FEEDING AND PREDATION DANGER TRADEOFFS IN STOPOVER SITE USAGE BY WESTERN SANDPIPERS (*CALIDRIS MAURI*)

by

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ABSTRACT

Migrant birds face a tradeoff at stopover sites between acquiring resources to fuel migration and avoiding predators. This tradeoff is crucial because the rapid acquisition of high-energy fuel for long-distance flight requires feeding in high-resource habitats, feeding intensely, and carrying heavy loads of fat, all of which elevate predation danger. I investigated how migrant western sandpipers (*Calidris mauri*) trade off food and safety at both the site (within stopover) and landscape (among stopovers) scales.

I studied within-site usage by sandpipers at Boundary Bay, located in the Strait of Georgia, in southwestern British Columbia. The mudflat is characterized by a strong feeding-danger gradient, with both food and danger decreasing with distance from the shoreline. I measured dropping densities on transects to evaluate how sandpipers distributed their usage across the mudflat. Dropping densities peaked at intermediate distances from shore, showing that sandpipers maximized neither energy gain (highest close to shore), nor safety (greatest far from shore). The observed pattern is that expected if these factors are traded off against each other. To test this hypothesis experimentally, I manipulating danger by adding obstructive cover to the open mudflat. As predicted, usage was lower on obstruction transects than controls; the difference in usage between control and obstruction transects was greatest near the obstruction; declined with distance from the obstruction; and was greater where food abundance was lower. Western sandpipers were also captured on noose carpets spread across these transects, which revealed that usage was mass-dependent: heavy individuals fed far from shore. A dynamic state variable model incorporating trade off assumptions predicted all of these patterns.

I investigated whether similar considerations applied at the landscape scale. Of 17 potential stopover sites for sandpipers in the Strait of Georgia and Puget Sound, only 8 were used on migration. Consideration of both food and safety better predicted stopover site usage than either factor alone. Furthermore, heavy sandpipers predominated at safe stopover sites, while leaner birds used more dangerous sites. This thesis highlights the importance of the interaction between food abundance and danger from predators in studies of stopover site behaviour, usage, and site selection by migrant birds.

Keywords: food abundance, migration, predation danger, stopover site usage, trade-off hypothesis, Western Sandpiper

DEDICATION

~To my loved ones~

For my parents who gave me every opportunity. For my Dad who taught me to walk softly and look for birds, for my Mom who supported me in all possible ways, and for Jason, who loves me every day, even when I am writing my thesis.

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CHAPTER 1:
GENERAL SYNTHESIS

Introduction

Tradeoffs are the fitness costs to individuals that take place when a beneficial change in one trait is linked to a detrimental change in another (Stearns, 1989). They occur when two traits are limited by time, energy, or any other resource that can be utilized only once. Addressing how tradeoffs influence the evolution of structures and traits has played a central role in the study of biology.

The role of tradeoffs has predominated in the development of life history theory (Stearns, 1992). Many studies of life history concern the timing and intensity of reproduction and address how tradeoffs affect attributes such as somatic growth, maintenance and repair trade off with reproduction, the tradeoff between offspring number and offspring quality, and the tradeoff between investment in current and future reproductive attempts. Tradeoffs are also central in studies of sexual selection. Sexual selection on traits arises when a phenotypic trait leads to differences in mating success among individuals (Andersson, 1994). However, many sexually selected traits exact survival costs so that as an individual's attractiveness increases its survival is negatively affected (Gray and Cade, 1999; Vehrencamp et al., 1989; and reviewed by Zuk and Kolluru, 1998). Animals also experience tradeoffs at the physiological level. Recent experimental evidence shows that in the mealworm beetle (*Tenebrio molitor*), a mating-induced hormone positively affects gamete and accessory gland production, but, the same hormone negatively affects immune function (Rolff and Siva-Jothy, 2002).

Behavioural ecologists are particularly interested in tradeoffs since behaviour is a trait that uses both time and energy, and these resources cannot be allocated to all behaviours simultaneously (Cuthill and Houston, 1997). For foraging animals, the acquisition of energy is inextricably linked with avoiding predation since behavioural adjustments made by individuals to increase energy intake generally increase exposure to predators (Lima and Dill, 1990). Under dangerous conditions foragers can use a variety of behavioural tactics to mitigate the threat due to predation such as increasing group size, vigilance, or moving to safer feeding locations, but all of these tactics reduce the attainable intake rate.

Feeding decisions by animals are consequently affected by the environmental level of food abundance, and by the danger posed by predators. Greater danger generally makes foragers more cautious, while higher food availability makes foragers more accepting of danger (Brown et al., 1999). Changes in the marginal value of food or safety have analogous effects on behaviour. For example, hungry individuals (for whom food is valuable) accept higher danger, while those for whom safety is at a premium (e.g. due to poor escape ability) are willing to accept poorer feeding opportunities to avoid danger (Brown, 1999). A wide range of studies in a variety of ecological situations have confirmed these general predictions (see reviews in Brown and Kotler, 2004; Lima and Dill, 1990).

For migrant birds this tradeoff is crucial because the rapid acquisition of high-energy fuel for long-distance flight requires feeding in high-resource habitats, feeding intensely, and carrying heavy loads of fat, all of which elevate predation danger. This thesis investigates how migrant western sandpipers (*Calidris mauri*) adjust their foraging behaviour to trade off food and safety at both the site (within stopover) and landscape (among stopovers) scales.

Study system

Western sandpipers are small (~25 g on migration) calidrine shorebirds that are primarily distributed along the west coast of the Americas. During the non-breeding season, most of the population is distributed between northern Oregon and Péru, though small numbers also winter along the east coast between New Jersey and Surinam (Wilson, 1994). Western sandpipers are differential migrants. Males tend to winter north of females, and proportionately more juveniles are found at the northern- and southernmost regions of the non-breeding distribution (Nebel et al., 2002). They migrate annually between southern non-breeding sites to breeding grounds on the arctic tundra of western and northern Alaska and eastern Siberia (Wilson, 1994). En route to their destination, they use mud- and sandflats on the Pacific coast as stopover sites (Iverson et al., 1996; Warnock and Bishop, 1998). On stopover sandpipers feed on a variety of small epibenthic and infaunal invertebrates to fuel their journey (Mathot and Elner, 2004; Sutherland et al., 2000; Wolf, 2001).

Migrant western sandpipers use a variety of mud- and sandflats in the Georgia Basin (British Columbia, Canada) and Puget Sound (Washington, USA) as stopover sites (Buchanan, 1988; Butler et al., 1987; Evenson and Buchanan, 1997; Iverson et al., 1996). Northward passage through the region extends from mid-April to mid-May, while adults migrate southward in July and juveniles in August and early September (Butler et al., 1987). Boundary Bay, in Delta, British Columbia (N 49°4.13′ W 122°58.05′), is a large mudflat of the Fraser estuary complex with approximately 60 km^2 of mud and sand exposed at the lowest tide. The bay is bordered by a dike and a 10-200 m wide strip of saltmarsh. The tidal rhythm at Boundary Bay is semi-diurnal, with the time of the highest tide shifting later by approximately 45 minutes per day. The mudflat at Boundary Bay is wide (~4 km at low water), but due to its shallow slope, the top portion of the mudflat is immersed and drained rapidly as the tide shifts.

During migration hundreds of thousands of western sandpipers stop at Boundary Bay for several days (Iverson et al., 1996; Warnock and Bishop, 1998). As the tide falls western sandpipers arrive at the study site where they hunt for epibenthic and infaunal invertebrates using both surface (pecking) and subsurface (probing) feeding behaviours (Ashmole, 1970; Sutherland et al., 2000). They feed for much of the tidal cycle within 600 m of the shoreline. At low tide many sandpipers leave the near shore area (especially if attacked repeatedly by falcons) and roost or feed elsewhere. They return to the near shore feeding areas as the tide advances and likely roost in nearby farm fields during high tide.

Sandpipers are hunted on stopover by peregrine falcons and merlins (Lank et al., 2003; Ydenberg et al., 2002) and implement anti-predator behaviours to avoid becoming prey. While foraging, sandpipers are vigilant for predators, as they repeatedly pause from feeding to raise their head and scan the horizon for approaching falcons. At Boundary Bay, tens of thousands of sandpipers spread across the mudflat, feeding less than a meter apart from one another. Although the birds do not appear to form distinct flocks, they benefit from feeding in such large numbers through the effects of dilution, and from the collective detection of predators.

Boundary Bay is characterized by a strong food-danger gradient, both decreasing with increasing distance from the shoreline. Macro invertebrate abundance at Boundary

Bay declines sharply with increasing distance from the shoreline (Chapter 3) as does predation danger. A study of peregrine falcons hunting dunlins (*Calidris alpina*) during winter at Boundary Bay by Dekker and Ydenberg (2004) found that falcons hunt most intensively and successfully close to shore, where they use the natural vegetation as cover to conceal their approach. Dekker and Ydenberg (2004) showed that the kill rate of peregrines declined as the tide fell and dunlins fed at increasing distance from the vegetated zone along the shore.

These opposing spatial gradients in food and safety at Boundary Bay allowed natural experiments (Chapter 3) and field manipulations (Chapter 4) to test whether migrant sandpipers adjust habitat usage to trade off food and safety. I examined how birds adjust vigilance (Chapter 3), habitat usage (Chapter 3, 4, and 5), and mass-dependent habitat usage (Chapter 5) at Boundary Bay and applied these concepts to the landscape scale to investigate the factors underlying stopover site selection by migrant sandpipers (Chapter 6).

Thesis overview

The thesis consists of five independent research chapters; Chapter 2 tests the applicability of color infrared photography to predict prey abundance for shorebirds indirectly by measuring the chlorophyll concentrations of primary producers on the sediment surface at mud and sandflats in Georgia Strait, British Columbia. Many shorebirds are associated with regions of high coastal zone productivity, which may contribute to high prey abundance (Butler et al., 2001) and chlorophyll levels of primary producers contribute to the red tones of an infrared photograph. While the infrared photograph hue was positively related to the chlorophyll concentration of the sediment surface among sites, invertebrate density was not strongly related to surficial sediment chlorophyll concentration or photograph hue. Color infrared photography is therefore not useful to predict macro-invertebrate abundance. However, it is a useful method to quickly assess the concentration of the phytobenthos in surficial sediment. Evidence from electron microscopy of the bill and tongue of western sandpipers suggests that biofilm (the extracellular carbohydrate matrix of diatoms and bacteria on the surface of sand and mudflat sediments) may be an important component of the western sandpiper diet (Elner et al., 2005; Nebel et al., 2005). Chlorophyll a concentration in the sediment surface has previously been shown to strongly correlate with biofilm density (Underwood and Smith, 1998). Therefore, while infrared photography is not a useful method for predicting invertebrate densities, it may prove a useful tool for estimating biofilm abundance for shorebirds.

Chapter 3 tests how western sandpipers adjust anti-predator behaviours (vigilance and within site usage) at Boundary Bay where food abundance and predation danger vary spatially (both decline with distance from shore) and temporally (food and safety are both greater during southward migration). Within site usage by sandpipers was measured along transects using dropping densities. Dropping densities peaked at intermediate distances from shore, showing that sandpipers maximized neither energy gain (highest close to shore), nor safety (greatest far from shore). The observed pattern is that expected if these factors are traded off against each other.

In Chapter 4 I experimentally tested the hypothesis that western sandpipers trade off food and safety by manipulating predation danger. I added obstructive cover to the open mudflat and compared usage (dropping densities) along transects extending 100 m on either side of the obstruction with that on matched control transects without obstructions. As predicted by the tradeoff hypothesis, usage by sandpipers was lower on obstruction transects than controls, furthermore the difference in usage between control and obstruction transects was greatest near the obstruction and declined as distance from the obstruction increased. Finally, the difference in usage between control and obstruction transects was greater on the oceanward side of the obstruction where food abundance was lower. This work provides experimental evidence that migrant western sandpipers avoid obstructions and adjust their habitat usage according to tradeoffs between food abundance and predation danger.

Chapter 6 uses a dynamic state variable model to test the assumptions underlying within site habitat usage by migrant sandpipers. In the model, I vary the probabilities of acquiring energy, attack by a predator, and escape in habitats within the stopover site and analyzed feeding decisions by migrants. Model predictions were tested using data collected from western sandpipers feeding at Boundary Bay. I tested the model using data on the distribution of sandpipers at various distances from shore (usage) by counting dropping densities, and their state dependent usage of the site by measuring the fuel load of birds at different distances. Model results predicted the observed patterns of usage and mass dependent usage of the stopover site. The pattern of state dependent usage (lean birds using dangerous-high resource habitats and heavy birds using safe-low resource habitats) is a robust pattern in the model, and persists even with no negative effect of state on escape performance. This result suggests that asset protection (Clark, 1994) rather than escape performance (Kullberg et al., 1996; Metcalfe and Ure, 1995; Witter and Cuthill, 1993) underlies state-dependent usage of stopover sites.

Observational (Chapter 3), experimental (Chapter 4), and theoretical (Chapter 5) evidence support the hypothesis that western sandpipers trade food for safety by adjusting habitat usage within stopover sites. The final thesis chapter (Chapter 6) applies this concept to the landscape scale to test the hypothesis that sandpipers consider both food and danger in their stopover site selection. Here I survey 17 mud and sandflats in the Georgia Basin/Puget Sound region and measure the food abundance, safety, and usage by migrant western sandpipers at each site. At sites that were used by sandpipers I measured the mass of birds captured to test the hypothesis that stopover site usage would be state-dependent with heavier sandpipers (that need not risk feeding at dangerous sites) using safer sites. Sandpipers used 8 of the 17 sites surveyed during migration. Sites that offered high levels of food and safety were used, while sites with low levels of food and safety were not. Dangerous sites were used if food was abundant, and sites with low food abundance were used if they were very safe. Furthermore, lean sandpipers used the most dangerous sites, while heavier birds used safe stopover sites.

Implications and future work

This thesis provides evidence that migrant western sandpipers adjust multiple behavioural attributes (vigilance, within site usage, and state-dependent usage) to trade off food and safety at both the site (within stopover) and landscape (among stopovers) scales. Understanding the factors influencing habitat use decisions may prove useful for making predictions of changes in stopover site usage that may arise if there are changes in attributes of the site. For example, if levels of food or danger change, then usage by migrants will change depending on both the magnitude of the change, and the level of the other attribute. If food abundance declines at a safe location, usage by migrants might not change, whereas if the location is dangerous the site or habitat might no longer be used. To identify migration stopover sites for conservation purposes both the food and danger attributes must be considered. Usage of stopover sites by migrants also depends on state. As danger from predators changes on the landscape the state of the birds using those sites might also change (Ydenberg et al., 2004). Increasing predator abundances might shift usage of sites so that safe feeding sites are more important for heavy birds while dangerous sites might be important for lean birds if they offer enough food to make the risk worthwhile.

Since usage and state-dependent usage of stopover sites by migrants is affected by food and danger attributes within and between sites, there are possible sources of error in studies of stopover site usage if danger is not considered. Migrant birds have been shown to alter their behaviour at stopover sites as danger from predators increases by decreasing length of stay at the site (Ydenberg et al., 2004), allocating more feeding time to vigilance (Cimprich et al., 2005; Pomeroy, 2006), and carrying lower fuel loads (Schmaljohann and Dierschke, 2005; Ydenberg et al., 2002; Ydenberg et al., 2004). Migrants might also shift usage from small dangerous sites to larger, safer ones. If danger from predators is not considered in the study of migrants on stopover, each of these behavioural adaptations to avoid mortality by predation could instead be attributed to declines in food abundance at a site or as population decline (see Butler et al., 2003; Ydenberg et al., 2004). The effects are amplified if data are collected solely at dangerous sites (which may be preferred for research due to ease of access and coverage) or locations (bird capture may occur close to shore where birds are constrained by tide).

Finally, this work cautions against the application of mass or usage data to indicate habitat quality. Had I applied the data to indicate habitat quality, I would have likely concluded that the near shore habitats were low quality habitats, as evidenced by lack of usage and the presence of lean birds, and that the high quality habitats were further from shore, where birds are heavy. However, as demonstrated in the thesis, the near shore habitats were those with the most food, offering the highest rates of energy gain, and the far shore habitats were where the ones where food was least abundant.

The idea that birds should adjust usage and fuelling behaviour at stopover sites to avoid mortality from predators is not new. In their models of optimal migration Alerstam and Lindström (1990) hypothesised that migrants may be selected to minimize either time, energy or mortality during migration. They assumed that time- and mortality-minimizing behaviour were identical (i.e. migrants minimize mortality by migrating as fast as possible). However relatively little work is concerned with the effects of danger shaping where, when and how quickly migrants travel, and how they use and select stopover sites (Lank et al., 2003). An increasing number of recent studies support the idea that migrants are sensitive to dangers, and when predation danger is high choose safer habitats, slow the rate of fuel deposition, and reduce fuel loads (Cimprich et al., 2005; Cresswell, 1994; Lindström, 1990; Pomeroy, 2006; Schmaljohann and Dierschke, 2005; Ydenberg et al., 2002; Ydenberg et al., 2004), thus slowing migration.

Future work should investigate how birds adjust multiple behavioural attributes to trade food for safety on migration (Lind and Cresswell, 2006) and how these behaviours affect the fitness of migratory birds (Lind and Cresswell, 2005). Our understanding of the evolution of migration strategies would benefit from addressing these questions in the context of the annual routine (McNamara et al., 1998). Although Alerstam and Lindström (1990) suggest that birds ought to migrate quickly to minimize mortality, an alternative strategy might be to migrate more slowly, and thus, more safely.

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CHAPTER 2:
COLOR INFRARED PHOTOGRAPHY IS NOT A GOOD PREDICTOR OF MACRO INVERTEBRATE ABUNDANCE ON MUDFLATS USED BY SHOREBIRDS

Pomeroy, A.C. and R.W. Butler. 2005. Waterbirds 281(1): 1-7

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Abstract

The applicability of color infrared photography to predict prey abundance for shorebirds indirectly was tested by measuring the chlorophyll concentrations of primary producers on the mudflat surface at eleven migratory stopover sites of shorebirds in Georgia Strait, British Columbia during southward migration in July and August 2002. Many shorebirds are associated with regions of high coastal zone productivity, which may contribute to high prey abundance. Chlorophyll levels of primary producers contribute to the red tones of an infrared photograph. The hue of an infrared photograph was positively related to the chlorophyll concentration of the sediment surface across all sites. However invertebrate density was not strongly related to surficial sediment chlorophyll concentration or photograph hue. The color infrared photography method is useful to quickly assess the surficial sediment concentration of the phytobenthos, but of low value to estimate invertebrate prey densities.

Introduction

Food density has been used by many authors to explain differential habitat use by shorebirds at migratory stop over sites (Hicklin and Smith 1984; Colwell 1993; Colwell and Landrum 1993; Tsipoura and Burger 1999; Gill *et al.* 2001). Many shorebirds are associated with regions of high coastal zone primary productivity. It is likely that the factors contributing to high primary ocean productivity inducing the growth of phytoplankton, also contribute to the growth of the benthic macro invertebrate fauna consumed by shorebirds (Butler *et al.* 2001). For example, Barnes and deVilliers (2000) found that the biomass of chlorophyll-consuming and deposit-feeding macro invertebrates increased with chlorophyll-α concentration across intertidal mudflats and lagoons in Norfolk, UK.

The sediments of intertidal mudflats support an assemblage of microphytobenthos that contribute significantly to the primary productivity of these habitats (Yallop *et al.* 1994; MacIntyre *et al.* 1996). Benthic epipelic diatoms are important primary producers in intertidal mudflats (Admiraal 1984; Smith and Underwood 1998). These organisms grow in the upper few millimeters of sediments the surficial layer exposed to light, where they form biofilms on the sediment surface (Cognie *et al.* 2001). Biofilms are made up of the extracellular polymeric substances, mainly consisting of carbohydrates, which are produced by surficial diatoms and bacteria (Baird and Thistle 1986; Hoagland *et al.* 1993).

Color infrared photography CIR is sensitive in the visible green, red, and near infrared spectral regions (Greer *et al.* 1990). Chlorophyll levels of primary producers contribute significantly to red tones on a color infrared photograph since vegetation reflects up to ten times as much energy in the near infrared part of the spectrum as it does in the wavelengths to which natural color films are sensitive (Everitt *et al.* 2001). Aerial CIR has been widely used to classify terrestrial plant communities (Holopaninen and Wang 1998; Ramsey *et al.* 1998; Nilsen *et al.* 1999; Ramsey *et al.* 2002).

Conventional methods of sorting and counting invertebrates from cores of mud to determine prey abundance are laborious and time consuming, especially on very large mudflats (Schneider and Harrington 1981; Hicklin and Smith 1984; Wilson and Vogel

1997; Sutherland *et al.* 2000). We tested the method of color infrared photography as an indirect measure of infaunal macro invertebrate abundance at eleven migration stopover sites for shorebirds in Georgia Strait, British Columbia. We examined the possibility that the hue of an infrared photograph is positively related to the abundance of chlorophyll producing organisms on the mudflat surface as measured by chlorophyll concentration. We also hypothesized that infaunal macro invertebrate abundance is positively related to the concentration of chlorophyll-α on the mudflat surface.

