidal species, including limpets (Wolcott 1973), bivalves (Britton 1983), and intertidal snails (McMahon & Britton 1983), and it has been suggested that thermal tolerance increases with decreasing latitude (Spicer & Gaston 1999). In insects, in contrast to amphibians and fish, lower lethal temperature declines towards higher latitudes, while the upper thermal limits show little geographic variation (Lutterschmidt & Hutchison 1997, Addo-Bediako et al. 2000). While our knowledge of how thermal physiology affects distribution patterns in marine ectothermes is limited (Clarke 2003), the possibility that intertidal invertebrates reach an upper thermal limit at the sediment surface at southern latitudes cannot be rejected and warrants further examination.

Temperature is just one possible factor that could affect niche depth. Another possibility is that competition for food by crabs could alter the relative availability of surface-dwelling prey and thus lead to the observed segregation (Elner & Seaman 2003). In tropical intertidal areas, crustaceans are far more abundant compared to northern latitudes (Swennen et al. 1982). Crabs might deplete most of the food resources on the surface of the sediment, which would force sandpipers to probe at greater depth for food in southern latitudes.

2. What other factors might affect Western Sandpipers nonbreeding distribution?

Latitudinal distribution is also affected by energy expenditure. Metabolic costs increase when environmental temperatures drop below the zone of thermoneutrality (Castro 1992, Piersma et al. 1995). Western Sandpipers, like other shorebirds, live exposed in open habitats. Cost of thermoregulation is therefore an important determinant of total energy expenditure (Piersma et al. 1991, Piersma 2002), and, as a consequence, of spatial distribution (Root 1988). Several species of shorebirds have been documented to substantially decrease energy expenditure by wintering in tropical compared to temperate latitudes (Castro 1988, Drent & Piersma 1990, Castro 1992, Wiersma & Piersma 1994, Kersten et al. 1998), even when taking into account the costs of the much longer flight (Piersma 1994).

Living in the Tropics, however, also comes with a cost, as birds have to migrate further, and they may face radiative heat gain, salt stress and evaporative water loss in hot climates (Marder et al. 1989, Klaassen & Ens 1990, Verboven & Piersma 1995, Battley 2002). But overall, wintering at southern latitudes may be advantageous, due to lower thermoregulatory costs (Castro 1988, Castro 1992, Cadee et al. 1996, Kersten et al. 1998), better flight performance when escaping predators, as less body fat is carried (Chapter 5), and less environmental uncertainty (Myers et al. 1985, Suter & van Eerden 1992, Lovvorn 1994). Interestingly, apparent survival rates of Western Sandpipers at a site in Panama were higher than those at a site in Mexico, which could be due to differences in local site quality (Fernández et al. 2003), but it might also be the result of a general pattern of latitudinal change in overwinter conditions.

3. Does intraspecific feeding niche divergence during the nonbreeding season underlie the sexual bill dimorphism?

Sexual size dimorphism has been the topic of much debate since Darwin (1871). Factors that are thought to affect the evolution of sexual size dimorphism include genetic correlations (Lande 1980), allometry (Lande 1980, Fairbairn 1997), intraspecific niche divergence (Bolnick & Doebeli *in press*, Reimchen & Nosil *in review*, Selander 1966, Slatkin 1984, Shine 1989, Butler et al. 2000), and sexual and fecundity selection (e.g. (Andersson 1994, Fairbairn 1997, Badyaev & Martin 2000, Ferguson & Fairbairn 2000, Székely et al. 2000). Niche divergence and sexual selection have received most attention, but niche divergence is thought to be far less frequent than sexual selection as the cause of sexual dimorphism (Hedrick & Temeles 1989, Fairbairn 1997, Badyaev & Martin 2000, Temeles et al. 2000). While resource partitioning between the sexes has been documented (e.g. Pasinelli 2000, Temeles et al. 2000, Pearson et al. 2002, Shine et al. 2002), intra- or inter-sexual selection on male or female body size could lead indirectly to resource partitioning if only because the relatively larger sex can consume larger prey (Bolnick & Doebeli in press).

In a comparative analysis on sexual size dimorphism, Székely et al. (2000) conclude that sexual size dimorphism in shorebirds has evolved primarily due to sexual selection, as a smaller body conveys an advantage in species using courtship aerial display (Jehl & Murray 1986). This explanation, however, does not account for why the difference in bill length is so much larger than that in body size. A shift in the relative size of the bill would not be predicted under the sexual selection scenario, unless its shape or size influences reproductive success (Shine 1989). Assortative mating seems to be generally rare in shorebirds (Wagner 1999), and in Western Sandpipers, there is little evidence that sexual selection processes might be driving sexual size dimorphism (Sandercock 1998).

According to Selander (1972), the only reliable evidence to infer natural selection as the cause of sexual dimorphism is a modification of the feeding structures, to a greater degree than would be expected from body size differences alone, and in a direction inconsistent with sexual selection. This has been documented only in a few species (Selander 1966, Temeles et al. 2000). However, Lande (1980) argued that assigning natural selection as the primary cause of sexual dimorphism also requires that a sex-specific difference exists in the use of the dimorphic character.

Not only is the difference in bill length between male and female Western Sandpipers larger than in body size, but there is also a sexual difference in feeding behaviour. Therefore, the criteria of both Selander (1972) and Lande (1980) are met, and I conclude that the evidence from morphometric and behavioural data are consistent with the idea that niche divergence during the nonbreeding season is resulting in sexual dimorphism in bill length in Western Sandpipers.

In conclusion, I provided evidence consistent with the hypothesis that in Western Sandpipers, location of feeding niche increases from north to south, perhaps caused by an increase in ambient temperature. Females, which have longer bills than males, exploit a feeding niche at greater vertical depth, resulting in intraspecific niche divergence. Concomitantly, individuals choose nonbreeding sites so as to match the sex-specific and the local feeding niche location, resulting in females overwintering further south. The hypothesis that intraspecific niche divergence affects large-scale spatial distribution patterns is novel and opens exciting avenues for further research.

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Table III-1. Number of Western Sandpipers used for morphometric comparison and for feeding behaviour observations.

Sex	Site	morphometric data	feeding observations
male	California	41	14
male	Mexico	243	none
male	South Carolina	none	30
male	Panama	27	59
female	California	7	1
female	Mexico	54	none
female	South Carolina	none	16
female	Panama	35	153

Table III- 2. Mean temperature of the sediment at Costa del Este, Panama Bay (no. of readings=803).

depth (cm)	°C maximum	°C mean	°C range
0	39.5	31.5	17
1	38.0	31.3	15
3	35.5	30.6	12

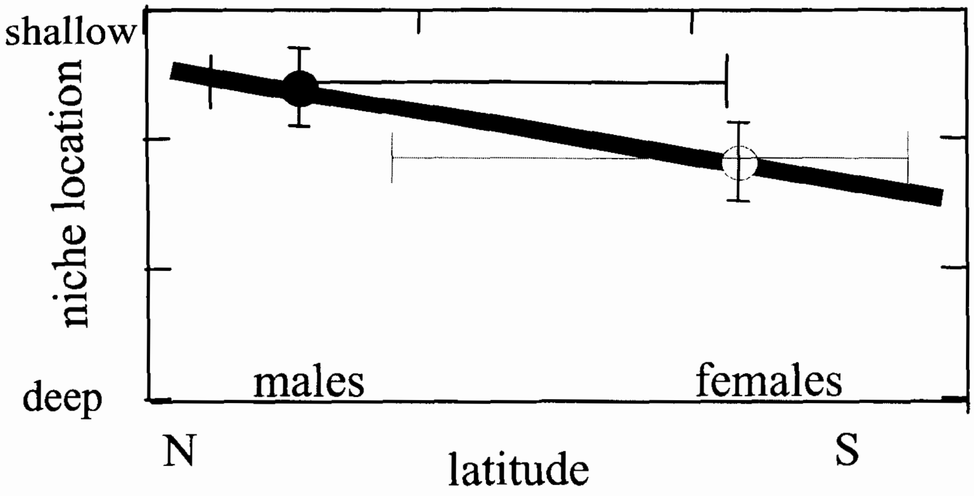

Figure III-1. Hypothesised change in vertical location of feeding niche (thick line) of Western Sandpipers with latitude.

Individuals distribute themselves such that the sex-specific niche location (determined by length of bill) matches local niche location (determined by ambient temperature).

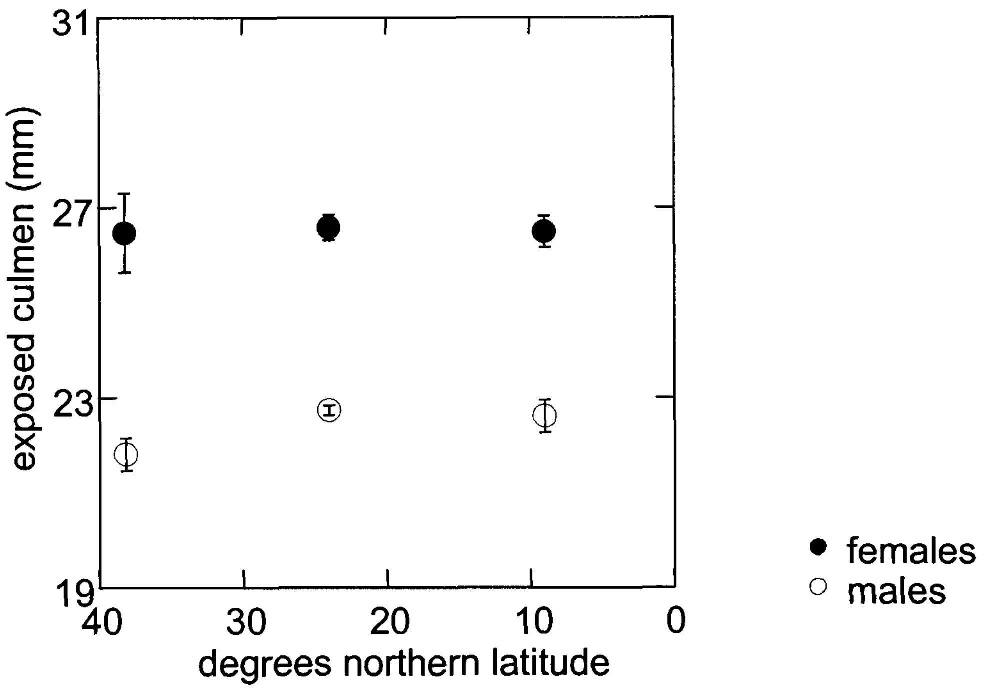

Figure III-2. Bill length (+/- 95% Confidence Interval) in male Western Sandpipers was shorter in California than in Mexico and Panama.

In females, no difference was detected. Sample sizes are given in Table III-1.

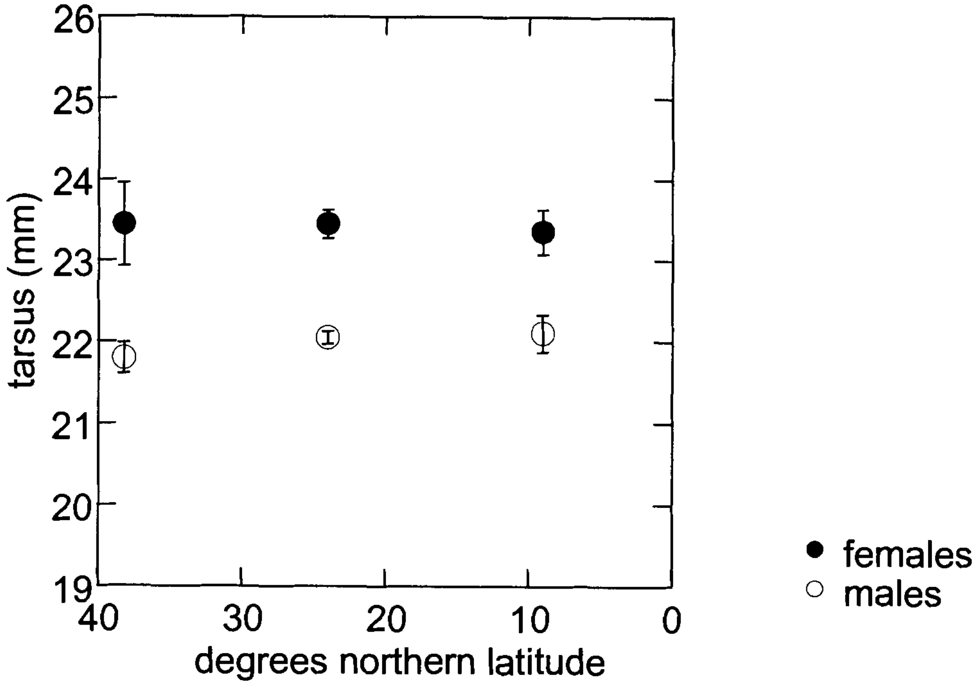

Figure III-3. Length of tarsus (+/- 95% Confidence Interval) in male Western Sandpipers was shorter in California than in Mexico.

In females, no difference was detected. Sample sizes are given in Table III-1.