Methods

Study area

The CIR method was tested at eleven sand and mudflats in the Georgia Strait in July and August 2002 (Figure 2-1). Sites ranged in sediment size class from very fine to very coarse sands 0.1 to 1.4 mm and the maximum mudflat area exposed at each site ranged from less than 1 to 60 km^2. Sites chosen were known or suspected stopover sites used by migratory shorebirds during the southward migration period in July and August.

Infrared photography

An infrared photograph was taken of approximately 0.75 m^2 of the sediment prior to extracting invertebrate, sediment and biofilm cores from the photographed area. Photographs were taken using a Nikon F401 camera with a yellow filter and Kodak Ektachrome Professional Infrared CIR slide film. The film was kept cool before and after use. The film was opened, loaded, and unloaded in total darkness, and developed using E-6 processing see (Greer *et al.* 1990).

Digitized images of each photograph were analyzed with Adobe Photoshop^{TM} v. 6.0 (Adobe Systems, Inc., San Jose, CA, USA). In each photograph, average hue was calculated using Photoshop's histogram function applied to an area of the mudflat outlined with the rectangular marquee. Photoshop assigns hue onto a 360° color wheel with pure red at 0° (or equivalently 360°) and pure green is at 180°. Hue is the color reflected from an object, and corresponds strongly with the wavelength of the reflected light (Dale 2000). In order to control for variation in ambient lighting conditions across different photographs we also scored the hue of a color-standard that was present in each photograph (Eastman Kodak Company 1997). Standardized hue values for the mud surface were calculated as the residuals of mudflat hue regressed onto color-standard hue (see also Kilner and Davies 1998; Dale 2000).

Core sampling

Immediately after each photograph was taken, we took invertebrate, biofilm, and sediment core samples, using a modified 60 cc syringe with a 2.6 cm inner diameter (Sutherland *et al.* 2000). Invertebrate and sediment core samples were taken to a depth of 4 cm. Wolf (2001) shows that the size of invertebrates ingested by the western sandpiper (*Calidris mauri)* are effectively sampled by this core size, since the size of the amphipod *Corophium* recovered from sandpiper feces were within the size range of those recovered from the core samples.

To assess the abundance of primary producers we measured the concentration of chlorophyll-α produced by the diatoms in the upper millimeters of sediment that contribute to the surficial biofilm layer. Biofilm samples were taken by slicing approximately 2 mm off the mud surface with a lifter, using the 2.6 cm core sampler to cut out a standard sediment surface area. All cores were taken within 1.5 h of the mudflat being exposed by a falling tide. All cores were taken within 500 m of the high water mark. Table 2-1 summarizes the number of macro invertebrate, sediment, and biofilm cores extracted at each site.

Infaunal macro invertebrates were quantified using the conventional method of mud core sampling. Invertebrate cores were frozen within 1 h of sampling. The cores were later thawed and rinsed through a 0.5 mm mesh sieve to retain the macro invertebrate fauna following Sutherland *et al.* (2000). The material on the sieve was preserved in vials containing 85% ethanol. Invertebrates in each core were identified and counted, using a dissecting microscope. The ash-free dry weight (AFDW) of invertebrates was determined from 35 randomly selected invertebrate cores by drying in an oven at 70 °C for 24 h to obtain dry weights, and then incinerated for 3 h at 550 °C to determine AFDW (de Boer and Prins 2002). Sediment cores were frozen, thawed, and dried for 24 h at 65 °C for analysis of sediment color. The hue of an infrared photograph of any sediment may be affected by substrate color, because of the semi-transparent nature of the diatom biofilm layer. To correct for this effect, infrared photographs were also taken of the sediment cores after they had been dried and placed in weigh boats. The hue of the photograph of the mud surface was standardized to that of the sediment hue.

Chlorophyll analysis

The methods outlined in Sutherland *et al.* (1998) were followed to analyze biofilm samples for chlorophyll-α concentration. A sub sample of sediment from each biofilm sample was placed in 10 ml of 90% acetone:water solution, contained in scintillation vials and stored for 24 h in a dark refrigerator to extract the chlorophyll from the sediment. The amount of chlorophyll in the supernatant was determined fluorometrically (Parsons *et al.* 1984). Chlorophyll levels were then divided by the mass of sediment that had been sub sampled, giving chlorophyll concentrations as the amount of chlorophyll per unit mass of sediment ($\mu g_{chl}/g_{sed}$).

Statistics

Variables for invertebrate density (invertebrates/core), biomass (g) and chlorophyll concentration ($\mu g_{chl}/g_{sed}$) were transformed by log(x+1) prior to analysis to satisfy normality assumptions. We used linear regression to determine the relationship between variables.

Results

There was a significant positive relationship between the hue of each infrared photograph and the chlorophyll concentration of the sediment surface (Figure 2-2). Photograph hue explained 21% of the variation in chlorophyll concentration (µg/g; $P < 0.001$, $r^2_{161} = 0.21$).

There was a positive and significant relationship between chlorophyll concentration and invertebrate density; however, chlorophyll concentration explained very little of the variation in invertebrate density ($r^2_{161} = 0.04$, $P < 0.02$). There was not a significant relationship between the hue of each infrared photograph and invertebrate density ($r^2_{184} = 0.001$, n.s.). There was not a significant relationship between chlorophyll concentration and macro invertebrate biomass ($r^2_{33} = 0.02$, n.s.) or between the hue of each infrared photograph and macro invertebrate biomass ($r^2_{33} = 0.002$, n.s.).

The mean number of invertebrates sampled was 76 individuals per core (N=186, range; 1-462). The major taxa recovered were polychaetes, nematodes, amphipods, tanaids, ostracods, copepods, foraminiferans, insect larvae, and small mollusks gastropods and bivalves. The mean density of each invertebrate taxa collected at each sampling site is shown in Appendix 1. Each taxa sampled has been shown to be ingested intentionally (Wolf 2001 and references therein) or unintentionally (Sutherland *et al.* 2000) by the western sandpiper a small calidrine shorebird.

To compare surficial chlorophyll concentration between sites we examined the data at the site level. The relationship between the site means of the infrared photograph hue and chlorophyll concentration was highly significant (Figure 2-3). Furthermore, photograph hue explained 84% of the variation in chlorophyll concentration ($r^2_9 = 0.84$, $P < 0.001$). However, there was no significant relationship between the mean infrared photograph hue at each site and the mean invertebrate density ($r^2_9 = 0.02$, n.s.) or the mean chlorophyll concentration at each site and mean site invertebrate density ($r^2_9 = 0.01$, n.s.).

Discussion

The aim of this study was to test the applicability of color infrared photography as an indicator of the abundance of primary producers and subsequently macro invertebrate abundance at intertidal mudflats. We showed that the hue of an infrared photograph was positively related to chlorophyll concentration across all sites and between sites when using site means. However contrary to our expectation, invertebrate density was not significantly related to chlorophyll concentration, and therefore was not related to photograph hue.

Across sites photograph hue was a poor predictor of chlorophyll concentration and explained only 21% of the variation in chlorophyll concentration. It is likely that the significant positive relationship between these two variables was driven by the relationship between photograph hue and chlorophyll concentrations between sites. The relationship improved when site means for photograph hue and chlorophyll concentration were compared ($r^2 = 0.84$), indicating that CIR as a technique may be most valuable to compare the surficial sediment concentration of benthic epipelic diatoms, between sampling sites.

The relationship between chlorophyll concentration and invertebrate density had nearly no predictive power ($r^2 = 0.04$). There are several possible reasons for this poor relationship. The abundance of chlorophyll producing organisms varies with season and the presence of grazers, providing inconsistent results (Underwood 1984; MacLulich 1986; Anderson 1995; Hillebrand *et al.* 2002). Furthermore, while dense biofilm assemblages may be able to support high densities of grazers, the presence of macrograzers, such as gastropods and crustaceans, can significantly decrease the biomass of biofilm assemblages and algae (Anderson 1995; Hillebrand *et al.* 2002).

In intertidal ecosystems, benthic diatoms, bacterial mats, and their associated exopolymers provide food for filter-feeding bivalves (Newell *et al.* 1989; Cognie *et al.* 2001), deposit-feeding holothurians sea cucumbers and deposit feeders and grazing organisms in general (Baird and Thistle 1986). Biofilm layers on intertidal surfaces may also provide food sources for organisms in higher trophic levels such as juvenile Dungeness Crabs (Stevens *et al.* 1982; Jensen 1998). In systems where the relationship between chlorophyll and macro invertebrate biomass is known (Barnes and deVilliers 2000), relative macro invertebrate biomass may be estimated using CIR.

The utility of CIR has been applied to studies of the distribution and health of plants (Field and Philipp 2000; Weber and Dunno 2001; Ramsey *et al.* 2002). The CIR method was useful for comparing the surficial chlorophyll concentration of mudflats between sites in our study, but of no use to predict macro invertebrate abundance.

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Table 2-1: Sample sizes and dates of cores extracted at each site.

Site	Date sampled	Infrared photograph N	Invertebrate cores N	Sediment cores N	Biofilm cores N
Boundary Bay	14 - 23 Jul	45	45	43	34
Comox Harbor	2 Aug	15	15	14	13
Cordova Bay	29 Jul	14	14	14	14
Cowichan Bay	30 Jul	14	14	11	14
Deep Bay	1 Aug	11	11	14	11
Fanny Bay	1 Aug	15	15	15	11
Kye Bay	1 Aug	15	15	15	11
Rathtrevor Beach	31 Jul	15	15	14	15
Robert's Bank	19 Aug	14	14	14	13
Tseum Harbor	29 Jul	15	15	14	14
Walker's Hook	30 Jul	13	13	13	13
Total		186	186	181	163

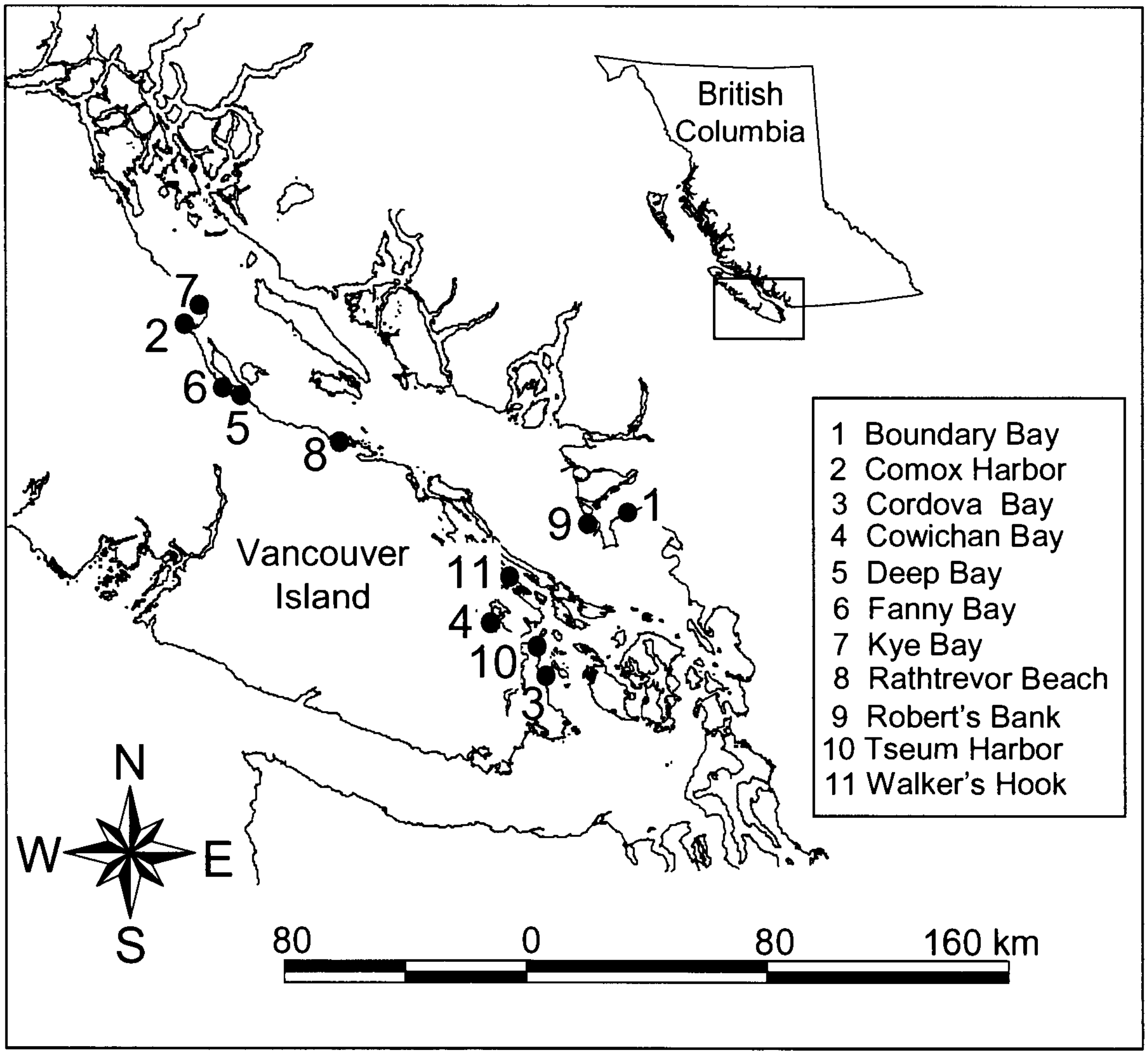

Figure 2-1: Sample locations in Georgia Strait, British Columbia, Canada

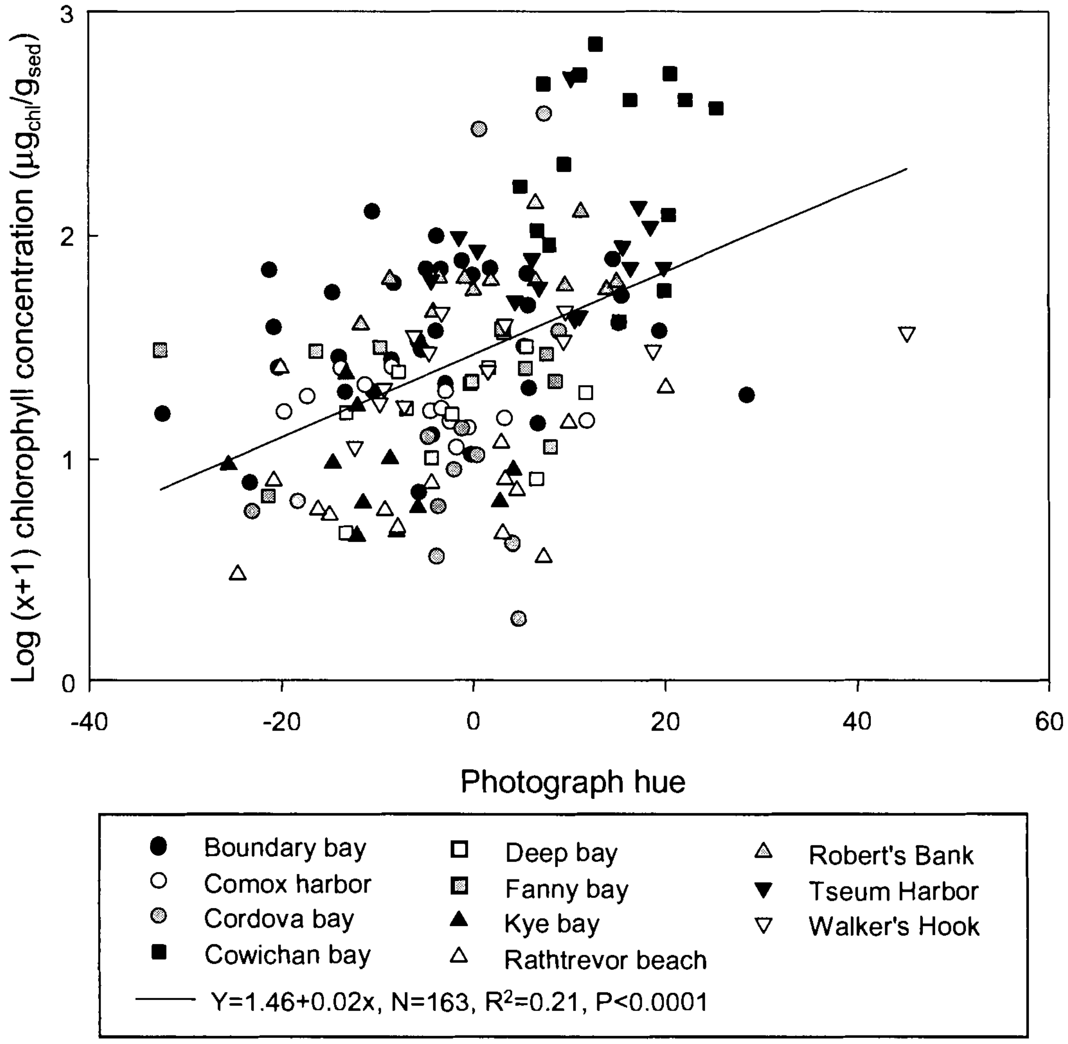

Figure 2-2: Photograph hue vs. chlorophyll concentration of surficial sediments on intertidal mudflats at migratory stopover sites for shorebirds in the Georgia Strait, British Columbia, Canada. Chlorophyll concentrations ($\mu g_{chl}/g_{sed}$) were transformed by log(x+1) prior to analysis see methods.

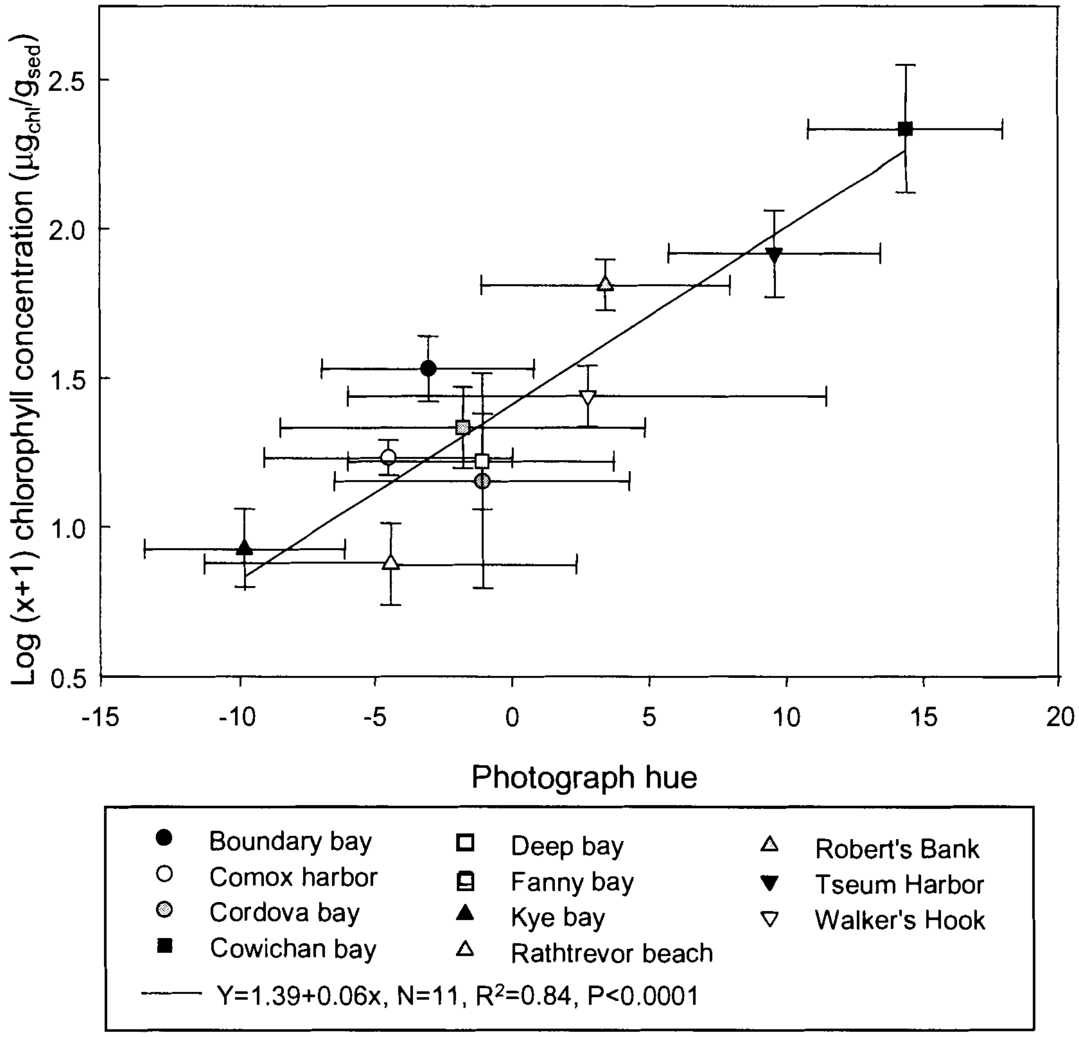

Figure 2-3: The mean photograph hue at each site is a significant predictor of the mean site chlorophyll concentration. Chlorophyll concentrations ($\mu g_{chl}/g_{sed}$) were transformed by log(x+1) prior to analysis (see methods). Error bars represent 95% confidence limits.

Appendix 2-1: The mean density per m^2 of invertebrate taxa collected at each sampling site (standard error shown in brackets).

Phylum	Class	Order		Site				
				Boundary Bay (N=45)	Cordova Bay (N=14)	Comox Harbor (N=15)	Cowichan Bay (N=14)	Deep Bay (N=11)
Sarcomastigophora	Granuloreticulosea	Foraminifera		962	403	125	10224	0
				(297)	(403)	(125)	(5569)	(0)
Nematoda	Adenophorea			44952	13318	8538	7668	17807
				(5703)	(3265)	(2118)	(4115)	(6634)
Mollusca	Bivalvia			42	0	502	135	342
				(42)	(0)	(222)	(135)	(229)
	Gastropoda			841	134	0	0	171
				(59)	(134)	(0)	(0)	(171)
Annelida	Polychaeta			215345	403	5273	1614	1198
				(31837)	(291)	(885)	(587)	(730)
	Branchiopoda	Cladocera		460	0	0	0	0
				(379)	(0)	(0)	(0)	(0)
Arthropoda	Ostracoda			24443	0	1255	807	1712
				(3960)	(0)	(397)	(548)	(593)
	Copepoda			10087	2287	8161	1345	3253
				(2482)	(1875)	(1431)	(800)	(883)
	Malacostraca	Amphipoda	Genus:	18500	0	13937	403	1883
			Corophium	(3617)	(0)	(3256)	(403)	(803)
			Suborder:	84	0	0	0	342
			Gammaridea	(59)	(0)	(0)	(0)	(342)
		Cumacea		42	0	502	0	171
				(41)	(0)	(288)	(0)	(171)
		Tanaidacea		24359	0	19462	0	0
				(5560)	(0)	(4948)	(0)	(0)
	Insecta	Diptera		841	0	502	14529	171
				(59)	(0)	(388)	(3578)	(171)

Phylum	Class	Order		Fanny Bay (N=15)	Kye Bay (N=15)	Rathtrevor Beach (N=15)	Robert's Bank (N=14)	Tseum Harbor (N=15)	Walker's Hook (N=13)
Sarcomastigophora	Granuloreticulosea	Foraminifera		0 (0)	0 (0)	0 (0)	1749 (574)	1256 (750)	8983 (2798)
Nematoda	Adenophorea			10924 (2522)	80990 (18483)	34028 (8812)	27580 (3867)	80111 (12224)	91856 (19480)
Mollusca	Bivalvia			251 (171)	251 (171)	1005 (516)	135 (135)	0 (0)	1594 (764)
	Gastropoda			628 (237)	0 (0)	1632 (798)	0 (0)	0 (0)	0 (0)
Annelida	Polychaeta			2888 (1601)	43320 (10626)	7785 (1021)	212296 (26169)	2637 (731)	6230 (1657)
	Branchiopoda	Cladocera		0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Arthropoda	Ostracoda			1005 (445)	0 (0)	5148 (2673)	269 (269)	502 (289)	3477 (1184)
	Copepoda			1381 (430)	9920 (3831)	4269 2299)	2691 (548)	3014 (1053)	6810 (2492)
	Malacostraca	Amphipoda	Genus: *Corophium*	5776 (1719)	0 (0)	24109 (6301)	2287 (1356)	753 (443)	21443 (4828)
			Suborder: Gammaridea	0 (0)	126 (126)	377 (201)	0 (0)	0 (0)	724 (724)
		Cumacea		0 (0)	0 (0)	377 (201)	0 (0)	126 (126)	290 (196)
		Tanaidacea		0 (0)	0 (0)	0 (0)	6727 (1881)	0 (0)	724 (340)
	Insecta	Diptera		126 (126)	0 (0)	0 (0)	269 (269)	126 (126)	290 (196)

CHAPTER 3:

TRADE-OFFS BETWEEN FOOD ABUNDANCE AND PREDATION DANGER IN SPATIAL USAGE OF A STOPOVER SITE BY WESTERN SANDPIPERS (*CALIDRIS MAURI*)

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Abstract

Foragers use a variety of anti-predator behaviours to increase their safety from predators. While foraging, animals should alter usage within or between sites to balance the benefits of feeding with the costs of predation. I tested how the distribution of food abundance and predation danger interacts to explain spatial usage (i.e. distance from shore) by migratory western sandpipers (*Calidris mauri*) at Boundary Bay, British Columbia, Canada during northward and southward migrations. At Boundary Bay there are opposing spatial gradients in the distribution of food abundance and safety from predators. Predation danger for sandpipers is high near the shoreline where there is approach cover for falcons and decreases with distance from shore. Food abundance for sandpipers declines as distance from the shoreline increases. Food and danger attributes at Boundary Bay also differ temporally, such that food abundance is higher during southward migration, and predation danger is higher during northward migration. The spatial usage by western sandpipers balances the trade-off between the opposing spatial gradients in food and safety. For both migratory periods spatial usage of the mudflat by sandpipers is highest at distances from the shoreline where food abundance and predation danger are intermediate. During the northward migration sandpiper usage is highest between 150 and 500 m from the shoreline, and during the southward migration sandpiper usage is highest between 100 and 600 m from the shoreline. Despite temporal differences in food and danger attributes, spatial usage of the site by sandpipers does not differ between migratory periods. Understanding how the distribution of food abundance and predation danger interact to affect the within site usage by shorebirds has important implications for assessments of site quality.

Introduction

Trade-offs between predation danger and energy intake affect the foraging behaviour of animals (Lima and Dill 1990). Foragers employ a suite of behaviours including increasing group size and vigilance levels (Bednekoff and Lima 1998, Downes and Hoefer 2004, Elgar 1989) and altering habitat usage (Grubb and Greenwald 1982, Lindström 1990, Suhonen 1993) to increase their safety from predators. While foraging, animals should alter habitat usage such that they use habitats (or patches within a habitat) that balance the benefits of feeding with the costs of predation (MacArthur and Pianka 1966). When faced with two habitats (or patches) similar in food abundance animals should spend more time foraging in the safer habitat (Brown 1988, Kotler 1992, Kotler, Brown, Slotow, Goodfriend and Strauss 1993). The distribution of food abundance and predation danger a forager faces within a site may vary both spatially and temporally, and where an animal chooses to forage within that site indicates how it considers the relative importance of these two factors. The spatial distribution of the food and danger attributes of a site may affect overall site quality, particularly if both food and danger are highest at the same location within a site.

Shorebirds use a variety of anti-predator behaviours to trade-off energy acquisition with avoiding predation. They increase flock size to reduce danger (Barbosa 1997, Cresswell 1994, Whitfield 2003) despite potential costs of interference competition that can occur between foragers at high densities (Yates, Stillman and Goss-Custard 2000), and decrease feeding rates to increase vigilance (Barbosa 1997, Cresswell 1994). Shorebirds balance the benefits of feeding with the costs of predation by using sites with low energy-intake rates in order to gain safety from predators (Cresswell 1994, Yasué, Quinn and Cresswell 2003, Ydenberg, Butler, Lank, Guglielmo, Lemon and Wolf 2002), furthermore they can alter their usage within a site to optimize this trade-off.

How the distribution of food abundance and predation danger within a site interacts to affect usage by shorebirds is critical to understanding how they select migration stopover and non-breeding sites, and has implications for habitat conservation. These factors likely vary spatially and temporally both within and between sites. Assessments of food abundance alone are insufficient to measure site quality since the distribution of danger within a site may affect the value of food (Butler, Bradbury and Whittingham 2005, Butler, Whittingham, Quinn and Cresswell 2005).

The objective of this study was to evaluate three alternative hypotheses to explain how food abundance and predation danger affect spatial usage of a stopover site by the western sandpiper at Boundary Bay, British Columbia, during northward and southward migration. On migration, birds need to sustain high feeding rates to acquire the fuel reserves necessary to reach subsequent stopover sites (Alerstam and Lindström 1990) while avoiding the predators that hunt them there. Intertidal mudflats used by shorebirds may show strong spatial differences in food abundance and predation danger within a site and these attributes may differ temporally between migratory periods.

Spatial usage is a measure of the intensity of usage by sandpipers at the site that includes both the density of shorebirds and the amount of time they foraged there. I measured the spatial usage of Boundary Bay by migratory western sandpipers to test the following hypotheses: 1) that spatial usage of the mudflat by sandpipers is affected by food abundance only, 2) that spatial usage by sandpipers is affected by predation danger only, and 3) that spatial usage of the mudflat by sandpipers reflects a trade-off between food abundance and safety from predators. I predict that if spatial usage is affected by food abundance only then bird usage will match the distribution of food in an ideal free manner, if spatial usage is affected by predation danger only then bird usage will increase as distance from the shoreline increases reflecting the gradient in predator safety, and if spatial usage reflects a trade-off between food abundance and safety then spatial usage will be less than expected by the distribution of food where danger is high and greater than that expected by the distribution of food where danger is low.

Methods and material

Study system

The western sandpiper (*Calidris mauri)* is a small scolopacid wader that migrates along the Pacific Coast from non-breeding grounds between northern Oregon and Peru, to breeding grounds in western and northern Alaska and eastern Siberia (Wilson 1994). Hundreds of thousands of western sandpipers forage on the mudflats of the Fraser Delta and Boundary Bay, Canada during each migratory period (Butler, Kaiser and Smith 1987). Boundary Bay (N 49°4.13′ W 122°58.05′) is a large mudflat on the Fraser estuary with approximately 60 km^2 of mud and sand exposed at the lowest tide. Shorebirds are hunted over mudflats there by peregrine falcons (*Falco peregrinus*) and merlins (*F. columbarius*, (Dekker 1998)), which are present on the study site during northward and southward migrations (Lank, Butler, Ireland and Ydenberg 2003). Danger is low for sandpipers during July as they migrate southward through the Fraser Estuary since falcons do not pass through the study site in high abundance until August (Lank, Butler, Ireland and Ydenberg 2003).

Predation danger for western sandpipers also differs spatially, as the hunting success of predators varies between different stopover sites, and in different foraging patches within sites (Dekker and Ydenberg 2004, Quinn and Cresswell 2004). The Boundary Bay mudflat is bordered by a protective dyke near the high tide line, with a narrow band of hummocks and marsh grasses along the shoreward side. Predation danger for shorebirds increases near the shoreline (the interface between marsh grasses and the mudflat), because falcons use the cover of vegetation to conceal their approach (Lazarus and Symonds 1992) and are most successful when mounting a surprise attack (Buchanan 1996, Cresswell 1996, Dekker 1998, Dekker and Ydenberg 2004, Whitfield 2003). At Boundary Bay peregrine falcons hunting dunlin (*Calidris alpina*) in winter experienced the highest success rate (44%) when hunting close to shore than compared to hunts made over the tidal flats and ocean (Dekker and Ydenberg 2004). Therefore, in the case of falcons hunting shorebirds, cover is obstructive for shorebirds (Lazarus and Symonds 1992).

Data were collected at Boundary Bay in April, May, and July 2002, on three 1 km long transects oriented perpendicularly to the shoreline. Transects were spaced approximately 3 km apart. Sample stations (see below) were placed along each transect at distances from the shoreline of 1, 50, 100, 150, 200, 250, 300, 400, 500, 600, 700, 800, 900 and 1000 m.

Distribution of food

Western sandpipers are considered invertebrate generalists opportunistically feeding on a variety of benthic macro invertebrates (Wilson 1994). To measure the distribution of shorebird food abundance I quantified benthic macro invertebrate abundance in mud cores extracted at sample stations according to the methods described by (Sutherland, Shepherd and Elner 2000). Each taxon sampled (see Results) has been shown to be consumed intentionally (Wolf 2001) and references therein) or unintentionally (Sutherland, Shepherd and Elner 2000) by western sandpipers.

Briefly, samples were extracted using a 60 ml syringe (26 mm inner diameter) to a depth of 40 mm, within 1.5 hours of mud exposure by the receding tide and frozen within 1 h of sampling. Cores were later thawed and rinsed through a 0.5 mm mesh sieve. Material on the sieve was preserved in vials with 85% ethanol. Invertebrates in each vial were identified to the lowest taxon possible and counted under a 40X dissecting microscope. Wolf (2001) shows that the size of invertebrates ingested by the western sandpiper are effectively sampled by this core size, since the size of the amphipod *Corophium* recovered from sandpiper feces were within the size range of those recovered from the core samples. Unfortunately due to the small size of invertebrates available for and consumed by western sandpipers (< 5 mm; Sutherland et al. 2000, Wolf 2001) their intake rates could not be measured in the field. However, technological advances in high-speed video imaging might provide insight into questions relating to sandpiper intake rates in the future.

Transects were sampled for invertebrates a total of 10 times at each of 14 sample stations. Transects 1 and 3 were sampled twice, and transect 2 was sampled three times during the northward migration (April 20 – May 15). Because invertebrate densities did not differ between transects during the northward migration (ANCOVA: $F_{2,95} = 1.54$, effect of transect $P > 0.20$) only transect 2 was sampled 3 times during the southward migration.

Vigilance behaviour

Western sandpipers forage for invertebrates by pecking or probing their bills into the mud, they often stop pecking or probing for prey and raise their heads briefly to scan for predators. In this case, scanning for predators (vigilance) and pecking for food is assumed to be incompatible (Elgar 1989). A sandpiper was considered to be vigilant if its head was up with the bill held parallel to the mud surface. I measured vigilance rates by randomly selecting individuals and observing their behaviour for one minute (Altmann 1974). Focal observations of 240 individuals (northward n=131, southward n=109) were made through a 25-60X zoom spotting scope at transect 2 and spoken into a tape recorder for later transcription.

Despite the well known relationship between decreasing vigilance levels of individuals with increasing group size (see reviews in Barnard and Thompson 1985, Elgar 1989, Lima 1990, Lima and Dill 1990, Quenette 1990) this study does not correct for the possible confounding effect of flock size in the relationship between vigilance and distance from the shoreline. The reasons for this are two fold; firstly the size of western sandpiper flocks does not differ as distance to the shoreline increases (pers. obs.), secondly their flock sizes range from hundreds to thousands of individuals, far above reported thresholds for effects of decreasing vigilance with increasing group size (Barbosa 1997, Cresswell 1994).

Spatial usage

I measured spatial usage (i.e. distance from the shoreline) by sandpipers by counting dropping (faecal) densities at sampling stations along each transect. Dropping densities provide a convenient measure of the intensity of spatial usage because they are produced frequently (0.5 dropping min^{-1} (unpubl. data)) by foraging sandpipers and are washed away by the tide between low tide periods. To avoid including droppings of other shorebird species present on the study site only droppings that were smaller than a Canadian dime (~2 cm diameter) were counted. Also, since western sandpipers were the most abundant shorebird at the site during migration (other species representing less than 2% of the total number of shorebirds) including other species droppings was unlikely to affect the outcome of the study. Droppings were counted in 1-m^2 quadrats randomly placed at each sampling station along each transect when the tide was low. Nine dropping counts were conducted during the northward migration and eleven counts were made during the southward migration. Because the receding tide exposes the mud closest to the shoreline for the longest period of time, dropping densities (droppings m^{-2}) were adjusted by sample station to account for the total duration of tidal exposure (droppings $\mathrm{m}^{-2}\ \mathrm{min}^{-1}$), to control for the differential availability of the mudflat habitat along the transect.

Statistical analyses

For analysis of the distribution of food abundance for western sandpipers at Boundary Bay, I tested the relationship between invertebrate density (invertebrates core^{-1}) and distance from the shoreline for each transect using analysis of covariance (ANCOVA) with transect as a group variable. A separate ANCOVA was used to test for an effect of migratory period in the relationship between invertebrate density and distance from the shoreline at transect 2 only. Invertebrate density measures were log(x+1) transformed to satisfy the assumptions of linear regression.

I investigated how sandpipers alter predator scanning behaviour at different levels of predation danger by measuring vigilance rates at various distances from the shoreline. For analysis vigilance was reduced to a binary variable (vigilant or not) because of the 240 focal observations nearly half (46.6%) of the birds displayed no vigilance behaviour. Of the remaining 128 birds nearly half of those (46 %) were vigilant only once, and the remaining were vigilant between 2 and 9 times. I used logistic regression to predict the probability of birds being vigilant (=1) or not (=0) at various distances from the shoreline.

I used a regression model with distance and distance^2 to test for trends in spatial usage in relation to distance from the shoreline. To test if spatial usage (as measured by dropping densities) proportionately matched the distribution of invertebrates at Boundary Bay I compared the ratio of droppings (m^{-2} min^{-1}) to invertebrate densities at each distance from the shoreline to the expected ratio of dropping to invertebrate densities if spatial usage matched invertebrate densities. The expected (null) ratio was calculated using the mean values over the entire transect range of dropping and invertebrate densities for each migratory period. Likewise I calculated the standard errors (SEs) of the null and measured ratios (Cochran 1977). I then tested for a difference between the observed and expected ratios of dropping to invertebrate densities at each distance from the shoreline using a two-tailed Z-test. A negative difference between observed and expected ratios indicates that the spatial usage was less than expected, and a positive difference indicates that spatial usage was greater than expected, than if sandpiper usage matched invertebrate densities.

To compare the spatial usage of sandpipers between migratory periods I scaled the measured ratios, and their SEs, of dropping to invertebrate densities to a value of unity for each migratory period by dividing the ratio at each distance by the average for each migratory period. I then tested for differences between the scaled ratio of droppings to invertebrate densities for the northward and southward migration at each distance from the shoreline using a two-tailed Z-test.

JMP*IN* V. 4.0.4 (2001) was used for all statistical analyses.

Results

Distribution of food

Macro invertebrate density decreased with distance from the shoreline for all transects during the northward migration period (Figure 3-1a; ANCOVA: $R^2 = 0.53$, $F_{1,95} = 76.80$, effect of distance $P < 0.0001$) and for each migratory period at transect 2 (Figures 3-1a & 3-2a; ANCOVA: $R^2 = 0.66$, $F_{1,83} = 124.97$, effect of distance $P < 0.0001$). Invertebrate density at the shoreline was two times greater than the invertebrate density at

350 m, and was approximately 6 times greater at the shoreline than at the 1 km mark. The average invertebrate density was significantly greater during the southward migration (least squares mean = 159.6 invertebrates core^{-1}, $P < 0.0001$) than during the northward adult migration (least squares mean = 88.9 invertebrates core^{-1}). There was a significant interaction in food density and distance from the shoreline between migratory periods (Figures 3-1 & 3-2a; ANCOVA: $R^2 = 0.66$, $F_{1,83} = 6.03$, migration*distance $P = 0.016$) such that in the northward migration the slope of decline of invertebrate density with distance from the shoreline was steeper than the southward migration.

Polychaetes were the dominant taxa among potential prey items followed by nematodes, copepods, tanaids, ostracods and *Corophium* (Table 3-1). In separate regression analyses, polycheate ($F_{1,137} = 198.13$, $R^2 = 0.59$, $P < 0.0001$), nematode ($F_{1,137} = 31.04$, $R^2 = 0.10$, $P < 0.0001$), foraminifera ($F_{1,137} = 14.76$, $R^2 = 0.10$, $P = 0.0002$), and insect larvae ($F_{1,137} = 5.68$, $R^2 = 0.02$, $P = 0.02$) densities declined significantly with distance from the shoreline in both migratory periods. The only taxa that increased significantly with distance from the shoreline were copepods ($F_{1,41} = 12.50$, $R^2 = 0.24$, $P < 0.001$) and *Corophium* ($F_{1,41} = 41.33$, $R^2 = 0.51$, $P < 0.0001$) during the southward migration.

Vigilance behaviour

If predation danger is highest at the shoreline then sandpiper vigilance should also be higher there. Consistent with that prediction the probability that an individual western sandpiper was vigilant during the focal observation increased significantly toward the shoreline (Figure 3-3; Logistic regression: Wald $\chi 2 = 9.45$, $n = 240$, d.f. = 1, $P = 0.0021$).

This effect did not differ between migratory periods (Logistic regression: Wald $\chi 2$ = 0.094, n =240, d.f. = 2, P = 0.76). The probability that a western sandpiper was vigilant within a one minute period was 0.69 at the shoreline and declined to 0.24 at 600 m from the shoreline.

Spatial usage

The day-to-day variation in spatial usage was high, likely due to the large fluctuations in the number of western sandpipers present on the study area, as they passed through on migration. However, despite the day-to-day variation the overall profile clearly shows that spatial usage by western sandpipers did not closely match the distribution of food.