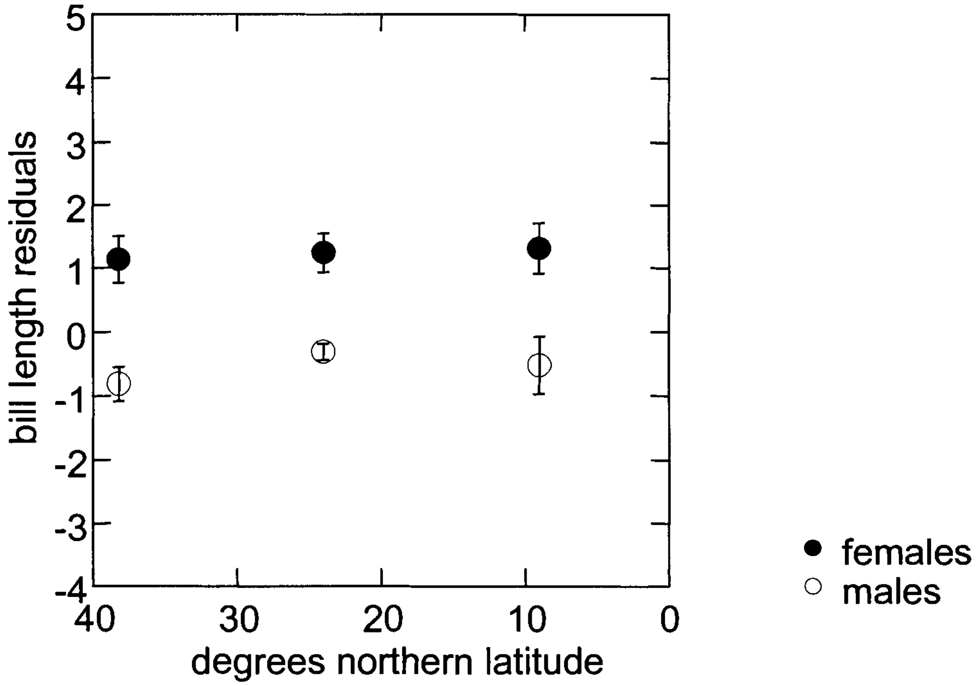

Figure III-4. Bill length residuals corrected for length of tarsus (+/- 95% Confidence Interval) in male Western Sandpipers were smaller in California than in Mexico.

In females, no difference was detected. Sample sizes are given in Table III-1.

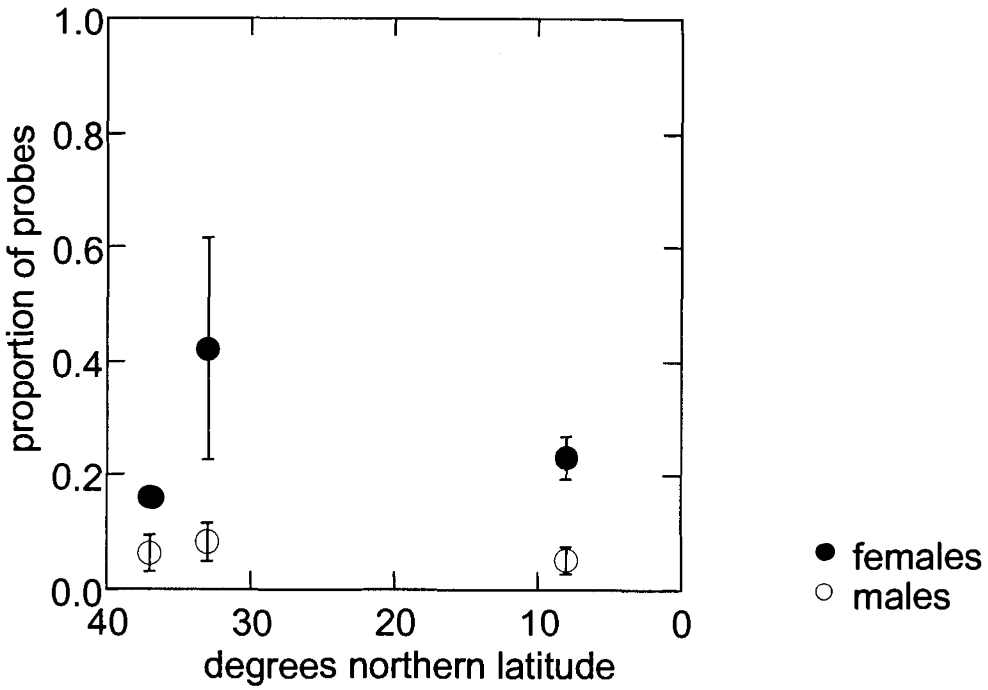

Figure III-5. Proportion of probes (+/- 95% Confidence Interval) was higher in female than in male Western Sandpipers.

It did not differ among sites in either sex. Sample sizes are given in Table III-1.

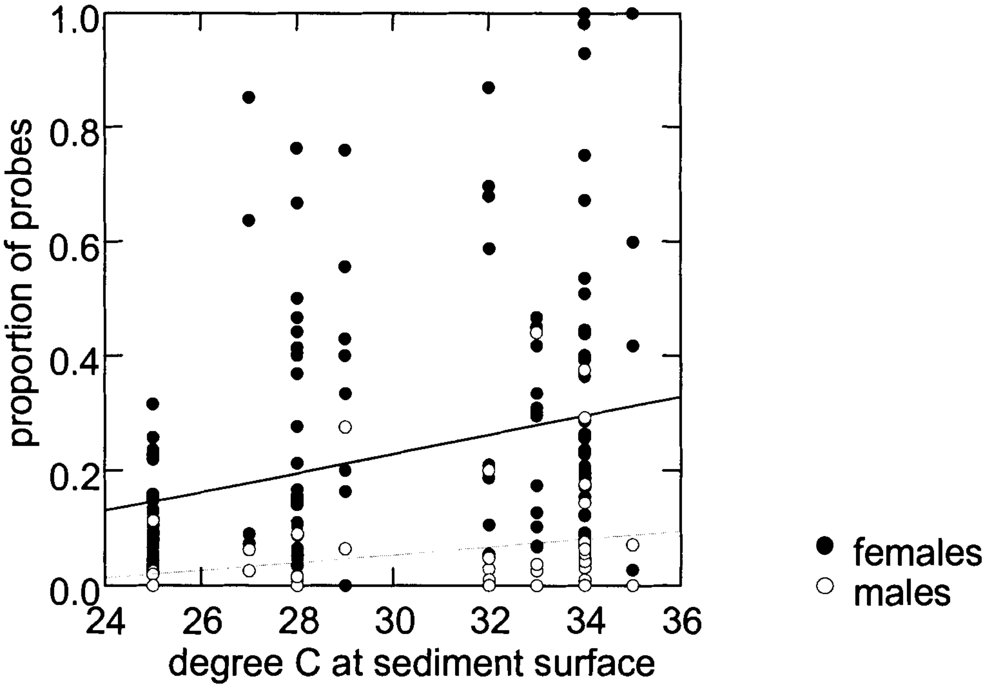

Figure III-6. Both males and females increased the proportion of probes with increasing temperature of the sediment surface at Costa del Este, Upper Panama Bay.

IV. BILL MORPHOLOGY AND ITS ASSOCIATION WITH FORAGING BEHAVIOUR IN SANDPIPERS

Nebel, S., D.L. Jackson & R.W. Elner

Summary

Evolution of intraspecific feeding niche divergence has been attributed to either dominance relationships between males and females or sexual differences in the trophic apparatus. Female Western Sandpipers (*Calidris mauri*) employ a probing foraging mode more than males, and it has been shown in other shorebirds that probing is facilitated by bill curvature. Female Western Sandpipers were thus predicted to have more decurved bills than males. High resolution microscopy revealed that bills of male and female Western Sandpipers differed with regard to length, but not curvature or depth. This was discussed in the context of species-specific diet choice. Gross bill morphology differed between Western Sandpipers, Least Sandpipers (*C. minutilla*) and Dunlin (*C. alpina*) again only with regard to length, not curvature or depth. Sensory pits, located under the keratin layer of the bill, host Herbst corpuscles, which detect pressure gradients caused or reflected by prey buried in the sediment. These pits occurred in all three species, suggesting that this method of prey localisation might be more common among sandpipers than previously assumed.

Introduction

Intraspecific feeding niche divergence has evolved in many taxa, and has usually been attributed to either dominance relationships between males and females (Peters & Grubb 1983, Matthysen et al. 1991, Pasinelli 2000), or to sexual differences in the trophic apparatus (e.g. Temeles & Roberts 1993, Temeles et al. 2000). Differentiating between the two factors can make a substantial contribution to our understanding of the evolution of sexual size dimorphism (Selander 1972, Lande 1980).

Shorebirds (family Scolopacidae) are a candidate group to study the association between sexual bill dimorphism and foraging behaviour. At least 13 species of shorebirds display sexual differences in diet and foraging behaviour (Durell 2003). Pronounced intra- as well as inter-specific differences in length and shape of the bill are common (Prater et al. 1977, Durell 2000), and a few studies were able to link these to differences in foraging behaviour. Long and decurved bills are thought to be adaptive for a probing foraging mode, where the bill is deeply inserted into the sediment, whereas short and straight bills are related more to a pecking foraging mode, where the individual is feeding off the surface (Ferns & Siman 1994, Zweers & Gerritsen 1997, Barbosa & Moreno 1999).

Foraging behaviour has also been associated with bill micro-anatomy. Several species of sandpipers (genus *Calidris*) can detect pressure gradients caused or reflected by prey items buried in the sediment (Gerritsen & Meiboom 1986, Piersma et al. 1998). Herbst corpuscles, mechanoreceptors located in small cavities ('sensory pits') under the keratin layer of the bill, are structures that can sense these pressure gradients (Gottschaldt 1985). High densities of Herbst corpuscles are thought to be associated with the probing foraging mode (Gottschaldt 1985, Barbosa & Moreno 1999).

The Western Sandpiper (*Calidris mauri*) is a small shorebird which breeds in Alaska and overwinters mainly along the American Pacific coast between southern Canada and Peru (Wilson 1994, Nebel et al. 2002). Females are slightly larger than males (about 3%), but have disproportionately longer bills (about 10%, Cartar 1984). Western Sandpipers employ two main modes of feeding, which are probing and pecking (Sutherland et al. 2000). Female Western Sandpipers use the probing foraging mode more than males (Nebel 2003), and are therefore predicted to have a more decurved bill. Whether sensory pits occur in this species is not known.

The purpose of this paper is two-fold. First, we investigate whether in Western Sandpipers, sexual differences in foraging behaviour are associated with differences in bill morphology and micro-anatomy. Second, we conduct an interspecific comparison of bill morphology between Western Sandpipers, Least Sandpipers (*C. minutilla*) and Dunlins (*C. alpina*). These three sandpiper species forage in intertidal habitats during the nonbreeding season, but show differences in micro-habitat choice. Unlike Western Sandpipers, Least Sandpipers also use freshwater creeks as foraging grounds, and Dunlin frequently feed in terrestrial fields (Colwell & Landrum 1993, Warnock & Gill 1996). Whether differences in micro-habitat use are reflected in bill morphology has hitherto not been explored.

Methods

Study sites

For an analysis of the length of the bill relative to tarsus length, birds were caught with mist-nets and released after measurements were taken. For the analysis of bill shape (Table IV-1), mist-netting casualties were used or collected under the authority of Special Permit No. PK BC 92/13 issued by Environment Canada's Canadian Wildlife Service The protocol was approved by the University of British Columbia Committee on Animal Care.

Birds were captured or collected at Boundary Bay, British Columbia, Canada (49.1°N, 123.0°W); Bodega Bay (38.2°N, 123.0°W), Tomales Bay (39.2°N, 123.0°W), San Francisco Bay, (37.5°N, 122.3°W), California, USA; and in Bahía Santa María, Sinaloa, Mexico (24.0°N, 108.0°W), Costa del Este, in the upper Bay of Panama (09.0°N, 79.3°W). Specimens were stored in a freezer within hours after collection.

Light microscopy

Observation of the bills were made with a Nikon SMZ-1500 stereomicroscope, fitted with either an HR Plan Apo 0.5x objective (for larger specimens) or an HR Plan Apo 1x objective. A combination of transmitted light from the base stand and epi-illumination from a fibre optic light ring was used to illuminate the specimens. We took digital images using a Nikon DXM-1200 high-resolution microscope camera, operating at a pixel resolution of 1280x1024. Additional image manipulations were performed using Adobe Photoshop, and Optimas® version 6.1 1 image analysis software (Media Cybernetics Inc., Silver Spring, MD, USA) was used for image analysis and measurements.

Measurements of bill morphology

Bill dimensions were quantified as follows (Fig. IV-1): exposed culmen, which is the distance from the tip of the bill to the line of feathering on the dorsal surface of the upper jaw (a); the distance from the tip of the bill to the ring at the dorsal end of the bill (b); the distance between the tip of the bill and the anterior margin of the nares (c); depth at nares (d); curved arch (e); width at ring (f); and width at notch (g). Length of tarsus was measured with calipers to the nearest 0.1 mm, and in some cases, length of wing (flattened and straightened) was measured to the nearest 0.1mm using a wing ruler (Table IV-1). To determine bill curvature, the ratio of the arch to the length of the exposed culmen was taken (after Stiles 1995).

To assess the density of sensory pits, the bill was soaked in water and the skin was peeled off subsequently. The bill was then soaked in bleach to dissolve remaining soft tissue and to display the pits. Occurrence of sensory pits was quantified by counting the number of pits on a transect drawn through the widest part of the bill, on the outside of the upper and lower bill. Sex was assigned using the length of the exposed culmen (Western Sandpiper: <24.3 mm = male, >24.7 mm = female, Page & Fearis 1971; Least Sandpiper: <17.5 mm = male, >18.6 mm = female, Page 1974a; Dunlin: <37.8 mm = male, >39.9 mm = female, Page 1974b).

Results

Bill shape: intraspecific comparison in Western Sandpipers

A Principal Component Analysis (PCA) was performed to detect differences in bill shape between male and female Western Sandpipers. All variables were used in the analysis, except for width at ring (g) and width at notch (h), which could only be quantified in a small number of individuals (Table IV-1).

Factor (or Component) 1 and 2 explained 84.1% and 15.2% of the total variance, respectively. Factor 1 constituted measures of bill length, while Factor 2 constituted bill depth (Fig. 2). Males (n=17) and females (n=14) differed with regard to Factor 1 (t=10.67, df=25, p<0.001), but not Factor 2 (t=0.40, df=21.4, p=0.70; Fig. IV-3). Bill curvature did not differ between males and females (General Linear Model (GLM): F=0.01, p=0.91).