Overall the relationship between spatial usage of the mudflat by sandpipers and distance from the shoreline showed a peak in usage at intermediate distances from the shoreline (Figures 3-1 & 3-2b; regression: $F_{1,279} = 16.02, P < 0.0001$). The spatial usage of Boundary Bay by western sandpipers was greater during the northward migration than in the southward migration ($F_{1,279} = 24.61, P < 0.0001$, northward: n = 126, least squares mean = 0.01 droppings m^{-2} min^{-1}, southward: n = 154, least squares mean = 0.003 droppings m^{-2} min^{-1}) because of the higher densities of sandpipers at the site during the northward migratory period.

For both migratory periods the pattern of usage was similar, for the northward migration (Figure 3-1b) the pattern was more peaked than the southward and the bulk of usage occurred between 150 and 500 m from the shoreline. For the southward migration the pattern of spatial usage is broader, with the peak usage 100 to 600 m from the shoreline (Figure 3-2b). The shape of the curves differs between the migratory periods as indicated by a significant migration by distance^2 interaction term ($F_{1,279} = 9.82$, $P = 0.002$).

Food abundance and spatial usage

The observed ratio of dropping to invertebrate densities did not closely match the expected ratio of dropping to invertebrate densities if spatial usage of Boundary Bay by sandpipers proportionally matched invertebrate abundance (Figures 3-1 & 3-2c). The observed pattern of usage supports the hypothesis that spatial usage reflects a trade-off between food and safety.

During both migratory periods spatial usage was less than expected at distances close to the shoreline (less than 150 m in northward and 100 m in southward migration) where predation danger is high (Table 3-2). Spatial usage was also less than expected at distances from the shoreline greater than 700 m in both migratory periods. At the furthest distances from the shoreline no sandpiper usage was measured where mean invertebrate densities dropped below 100 invertebrates per core. In the southward migration, except for those distances closest to (≤50 m) and furthest (≥700 m) from the shoreline, spatial usage by sandpipers did not differ significantly from expected usage (Table 3-2). However, in the northward migration spatial usage by sandpipers was greater than expected at intermediate distances (250 to 400 m) from the shoreline (Table 3-2).

The pattern of spatial usage by sandpipers did not differ between migratory periods when the ratios of dropping to invertebrate densities are scaled to unity and directly compared (Figure 3-4). The only significant difference in usage was that during the southward migration sandpiper usage extends to 700 m from the shoreline, where as in the northward migration sandpipers do not use distances greater than 600 m.

Discussion

This study examined how within site spatial usage by migratory western sandpipers is affected by food abundance and predation danger at Boundary Bay, British Columbia, Canada during northward and southward migrations. Data presented in this paper indicate that food abundance at Boundary Bay declines with distance from the shoreline. Evidence from several shorebird systems indicates that safety from avian predators increases with distance from the shoreline (Buchanan 1996, Cresswell 1996, Dekker 1998, Dekker and Ydenberg 2004, Lazarus and Symonds 1992, Whitfield 2003). Given these opposing spatial gradients in food abundance and safety, spatial usage by sandpipers is consistent with the hypothesis that sandpipers trade-off food with safety. Spatial usage by sandpipers is lower than expected on the basis of food alone where danger is high and greater than expected as safety increases.

The spatial pattern of dropping densities can not be explained simply by sandpipers foraging along the receding tide (c.f. Colwell and Landrum 1993). If this were the case dropping densities across the mudflat would be directly proportional to the speed with which the tide recedes. At Boundary Bay the tide edge recedes at about 10 m min^{-1} to a distance of about 4 km at mean low tide (unpubl. data). Therefore the width of mudflat over which western sandpipers actively forage is exposed in less than one hour. If sandpipers foraged over this expanse by following the tide edge droppings would be evenly distributed. With the correction for exposure, the expected distribution would be a slight linear increase in dropping density with distance from the shoreline, which is clearly not the case. In fact, western sandpipers foraging at Boundary Bay spread out over the mudflat as the tide recedes.

The opposing gradients of food and safety at Boundary Bay provide a natural analogy to a giving up density (GUD) experiment. GUDs offer an effective measure of the cost to an animal foraging under the danger of predation (Altendorf, Laundre, Gonzalez and Brown 2001, Brown 1988, Kotler, Brown and Bouskila 2004). The GUD of an animal in a controlled food patch measures the amount of food an animal is willing to give up for a certain level of safety (Brown 1988). The position of a sandpiper along the food and safety gradients serves as an index of how it evaluates these two things. For example, a bird observed feeding any distance away from the shoreline is apparently unwilling to feed in a more dangerous location despite the benefits of increased food abundance.

Despite temporal differences in both food abundance and predation danger at Boundary Bay between migratory periods the pattern of usage by sandpipers does not differ (Figure 3-4). For southbound adults food abundance at Boundary Bay is higher (Figures 3-1 & 3-2a) and predator abundance is lower (Lank, Butler, Ireland and Ydenberg 2003) than for northbound migrants. Southbound adults also face much lower competitor densities than northbound migrants, such that the ratio of dropping to invertebrate densities is 10 times lower for southbound sandpipers. One might expect that since predator abundance is lower for southbound adults they would adjust their spatial usage to feed closer to the shoreline than northbound adults. However, predators are not completely absent from the Fraser Estuary during the southward sandpiper migration.

Prey that ignore predation danger may become victims as their predators quickly respond to these more catchable prey (Brown, Laundre and Gurung 1999). The increase in food abundance and decrease in competitor densities for southbound migrants might allow them to feed at safer distances while achieving higher food intake than northbound migrants.

Spatial differences in food abundance and/or predation danger are likely widespread both within and between feeding sites used by shorebirds. Many intertidal mudflats used by shorebirds may show similar spatial gradients in food abundance to Boundary Bay (Swennen, Duiven and Spaans 1982). On intertidal mudflats macro invertebrate densities are influenced by sedimentary grain size. High macro invertebrate densities are often associated with fine-grained sediments (silt and mud) and densities decline with increasing grain size (Kennish 1990, Yates, Goss-Custard, McGrorty, Lakhani, Durell, Clarke, Rispin, Moy, Yates, Plant and Frost 1993). On large open tidal flats, such as Boundary Bay, the bed slope is often shallow and constant in an on-offshore direction, as water depth decreases close to the shoreline fine sediment particles such as silt and mud settle there (Kennish 1986, Reise 1985). At Boundary Bay the deposition of the finer grained sediments close to the shoreline offers an explanation for the high abundance of macro invertebrates there. Spatial gradients in food abundance for shorebirds on intertidal flats will depend on interactions between the topography of the site, tidal inundation, grain size and the prey type of interest.

Spatial gradients in predation danger for shorebirds at a feeding site depend on the proximity to cover at which an individual can forage. In several shorebird systems it has been shown that avian predators are more successful when mounting a surprise attack, flying low over the marsh grass, using the cover of vegetation at the shoreline to conceal their approach (Buchanan 1996, Cresswell 1996, Lazarus and Symonds 1992, Whitfield 2003). Although data on raptor predation on western sandpipers were not collected for this study, evidence from Dekker (1998) and Dekker and Ydenberg (2004) at this study site concur with others that danger for shorebirds is highest near the shoreline. In this study I show that the frequency of vigilance by sandpipers is highest close to the shoreline, indicating that foraging sandpipers perceive a high level of danger close to cover at Boundary Bay.

Predation danger varies between sites, since the distance from cover at which an individual can forage differs depending on the size and shape of a site. At a very small site all feeding locations may be close to the shoreline, resulting in a site that is very dangerous, whereas, a large open mudflat would offer many safe feeding locations far from the shoreline. The geometry of the site also plays a role since proximity of an individual to the shoreline will differ depending on the shape of the site, especially if the perimeter of a site is surrounded by more than one marsh lined shore.

Differences in the spatial distribution of food abundance and predation danger at feeding sites predict different patterns of usage by shorebirds. The quality of a feeding site for shorebirds will be determined by spatial gradients in both food abundance and predation danger. Measurements of food abundance alone cannot adequately assess site quality since the distribution of danger within a site affects the value of food. For example at Boundary Bay food abundance is highest where predation danger is also higher, since few sandpipers are willing to feed where it is most dangerous, the quality of the site is lower than expected by food alone. Alternatively a site where food abundance is high in the safest locations would be of a higher quality than predicted based on an assessment of food only.

This work strongly suggests that both food abundance and predation danger influence the distribution of sandpipers over short distances at a migratory stopover site. These results have implications for understanding how usage both within and between sites depends on the interaction between food and danger. Assessments of site quality need to consider both food and danger attributes at a site to predict which sites should be used or not by shorebirds. This work also indicates that food and danger attributes of shorebird feeding sites may differ temporally. For migratory birds, recognizing temporal differences in food and danger attributes may be an essential component of predicting site usage, since temporal differences may affect which sites are used at different stages of the annual cycle.

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Table 3-1: The mean number of invertebrates per core (± 95% confidence limits) of the major invertebrate taxa sampled for each migratory period.

Invertebrate Taxa	Northward	Southward Adult
Polycheate	67.09 (16.16)	64.37 (20.34)
Nematode	31.53 (9.16)	14.46 (5.52)
Copepod	12.66 (2.52)	2.78 (1.19)
Tanaid	0.14 (0.10)	19.51 (8.69)
Ostracod	4.48 (3.30)	16.07 (3.80)
Corophium	0.15 (0.09)	13.78 (4.18)
Molluscs	0.18 (0.13)	0.90 (0.49)
Foraminiforam	0.24 (0.14)	0.32 (0.27)
Insect larvae	0.05 (0.09)	0.12 (0.14)
Cumacean	0.10 (0.08)	0 (0)
Cladoceran	0.01 (0.02)	0 (0)

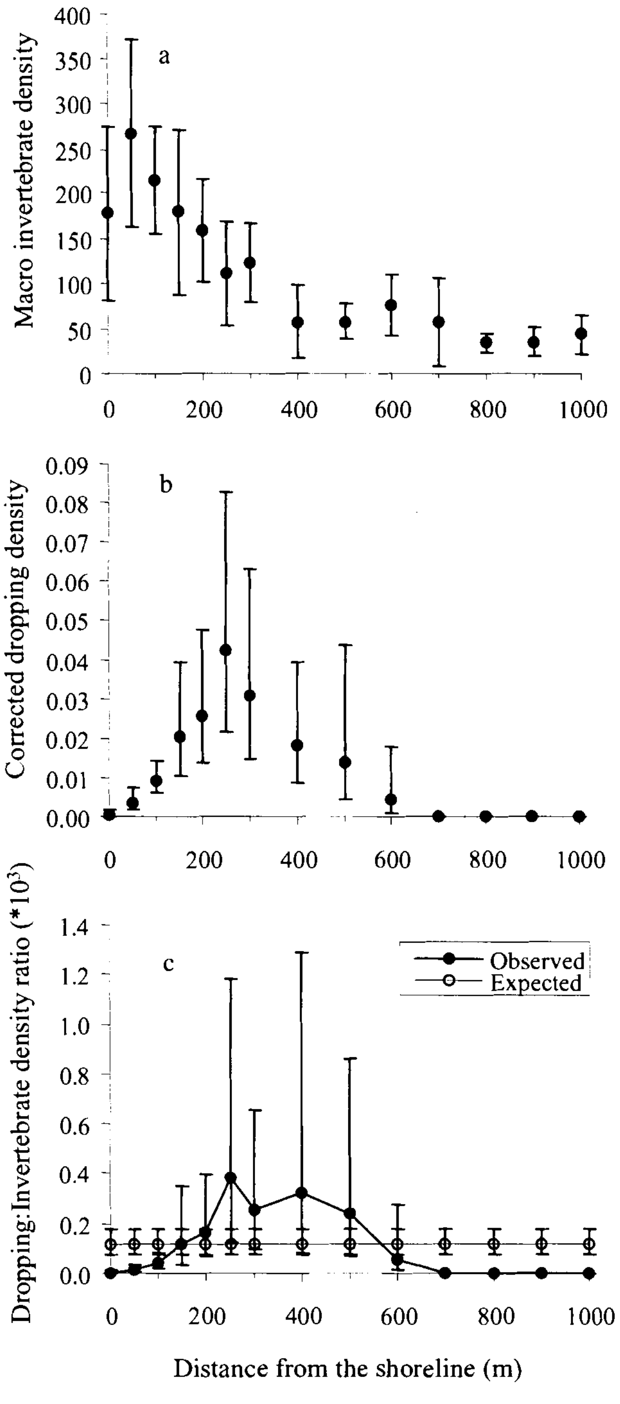

Figure 3-1: Northward migration - the mean density of macro invertebrates (invertebrates core^{-1}) (a) and sandpiper droppings (droppings m^{-2} min^{-1}) (b) as distance from the shoreline increases. The observed ratio of dropping to invertebrate densities (c) does not closely match the expected ratio based on food. Error bars are 95% confidence limits.

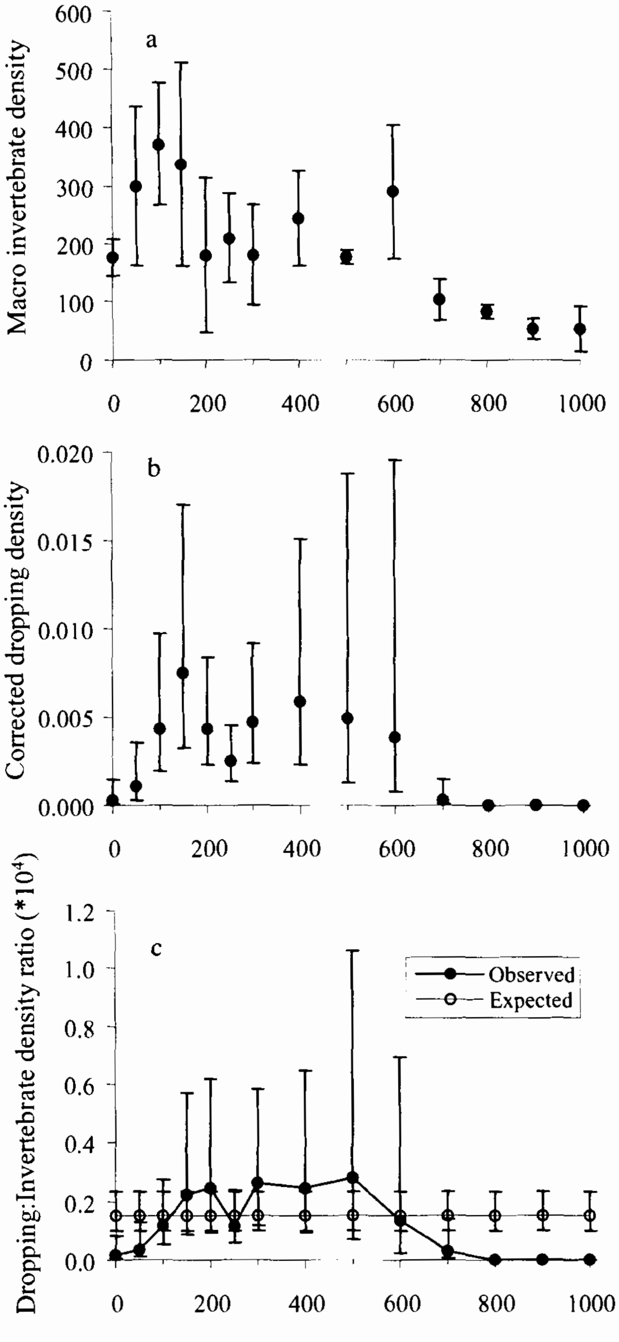

Figure 3-2: Southward migration - the mean density of macro invertebrates (invertebrates core^{-1}) (a) and sandpiper droppings (droppings m^{-2} min^{-1}) (b) as distance from the shoreline increases. The observed ratio of dropping to invertebrate densities (c) does not closely match the expected ratio based on food. Error bars are 95% confidence limits.

Table 3-2: Differences between observed and expected ratios of dropping to invertebrate densities for northward (*10^3) and southward (*10^4) migratory periods. The p-value from the two-tailed z-test is shown in brackets.

Distance from the shoreline (m)	1	50	100	150	200	250	300	400	500	600	700	800	900	1000
Northward	-0.12 (<0.0001)	-0.10 (<0.0001)	-0.07 (0.0012)	-0.004 (0.94)	0.05 (0.41)	0.26 (0.009)	0.13 (0.09)	0.20 (0.05)	0.12 (0.26)	-0.06 (0.33)	-0.12 (<0.0001)	-0.12 (<0.0001)	-0.12 (<0.0001)	-0.12 (<0.0001)
Southward	-0.13 (0.008)	-0.12 (0.03)	-0.04 (0.57)	0.07 (0.49)	-0.09 (0.38)	-0.04 (0.52)	0.11 (0.24)	0.09 (0.40)	0.12 (0.41)	-0.02 (0.86)	-0.13 (0.04)	-0.15 (<0.0001)	-0.15 (<0.0001)	-0.15 (<0.0001)

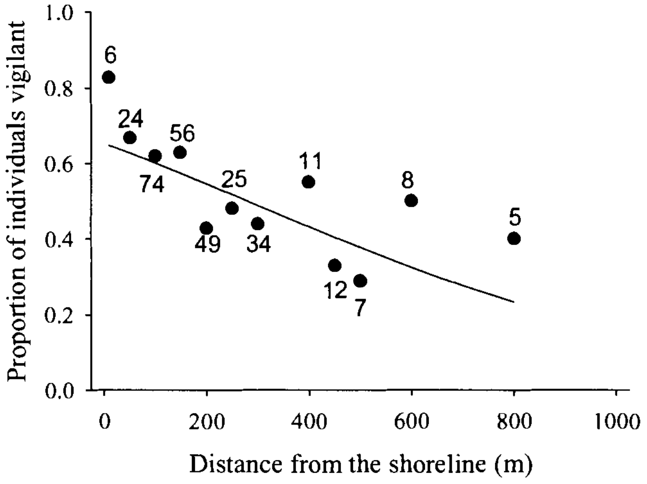

Figure 3-3: The proportion of individuals vigilant (1) as distance from the shoreline increases (solid circles). The sample size for each point is shown on the figure. The logistic regression curve (solid line) shows the probability of an individual being vigilant as distance from the shoreline increases

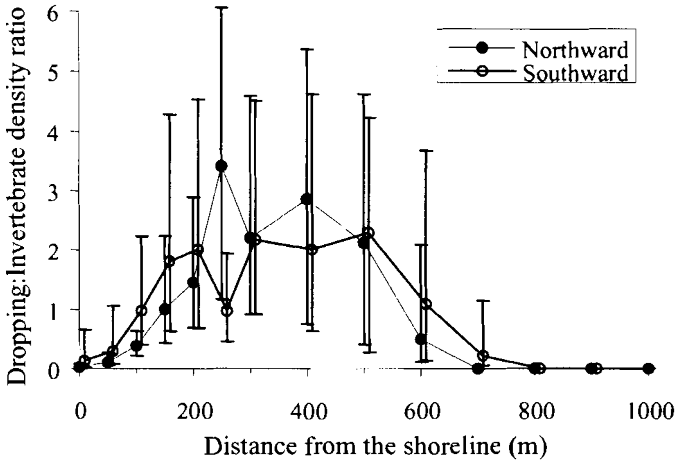

Figure 3-4: The overall pattern of spatial usage of Boundary Bay between migratory periods when the ratio of dropping to invertebrate densities is scaled to unity for each migratory period. Error bars are 95% confidence limits. Data points are offset slightly for clarity.

CHAPTER 4:

EXPERIMENTAL EVIDENCE THAT MIGRANTS ADJUST USAGE AT A STOPOVER SITE TO TRADE OFF FOOD AND DANGER

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Abstract

Rich habitats, intensive feeding and large fuel deposits are assumed to improve the capability for long distance migration by birds, but may also heighten their vulnerability or exposure to predators. Studies of habitat use by migrants have emphasized the importance of feeding, and relatively few studies have considered how migrants manage the dangers inherent in acquiring and storing fuel. Migrant western sandpipers (*Calidris mauri*) stop over on coastal mudflats characterized by a strong feeding-danger gradient, with both food and danger decreasing with distance from the shoreline. We experimentally manipulated danger by adding obstructive cover, and measured sandpiper usage along this gradient. We compared sandpiper usage along a transect extending 100 m on either side of the obstruction to that on matched control transects without obstructions. The dropping density accumulated during a low tide period provided a sensitive measure of sandpiper usage. Mean usage on control transects was 2.3 droppings m^{-2}, and was lower by 1.5 droppings m^{-2} (65%) on treatment transects. Usage did not differ between control and treatment transects at the furthest distances from the obstruction, the difference increased with proximity to the obstruction, and was greater by on average 0.9 droppings m^{-2} on the oceanward side (low food abundance) than on the shoreward side (high food abundance). All of these findings were predicted by danger management theory. Our study provides experimental evidence that migrant birds are sensitive to danger on stopover and has implications for understanding migration strategies.

Introduction

There is mounting evidence that every facet of the foraging behavior of animals has an effect on both the rate or ease of food gain, and the danger to which the forager must expose itself (Lima and Dill, 1990). This association is so profound that one can think of a trade off between energy intake and predation danger underlying decisions in almost any foraging situation. The choice of behavior is affected by the environmental levels of food abundance and danger. Generally (but not always) greater danger makes foragers more cautious, while higher food availability makes foragers more accepting of danger. Changes in the value of food or safety have analogous effects on behavior. For example, hungry individuals (for whom food is valuable) accept higher danger, while those for whom safety is at a premium (e.g. due to poor escape ability) are willing to accept poorer feeding opportunities to avoid danger. Studies in a variety of ecological situations have amply confirmed these general expectations (Laundre et al., 2001; Lima, 1988; Sih, 1980). Under dangerous conditions, foragers become more vigilant, join larger flocks, or move to safer (but poorer) feeding sites (see reviews in Brown and Kotler, 2004; Lima and Dill, 1990).

In spite of these findings, most research on the ecology of migration remains concerned with energetics, and comparatively little effort has examined the potential importance of danger, or its potential trade off against foraging needs (Lank et al., 2003). For example, neither Rappole's (1995) book 'The Ecology of Migrant Birds' nor 'Birds of two worlds: the ecology and evolution of migration' by Greenberg and Marra (2005) mention predators or predation danger as selective forces on migration. But since Lindström's (1990) paper, several authors have begun to recognize a role for predation danger in shaping where, when and how quickly migrants travel, and how they use and select stopover sites. The demand for high-energy fuel to power long migratory flights requires feeding in high-resource habitats, feeding intensely, or carrying heavy loads of fat. Thus, trade offs would appear to be central, because all of these activities elevate predation danger. Lindström (1990), for example, showed that dangerous stopover habitats were used by migrant bramblings (*Fringilla montifringilla*) only in years when the food supply there was unusually high (in this case, mast years for beech seeds). Quinn and Cresswell (2004) showed that intensively-feeding redshanks were selectively targeted by predators, while Burns and Ydenberg (2002) show that more heavily wingloaded western sandpipers (*Calidris mauri*) are slower to escape on take off.

Field studies support the notion that migrants are sensitive to dangers, and trade off food and danger by choosing safer habitats, slowing the rate of fuel deposition, or reducing fuel loads when predation danger is high (Cresswell, 1994; Lindström, 1990; Pomeroy, 2006; Schmaljohann and Dierschke, 2005; Ydenberg et al., 2002; Ydenberg et al., 2004). However, experimental work to confirm that migrants are sensitive to predation danger is scant. Cimprich et al. (2005) found that blue-grey gnatcatchers, *Polioptila caerulea*, reduced movements and foraging rates after exposure to a gliding model hawk.

Here we describe a field experiment designed to test the idea that migrants make small scale decisions at stopover sites in response to variations in both the potential level of danger and the abundance of food. Visual obstructions are dangerous for shorebirds if they obscure approaching predators (Lazarus and Symonds, 1992). Peregrine falcons (*Falco peregrinus*), merlins (*F. columbarius)* and other raptors hunt shorebirds, including western sandpipers (Buchanan et al., 1988; Cresswell, 1994; Cresswell, 1996; Dekker, 1988; Page and Whitacre, 1975; Whitfield, 1985), and achieve greatest hunting success using cover to conceal their approach (Cresswell, 1994; Dekker and Ydenberg, 2004; Whitfield, 1985; Whitfield, 2003). To test whether migrants adjust habitat usage to trade off food and safety at a stopover site, we placed obstructive cover on our study mudflat to manipulate danger. We compared usage by sandpipers on those treatment transects to usage on nearby control transects.

We predicted that the presence of the obstruction would lower the amount of feeding by western sandpipers in the vicinity. The size of this effect should increase with proximity to the obstruction, because the ability of a sandpiper to detect an approaching predator declines closer to the obstruction. Food abundance should also affect the trade off, because the value of feeding under predation danger is greater when food abundance is high. The natural gradient of food abundance across the mudflat on our study site (declining food abundance with distance from the shoreline) allowed us to compare usage on the shoreward (higher food) and oceanward sides (lower food) sides of the obstruction.

Methods

Study System

The western sandpiper is a small (~ 25 g when on migration) calidridine shorebird, stopping in large numbers at Boundary Bay, southwestern British Columbia, Canada (N 49°4.13′ W 122°58.05′) twice annually while travelling between tropical non-breeding sites and arctic breeding grounds (Butler et al., 1987; Wilson, 1994). Part of the estuarine complex of the Fraser River, Boundary Bay contains large tidal flats, with approximately 60 km^2 of mud and sand exposed at the lowest tide. The bay is bordered by a dike and a 10-200 m wide strip of saltmarsh. During northward migration (mid April to mid May), hundreds of thousands of western sandpipers stopover en route to breeding areas in Alaska, and feed on a variety of small epibenthic and infaunal invertebrates (Mathot and Elner, 2004; Sutherland et al., 2000). Peregrine falcons and merlins hunt sandpipers there (Lank et al., 2003; Ydenberg et al., 2002).

Experimental design

From the point-of-view of migrant sandpipers, Boundary Bay is characterized by a strong on-offshore food-safety gradient, with both food abundance and predation danger decreasing with distance from the shoreline (Figure 4-1b and 4-1c). Other intertidal mudflats used by shorebirds likely show similar spatial gradients in food abundance (Swennen et al., 1982). For many large open tidal flats, the bed slope is shallow and constant in an on-offshore direction. Fine sediment particles such as silt and mud settle close to the shoreline (Kennish, 1986; Reise, 1985), and high macro-invertebrate densities are associated with these fine grained sediments (Kennish, 1990; Yates et al., 1993).

Predation danger also falls with distance from the shoreline. In their analysis of peregrine falcons hunting dunlins (*Calidris alpina*) during winter at Boundary Bay by Dekker and Ydenberg (2004) found that falcons hunt most intensively and successfully close to shore, where they use the available cover to advantage. Peregrines hunting over the open bay had to make repeated attacks and had to persist in often-lengthy pursuits to capture sandpipers, whereas along the fringes of the bay they were able to succeed in surprise attacks, and did not persist if the initial attack failed. Dekker and Ydenberg (2004) showed that the kill rate of peregrines declined as the tide fell and dunlins fed at increasing distance from the vegetated zone along the shore (Figure 4-1c). The natural pattern of western sandpiper usage across the mudflat peaks at intermediate distances (Figure 4-1d), avoiding the high food – high danger areas close to shore, as well as the low food – low danger zone far offshore.

To manipulate danger, we placed an obstruction on each of three treatment transects in Boundary Bay during northward migration in 2003 (Figure 4-1a). The three treatment transects were approximately 5 km apart. Transects were oriented perpendicular to shore, and extended 250 m onto the mudflat. The obstruction consisted of a 20 m length of 1 m high black plastic tarp, supported by metal poles at 5 m intervals, placed parallel to the shore at a distance of 150 m. A control transect, with obstruction consisting of poles only, paralleled each treatment transect at a distance of 200 m. Due to the natural gradient in food abundance, the mean macro invertebrate abundance (invertebrates cm^{-3} ± 95% C.I.) on the shoreward side of the obstruction (50 to 150 m along the transect) was almost twice that on the oceanward side (150 to 250 m; shore side: 11.28 ± 1.39, ocean side: 6.31 ± 0.96, based on data in Pomeroy 2006; see Figure 4-1b).

The tidal rhythm at Boundary Bay is semi-diurnal, with the time of the highest tide shifting later by approximately 45 minutes per day. The mudflat at Boundary Bay is wide (~4 km at low water), but due to its shallow slope, the top portion of the mudflat where our study transects were located was immersed and drained rapidly as the tide shifts. The obstruction was erected just as the tide began to fall, was left in place for 6 hours and was removed between replicates. The procedure was replicated three times on two transects, and four times on the third, for a total of 10 replicates.

We evaluated sandpiper usage of the mudflat by measuring dropping densities along both control and obstruction transects at the end of each 6h foraging period. Western sandpipers are by far the most abundant shorebird on the mudflats during the northward migration period, and their small droppings are easily distinguished from those of other, larger species. Western sandpipers produce droppings at a rapid, regular rate while foraging (mean droppings min^{-1} ± 95% C.I. = 0.48 ± 0.10, N=66). These are washed away with each tidal inundation (unpubl. data), and hence provide a sensitive measure of use since the previous high tide. We counted droppings in 1m^2 quadrats placed along each transect at distances of 1, 10, 20, 30, 40, 50, 75, and 100 m from the obstruction, on both the shoreward and oceanward sides. Five 1 m^2 plots were measured at each distance interval, for a total of 40 on each side, 80 per transect, and 160 per treatment/control pair or transects.

Dropping densities (droppings m^{-2}) at each station were adjusted to account for the total duration of tidal exposure (droppings m^{-2} min^{-1}) even though the tide fell quickly (see above), exposing the entire 200 m transect within 20 min. We use corrected values in all analyses presented here, but for simplicity display uncorrected values in our graphical results.

Statistical analyses

A matched pairs analysis was used to test for an effect of the obstruction treatment on sandpiper usage as measured by mean dropping densities on entire control and obstruction transects. Because paired control and obstruction transects were sampled on multiple days and transects for a total of 10 replicates we included replicate as a random factor in subsequent analyses.

A mixed model analysis was used to test the effects of distance from the obstruction and food abundance (high or low) on the difference in the mean counts of dropping densities at each distance (control - obstruction). We included distance from the obstruction^2 (to test for non-linearity) and all interactions between the three main factors as dependent variables. All variables were entered into the model and non-significant variables were removed sequentially ($p>0.05$) until the minimum adequate model was derived. The change in deviance, which approximates a chi-square distribution, was used to determine the significance of changes made to each model. Means ± 95% confidence intervals are presented throughout. Genstat V. 8.2 (GenStat, 2005) was used for all statistical analyses.

Results

Our activities had no significant effect on western sandpiper usage of the mudflat as a whole. We compared measures of usage (as described above) in 2003 with that same measure in 2004 when no obstructions were erected. The overall density and pattern of sandpiper usage was similar to that observed in 2003 (see Figure 4-2) indicating that normal usage of the mudflat continued when the obstructions were present.

Overall, western sandpiper usage of treatment transects was lower than on control transects by on average 1.5 droppings m^{-2}, or about 65% (Figure 4-2; matched pairs, $t = 2.30$, d.f. = 9, $p = 0.02$). As predicted, the difference in dropping densities between control and treatment transects was greatest close to the obstruction, and decreased with distance on both the shoreward and oceanward sides (Figure 4-3; $\chi^2 = 4.7$, d.f. = 1, $p = 0.03$, $N = 160$).

Food abundance also affects the usage pattern as predicted. The difference in dropping density between treatment and control transects was greater on the low-food oceanward side of the obstruction than on the high-food shoreward side (Figure 4-3; $\chi^2 = 4.5$, d.f. = 1, $p = 0.03$, $N = 160$). Non-significant variables removed from the model were distance from the treatment^2 ($p = 0.29$), distance from the treatment^2*food interaction ($p = 0.48$) and distance from the treatment*food interaction ($p = 0.75$). These results suggest that danger was the factor that affected the level of usage as predicted by the trade off hypothesis.

Discussion

Our results show that during northward migration, usage of Boundary Bay by western sandpipers was lower on treatment transects with visual obstructions than on control transects, and the difference in usage was greatest close to the obstruction. Western sandpipers also adjusted their usage of the mudflat according to food abundance on either side of the obstruction, with the difference in usage between control and treatment transects greater where food abundance was low. These experimental results support the predictions of the trade off hypothesis that mudflat usage is affected by both predation danger and food abundance, with these factors traded off one against the other.

Giving-up density (GUD) experiments are a powerful method to titrate the costs of predation by foraging animals (Brown, 1988). GUD experiments have generally shown that foragers 'give up' at higher densities of food when they are in dangerous habitats (Kotler et al., 2004; Kotler et al., 1991), have ample reserves (Kotler, 1997), and when predators are abundant (Kotler, 1992; Kotler et al., 2004; Kotler et al., 1991) indicating that the costs of foraging are greater in more dangerous situations. GUDs are usually measured by quantifying removal of food from experimental food patches (Brown and Kotler, 2004). However for the western sandpiper manipulating food densities on the large scale of a mudflat is impossible. Our experimental manipulation of danger on a gradient of decreasing food is analogous to giving-up density (GUD) experiments as we are able to investigate the relative spatial usage of sandpipers at various levels of food abundance. Our results confirm the general expectations of GUD experiments that animals should adjust time allocation between habitats to trade off food and danger, in that usage of safe habitats should be greater than dangerous ones, and that more food is required to entice animals to allocate their time in dangerous places.

General results from GUD experiments allow us to predict how individual migrant western sandpipers should adjust habitat usage during their stopover. For example, hungry individuals should take more risks to feed in the food rich but dangerous habitats close to shore than individuals that are satiated. Fat individuals with poor escape performance should take fewer risks and feed in safer habitats further from the shoreline than lean agile sandpipers.

Our study joins a growing body of evidence that shows that like many other animals, migrants, make fine-tuned adjustments of habitat usage to balance the costs and benefits of feeding in a particular place (Apollonio et al., 2005; Cimprich et al., 2005; Cresswell, 1994; Dussault et al., 2005; Heithaus, 2005; Kamenos et al., 2004; Makino et al., 2003; Sapir et al., 2004; Sergio et al., 2005; Spencer et al., 2005). As a general rule, we conclude that food and danger attributes of a site have a strong influence on habitat selection by foraging animals. Since these factors are so important to animals feeding within a site, habitat, or microhabitat, it is also likely that these factors affect how animals make between site foraging decisions. Migrants likely use features of the environment to approximate levels of food abundance and predation danger to decide whether to use the site as a stopover. For example, high densities of macro invertebrates, on which many shorebirds feed, are often associated with fine-grained sediments (Kennish, 1990, Yates et al., 1993). It is possible that migratory shorebirds can visually assess food abundance of potential stopover sites from the air, for example by the reflectance or sediment properties of a beach or mudflat (Pomeroy and Butler 2005, Rainey et al., 2003). Proximity to cover may be used by migrants to remotely assess the predation danger at a site. Large mudflats with a vast expanse of foraging habitats many kilometres from the shoreline is indicative of relatively safe site for a migrant shorebird, whereas a small mudflat surrounded by marsh grass would be deemed a potentially dangerous place to stop. Upon selecting a stopover site migrants can assess the levels of food abundance, and gauge the level of danger there based on their encounters with predators, then they can make appropriate adjustments of anti-predator behaviors to carefully balance food and danger over short temporal and small spatial scales.

We show here that migrant western sandpipers avoid obstructions and adjust their habitat usage according to tradeoffs between food abundance and predation danger. This study suggests that migratory shorebirds use features of the habitat such as obstructive cover as a measure of predation danger, and that they mediate their probability of mortality by predation by adjusting habitat usage on the scale of a stopover. Results such as these can be applied to predict the behavior of migrants at stopover sites, and at the landscape level to predict site selection between stopover sites on the scale of the entire migration.

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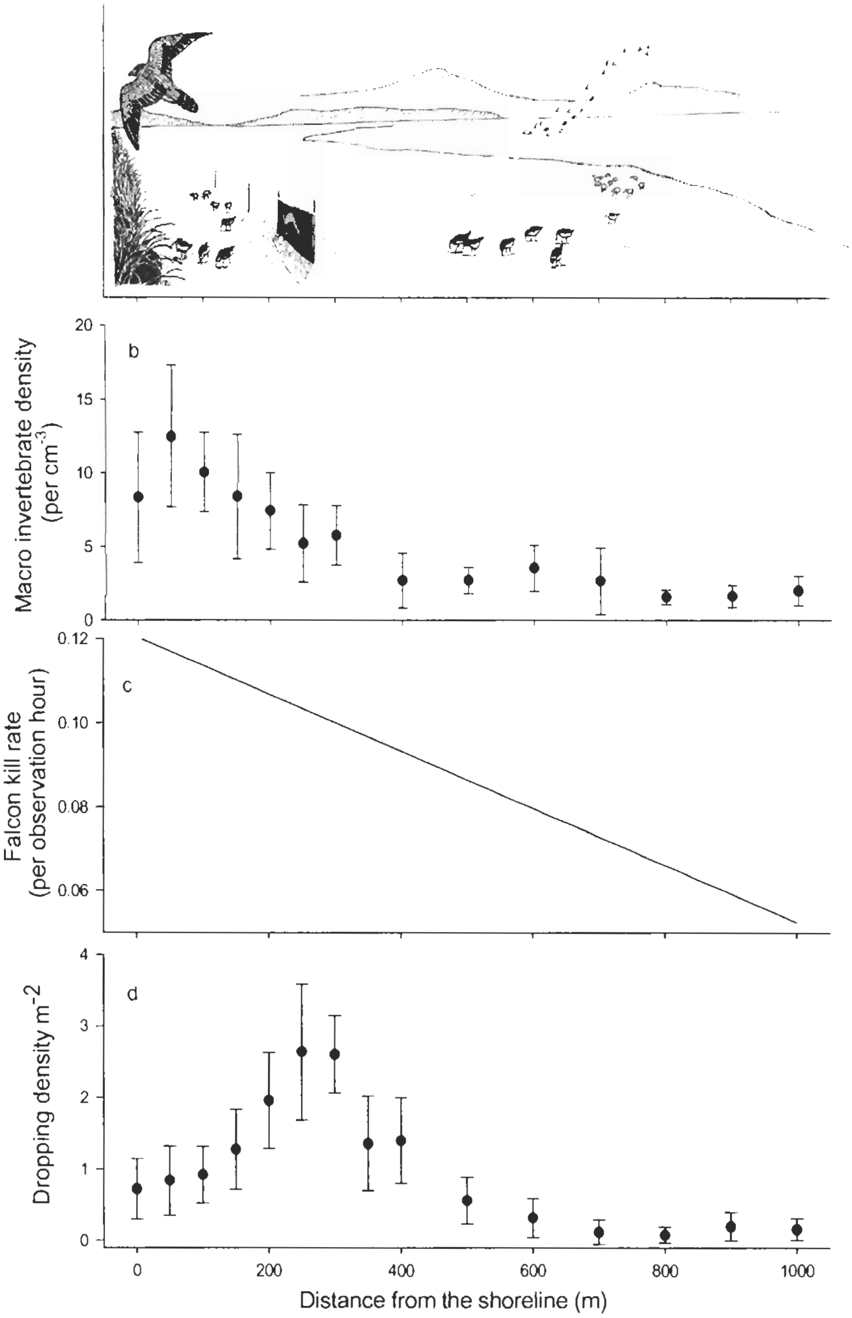

Figure 4-1: a) Experimental design with location of control and treatment transects relative to the shoreline at Boundary Bay, b) the distribution of macro invertebrates at the study site as sampled in 2002 (adapted from Pomeroy 2006) c) the kill rate of peregrine falcons hunting dunlin in winter at the study site (adapted from Dekker and Ydenberg 2004) d) natural dropping densities as sampled in 2004.

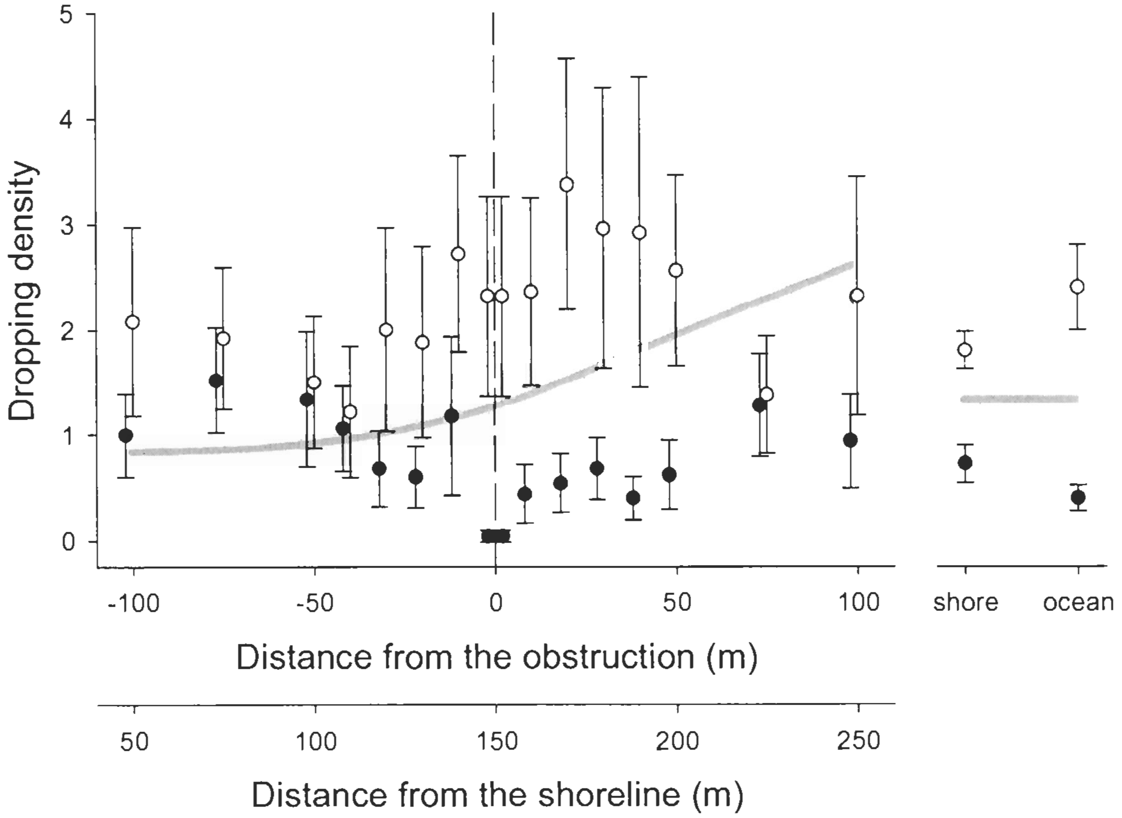

Figure 4-2: The effect of an experimental obstruction at 150 m (indicated by dashed vertical line) on usage of western sandpipers at a stopover site during northward migration. Open circles are mean dropping densities on control while closed circles are densities on treatment transects. The grey line represents the natural pattern of dropping densities at the study site sampled in 2004. Error bars are 95% confidence intervals. Points are jittered for clarity. The offset panel displays mean dropping densities in the high (shoreward) and low (oceanward) food sides of the obstruction.