Bill shape: intraspecific comparison in Dunlins

In Dunlin, a GLM was performed to test for differences between males (n=1) and females (n=3), as the sample sizes were not sufficient to run a PCA. Females had longer bills than males (n=4, F=29.06, p=0.033), while no difference was detected in depth of the bill (F=1.56, p=0.34) nor in curvature (F=0.06, p=0.83).

Bill shape: interspecific comparison

A PCA was performed to test for interspecific differences in bill shape, using the same variables as in the intraspecific comparison. Factor 1 and 2 explained 96.1% and 3.8% of the total variance, respectively. Again, Factor 1 constituted measures of bill length, Factor 2 of bill depth (Fig. IV-4). Each species pair differed with regard to Factor 1 (F=112.77, p<0.001), but not Factor 2 (F=1.06, p=0.36). This indicates that bills of the three species differ only with regard to length, but not depth (Fig. IV-5). Bill curvature did not differ between species (GLM: F=1.63, p=0.21). A visual comparison of the bills of all three species confirmed the similarity of the bill shape (Fig. IV-6).

Bill size relative to tarsus: intra- and interspecific comparisons

Residuals of culmen corrected for tarsus were larger in females than in males in all three species (Western Sandpipers: n=407, F=65.83, p<0.001, Least Sandpipers: n=120, F=35.08, p<0.001, Dunlin: n=17, F=24.25, p<0.001; Fig. IV-7).

Occurrence of sensory pits

Sensory pits occur in all three species (Fig. IV-8). Frequency of sensory pits as quantified by the transects did not differ substantially between males and females within and between species (Fig. IV-9, Table IV-1).

Discussion

In shorebirds, sexual differences in foraging behaviour and in bill morphology are common (see Durell 2003), but few studies have looked at their association (Hulscher &

Ens 1992, Durell 2000). Here, we used data on bill morphology and micro-anatomy to explain intraspecific feeding niche divergence and make inferences about diet and micro-habitat choice.

Female Western Sandpipers use a probing foraging mode more than males (Nebel 2003). This does not seem to be caused by behavioural dominance, which as of yet has not been reported from the nonbreeding grounds (Wilson 1994, Nebel & Lank 2003). Moreover, there is strong latitudinal segregation of males and females during the nonbreeding season (Nebel et al. 2002), but females were shown to probe more than males at sites at both northern and southern latitudes (Nebel 2003). If competition was forcing females to probe more when males are present (or vice versa), we would expect to see a change in feeding behaviour with a change in local sex ratio.

Alternatively, the sex-specific foraging niche might be based on morphological adaptations. Decurved bills are known to facilitate probing (Zweers & Gerritsen 1997), female Western Sandpipers were therefore predicted to have more decurved bills than males. However, the only dimension of gross bill morphology that differed between the sexes was length. Thus, in Western Sandpipers, the propensity for probing does not appear to be associated with bill curvature.

The reasons underlying the relatively straight bills of females Western Sandpipers might become apparent when taking their diet into consideration. Curlews (*Numenius arquata*) have strongly decurved bills and extract crabs and large worms from their burrows, and bill decurvature has been argued to be an adaptation to their three-dimensional probe path (Davidson et al. 1986). A decurved bill allows further penetration into crab burrows and gaps under rocks than straight bills (Ferns & Siman 1994). Unlike Curlews, Western Sandpipers mainly feed on small invertebrates and meiofauna which are buried in the sediment rather than inhabiting structured burrows (Sutherland et al. 2000, Wolf 2001). Concomitantly, a strongly decurved bill is not likely to facilitate foraging in Western Sandpipers. In fact, curvature incurs a cost, as a decurved bill is structurally weaker than an equivalent straight bill (Burton 1974), and therefore less suitable for hard substrates (Davidson et al. 1986).

The similarity in bill shape in Western Sandpipers, Least Sandpipers and Dunlin suggests that they share a common archaeotype and/or gross bill morphology evolved in response to similar selective pressures. They might also use pressure waves to detect prey items (Gerritsen & Meiboom 1986; Piersma et al. 1998), as they all exhibit high densities of sensory pits. This method of prey detection might be much more widespread then previously assumed (see also Bolze 1968). It seems that the features of diet and habitat the three species have in common exert stronger selective pressures than those that differ (Cooper 1994, Wilson 1994, Warnock & Gill 1996).

In all three species, females had longer bills than males. Differences in bill length can lead to intraspecific feeding niche divergence (Suhonen & Kuitunen 1991), which may underlie the large-scale spatial segregation of male and female Western Sandpipers (Elner & Seaman 2003, Nebel 2003). It has been suggested that intertidal invertebrates increase burying depth with increasing temperature of the sediment; birds in warmer regions would therefore require a longer bill to be able to forage successfully (Chapter 3). Indeed, Western Sandpipers wintering at southern latitudes have longer bills than individuals further north, both within and between sexes (Nebel et al. 2002, O'Hara 2002). A similar pattern is documented in Least Sandpipers (Nebel & Fernández *in review*), and evidence exists for a male-biased sex ratio at northern nonbreeding sites in Dunlins (Shepherd et al. 2001). These patterns of a latitudinal change in sex ratio and in bill length are consistent with the idea that an association exists between sexual bill dimorphism and nonbreeding latitude in all three species (Chapter 3).

What does the occurrence of sensory pits tell us about feeding behaviour? It has been suggested earlier that Western Sandpipers might use pressure gradients to identify large prey items as they move in wet sediment (Sutherland et al. 2000). The fact that in all three species, sensory pits occur at high densities suggests that this method of localising prey might be much more widespread than previously assumed. While the data on density of sensory pits is only preliminary and needs to be interpreted with caution, it is nevertheless evident that no pronounced differences in the occurrence of sensory pits existed between male and female Western Sandpipers. Given that females probe more than males, we may have expected that females have a higher occurrence of sensory pits, as they feed less on visual cues than males (Barbosa & Moreno 1999).

According to Selander (1972), the only reliable evidence to infer natural selection as the cause of sexual dimorphism is a modification of the feeding structures, to a greater degree than would be expected from body size differences alone, and in a direction inconsistent with sexual selection. This has been documented only in a few species (Selander 1966, Temeles et al. 2000). In Dunlin and Least Sandpipers, no data on sex-specific feeding behaviour were available to test for an association with sexual bill size dimorphism. In Western Sandpipers, the increased use of the probing foraging mode in females was associated with increased bill length, the sexually dimorphic bill is subject to differential use by males and females. Therefore these findings provide evidence for the hypothesis that sexual bill dimorphism in Western Sandpipers can be attributed to natural sexual selection (Lande 1980, Nebel 2003).

Our work highlights the importance of incorporating morphological aspects into the study of evolutionary ecology. It suggests that a more thorough consideration of bill morphology and morphometrics can assist in understanding patterns in foraging behaviour and life history.

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Species	Site[1]	#pits LB[2]	#pits UB[3]	day/mo 2000	Mass (g)	Tarsus	Wing	Age	Sex	Exposed culmen: a	Chord: b	Nares to tip: c	Depth at nares: d	Curved arch: e	Width at ring: f	Width at notch: g	Cause of death[4]
WESA	BS			1/29	22.0	22.6	102.0	ad.	M	22.67	22.04	18.77	5.09	22.37	4.68	4.53	hc
WESA	BS			1/29	22.0	22.2	96.0	ad.	M	20.57	20.12	17.15	4.14	20.35	4.70	4.31	hc
WESA	BS			1/29	20.0	21.2	100.5	ad.	M	22.01	21.52	18.24	4.70	21.86	4.84	4.57	hc
WESA	BS			1/29	21.0	20.6	100.5	ad.	M	21.37	20.60	17.34	4.72	20.90	4.85	4.60	hc
WESA	BS			1/29	21.5	20.9	99.5	ad.	M	20.84	20.48	17.84	4.24	20.67		4.87	hc
WESA	BS	5	5	1/29	21.0	21.6	101.0	ad.	M	22.00	21.59	18.38	4.29	21.84		4.57	hc
WESA	BS			1/29	20.5	21.2	100.0	ad.	M	22.22	21.38	17.72	5.32	21.79		4.82	hc
WESA	BS			1/29	20.0	22.5	98.5	ad.	M	23.04	22.57			22.87			hc
WESA	BS			1/29	22.5	20.8	99.0	ad.	M	23.27	22.92	19.46	4.53	23.25		4.72	hc
WESA	BS			1/29	24.5	22.5	95.0	ad.	?	24.70	23.60	20.45	4.39	23.99	4.97	4.54	hc
WESA	BS			2/27		21.5		ad.	M	22.14	21.08	18.45	4.41	21.30		4.22	mc
WESA	BS			3/24	20.0	22.1	95.0	ad.	M	21.61	21.01	18.58	4.74	21.31			?
Dunlin	RB			5/5	73.4	30.7		?	F	42.35	41.34	35.07	6.09	43.20	6.36		coll.
Dunlin	RB			5/5	60.2	30.7		?	F	40.68	39.59	34.36	6.71	39.67	7.01	6.66	coll.
Dunlin	RB			5/5	60.8	28.5		?	F	41.17	39.88	34.52	6.57	40.38		6.13	coll.
WESA	RB		6	5/5	26.8	23.7		?	F	28.37	27.43	24.14	4.70	27.78	4.42	4.33	coll.
WESA	RB			5/5	30.4	25.0		?	F	26.81	26.44	22.30	5.28	26.65	4.64		coll.
WESA	RB			5/5	24.9	23.8		?	F	26.46	25.64	21.24	4.92	25.96	5.21	5.05	coll.
WESA	RB			5/5	26.8	23.0		?	F	26.02	25.24	22.32	5.15	25.59	5.89		coll.
WESA	RB			5/5	28.1	22.9		?	F	25.03	24.60	20.60	5.05	24.98		4.43	coll.
WESA	RB			5/5	26.1	22.5		?	F	25.04	24.12	20.17	4.23	24.53			coll.
WESA	RB			5/5	26.3			?	F	25.21	24.66	21.44	4.76	24.91		4.70	coll.
WESA	RB			5/5	29.8	25.1		?	F	25.72	25.21	21.89	5.47	25.77		4.40	coll.
WESA	RB			5/5	30.4	24.6		?	F	26.82	25.73	22.77	4.97	26.04		5.06	coll.
WESA	RB	6	6	5/5	30.3	23.9		?	F	27.14	26.61	22.97	5.07	26.92		4.96	coll.
WESA	RB			5/5	27.3	26.1		?	F	27.95	27.37	23.20	5.06	27.73			coll.
Dunlin	RB	2	3	5/5	56.0	30.0		?	M	36.05	34.97	30.28	5.98	35.44	5.39		coll.
WESA	RB			5/5	26.7	20.6		?	M	19.55	19.08	16.68	4.83	19.39	4.70	4.35	coll.
WESA	RB	3		5/5	25.9	22.3		?	M	22.62	22.06	18.19	4.71	22.35	5.34	5.09	coll.
WESA	RB			5/5	28.2	22.5		?	M	21.78	21.04	17.34	4.82	21.55		4.25	coll.
WESA	RB			5/5	26.5	21.5		?	M	22.96	22.52	19.23	4.54	22.76		5.23	coll.
WESA	RB			5/5	26.2	22.9		?	M	23.29	22.66	19.12	4.62	22.96		5.05	coll.
Dunlin	RB	3	4	5/5	60.5	29.6		?	?	38.75	37.45	32.42	5.80	38.34	5.79		coll.
LESA	BB	5	2	11/3	21.0	18.9	92.0	?	M	17.20	16.72	13.15	3.57	16.92		4.37	mc
WESA	SF			11/15	25.5	22.6	105.0	juv.	M	22.28	21.57	18.77	4.95	21.70	5.44	5.03	mc
LESA	TB	4	2	12/3		19.2		?	M	17.47	16.89	13.91	4.02	17.10	4.60		mc

Table IV-1. Measurements of specimens.

All linear measurements are in mm.
[1] BS = Bahía Santa María, Sinaloa; BB = Bodega Bay, California; RB = Roberts Bank, British Columbia; SF = San Francisco Bay, California; TB = Tomales Bay, California.
[2] LB = lower bill
[3] UB = upper bill
[4] coll. = collected; hc = hunting casualty; mc = mistnetting casualty.