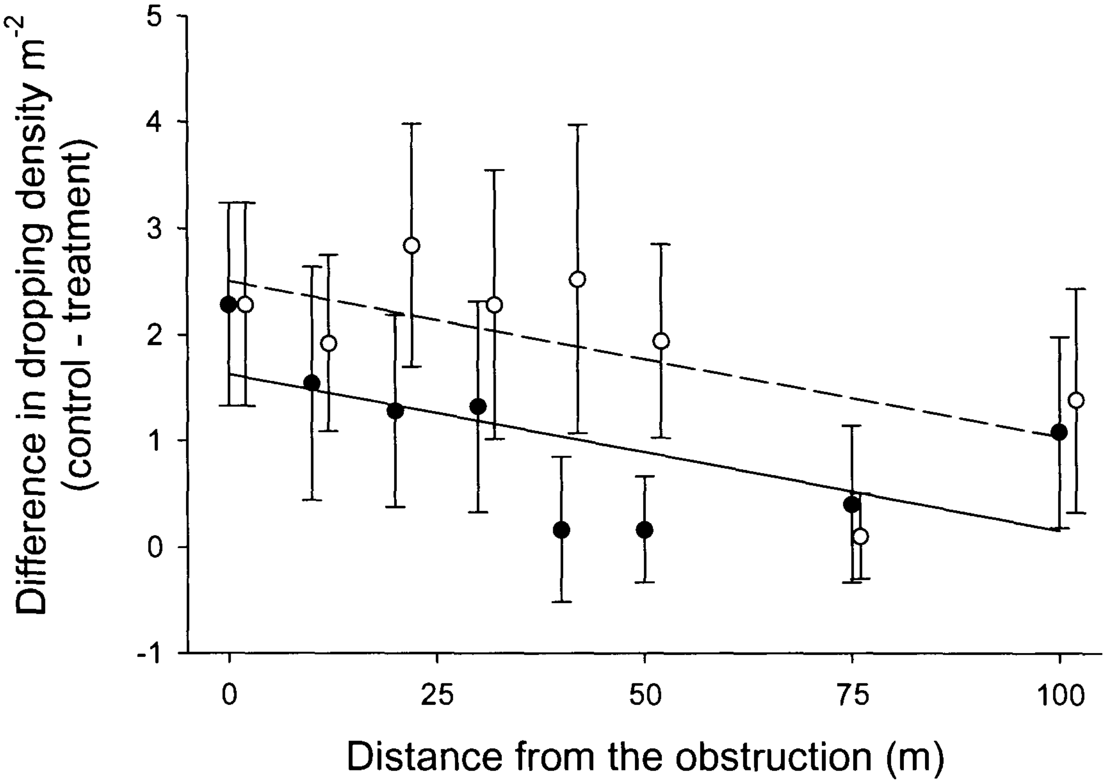

Figure 4-3: The difference in usage (droppings m^{-2}) between matched control and treatment transects on high (shore - filled circles) and low food (ocean - open circles) sides as distance from the obstruction increases. The lines are those predicted from the statistical model. Error bars are 95% confidence intervals. Points are jittered for clarity.

CHAPTER 5:
A TEST OF THE ASSUMPTIONS UNDERLYING STOPOVER SITE USAGE BY MIGRANTS

Andrea C. Pomeroy, Gregory G. Baker, Ronald C. Ydenberg

Abstract

Birds on migration face the problem of acquiring fuel for migration while avoiding mortality by predators. To decide where to feed a migrant should consider the expected rate of energy gain, the likelihood of predator attack, the probability of escaping a predator and the individual's current and future state. Here we use a dynamic state variable model to test the assumptions underlying within site habitat usage by migrant sandpipers. In the model, we varied the probabilities of acquiring energy, attack by a predator, and escape in habitats within the stopover site and analyzed feeding decisions by migrants. Model predictions were tested using data collected from western sandpipers feeding at Boundary Bay. The distribution of sandpipers at various distances from shore (usage) was measured by counting dropping densities (per m^2), and the state dependent usage of the site was assessed by measuring the fuel load of birds at different distances. Model results predicted the observed patterns of usage and mass dependent usage of the stopover site. The pattern of state dependent usage (lean birds using dangerous-high resource habitats and heavy birds using safe-low resource habitats) is a robust pattern in the model, and persists even with no negative effect of state on escape performance. This result suggests that asset protection rather than state-dependent escape performance underlies usage of stopover sites.

Introduction

While foraging, it is necessary that animals consider the danger posed by their predators, and adjust their foraging behaviours accordingly, to avoid becoming prey themselves. The possibility of mortality from predators forces animals to behave in ways that balance the benefits of feeding with the costs of predation (Brown 1999). Instead of maximizing energy gain or resource acquisition a forager may accept a lower rate of gain if it means greater safety from predators. To increase safety from predators, foragers may become more vigilant, join larger groups, or switch to safer (but poorer) feeding sites, all of which are known to decrease the rate of energy gain (see reviews in Brown & Kotler 2004; Lima & Dill 1990).

Feeding-danger tradeoffs are central for migrant birds on stopover. Rapid fuel deposition increases the speed of migration and provides migrating birds with reserves of energy (Alerstam & Lindström 1990). However, to acquire high energy fuel requires feeding in resource-rich habitats, feeding intensely, and carrying heavy loads of fat, all of which are thought to increase a migrants probability of mortality by predation (Witter & Cuthill 1993). At stopover sites migrant birds should choose feeding habitats that optimize fuel deposition (Alerstam & Lindström 1990). Within a stopover site habitats may vary in food abundance and the danger posed by predators. To decide where to feed a migrant should consider the expected rate of energy gain, the likelihood of attack by a predator there, and the probability of escaping the predator if attacked. Foragers can not alter the food attributes of a habitat or affect the probability of being attacked by a predator, however they can implement a variety of anti-predator behaviours to adjust their probability of escape (Lind & Cresswell 2006).

The probability of escaping a pursuing predator is a function of the predator's speed, the time for prey to detect the predator, and the time for prey escape (Bednekoff 1996; Lind 2004), which is negatively affected by increases in fuel load (Burns &

Ydenberg 2002; Kullberg et al. 1996; Kullberg et al. 2000). The probability of escaping a predator is also affected by a forager's proximity to cover (Lind 2004). For small passerine birds a successful escape is achieved once they reach the safety of cover, while for shorebirds on mudflats, cover obstructs the view of oncoming predators, so increasing their distance from cover increases their probability of escape.

Western sandpipers (*Calidris mauri*) on stopover face the crucial decision of where to feed at stopover sites in light of the danger posed by falcon predators. The western sandpiper is a small (~ 25 g when on migration) calidridine shorebird, stopping in large numbers at Boundary Bay, southwestern British Columbia, Canada (N 49°4.13′ W 122°58.05′) twice annually while travelling between tropical non-breeding sites and arctic breeding grounds (Butler et al. 1987; Wilson 1994a). Part of the estuarine complex of the Fraser River, Boundary Bay contains large tidal flats, with approximately 60 km^2 of mud and sand exposed at the lowest tide. The bay is bordered by a dike and a 10-200 m wide strip of saltmarsh. During northward migration (mid April to mid May), hundreds of thousands of western sandpipers stopover en route to breeding areas in Alaska, and feed on a variety of small epibenthic and infaunal invertebrates (Mathot & Elner 2004; Sutherland et al. 2000). On stopover at Boundary Bay western sandpipers are hunted by peregrine falcons and merlins (Lank et al. 2003; Ydenberg et al. 2002).

We used a dynamic state variable modelling (DSV) approach (Clark & Mangel 2000; Houston & McNamara 1999) to test the assumptions underlying feeding decisions by migrants on stopover. This technique has been widely applied to questions of migratory fuelling and stopover behaviour (e.g. Clark & Butler 1999; Farmer & Wiens

1999; Weber et al. 1998) and is ideal to address questions such as these, since feeding decisions made by migrants depend on both their current and future state.

We varied the probability of a sandpiper acquiring food, being attacked by a predator, and, if attacked, its probability of escape in habitats within the stopover site and analyzed the feeding decisions by migrants. Model predictions were tested using data collected from western sandpipers feeding on stopover during northward migration at Boundary Bay where food and danger varies with distance from the shoreline. We tested data on the distribution of sandpipers at various distances from shore (usage) by counting faecal dropping densities, and their state-dependent usage of the stopover site by measuring the fuel load (size corrected body mass) of birds at different distances.

Methods

The model

Using a state variable dynamic approach, we modelled fitness-maximizing foragers, where fitness was defined as the probability of successful migration at the final time, T. Energy stores varied from 0 to 15 g (representing a sandpiper mass ranging from 20-35 g) in discrete steps of 1 g.

Time proceeded in discrete steps of 1 hour until the final time, T, of 50 hours. During the peak of northward migration the tide exposes the bay during the day for about 10 hours and little mud is exposed during the night. Thus, the time period of the model is based on 5 tidal cycles of 10 hours each, and assumes neither mass gain nor loss, or attack by predators, during the night or high tide periods. Telemetry studies in the Fraser

Estuary region suggests that the length of stay by western sandpipers during northward migration ranges from 1-5 days (2.2 days ± 0.23 SE, n = 25 (Warnock & Bishop 1998); 3.6 days, ± 0.66 SE, n = 10 (Iverson et al. 1996)).

At the onset of each time step the forager decides at which distance to feed, d, which ranges from 0-1000 m from shore in 50 m interval steps. The action that maximizes the probability of successful migration depends on the actions taken in the future; this problem can be solved using dynamic programming by working backwards in time (Clark & Mangel 2000; Houston & McNamara 1999). We therefore start with the final times step, T, where the probability of surviving until the final time is 1. The terminal reward function (Figure 5-1) is a function of state (mass, g), x, given by:

$$F(x,T)=\frac{1}{(1+e^{\left(\frac{27.5-x}{1.5}\right)})}$$

Surviving to the final time for all other times steps t, is the maximum probability of successful migration, until final time of all possible actions taken at t assuming that the animal behaves optimally from $t+1$ onward (Clark & Mangel 2000; Houston & McNamara 1999).

$$F(x,t)=\max_{d}\left(V_d\left(x,t\right)\right)$$

where:

$$V_d\left(x,t\right)=\left(\left(a_d E_{x,d}\right)F\left(x+\Delta x,t+1\right)\right)+\left(\left(1-a_d\right)F\left(x+\Delta x,t+1\right)\right)$$

V_d is the survival probability (until the final time) of decision d (feeding location). This decision leads to a change in energy stores by Δx in the next time step $(t+1)$, and depends on the probability of an attack (a) at d, and the probability of escaping an attack (E) which depends on both state x and time, t. In order to make $(x+\Delta x)$ discrete we used linear interpolation (Clark & Mangel 2000).

The distribution of food $g(d)$

Western sandpipers are considered invertebrate generalists opportunistically feeding on a variety of epifaunal and infaunal macro invertebrates (Mathot & Elner 2004; Sutherland et al. 2000; Wilson 1994b). Food abundance for western sandpipers at Boundary Bay declines with distance from the shoreline (Pomeroy 2006). The decline in food is described by the regression equation:

$$y = 10^{(2.4-0.001d)}$$

We assume that intake rate is related to invertebrate abundance by a constant b, giving the following relationship:

$$g(d) = b\left(10^{(2.41-0.001d)}\right)$$

We varied b to test how differences in food abundance (high, medium and low, b=0.002, 0.0015, 0.001) affect the usage and state-dependent usage of stopover sites by sandpipers (Figure 5-2).

The probability of attack $a(d)$

We assumed that the probability of an individual sandpiper being attacked during each time step was equal at all distances. We varied $a(d)$ (high, medium and low, $a(d)$ =0.1, 0.01, and 0.001) to test how increasing attack rates affected usage and state dependent usage by sandpipers (Figure 5-3).

The probability of escape $E(x,d)$

We tested three different models to describe the effect of feeding distance and state on the probability of escaping a predator (Figure 5-4). We varied the effect of state on escape to evaluate how negative effects of increasing fuel load affect usage and mass-dependent usage by birds.

1. Sigmoid curve

The probability of escaping an attack is related to state, x and distance, d :

$$E(x,d) = \frac{1}{\left(1 + e^{\left(\frac{-t_{ahead}}{1.5}\right)}\right)}$$

Where $t_{ahead} = t_{attack} - t_{escape}$. The time for a falcon to reach the sandpiper t_{attack} is a function of falcon speed (v_f) and the feeding distance of the sandpiper (d_s).

$$t_{attack} = \frac{d_s}{v_f}$$

The time for a sandpiper to escape an attack $\left(t_{escape}\right)$ is a function of its acceleration (a_s – which is negatively affected by increasing state, x) and the velocity of the falcon v_f (m/s).

$$t_{escape} = \frac{v_f}{a_s}$$

Where v_f = 30 m/s, and $a_s = 9 - 0.1x$ m/s^2 (Burns and Ydenberg 2002)

2. Exponential increase

In this case the probability of surviving an attack increases exponentially to a maximum as described by:

$$E(x,d) = 1 - \left(e^{-\left(\left(c_1 - \left(h_1\left(x-20\right)\right)\right)d\right)}\right)$$

Where the constant c_1 = 0.0075 and h_1 , the effect of state on escape, = 0.0001.

3. Linear increase

Here the probability of escape increases linearly with increasing feeding distance.

$$E(x,d) = dc_2 - \left(dc_2h_2\left(x-20\right)\right)$$

Where the constant c_2 =0.001 and h_2 , the effect of state on escape, = 0.01.

Forward simulation

For birds fuelling for migration the optimal feeding decision at a particular time is affected by the decisions made in the future. Dynamic programming works ‘backwards in time’ to calculate the optimal decision (i.e. where to feed) at each time step that maximizes the probability of successful migration (i.e. fitness) for every reserve level at each time period. To observe the consequences of using the optimal decision, Monte Carlo simulations were run forward in time. For each simulation 53% of the individuals were started at a mass of 20 g, 24% at a mass of 21 g, 12% at 22 g, 6% at 23 g, and 1% at 26 and 27g. Individuals were allowed to run through time periods 1-50 using the state-dependent choices calculated by dynamic programming. For 1000 simulations the percentage of foragers using each distance (decision) was calculated for each time period in each simulation.

For each Monte Carlo simulation an individual makes a sequence of decisions at each time period. We randomly selected 1000 decisions from the simulations and recorded the energy state of individuals making that decision. We used these samples to test against usage data collected in the field. To test the models against mass data collected in the field we further sub sampled 30 individuals at feeding decisions of 50, 150, 250 and 350 m from shore (where birds were captured), and recorded their energy state, to mimic the collection of field data.

Usage data

To test the assumptions of the model we compared model results to data collected on sandpiper usage and mass along a transect perpendicular from shore and recorded falcon attacks at the study site during northward migration (April 19 – May 5) in 2004 and 2005. Sandpiper usage was measured by counting dropping densities along transects at the end of each 6 h foraging period. We counted droppings in 5 1-m^2 quadrats placed along each transect at distances of 1, 50, 100, 150, 200, 250, 300, 350, 400, 500, 600, 700, 800, 900 and 1000 m from the shoreline. Dropping densities (droppings m^{-2}) at each station were adjusted to account for the total duration of tidal exposure (droppings m^{-2} min^{-1}). The frequency of usage for each distance was determined by calculating the percent of the dropping density (per m^{-2} min^{-1}) of the total at each distance.

To measure state-dependent usage by sandpipers along the transect, we set noose carpets (Mehl et al. 2003) on the mudflat to capture birds at distance intervals of 50, 150, 250, and 350 m from the shoreline. Sandpipers were removed from noose mats immediately after capture and weighed within 10 minutes. Tarsus was measured using callipers and included in analysis as a covariate to account for the effect of body size on mass.

Statistical analyses

Analysis of variance (ANOVA) was used to test for an effect of varying model parameters (food abundance, attack rate, escape) on feeding decisions by sandpipers. Analysis of covariance (ANCOVA) was used to test for an effect of varying model parameters (food abundance, attack rate, escape) on the mass of sandpipers at different feeding distances. The model effect (i.e. low, medium or high food abundance) was included as a factor in these analyses.

To compare the frequency of usage at each distance with the model predictions correlations were made and Pearson's correlation coefficients were reported.

To test if empirical data on state dependent usage were consistent with model predictions we compared field data to model predictions at each distance where birds were captured (50, 150, 250, 350 m). For field data, least square means (and their standard errors) of body mass were calculated from an ANCOVA including tarsus as a covariate, and year as a factor. Including tarsus as a covariate accounts for any differences in mass between individuals that differ in structural body size. The least square means (size corrected body mass) were then compared to the model predictions at each distance using z-tests. Means and 95% confidence intervals are used throughout. JMP*IN* V. 4.04 (SAS 2001) was used for all statistical analyses.

Results

To test how changes in each parameter affected usage and state dependent usage by sandpipers, baseline levels for each parameter were held constant while the parameter of interest was varied. The baseline parameters used were as follows: for the probability of acquiring energy, $g(d)=0.0015\left(10^{(2.41-0.001d)}\right)$, being attacked $a(d)=0.01$, and escaping predators $E(x,d)=1-\left(e^{-((0.0075-(0.0001(x-20)))d)}\right)$.

Food abundance

As food abundance is increased in the model sandpipers adjust their usage to feed further away from the shoreline (Figure 5-5). On average, birds feed in safer areas of the mudflat when food abundance is high, and move to feed in more dangerous locations when overall food abundance is low (ANOVA: $F_{2,\,2997} = 422.3$, $p < 0.0001$). The mean feeding distance (m) was furthest from shore when food abundance was high ($b = 0.002$; mean distance ± 95% C.I. = 354 ± 9.2) and birds moved closer to the shoreline when food abundance was lowered ($b = 0.0015$; mean distance ± 95% C.I. = 276 ± 8.4, $b = 0.001$; mean distance ± 95% C.I. = 186 ± 6.6).

In our model the sandpiper mass (g) increases with increasing distance from the shoreline (ANCOVA: $F_{1,\,2994} = 688.1$, $p < 0.0001$), and on average birds are heavier when food abundance is high ($F_{2,\,2994} = 26.6$, $p < 0.0001$; mean mass ± 95% C.I.: high food = 27.8 ± 0.2, medium food = 27.4 ± 0.2, low food = 25.9 ± 0.18). There is a significant interaction between feeding distance and food level on the effect of mass ($F_{2,\,2994} = 59.8$, $p < 0.0001$) indicating that the slope of the relationship between sandpiper mass and feeding distance was more steep when food abundance was low compared to when it was high (Figure 5-6).

Attack rate

As attack rates by falcons are increased in the model sandpipers adjust their usage by increasing their feeding distance further from the shoreline, to safer areas of the mudflat (Figure 5-7). On average, birds feed further away from shore when danger is high despite lower levels of food abundance, when attack rates are low birds feed in more dangerous locations where food is more abundant (ANOVA: $F_{2,2997} = 312.7$, $p < 0.0001$). The mean feeding distance was furthest from the shoreline when attack rates were high (high attack rate; mean distance ± 95% C.I. = 412 ± 7.1) and became closer as attack rates decreased (medium attack rate; mean distance ± 95% C.I. = 274 ± 9.0, low attack rate; mean distance ± 95% C.I. = 221 ± 15.5).

The average sandpiper mass increases with increasing distance from the shoreline (ANCOVA: $F_{1, 2994} = 1283.0$, $p < 0.0001$), and on average birds are lighter when attack rates are high ($F_{2, 2994} = 641.3$, $p < 0.0001$; mean mass ± 95% C.I.: attack rate = 0.1, mass = 25.6 ± 0.2, attack rate = 0.01 mass = 27.5 ± 0.2, attack rate = 0.001, mass = 28.8 ± 0.2). There is a significant interaction between feeding distance and attack rate on the effect of mass ($F_{2, 2994} = 34.4$, $p < 0.0001$) indicating that bird mass increased more quickly with feeding distance when attack rates were low compared to when they were high (Figure 5-8).