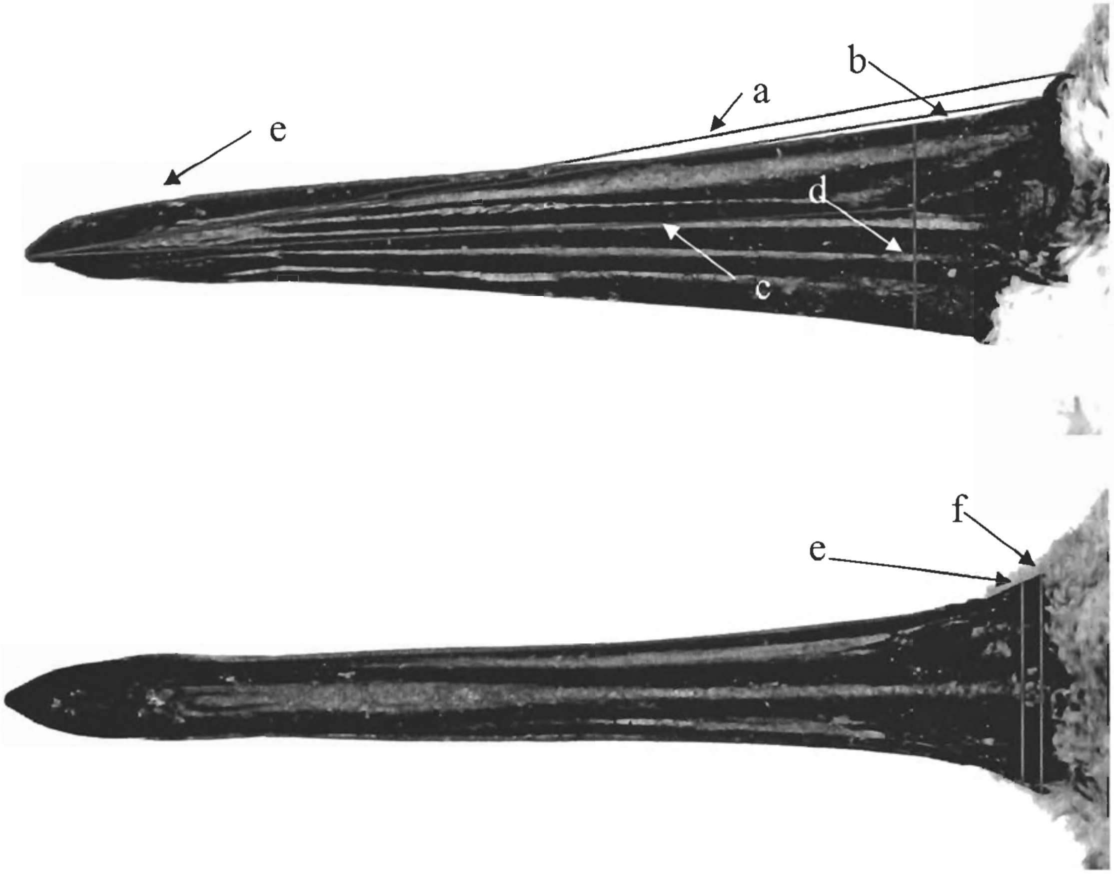

Figure IV-1 Diagram of bill measurements.

For explanation of the letters see Methods.

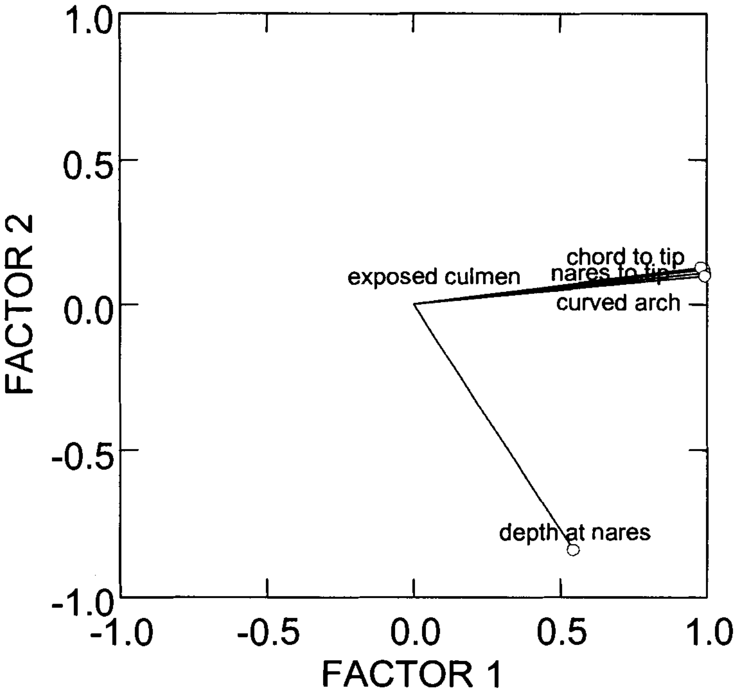

Figure IV-2. Factor 1 explained most (84.1%) of the variance in bill shape in Western Sandpipers.

Measurements of length way heavily on Factor 1, that of bill depth on Factor 2.

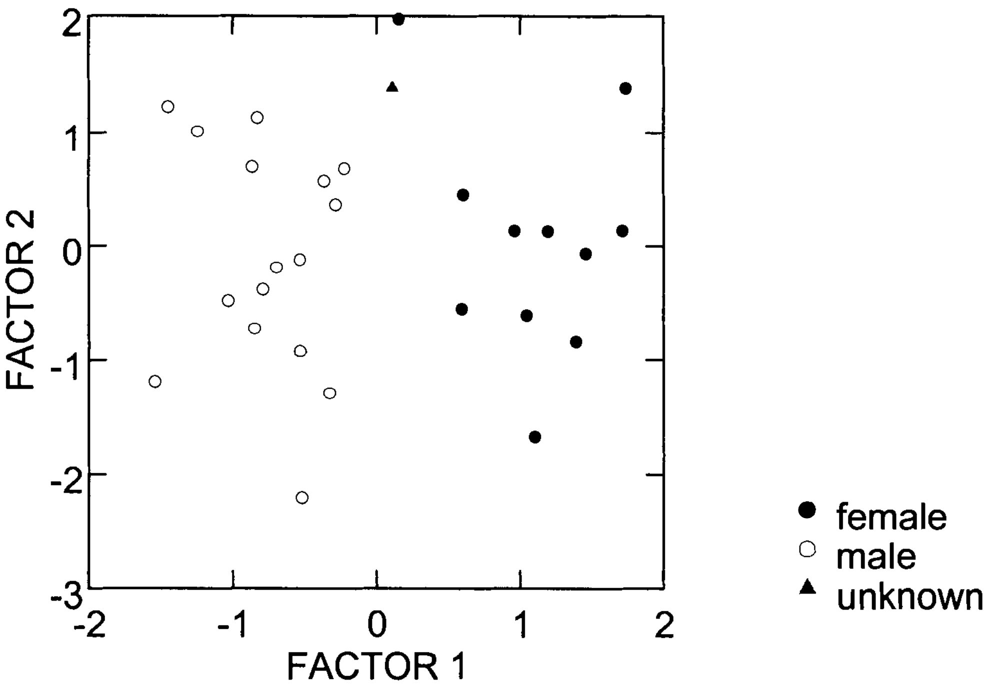

Figure IV-3. Location of specimens in factor space.

Males and females differed only with regard to Factor 1 (bill length), but not Factor 2 (bill depth).

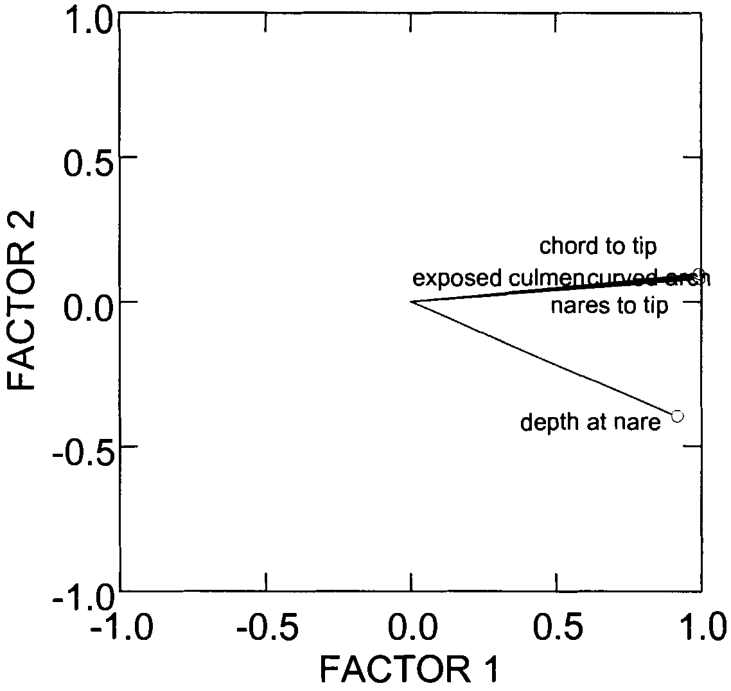

Figure IV-4. In the interspecific comparison, Factor 1, constituting measures of bill length, explained 96.1% of the total variance.

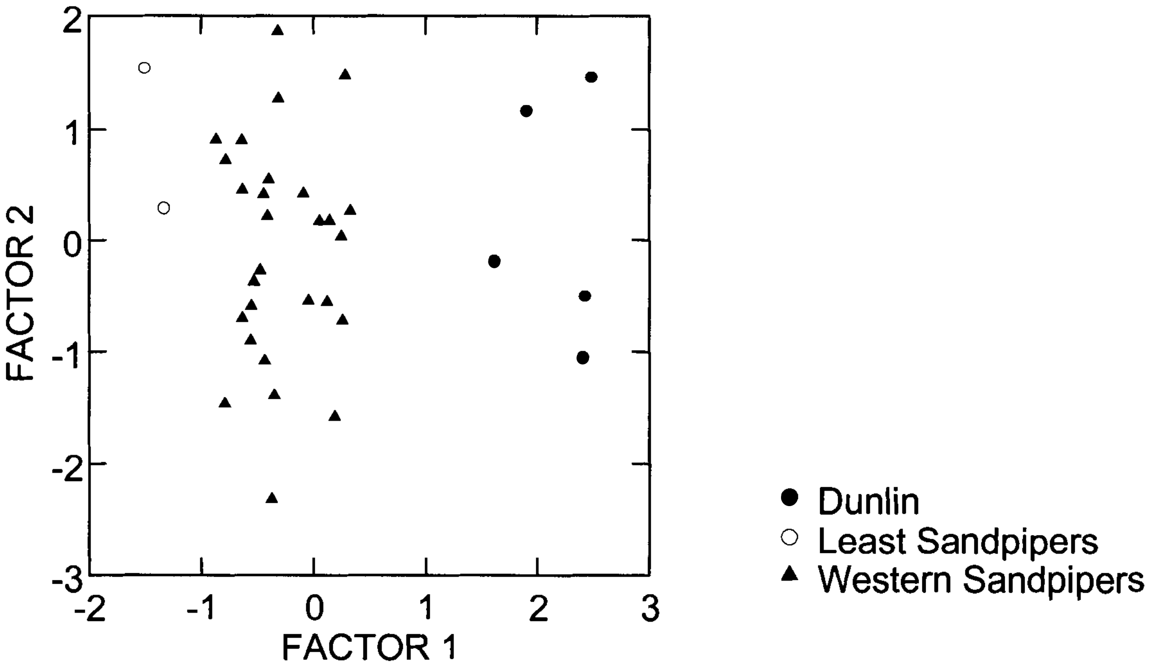

Figure IV-5. Factor scores differed between each species pair with regard to Factor 1, but not Factor 2 .

This indicates that bills of the three species differ only with regard to length.

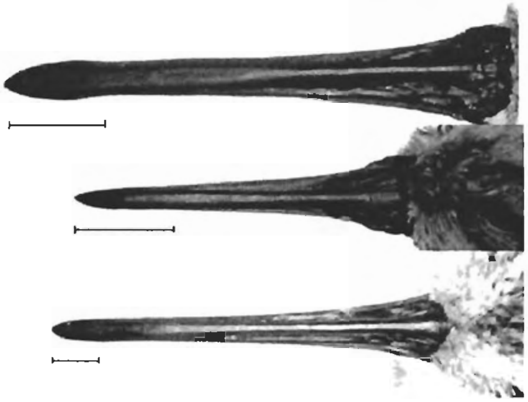

Figure IV-6. Dorsal view of the bill Western Sandpiper (A), Least Sandpiper (B) and Dunlin (C). Scales indicate 5 mm.

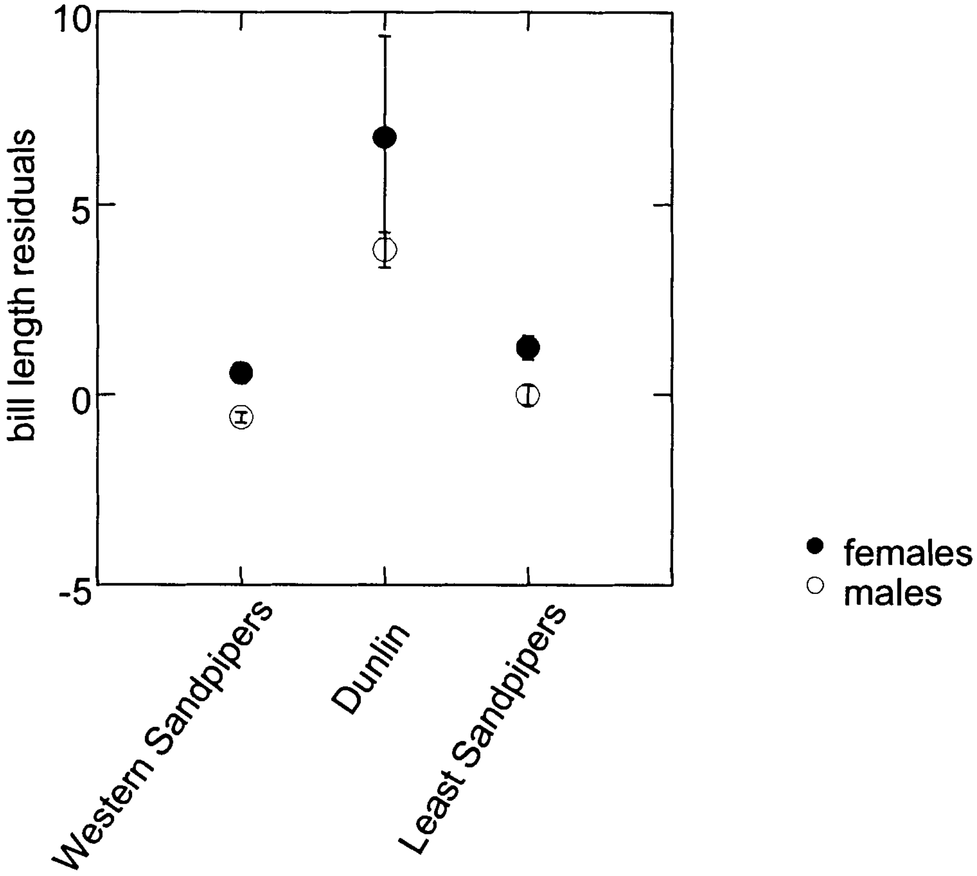

Figure IV-7. In all three species, residuals of culmen corrected for tarsus length were larger in females than in males.

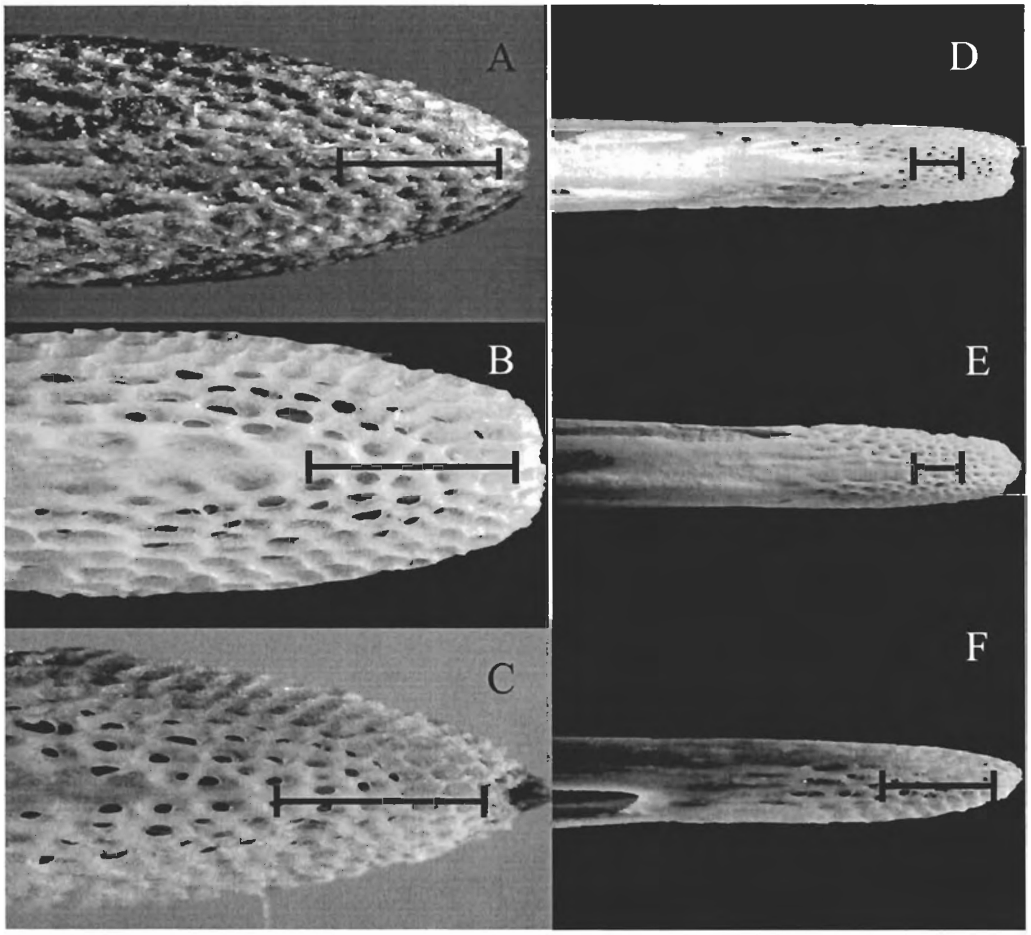

Figure IV-8. Sensory pits occur in all three species in both upper and lower bill.

The scale indicates 1 mm. (A) Western Sandpiper female, lower bill, unbleached; (B) Western Sandpiper female, upper bill, bleached; (C) Western Sandpiper male, lower bill, bleached; (D) Dunlin female, lower bill, bleached; (E) Dunlin male, upper bill, bleached; (F) Least Sandpiper male, upper bill, bleached, side view.

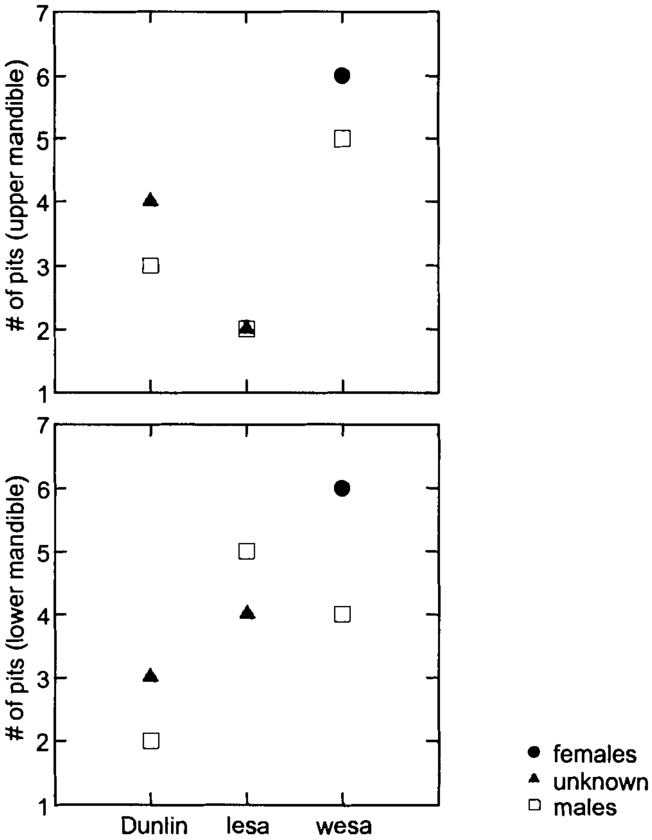

Figure IV-9. Occurrence of sensory pits along transects on the bill.

V. PREDATION DANGER, ESCAPE PERFORMANCE AND THE DIFFERENTIAL MIGRATION OF WESTERN SANDPIPERS (*CALIDRIS MAURI*)

Silke Nebel

Abstract

Species in which males and females migrate to different nonbreeding latitudes are called differential migrants. Here, we test the hypothesis that sex- and latitude-specific escape performance underlies the differential nonbreeding distribution of Western Sandpipers (*Calidris mauri*). This migratory shorebird breeds mostly in Alaska and spends the nonbreeding season mainly along the Pacific coast between southern Canada and Peru. Females migrate further south than males, creating a latitudinal cline in sex ratio. According to the predation danger hypothesis, predator escape performance of males and females, indexed by wing loading, differs consistently across latitudes. Escape performance is generally reduced with higher wing loading. Individuals with poorer escape performance were therefore predicted to prefer southern sites, where less fat is required as insurance against environmental variability. Data were collected at four onbreeding latitudes to test the predictions. Wing loading was higher overall for females, and it increased with latitude in both sexes, but an index of predation danger remained constant across latitudes. Within latitudes, wing loading was lower at smaller, and presumably more dangerous, sites.

Introduction

In most avian species, males and females migrate to different latitudes during the nonbreeding season (Cristol et al. 1999). Three main hypotheses have been proposed to explain this 'differential distribution' (Berthold 1996). The 'Dominance Hypothesis' assumes that behavioural interactions between males and females produce geographical segregation (Gauthreaux 1978), because individuals of the dominant sex monopolise preferred nonbreeding areas (e.g. close to the breeding sites). A second hypothesis is based on a physiological argument and suggests that body size differences between males and females interact with local climate to produce differing distributions ('Body Size Hypothesis', Ketterson & Nolan 1976). Larger individuals can survive longer periods of fasting and are therefore thought to be better suited to survive the colder and less predictable climates at higher latitudes. Finally, according to the 'Arrival Time Hypothesis', individuals benefiting more from earlier arrival on the breeding grounds will gain by wintering closer to the breeding grounds (Ketterson & Nolan 1976, Myers 1981). Empirical evidence supporting these hypotheses remains equivocal (Cristol et al. 1999).

Here we consider a different and novel idea, namely that the risks posed by predators underlie the differential nonbreeding distributions of male and female birds. The presence of raptors has been used to explain differences in local site use in shorebirds (e.g. Robert et al. 1989, Piersma et al. 1993), but investigators have neglected their possible importance on a large geographic scale. Castro et al. (1992) suggested that Sanderlings (*Calidris alba*) may approach an ideal free distribution over their large nonbreeding range, matching numbers to food availability, the thermal environment and the risks of starvation and predation, but provided no details.

We are aware of only one avian study suggesting a link between sexual size dimorphism, predation danger and segregation of males and females during the nonbreeding season (Erritzoe & Fuller 1999). However, several studies of fish have explored in some detail the association between predation danger, sexual dimorphism and sexual differences in spatial distribution. Female guppies (*Poecilia reticulata*) are larger than males, and are preferred as prey by an important predator, Hart's Rivulus (*Rivulus hartii*; Seghers 1973). Female guppies are more vigilant than males, respond to the presence of a predator with a greater increase in anti-predator behaviour (Magurran & Nowak 1991, Magurran & Seghers 1994), and are more prone to inhabit low-predation areas (Seghers 1973). Thus, sexes are differentially distributed across habitats, and females are actually killed by Hart's Rivulus less frequently than are males (Magurran 1999) in spite of the predator's preference. In the Threespine Stickleback (*Gasterosteos aculeatus*) in lakes of coastal British Columbia, spines function in defence against avian predators, but are a liability against grappling invertebrate predators (Reimchen 1980). Reimchen & Nosil (2002) show (see also Reimchen & Nosil *in review*) that males and females differ in habitat use (benthos vs. open water) and in the number and size of spines. They demonstrate rapid and reversible selection on spine development in association with differing exposure to predators in these habitats.

These studies illustrate that both 'danger' (i.e. properties of the environment) and 'escape performance' (i.e ability of the animal to escape an attack) can affect habitat choice. The level of danger at a given site changes with several site-inherent characteristics, such as the abundance of predators, and the presence of tall vegetation providing cover for a predator to hide. ‘Escape performance’, on the other hand, is a function of the physiological and morphological attributes of the prey (Lank & Ydenberg 2003). The escape performance of individual birds is reduced by extra body mass, as an increase in wing loading (mass/wing area) decreases take-off speed and manoeuvrability, traits crucial for escaping attacks by aerial predators such as Merlins (*Falco columbarius*) and Peregrines (*F. peregrinus*) (see Witter et al. 1994, Olsson et al. 2002).

The Western Sandpiper (*Calidris mauri*) is a small migratory shorebird. It breeds in western Alaska and eastern Siberia, and migrates southward to spend the nonbreeding season along intertidal areas of the Pacific coast from southern Canada to Peru, and, to a lesser extent, along the Atlantic coast of the Americas (Wilson 1994, Nebel et al. 2002). Western Sandpipers show strong latitudinal segregation with regard to sex, as females migrate further south than males, creating a latitudinal bias in sex ratio (Nebel et al. 2002). The negative relationship between wing loading and escape performance has been demonstrated in Western Sandpipers (Burns & Ydenberg 2002); and here we use wing loading as an indirect measure of escape performance.

The differing escape performance of individuals may have important effects on their latitudinal distribution, as individuals at northern nonbreeding sites usually carry more fat than southern conspecifics. This is widely interpreted as a survival hedge against environmental unpredictability (Blem 1975, Ketterson & Nolan 1976, Dugan et al. 1981, Ketterson & Nolan 1983, Nolan & Ketterson 1983, Davidson 1984, Lima 1986, Rogers 1987, Suter & van Eerden 1992, Lovvorn 1994), but has the consequence that any individual has poorer escape performance at a northern site than it would have a more southerly site, everything else being equal.

Aerodynamic theory suggests that this extra fat required is more costly for larger individuals in terms of reduced flight performance. On an interspecific basis, larger species have less surplus power and higher wing loading and are less maneuverable than smaller birds (Pennycuick 1972, Norberg 1995), and the same is thought to apply on an intraspecific basis. As female Western Sandpipers are slightly larger than males (ca. 3%; (Cartar 1984), this reasoning suggests that female escape performance is poorer than that of males, and that it deteriorates more rapidly as the extra fat required at northern sites is added.

Here, we test the hypothesis that the differing latitudinal distributions of male and female Western Sandpipers are related to the poorer escape performance of females. Specifically, the hypothesis is that the selection of a nonbreeding site balances the safety advantages of southern sites, where less fat is required, against the extra costs incurred by the longer migration required to arrive there. This hypothesis makes several predictions that, if upheld by data, would support it as a candidate explanation for the differential migration of Western Sandpipers.

The first prediction of the hypothesis is that wing loading increases with latitude (i.e. higher in the north) for both male and female Western Sandpipers. The second prediction states that at any latitude nonbreeding females have higher wing loading than males. Third, we predict that flight response to a predatory attack decreases from north to south. The length of time a flock stays airborne after an attack is thought to reflect how individuals perceive their probability of capture, which is supported by the observation that in Red Knots (*C. canutus*), flight response to approaching observers was stronger when disturbance by planes was high (Koolhaas et al. 1993). Thus, if probability of capture is perceived to be low, a flock should stay airborne only shortly, if it is perceived to be high, it should stay airborne for longer. As individuals with poor escape performance are predicted to migrate further south, flight response to a predatory attack should be more pronounced than further north. The fourth prediction, that predation danger in the south is equal to or lower than in the north, follows from predictions 1 and 2. If wing loading decreases towards the south (prediction 1) and females have higher wing loading than males (prediction 2), females should choose nonbreeding sites in the south, but only if predation danger does not increase towards southern latitudes.

Predictions 5-7 are concerned with the choice between small and large sites within latitude, and follow from the assumption that smaller sites are more dangerous than large sites. Vegetation and other visual obstructions can be used by aerial predators in making attacks, and small sites, due to the greater proximity to cover, are more dangerous than larger ones (Townshend 1984, Lissimore et al. 1999, Ydenberg et al. 2002, Whitfield 2003). Indeed, individual Western Sandpipers using a small stopover site while on migration had lower wing loading than those at a nearby large site (Ydenberg et al. 2002). Within latitudes, individuals at small site are therefore predicted to be better escapers and therefore to have lower wing loading (prediction 5), to show a less pronounced response to a predatory attack (prediction 6), and females, given their higher wing loading, are predicted to be relatively more abundant at small than at large sites (prediction 7).