Escape performance

The exponential escape model most closely matched the usage patterns observed in 2004 (Figure 5-9: $r_s = 0.86$ $p<0.0001$) and 2005 ($r_s = 0.80$, $p = 0.0003$). The sigmoid escape model was also significantly correlated with the data in 2004 ($r_s = 0.65$, $p = 0.008$) but was not as strongly related, and was not significantly correlated with the data in 2005 ($r_s = 0.42$, $p = 0.11$). The data from the linear escape model did not correlate significantly with either year of usage data ($p > 0.2$).

Using the exponential escape model, increasing the negative effect of state on escape performance has a very small, but significant effect on increasing the feeding distance of sandpipers (Figure 5-10: ANOVA; $F_{2, 2997} = 49.2$, $p < 0.0001$). There was no difference between feeding distances of sandpipers when the effect of mass on escape was increased from no effect (Figure 5-11: mean distance ± 95% C.I. = 270 ± 8.6) to a negative effect of 0.0001 for every 1-gram increase in mass (mean distance ± 95% C.I. = 274 ± 8.4). Increasing the effect of mass on escape to $-0.0004\,x$ (i.e. increasing state by 15 g reduced the probability of escape by 50% at a feeding distance of 300 m) increased sandpiper feeding distance by approximately 65 m (Tukey HSD $p < 0.05$, mean distance ± 95% C.I. = 338 ± 14.2).

Model test

The attack rate of falcons on foraging sandpipers was over 3 times greater in 2004 (2.5 attacks/day) than in 2005 (0.8 attacks/day; Pomeroy, unpubl. data). We tested the predictions of the model against sandpiper data on usage and state-dependent usage between these two years. Based on the unpublished data, the probability of an attack $(a(d))$ on an individual sandpiper was calculated as the number of attacks per hour in the 10 hour day (i.e. 0.25 attacks/hour in 2004) and assumes that an individual is attacked in a flock of 25 birds (i.e. a 1 in 25 chance of attack on an individual in the flock). For the high falcon year (2004) $a(d) = 0.01$ and for the low falcon year $a(d) = 0.003$. The baseline parameters were used for the probability of acquiring food, and escaping predators.

Usage

The usage distribution of sandpipers at feeding distances across the mudflat for the high falcon year (2004) was more closely correlated to the high falcon attack rate model (Figure 5-12, $a(d) = 0.01$; $r_s = 0.86$, $p < 0.0001$) than was the usage data from the low falcon year (2005; $r_s = 0.80$, $p = 0.0003$). Consistently, the usage distribution for the low falcon year (2005) was more closely correlated to the low falcon attack rate model ($a(d) = 0.003$; $r_s = 0.82$, $p = 0.0002$) than was the usage data from the high falcon year (2004; $r_s = 0.50$, $p = 0.06$).

Mass dependent usage

The high falcon year mass data (2004) was more consistent than the low falcon year (2005) data to the predictions from the high falcon attack model (Figure 5-13). The model predictions only differed significantly from the high falcon year data at the 50 m feeding distance (z-test, $p<0.01$), while the low falcon attack year data was only consistent with the model predictions at 50 m ($p = 0.40$). However, the low (2005) and high (2004) falcon year data were equally consistent with the predictions from the low falcon attack model. The model predictions differed significantly from the low falcon year data at 150 and 350 m ($p < 0.002$) feeding distances. While the high falcon attack rate data differed significantly with the model predictions only at 250 m ($p = 0.01$). The most striking result here is that the observed pattern of heavier birds feeding further from shore persists in the model, even with no negative effect of increasing mass on escape performance.

Discussion

Our model confirms, in general, our assumptions that food abundance, predator attack rates, and prey escape performance underlie feeding decisions made by migrant birds on stopover. The model supports the hypothesis that migrant sandpipers trade off food abundance and predation danger in their usage of Boundary Bay, and that the decisions they make on migration are affected by their state. In general, when danger (probability of attack) increases, migrants move to safer habitats and when food abundance is lowered, migrants are willing to feed in more dangerous places.

The most surprising finding of our model was that large increases in the negative effect of fuel load on escape performance had negligible effects on the usage of the mudflat by sandpipers and their pattern of state dependent usage. The pattern of state dependent usage (heavy birds feeding further from shore) is a robust persistent pattern in the model even if there is no mass-dependent predation (negative effect of state on escape) in the model parameters.

There are two hypotheses for how predation danger can affect the state-dependent usage of habitats by foragers. The first is that a foragers' probability of escaping a predator depends on its body mass (mass-dependent predation). According to this hypothesis as birds gain mass they should feed in safer habitats because of the negative effect of increasing fuel load on its escape performance or manoeuvrability (Kullberg et al. 1996; Metcalfe & Ure 1995; Witter et al. 1994). The asset protection principle makes the same prediction (heavier birds feeding in safer habitats) but for a different reason. The asset-protection principle is that as an animal's asset increases, the more important it becomes to protect it (Clark 1994). For birds fuelling for migration, individuals with ample fuel reserves are less willing to risk feeding in dangerous habitats than lean birds that benefit more from the high levels of food abundance.

This model provides a possible explanation for why we observe patterns of mass-dependent usage by birds (asset protection). Recently, it has been suggested that increases in a migrants' fuel load might not contribute as much as previously thought to the probability of a bird escaping predator attacks (Lind 2004). The effect of state on escape may be of less importance in these systems where vigilance or feeding distance has a relatively large effect on escape compared to escape performance; however, where initial take off is critical the effect of mass-dependent predation may be more important.

In this model we illustrate feeding danger trade offs by migrants that decide to feed in a particular habitat which varies in the abundance of food and the probability of attack and escape from predators. This tradeoff might also be thought of as analogous to tradeoffs between feeding intensity and vigilance, which we do not include here. Migrants on stopover are equipped with a suite of anti predator behaviours that they can employ to reduce their probability of capture by a predator. Not only can they adjust habitat usage, as demonstrated here, but they can also alter vigilance rates and join large flocks. As suggested by Lind and Cresswell (2006) studying multiple attributes of the behaviour of these migratory birds provided insight on the factors underlying western sandpiper usage of this stopover site.

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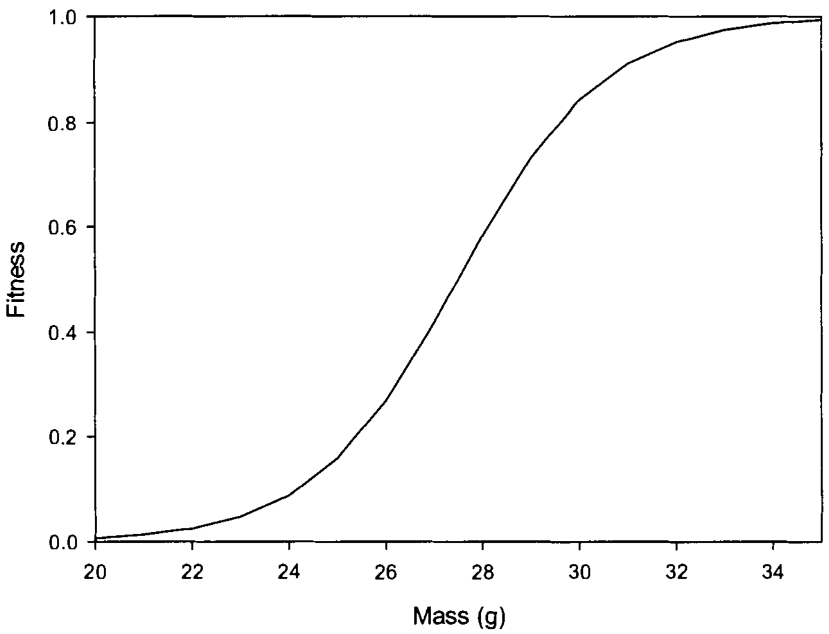

Figure 5-1: The terminal fitness function, the relationship between sandpiper mass and the fitness of a migrant sandpiper at the final time, T.

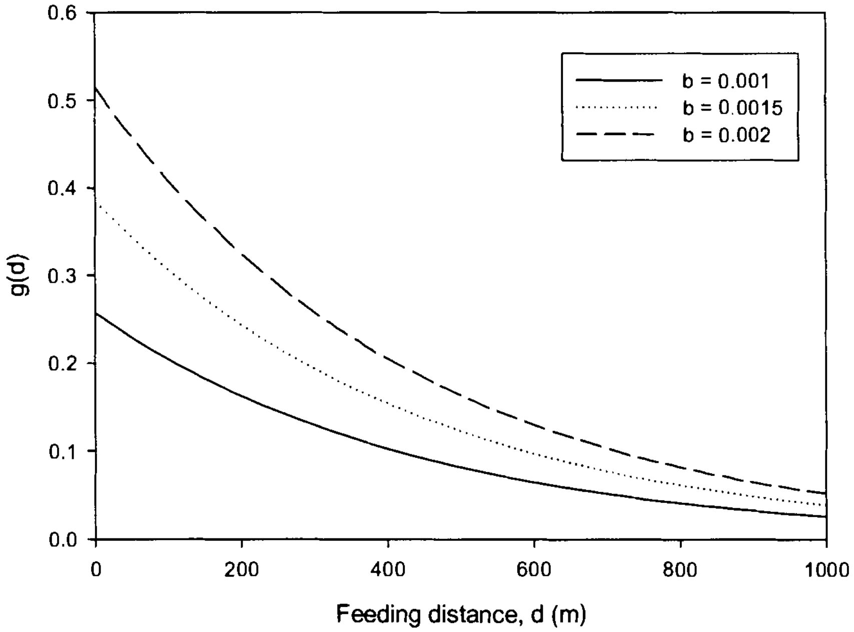

Figure 5-2: The distribution of food at low (b = 0.001, solid line), medium (b = 0.0015, dotted line), and high (b = 0.002, dashed line) levels of food abundance.

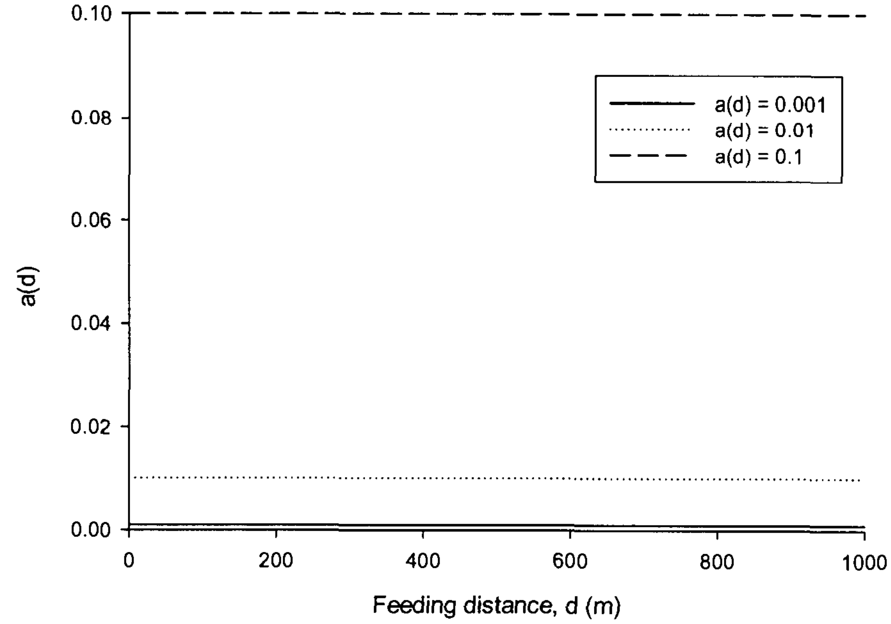

Figure 5-3: The probability of attack at each feeding distance where a(d) = 0.001 (low, solid line), a(d) = 0.01 (medium, dotted line) or a(d) = 0.1 (high, dashed line).

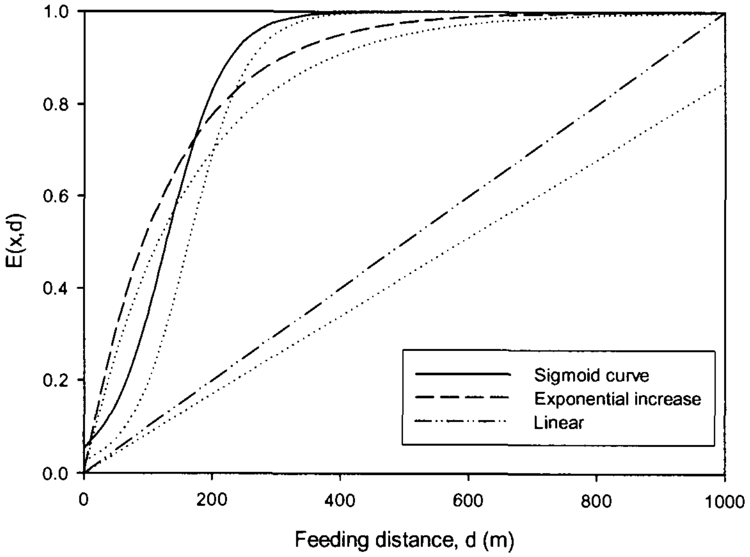

Figure 5-4: The probability of escape at each feeding distance declines with increasing state. The dotted lines adjacent to each curve represent the probability of escape with a 15 g increase in mass.

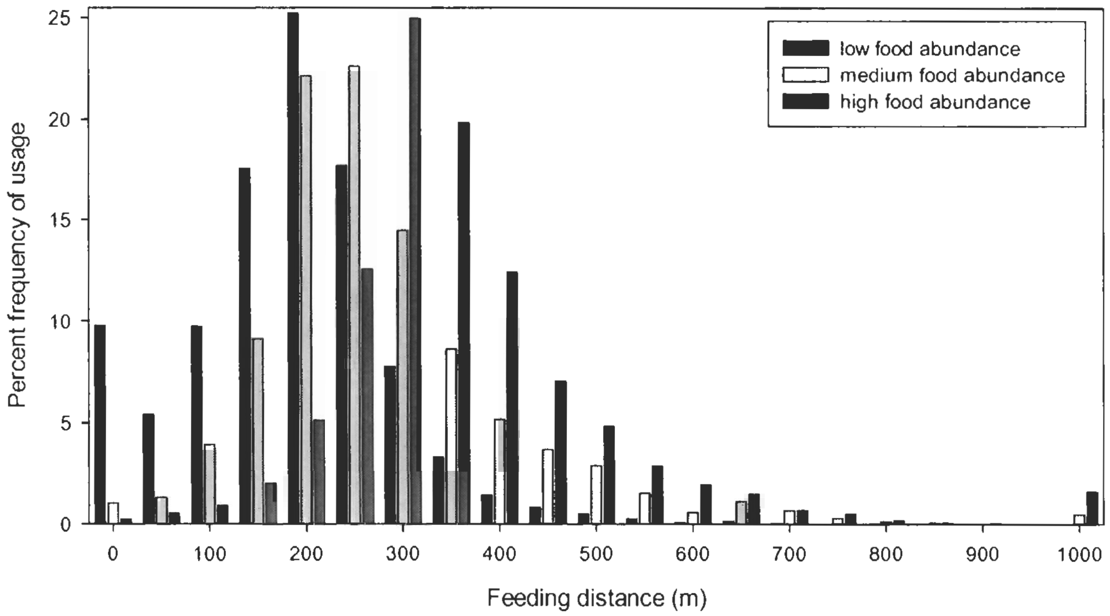

Figure 5-5: The predicted frequency of usage of each feeding distance by sandpipers at low (b = 0.001, black bars), medium (b=0.0015, light grey bars), and high (b=0.002, dark grey bars) levels of food abundance.

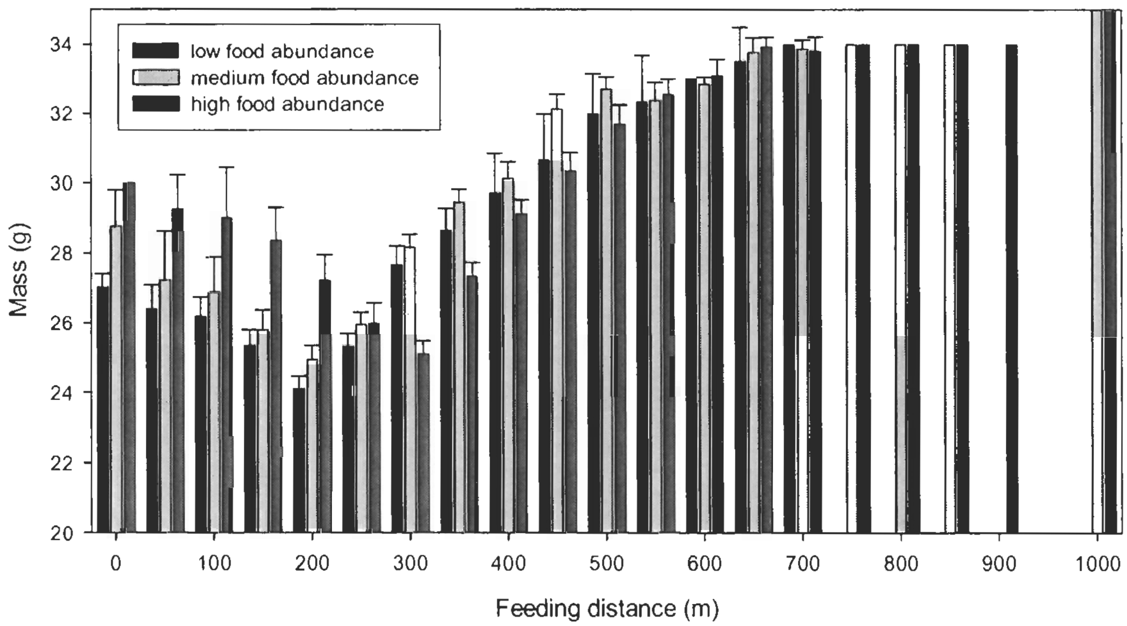

Figure 5-6: The predicted mean mass of sandpipers at each feeding distance at low (b=0.001, black bars), medium (b=0.0015, light grey bars), and high (b=0.002, dark grey bars) levels of food abundance. Error bars represent 95% confidence intervals.

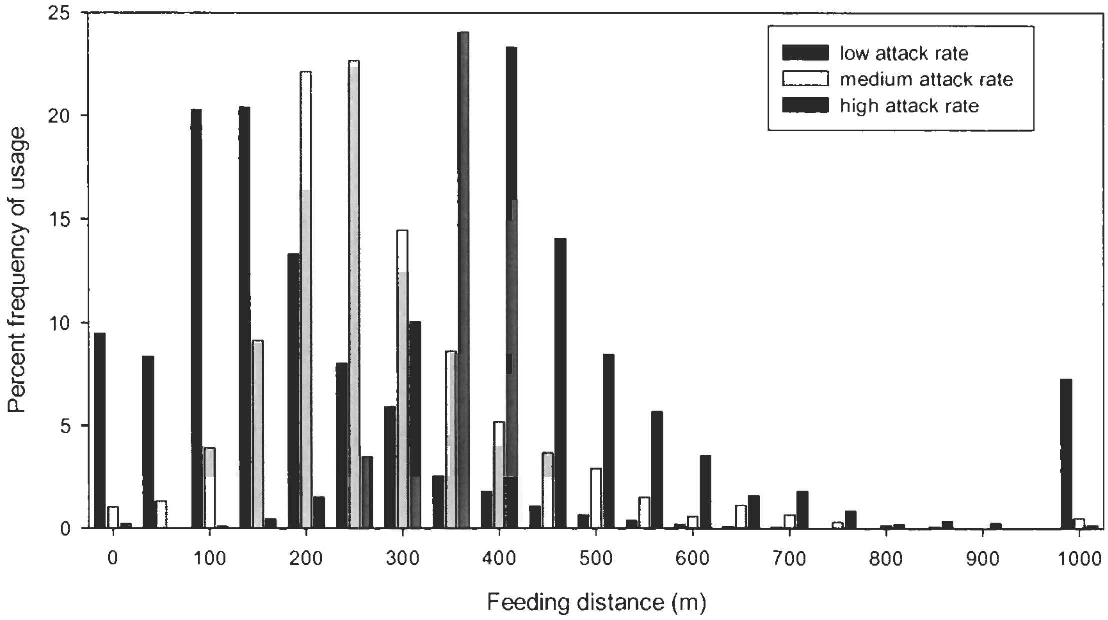

Figure 5-7: The predicted percent frequency of usage of each feeding distance by sandpipers at low (a_d = 0.001, black bars), medium (a_d =0.01, light grey bars), and high (a_d =0.1, dark grey bars) attack rates.