We collected data on predation danger, flight response to predation danger and wing loading for both male and female nonbreeding Western Sandpipers at small and large sites at four latitudes, allowing to test the predictions of the predation danger hypothesis.

Methods

Study sites

Data analysis was restricted to birds collected during the centre of the nonbreeding season in order to exclude migrating individuals. Data were collected in November-December 2000 at Bodega Bay (38.2°N, 123.0°W), Tomales Bay (39.2°N, 123.0°W), and San Francisco Bay, California, USA (37.5°N, 122.3°W), at the latter site data were also collected in February 2003; in December 2001 on Bull Island, South Carolina, USA (32.8°N, 79.6°W), in January-March 2000 in Bahía Santa María, Sinaloa, Mexico (24.0°N, 108.0°W); in early March 1998 in Chitré, Herrera, Panama (8.0°N, 80.5°W); and in January-February 2002 at Costa del Este, Rio Pacora, and Rio Chico in the upper Bay of Panama, Republic of Panama (9.0°N, 79.2°W). On Bull Island, only predation danger and flight response to predation danger were assessed, while in San Francisco Bay, only data on wing loading were collected.

San Francisco Bay and Costa del Este are extensive intertidal areas, while Bodega Bay, Tomales Bay, Rio Pacora, Rio Chico and Chitré are of small size. Bahía Santa María contains both large and small feeding areas.

Sex ratio and wing loading

Birds were caught with mistnets. Length of culmen was measured using calipers, and individuals with an exposed culmen of <24.3 mm were classified as males, those with an exposed culmen >24.7 mm were considered females (Page & Fearis 1971). A digital picture was taken of the wing held in a standardized manner on a custom board (Burns & Ydenberg 2002). Wing area was calculated using Scion Image (www.scioncorp.com). Mass was taken immediately after capture (to 0.1 g using a Pesola spring balance). Age class (adult of juvenile) was determined using plumage characteristics (Prater et al. 1977).

Predation danger

Flocks of Dunlin (*C. alpina*) and Sanderlings (*C. alba*) hunted by raptors show rapid, highly synchronised flight patterns (Bertochi et al. 1984, Buchanan et al. 1988, Buchanan 1996, Dekker 1998). Western Sandpipers display a similar response (pers. obs.), and we are therefore confident to recognise the presence of a hunting raptor on the basis of the flight response of the flock as well as by visual detection of the predator itself.

To assess flight response to a predatory attack, 'time in air/attack', measured in seconds, was calculated for each observation period during which an attack took place. As an index of predation danger, 'number of attacks/hour' was calculated for each observation period. The overall mean for each study site includes observation periods without attacks.

Statistical analysis

Data were analysed using General Linear Models in the statistical package Systat v. 10.2. Interaction terms are only reported when significant at the 0.05 level. Frequency distributions of males and females at small and large sites were compared via a multi-way contingency table; the Mantel-Haenszel test accounts for the effect of latitude.

Results

Wing loading

To better understand variation in wing loading, we included an analysis of both wing area and body mass, using a total of 276 individuals. Pooling all individuals, age did not have a significant effect on wing loading (F=1.53, p=0.22) nor mass (F=0.07, p=0.79), adults and juveniles were therefore pooled in subsequent analyses. Age did, however, affect wing area: adults had larger wings than juveniles (F=5.45, p=0.02).

Both wing loading and mass varied with latitude, sex, size of the intertidal area ('large' or 'small'), and the 'area size*latitude' interaction term (wing loading - latitude: N>S, F=110.41, p<0.001; sex: females>males, F=14.72, p<0.001; area size: large>small, F=49.88, p<0.001; area size*latitude: F=18.76, p<0.001; Figs V-1-3; mass - latitude: N>S, F=112.50, p<0.001; sex: females>males, F=99.69, p<0.001; area size: large>small, F=22.30, p<0.001; area size*latitude: F=8.96, p=0.003). Wing area, however, also varied with age (latitude: F=2.24, p=0.136; sex: females>males, F=35.20, p<0.001; area size: small>large, F=15.95, p<0.001; age: adults>juveniles, F=4.15, p=0.043; area size*latitude: F=5.91, p=0.016).

Wing loading decreased from north to south, which can be attributed primarily to a decline in mass rather than to an increase in wing area. Females had higher wing loading than males; they were both heavier and had larger wing areas. Interestingly, the interaction term 'area size*latitude' had a significant effect on all three variables: wing loading declined more steeply from north to south at small than at large sites, and this was the case in both males and females (Fig. V-2).

Flight response and predation danger

Flight response to predation danger (expressed as 'time in air/attack') changed with latitude (N<S, F=20.69, p<0.001) but did not differ with area size (F=0.22, p=0.65). Predation danger, measured in 'number of attacks/hour' did not change with latitude (F=0.08, p=0.778 nor area size (F=0.58, p=0.45; Fig. V-4).

Distribution of males and females at small and large sites

No significant difference was detected between the frequency distribution of males and females at large and small sites (Mantel-Haenszel χ^2=0.061, p=0.80; Table V-1, Fig. V-5).

Discussion

The reasons underlying differential nonbreeding distribution in migratory birds are still poorly understood, despite extensive literature documenting this pattern (Cristol et al. 1999). In Western Sandpipers, a particularly well-studied differential migrant, none of the existing hypotheses can fully account for the latitudinal cline in sex ratio (Nebel et al. 2002). Here, we proposed a novel hypothesis, namely that female Western Sandpipers migrate further south than males because of sex- and latitude-specific differences in escape performance. Escape performance is generally reduced with higher wing loading. Individuals with poorer escape performance were therefore predicted to prefer southern sites, where less fat is required as insurance against environmental variability. Are the seven predictions supported by the data?

1. Yes, wing loading did decrease in both males and females from north to south. 2. Yes, females did have higher wing loading than males. 3. Yes, flight response to a predatory attack increased from north to south. 4. Yes, predation danger did not change with latitude. 5. Yes, wing loading was lower at small than at large sites. 6. No, no difference was detected between the flight response at small and at large sites. 7. No, no difference was detected in sex ratio between small and large sites.

The data on wing loading and predation danger were consistent with the hypothesis that on a latitudinal scale, site choice is the outcome of sex- and latitude-specific escape performance. Interestingly, wing loading declined more steeply from north to south at small than at large sites. This is interpreted as strong support for the hypothesis, as individuals can 'afford' to be heavier at the large sites, and this difference increased towards the south. It seems unlikely that the difference in wing loading between large and small sites is a consequence of individual quality differences (Swennen 1984). Individuals had larger wings at small sites, and are therefore unlikely to be driven to the smaller sites by competitive exclusion.

Flight response to a predatory attack increased towards the south, but did not differ between large and small sites. Flight response can be affected by factors other than an individual's probability of capture. It was shown to increase with both wind speed and air temperature (McGowan et al. 2002), and is also interpreted to be a trade-off between food intake and perceived predation danger (Gill et al. 1996). It remains to be shown whether flight response to a predatory attack is a reliable indicator of the perceived probability of capture.

Contrary to our prediction (7), females did not choose large over small sites. However, only in Mexico, females occurred at higher proportions at small sites, but at the same time, no difference in wing loading was detected between males and females. In both California and Panama, females tended to occur in higher proportions at smaller sites, and had higher wind loading than males, which is in accordance with our hypothesis. A larger data set is needed to address this prediction.

Our hypothesis is based on the assumption that females have poorer escape performance than males. While it has been demonstrated that wing loading decreases take-off ability in Western Sandpipers (Burns & Ydenberg 2002), it still remains to be shown that females do indeed have poorer flight performance than males. Higher wing loading should result in higher mortality rates, if no habitat segregation takes place according to escape performance (but see Lank & Ydenberg 2003). A possible way to test for this effect is by determining fat content of wing remains of birds recently caught by predators, which allows estimation of wing loading, if the wing is left intact (Guglielmo & Burns 2001). The mean wing loading of birds taken by predators and those in the population can subsequently be compared, and it can thus be established whether high-wing loading individuals are over-represented among the victims of the aerial attacks. This test has not been performed to date.

At one study site, at Bahía Santa María, Mexico, sex-specific predation was estimated by comparing the sex-ratio of live Western Sandpipers to the molecular estimate obtained from depredated birds. The proportion of females estimated from living (~25%) versus dead (~24%) individuals was not significantly different, indicating an apparent absence of sex-biased predation (Chapter VI). However, escape performance is thought to be a function of wing loading, and at Bahía Santa María, no difference in wing loading was detected between males and females. The absence of a sex-bias in predator-induced mortality at this site is therefore in accordance with the prediction.

The data on wing loading and predation danger are consistent with the hypothesis that sex- and latitude-specific escape performance is driving the observed nonbreeding distribution, but other explanations for the latitudinal cline in sex ratio also need to be considered. It has for example been suggested that intertidal invertebrates are buried more deeply towards the south, possibly due to higher ambient temperature and/or desiccation. Longer bills enable foraging on more deeply buried prey. Females have disproportionately long bills, and can therefore exploit a feeding niche at greater vertical depth (Chapter III).

Predation affects every living organisms, as every individual is likely to be either prey or predator or both simultaneously during some stage of its life cycle (Sih et al. 2000, Banks 2001, Krams 2001, Downes 2002, Childress & Lung 2003, Mathisen et al. 2003, Sinclair et al. 2003). In the context of bird migration strategies, predation has been shown to play a role in stop-over ecology of migrants (Lindström 1989), and has been suggested to affect spatial distribution, but empirical evidence is mostly lacking (Alerstam 1990, Erritzoe & Fuller 1999). Only recently, the importance of predation for the evolution of the timing of migration (Lank et al. 2003) and large-scale nonbreeding distribution, as documented here, are starting to become recognised.

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Table V-1. Frequency distribution of males and females did not differ between large and small sites.

	California			Mexico			Panama		
	female	male	total	female	male	total	female	male	total
large	5	11	16	5	31	36	31	26	57
small	3	29	32	15	64	79	24	21	45
total	8	40	48	20	95	115	55	47	102

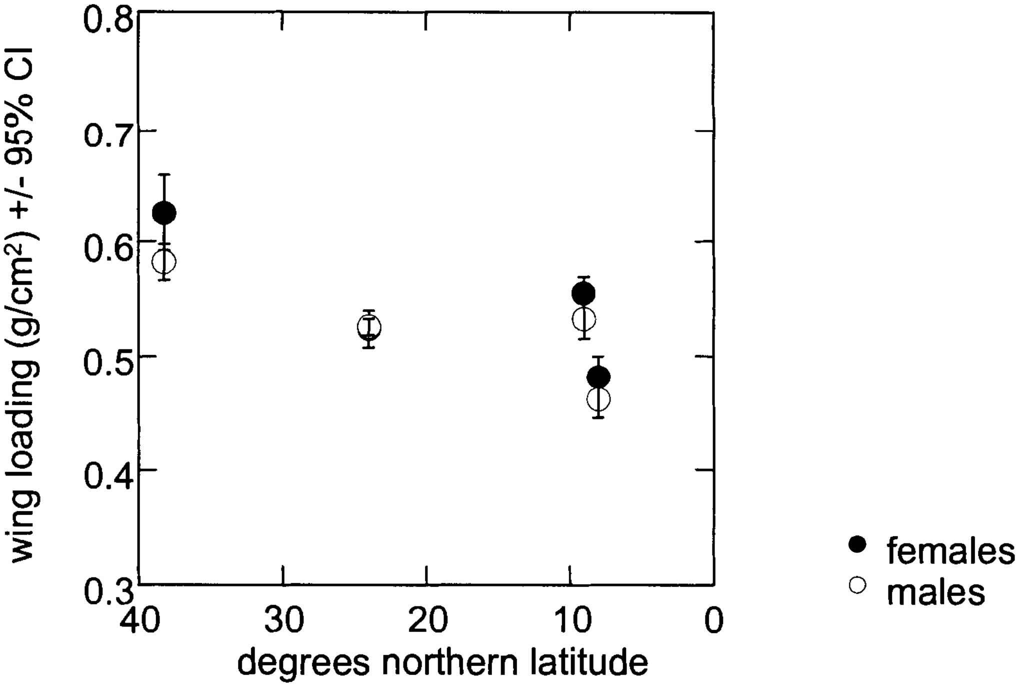

Figure V-1. Wing loading (mass/wing area +/- 95%CI) in Western Sandpipers decreased from north to south in both males and females.

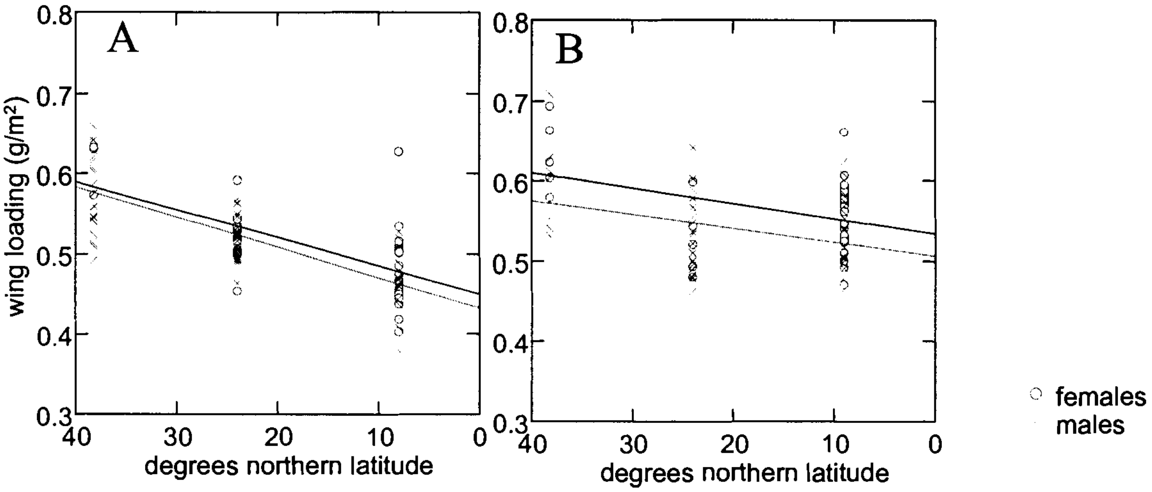

Figure V-2. Wing loading declined more steeply from north to south at small (A) than at large (B) sites.

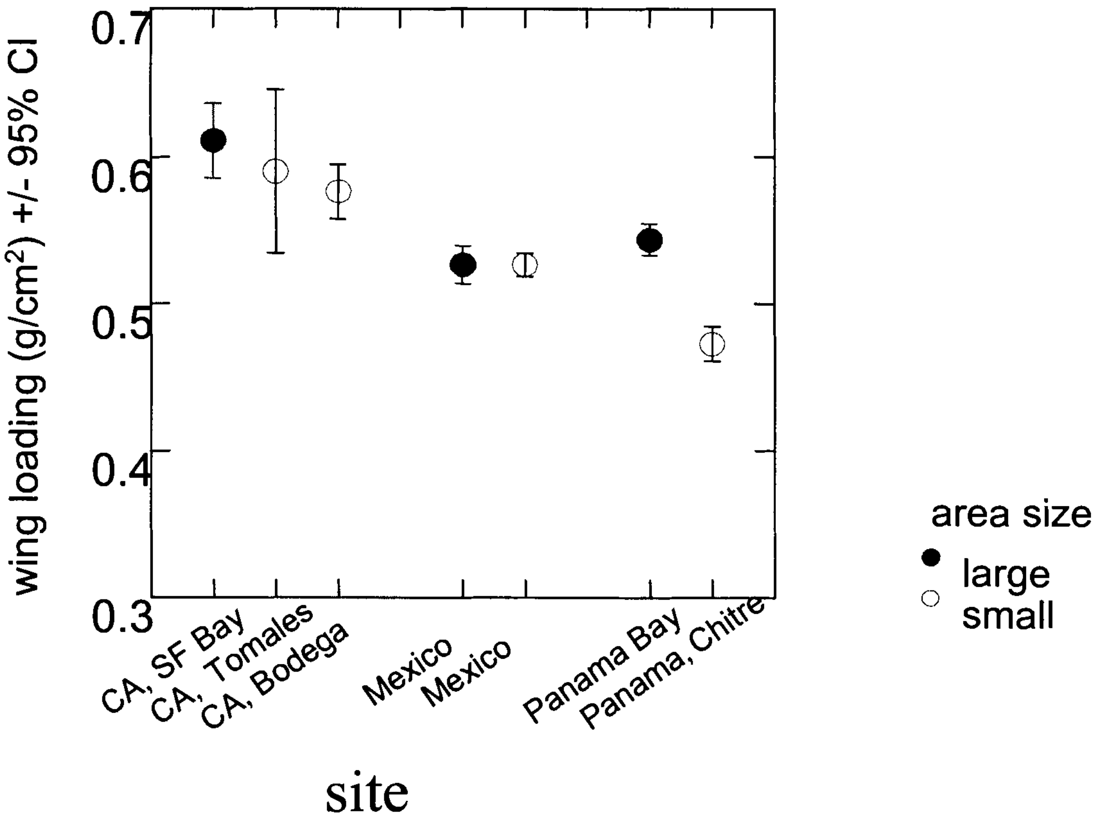

Figure V-3. Wing loading was higher at large than at small sites.

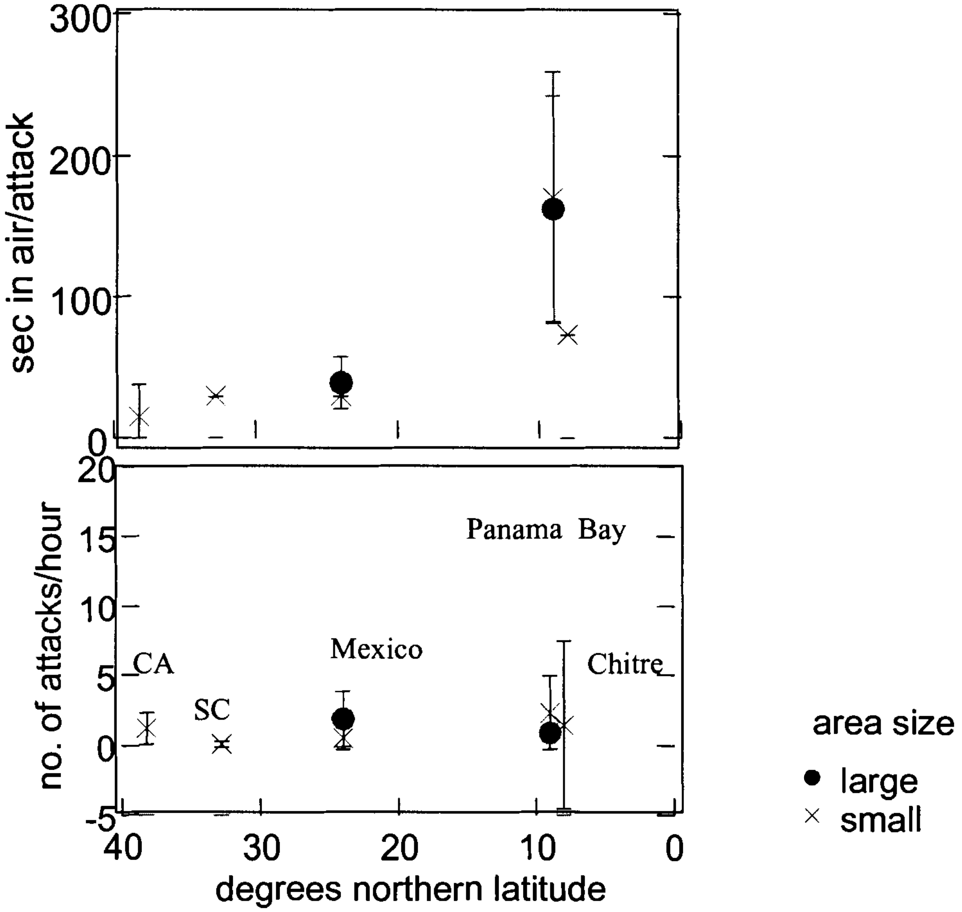

Figure V-4. 'Seconds in air per attack' increased from north to south, while the number of attacks per hours did not change.

Neither variable changed with area size. Bars indicate the 95% Confidence Interval.

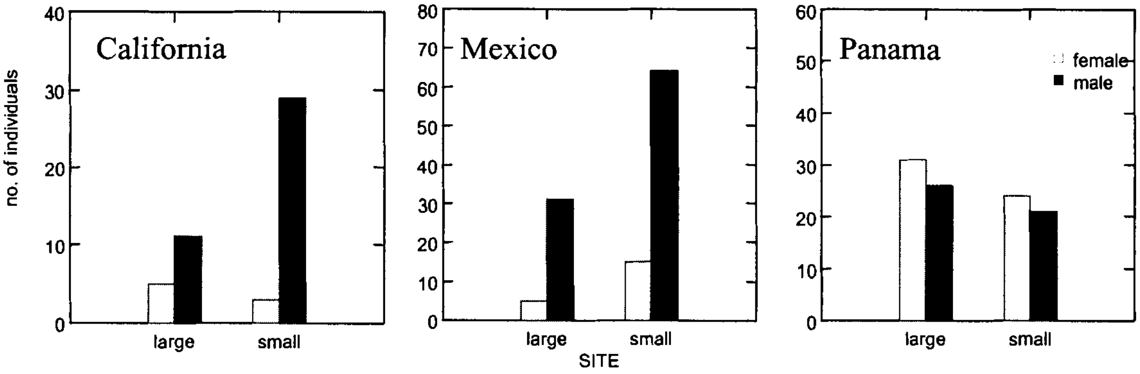

Figure V-5. Frequency distribution of males and females did not differ between large and small sites.

VI. MOLECULAR SEXING OF PREY-REMAINS PERMITS A TEST OF SEX-BIASED PREDATION IN A WINTERING POPULATION OF WESTERN SANDPIPERS

Manuscript in review

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Abstract

Population sex ratios in monogamous birds are often male-biased. One factor that can affect population sex ratios is sex-biased predation. However, most estimates of sex-biased predation in birds have focussed on species with pronounced sexual colour- or body-size dimorphism. Data on sexually monomorphic birds are generally lacking. In the present study, we adopt the PCR-based sexing procedure of Griffiths et al. (Mol Ecol 7: 1071-1075) to help test for sex-biased predation in a wintering population of Western Sandpipers (*Calidris mauri*), a shorebird with little sexual dimorphism. Specifically, by comparing the a priori determined sex-ratio of live birds wintering at a site in western Mexico to the molecular estimate obtained from depredated birds at this same site, we were able to perform a population-specific test for sex bias in predator-induced mortality. The proportion of females estimated from living (~25%) versus dead (~24%) individuals was not significantly different, indicating an apparent absence of sex-biased predation. Molecular sexing of prey-remains is here demonstrated to be a feasible and hitherto unexploited approach towards detecting sex-biased predation in birds.

Introduction

Population sex ratios in birds often diverge from parity and are, in fact, predominantly male-biased (Trivers 1971, Bellrose 1980, Dobson 1987, Breitwisch 1989, Sargeant & Raveling 1992). While recent studies have shown that birds are able to manipulate primary offspring sex ratio (e.g. Komdeur et al. 1997, Sheldon 1998, Green 2002), in many species, both sexes typically occur in equal proportions among nestlings (Clutton-Brock 1986, Breitwisch 1989). In such cases, any sex ratio skew observed must occur at later stages in life history via sex-biased mortality. Factors promoting sex-biased mortality can sometimes be attributed to causes not directly related to predation, such as sex-based differences in feeding specialisation (Durell & Goss-Custard 1996) or in parental investment (Trivers 1972), including the energetic costs of producing gametes, or of feeding of chicks (Owens & Bennett 1994). Alternatively, a population sex-bias could be directly associated with predation if, for example, morphological, physiological or behavioural differences rendered one sex significantly easier to detect and/or capture by predators than the other (Angelstam 1984, Widén et al. 1987, Götmark 1993, Slagsvold et al. 1995, Götmark et al. 1997).

While the need for better estimates of sex-specific mortality has been voiced (e.g. Promislow et al. 1992), such estimates remain uncommon, especially those that can clearly identify the cause of the sex ratio bias. Studies identifying predation as the cause for sex-biased mortality are usually restricted to species showing obvious sexual dimorphism, which permits the direct sexing of prey remains, or they focus on birds during the breeding season (Widén et al. 1987; Götmark 1993, Slagsvold et al. 1995; Götmark et al. 1997). New approaches to measuring differential predation are therefore desirable and, accordingly, we have adopted a novel approach that relies in part on the PCR-based sexing procedure of Griffiths et al. (1998), and is potentially applicable to any species for which prey remains can be gathered. In the present study, we demonstrate the application of this approach for, and conduct a test for sex-biased predation in, a wintering population of Western Sandpipers (*Calidris mauri*).

Western Sandpipers are small migratory shorebirds. Males and females do not show differences in plumage colouration (Wilson 1994), but females are slightly larger than males and have longer bills (Cartar 1984). Western Sandpipers breed in Alaska and eastern Siberia and spend the nonbreeding season mainly along the American Pacific coast between southern Canada and Peru (Wilson 1994, Nebel et al. 2002). Males and females are not distributed evenly across the nonbreeding range, however, as females tend to migrate further south than males, resulting in a latitudinal bias in population sex ratio (Nebel et al. 2002). Whether differential predation contributes to local sex biases has never been tested.

Study Area and Methods

Data were collected from January to March 2000 at Bahía Santa Maria, Sinaloa, Mexico (24.0°N, 108.0°W), one of the major nonbreeding sites of Western Sandpipers (Morrison et al. 2001). This Pacific estuary covers an area of about 1,350 km^2 and is composed of mangroves, intertidal and brackish mudflats and freshwater marshes (Engilis et al. 1998). Population sex ratios in this northern part of the nonbreeding range are biased towards males, and indeed, a mist-netted sample of 823 individuals collected during this study period contained only 25% females (Nebel et al. 2002). The main predators of Western Sandpipers at this site are Peregrines (*Falco peregrinus*) and Merlins (*F. columbarius*), and these predators have been shown to impose a significant mortality cost on other populations of wintering shorebirds (Page & Whitacre 1975, Whitfield 1985). In fact, prey remains, such as part of a wing, were commonly observed at this site, typically near plucking posts or close to the high-water mark on the mudflats (pers. obs.). To determine the sex ratio of recently depredated individuals, we removed 5-15 primary feathers from their carcasses. Feathers were then frozen, and transported back to the lab for DNA analysis.

Genomic DNA was extracted from feather shafts using a DNeasy Tissue Kit (Qiagen). The CHZ and, in the case of females, the CHW loci were PCR amplified following the procedure of Griffiths et al. (1998), using the primers P2 (5'-TCTGCATCGCTAAATCCTTT-3') and P8 (5'-CTCCCAAGGATGAGRAAYTG-3'). PCR products were then separated by electrophoresis on a 3% agarose gel, stained with EtBr, and visualised under UV light. As expected, females, being the heterogametic sex, were readily identified by the presence of two bands (~360 and ~380 bp), whereas males were identified by the presence of a single (~360 bp) band. Finally, the frequency distribution of males and females among living versus dead groups was compared via a 2x2 contingency table.

Results

We were able to determine the sex of 25 depredated individuals from their remains via molecular criteria. Of these, six individuals (24%) were found to be female. The frequency distribution of males and females among living birds at this site (25% females; Nebel et al. 2002) is therefore not statistically different from that of depredated individuals (Pearson $\chi^2=0.017$, df=1, p=0.90), indicating an absence of sex-bias in predation. A lack of evidence for differential predation is not likely to be a consequence of the relatively small number of depredated birds we were able to sample. An observation of less-than three (or greater-than ten) females would have been sufficient to detect differential predation, given our sample size ($p<0.05$, power=0.80).

Discussion

Population sex biases in avian species are common (Bellrose 1980; Dobson 1987; Breitwisch 1989; Sargeant & Raveling 1992), but the factors driving these biases are not well understood. Predation is one of the factors that could lead to a population sex-bias, however, estimates of sex-biased predation are difficult to obtain, particularly so in species with little or no morphological sexual dimorphism. We demonstrated that molecular sexing of prey remains can be used to test for sex-biases in predation rates. This approach, if applied widely, could potentially reveal new and large-scale patterns of sex-biased predation.

Based on studies conducted to date, population sex ratios in waterfowl and songbirds appear to be male-biased (Bellrose 1980; Breitwisch 1989; Sargeant & Raveling 1992). While these patterns are usually attributed to differential parental investment, where females typically bear higher costs in not only producing the egg, but also rearing the young (Breitwisch 1989; Sargeant & Raveling 1992), empirical evidence supporting this assumption is mostly absent (but see Owens & Bennett 1994). In Western Sandpipers, this explanation is unlikely to account for the male bias at northern wintering sites because, unlike songbirds, it is the males that do most of the chick rearing, as females depart several weeks before males from the breeding grounds (Wilson 1994).

Alternatively, a male bias in local sex ratio at wintering sites of Western Sandpipers may stem, at least in part, from differential predation. This hypothesis is motivated from the fact that female Western Sandpipers have a larger body size than males (Cartar 1984), and from this we generally expect females to have proportionally higher wing loading (mass/wing area) (Pennycuick 1972) and a concomitant decrease in escape performance (Norberg 1995, Burns & Ydenberg 2002). Quick take-off from the ground is crucial in escaping predators (Cresswell 1993), and wing loading might therefore lead to increased predator-induced mortality. This hypothesis has, however, never been tested and, to our knowledge, this study provides the first empirical test of sex-biased predator-induced mortality in a nearly-monomorphic bird at a nonbreeding site.

The sex ratio of Western Sandpipers at Bahía Santa Maria, Sinaloa, Mexico, did not differ between live birds in the population and those killed by predators. However, while female Western Sandpipers are generally larger than males, and are known to have higher wing loading at three other nonbreeding sites, no difference in wing loading has since been detected at our study site, despite a consistent difference in body size (Chapter V). The apparent absence of wing loading differences at our study site may therefore explain the absence of differential predation reported in the present study. Differential predation, if it occurs in Western Sandpipers, might be a population specific phenomenon and not a ubiquitous feature of the species. Future work, adopting the approach described here and expanding its application, will help build on the preliminary findings reported here and further document the presence and/or extent of sex-biased predation in birds.

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VII. SYNTHESIS

General Synthesis

One of the major goals in ecology is to understand the factors that determine animal distribution patterns (Heglund 2002). Detailed knowledge of the ecological factors underlying animal movements over smaller time spans will broaden our understanding of the selective forces shaping animal distributions over evolutionary time. It will also help us to predict the ecological consequences of human-caused changes in the environment and of global climate change (Goodchild 2002).

A candidate system to study these factors are avian species in which males and females migrate to different nonbreeding latitudes. Patterns of such differential distribution are common among migratory birds, but the factors driving these patterns are not well understood (Cristol et al. 1999). In this dissertation, I developed two new hypothesis regarding differential distribution and tested them with data collected at four nonbreeding latitudes. The General Introduction (Chapter 1) provides the relevant background and introduces the study species, the Western Sandpiper (*Calidris mauri*).

In Chapter 2 (published in Auk 2002), the nonbreeding distribution of Western Sandpipers was documented. Western Sandpipers showed latitudinal segregation with regard to sex and age. Females overwintered further south than males. A U-shaped pattern was found with respect to age, with juveniles occurring at higher proportions at both the northern and southern end of the range. The age class distribution might be related to higher cost of feather wear for juveniles compared to adults. Juveniles that breed in their first summer complete three long-distance migrations on one set of flight feathers whereas adults complete two. Two different life-history tactics of juveniles might exist where juveniles either breed in their first summer and overwinter far north, thereby reducing feather wear induced by ultraviolet light and/or migration, or they overwinter far south and spend the first summer on the non-breeding area.

In Chapter 3 (*in review*), I proposed that intraspecific feeding niche divergence underlies the latitudinal cline in sex ratio. I hypothesised that intertidal invertebrates are buried more deeply towards the south, possibly due to higher ambient temperature and/or desiccation. Longer bills enable probing (foraging on buried prey) to greater depths. Females have disproportionately long bills, and can therefore exploit a feeding niche at greater vertical depth. Bill length residuals, corrected for tarsus length, were predicted to increase towards the south, which was only found in males. No clear trend of proportion of probes with latitude was detected. Females probed more than males at all locations. At the one site where the relationship was measured, both sexes probed more with increasing sediment temperature. These results are consistent with the hypothesis that intraspecific feeding niche divergence underlies the spatial distribution pattern.

In Chapter 4, we investigated whether sexual differences in feeding behaviour in Western Sandpipers were associated with sexual size dimorphism. Females employed a probing foraging mode significantly more than males do, and in other shorebird species, curved bills have been shown to be better suited for probing than straight bills. Female Western Sandpipers were therefore predicted to have more decurved bills than males. Using high resolution microscopy and digital imaging, we showed that, in contrast to our prediction, bills differed between males and females only with regard to length, but not curvature nor depth. An intraspecific comparison revealed that gross bill morphology differed between Western Sandpipers and two close relatives, Least Sandpipers (*C. minutilla*) and Dunlins (*C. alpina*) again only with regard to length. Sensory pits, located in the keratin layer of the bill, occurred in all three species. These host Herbst corpuscles, which can detect pressure gradients caused or reflected by prey buried in the sediment. This suggested that this method of prey localisation might be more widespread than previously assumed.

In Chapter 5, the hypothesis was tested that sex- and site-specific probability of capture by predators affects nonbreeding distribution of Western Sandpipers. An increase in body mass has been documented to decrease escape-performance. Individuals with poorer escape ability were therefore predicted to prefer southern sites, where less fat is required as insurance against environmental variability. Wing loading was higher overall for females. Wing loading increased with latitude in both sexes, but an index of predation danger remained constant across latitudes. Within latitudes, wing loading was lower at smaller sites, which were thought to be more dangerous. This results are consistent with the hypothesis that differential predator escape ability underlies the nonbreeding distribution pattern.

In Chapter 6 (*in review*), a PCR-based sexing procedure (Griffiths et al. 1998) was adopted to help estimate sex-specific predation in a wintering population of Western Sandpipers. Specifically, by comparing the *a priori* determined sex-ratio of live birds wintering at a site in western Mexico to the molecular estimate obtained from depredated birds at this same site, we were able to perform a population-specific test for sex bias in predator-induced mortality. The proportion of females estimated from living (~25%) versus dead (~24%) individuals was not significantly different, indicating an apparent absence of sex-biased predation.

Conclusions and Implications

The data presented in this dissertation suggest that in Western Sandpipers, sex-specific differences in feeding behaviour as well as in escape performance are important in determining large-scale spatial distribution. Sexual size dimorphism, which underlies both hypotheses, is common in animals (Fairbairn 1997). Intraspecific niche divergence has been attributed to sexual size dimorphism (e.g. Mysterud 2000, Temeles et al. 2000), but its association with large-scale spatial distribution has, to my knowledge, not been considered previously. Predation has been shown to play a role in stop-over ecology of migrants (Lindström 1989), and has been suggested to affect spatial distribution, but empirical evidence is mostly lacking (Alerstam 1990, Erritzoe & Fuller 1999). Only recently, the importance of predation for the evolution of the timing of migration (Lank et al. 2003) and large-scale nonbreeding distribution (this dissertation) are starting to become recognised.

Systems are often shaped by a number of selective pressures (e.g. Schluter et al. 1991, Grant & Grant 2002), but predation riski and feeding niche divergence might be of particular importance. Another example of where they affect sexual segregation is the Threespine Stickleback (*Gasterosteus aculeatus*), a species complex inhabiting marine, brackish and fresh-water habitats (Bell & Foster 1994). They exhibit high morphological diversity, which is particularly pronounced on the Queen Charlotte Islands, Canada (Reimchen 1994). In one lake located on the Islands, male and female Threespine Stickleback show spatial segregation: males were more abundant near shore, while females occurred primarily in open water (Reimchen 1980). This habitat segregation can partly be attributed to differences in parental care, as males establish the territories, and after the eggs are laid, females leave the breeding grounds, and the males care for the young (Whoriskey & FitzGerald 1994).

However, the habitat segregation is also associated with a reduction of intraspecific competition for food. Gill rakers, which are part of a stickleback's trophic apparatus, help to gather and manipulate food (Hagen & Gilbertson 1972, Hart & Gill 1994), and are often sexually dimorphic (see Bolnick & Doebeli *in press*). Resource competition can promote morphological diversification (Schluter 1994), which in turn has been demonstrated to lead to habitat segregation between populations (Schluter 1993).

Sticklebacks also exhibit sexual dimorphism with regard to their spines. The dorsal and pelvic spines serve as a defence against gape-limited predators such as other fish or birds, while they are detrimental in the presence of grappling predators, such as invertebrates (Reimchen & Nosil *in review*). And indeed, spines were larger or more robust in populations exposed to elevated levels of vertebrate predation (Hagen & Gilbertson 1972). On the Queen Charlotte Island, predation regimes varied spatially such that avian predators foraged primarily in open-water regions of the lake, whereas invertebrate predators were prevalent in benthic regions. Females, occupying a more open water ecological niche, exhibited a greater number of both dorsal and pelvic spines than males. This shows that selection favoured increased spine number in females and decreased spine number in males (Reimchen 1980), but only when pronounced ecological differences between the sexes result in differential exposure of the two, divergent predation regimes (Reimchen & Nosil *in review*). Predation and feeding niche divergence both act on sexual dimorphism as well as spatial distribution, providing another example of where the interplay of the two factors exert selection pressure within a single system.

Future directions

The data presented in this dissertation are consistent with both the feeding niche and the predation danger hypothesis. However, a few pieces in the puzzle are still missing. With regard to the feeding niche hypothesis, the next logical step is to provide empirical evidence as to whether invertebrate burying depth does increase with latitude and with increasing environmental temperature. The first aspect could be addressed by measuring invertebrate burying depth throughout the nonbreeding range of Western Sandpipers, a project which is currently underway (K. Mathot, unpubl.). To address the second issue, the experimental approach is called for. One possibility is to increase surface temperature of a small patch of intertidal sediment, and measure mean burying depth of invertebrates before and after. Repetition of this experiment at several latitudes with different temperature regimes will provide evidence as to whether intertidal invertebrates increase burying depth at lower latitudes due to the effect of high temperatures and/or desiccation.

The predation danger hypothesis hinges on the assumption that females have poorer escape performance than males. While it has been demonstrated that wing loading decreases take-off ability (Burns & Ydenberg 2002), it still remains to be shown that females do indeed have poorer flight performance than males. A possible way to do this is to set up a flight maze, which allows assessment of individual flight performance (Witter et al. 1994, Niehaus unpubl.). In the natural environment, higher wing loading should result in higher mortality rates, if no habitat segregation takes place according to escape performance (but see Lank & Ydenberg 2003). A possible way to test for this effect is by determining fat content of wing remains of birds recently caught by predators, which allows estimation of wing loading, if the wing is left intact (Guglielmo & Burns 2001). The mean wing loading of birds taken by predators and those in the population can subsequently be compared, and it can thus be established whether high-wing loading individuals are over-represented among the victims of the aerial attacks.

What predictions can we make with regard to the nonbreeding distribution of other shorebird species? Assuming a latitudinal cline in invertebrate burying depth, any shorebird species feeding on a diet similar to that of Western Sandpipers is predicted to increase bill length towards southern latitudes. However, only in species with pronounced sexual bill dimorphism, a shift in invertebrate burying depth is predicted to result in spatial segregation of males and females, such that the sex with the longer bill occurs further south. The only other shorebird species for which currently data on sex ratio as well as morphometrics are available from different latitudes is the Least Sandpiper (*C. minutilla*). This small sandpiper also occurs on intertidal mudflat with a nonbreeding distribution similar to the Western Sandpipers, and females have longer bills than males (Cooper 1994). As predicted, females occur at higher proportion towards southern latitudes, and bill length increases from north to south (Nebel & Fernández *in review*).

The predation danger hypothesis predicts that the degree of sexual segregation increases with the degree of sexual differences in wing loading. Wing loading and bill length are not independent character traits, however, recent advances in comparative phylogenetics permit trends to be detected at the interspecific level. A powerful test for an association between sexual bill dimorphism or wing loading with differential distribution patterns is plotting character values for these attributes onto a phylogenetic tree of the whole family. The trait that provides the closer fit with the distribution pattern probably exerted stronger selective pressure. In only 14 out of the 88 species in the family Scolopacidae, data on nonbreeding distribution of the sexes are available (Cristol et al. 1999), and even less is known about wing loading and morphometrics from different sites. While currently this lack of data prevents answering this question with the comparative approach, it nevertheless offers a promising avenue for future research on the evolution of bird migration strategies and animal distribution patterns in general.

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