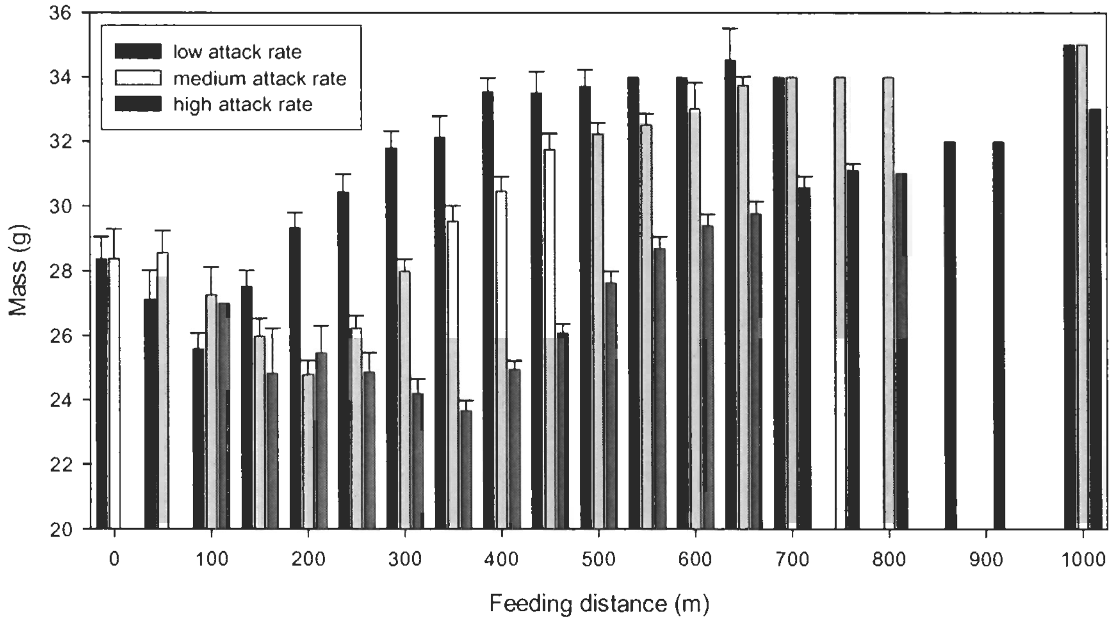

Figure 5-8: The predicted mean mass of sandpipers at each feeding distance at low (a_d = 0.001, black bars), medium (a_d =0.01, light grey bars), and high (a_d =0.1, dark grey bars) attack rates. Error bars represent 95% confidence intervals.

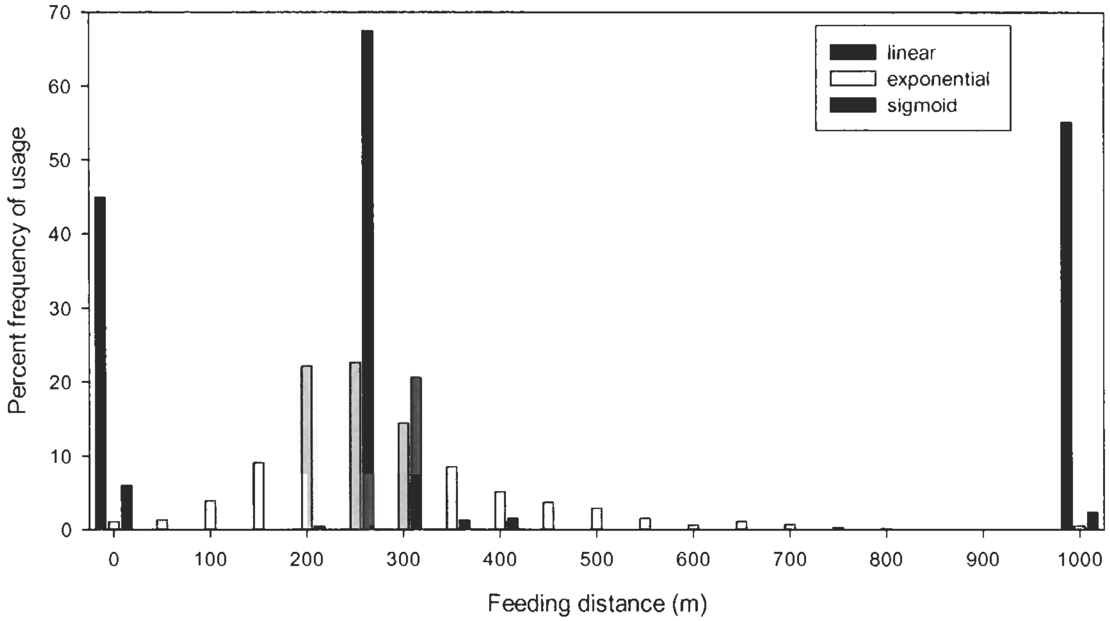

Figure 5-9: The predicted percent frequency of usage of each feeding distance by sandpipers when the relationship between the probability of escape and feeding distance is linear (black bars), exponential (light grey bars), or sigmoid (dark grey bars).

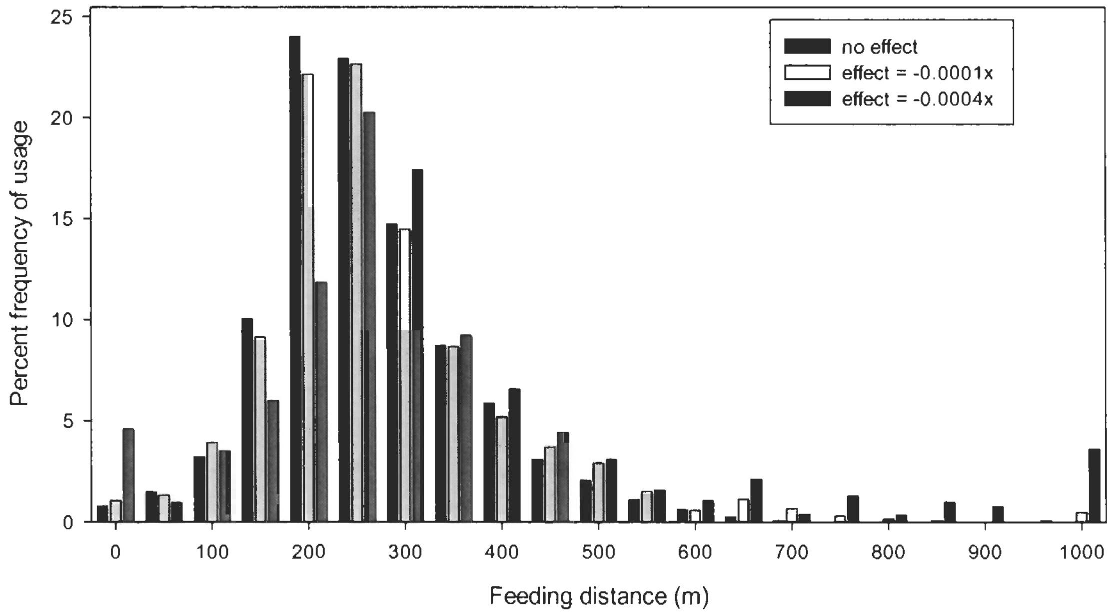

Figure 5-10: The predicted percent frequency of usage of each feeding distance by sandpipers when there is no effect of increasing mass on escape (black bars), when the effect of mass on escape = -0.0001x (light grey bars), and when the effect of mass on escape = -0.0004x (dark grey bars).

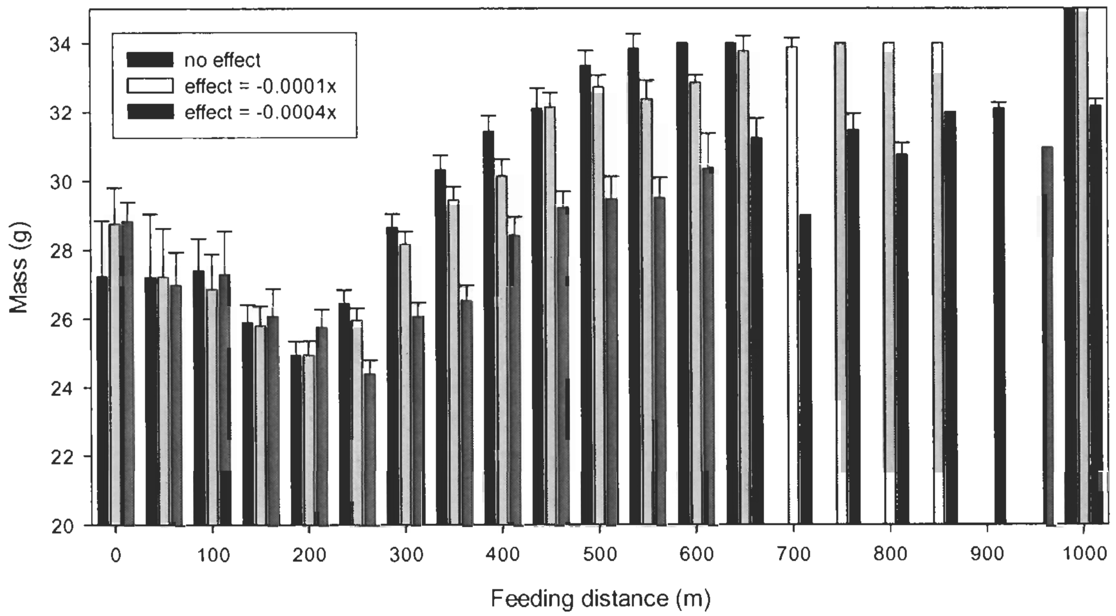

Figure 5-11: The predicted mean mass of sandpipers at each feeding distance when there is no effect of increasing mass on escape (black bars), when the effect of mass on escape = -0.0001x (light grey bars), and when the effect of mass on escape = -0.0004x (dark grey bars). Error bars represent 95% confidence intervals.

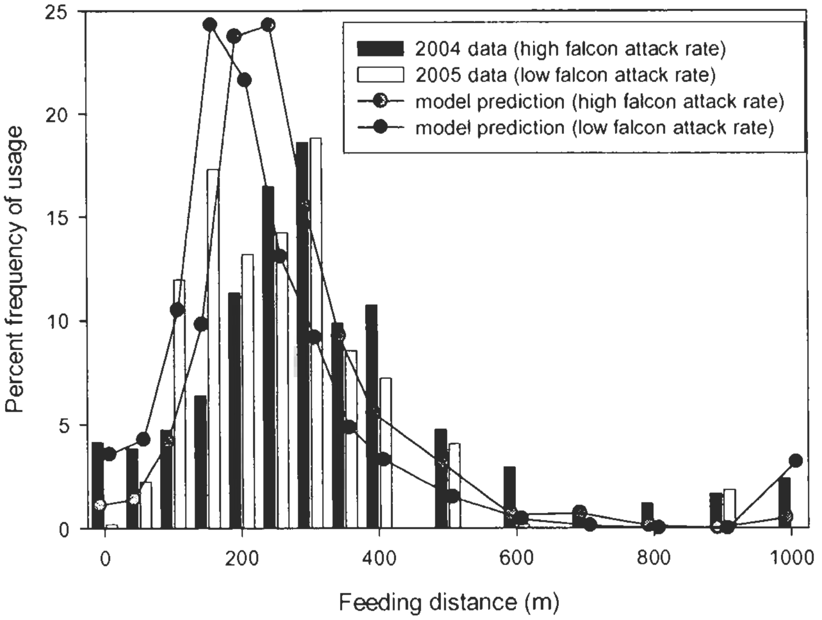

Figure 5-12: The actual and predicted frequency of usage sandpipers at each feeding distance at high (2004 data – black bars, model $a_d = 0.01$ – grey dots) and low (2005 data – white bars, model $a_d = 0.003$ – black dots) falcon attack rates.

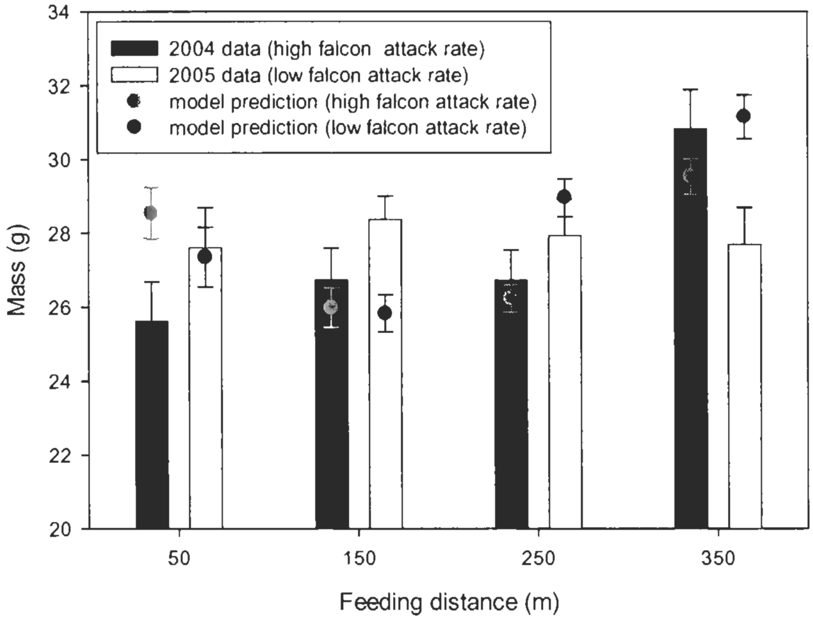

Figure 5-13: The actual and predicted frequency of sandpiper mass at each feeding distance at high (2004 data – black bars, model $a_d = 0.01$ – grey dots) and low (2005 data – white bars, model $a_d = 0.003$ – black dots) falcon attack rates. Error bars are 95% confidence intervals.

CHAPTER 6:
FEEDING-DANGER TRADEOFFS UNDERLIE STOPOVER SITE SELECTION BY MIGRANTS

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and R.C. Ydenberg

Abstract

To migrate successfully birds must acquire sufficient energy reserves at stopover sites while avoiding the predators that hunt them there. Since acquiring fuel also increases predation danger migrants should choose stopover sites that are rich in resources and offer safety from predators. Furthermore, decisions by migrants may differ depending on their state (fuel load). Here we evaluate the factors underlying stopover site usage by migrant western sandpipers on the landscape scale. We measured the food and danger attributes of 17 potential stopover sites and measured their usage by sandpipers. Of the sites surveyed 8 of 17 were used by sandpipers on migration. Sites that were high in food and safety were used, while sites that were low in food and safety were not. Dangerous sites were only used if there was ample food abundance, and sites with low food abundance were used only if they were very safe. Furthermore, lean sandpipers used the most dangerous sites, while heavier birds (that do not need to risk feeding in dangerous locations) used relatively safer sites. This study indicates that both food and danger attributes of stopover sites are considered by migrant birds when selecting stopover sites and thus should both be considered to prioritize sites for conservation.

Introduction

One challenge to understanding the causes underlying population declines of Neotropical migrants is that declines may be caused by a suite of factors operating at various stages of a migrant's life cycle. Most research on factors limiting these populations (i.e. reproduction and mortality) has focused on breeding and non-breeding stages (Burke & Nol 1998; Gill et al. 2001; Latta & Faaborg 2002; Robinson et al. 1995; Rodewald & Yahner 2001; Stillman et al. 2005; Whitfield 2003a; Zannette et al. 2000), while comparatively less work has been carried out on limiting factors during migration (Hutto 1985; Moore et al. 1995). A growing number of studies suggest that mortality on migration has a significant effect on population regulation (Baker et al. 2004; Sillett & Holmes 2002). Biologists have advocated that the protection of high quality stopover habitat is essential to conserve migratory bird species (Donovan et al. 2002; Mehlman et al. 2006; Skagen & Knopf 1993). To identify appropriate stopover sites for conservation, an understanding of the factors underlying their usage at a broad scale is required.

To migrate successfully, sufficient energy reserves are needed to fuel long distance flights. In light of the rapid, impressive fuelling by long distance migrants, high quality stopover sites are generally considered those that can provide the required energy. Therefore much research on stopover site usage has focussed on the abundance and distribution of food (Baker et al. 2004; Colwell & Landrum 1993; Hicklin & Smith 1984; Loria & Moore 1990; Piersma et al. 1994; Placyk & Harrington 2004; Schneider & Harrington 1981).

However, more recently, authors have begun to recognize a role for predation danger in shaping where, when and how quickly migrants travel, and how they select and use stopover sites (Clark & Butler 1999; Lank et al. 2003; Moore 1994; Weber et al. 1998). Fore example, migrants may adjust their fat loads (Schmaljohann & Dierschke 2005; Ydenberg et al. 2002; Ydenberg et al. 2004) and alter the amount of time spent being vigilant (Cimprich et al. 2005; Pomeroy 2006) with changing levels of predation danger, and avoid feeding in dangerous places (Cimprich et al. 2005; Pomeroy 2006;

Pomeroy et al. 2006; Sapir et al. 2004). While these studies are informative at the site level, stopover site selection is likely hierarchical (Hutto 1985). Migrants likely use site level attributes to determine if the site is suitable, and later adjust within site usage to optimize fuel deposition. Therefore, studies of within site usage do not necessarily inform managers of the appropriate attributes used by migrants to select between sites (Wiens 1989). Large scale studies are needed to understand how food and danger affect selection and usage of stopover sites by migrants. The physical attributes or current state (fuel load) of individuals might influence their stopover site selection. For example, lean migrants may be more willing to risk using dangerous sites that offer greater feeding benefits, while birds with ample fat reserves might use sites that offer greater safety (i.e. Ydenberg et al. 2004).

Here we designed a landscape scale field study to assess the food and danger attributes of a variety of potential stopover sites to evaluate the factors underlying their usage by western sandpipers (*Calidris mauri*). Where sites were used we captured sandpipers and measured their state (fuel load). We predicted that if usage of stopover sites depends on either food abundance or safety from predators alone, then sandpipers will use sites with high food abundance or safety and avoid sites with low food abundance or safety. If usage of stopover sites by sandpipers reflects a trade off between food abundance and predation danger, then we predict that migrant sandpipers will use stopover sites high in both food and safety and not use sites that are low in both food and safety. Furthermore, birds should use dangerous sites only if they offer high food abundance and sites low in food abundance only if they are safe from predators. If the individual state (fuel load) of migrant sandpipers affects stopover site usage, then we predict that lean birds should be willing to use dangerous sites whereas heavy birds with ample fuel reserves will use only sites that offer safety from predators (i.e. Ydenberg et al 2004).

Methods

Study system

Western sandpipers are small (25-30 g on migration) calidrine shorebirds that migrate along the Pacific Coast from non-breeding grounds between northern Oregon and Peru, to breeding grounds in western and northern Alaska and eastern Siberia (Wilson 1994). En route to their destination, they use mud- and sandflats in the Georgia Basin (British Columbia, Canada) and Puget Sound (Washington, USA) as stopover sites (Buchanan 1988; Butler et al. 1987; Evenson & Buchanan 1997; Iverson et al. 1996). During their migration northward, western sandpipers use stopover sites in this region from mid-April to mid-May; adults migrate southward in July and juveniles from August to early September (Butler et al. 1987). We collected food abundance, safety, and site use data from 17 mud- and sandflats in the Georgia Basin/Puget Sound (GB/PS) region in 2002 (Figure 6-1). Three sites, Boundary Bay (BB), Roberts Bank (RB), and Skagit Bay (SB), were sampled in more than one migratory period; all other sites were only sampled once during either the northward or southward migratory period (Table 5-1).

Food abundance

Western sandpipers are invertebrate generalists feeding opportunistically on a variety of epibenthic and infaunal invertebrates (Mathot & Elner 2004; Sutherland et al.

2000; Wilson 1994). To measure food abundance for western sandpipers, we quantified benthic macro-invertebrate abundance in sediment cores according to the methods described by (Sutherland et al. 2000). Each taxon sampled has been shown to be consumed intentionally or unintentionally by western sandpipers (Wolf 2001 and references therein). Samples were extracted from the sediment within 500 m of the shoreline using a 60 ml syringe (26 mm inner diameter) to a depth of 40 mm, within 1.5 hours of mud exposure by the receding tide and frozen within 1 h of sampling. Cores were later thawed and rinsed through a 0.5 mm mesh sieve. Material on the sieve was preserved in vials with 85% ethanol. Invertebrates in each vial were identified to the lowest taxon possible and counted under a 40X dissecting microscope. Wolf (2001) shows that the size of invertebrates ingested by the western sandpiper are effectively sampled by this core size, since the size of the amphipod *Corophium* recovered from sandpiper feces were within the size range of those recovered from the core samples.

We sampled macro-invertebrate abundance at each site during at least one migratory periods, sample sizes ranged from 15-146 (Table 5-1). For the three sites sampled in multiple migratory periods, invertebrate abundance did not differ among migratory periods at either Boundary Bay (ANOVA, $F_{2, 144}$=1.97, P=0.14) or Roberts Bank (ANOVA $F_{1, 53}$=2.89, P=0.10). At Skagit Bay, invertebrate abundance differed significantly between northward (N=30) and southward adult (N=30) migratory periods ($F_{1, 59}$=25.4, p<0.0001); however, these differences are likely due to sampling location since it was sampled at a microsite called Jensen Access during northward migration and at English Boom during southward adult migration. Despite the difference in food abundance between these two microsites (Jensen Access mean invertebrate abundance ±

95% C.I. = 76.5 ± 19.0; English Boom; invertebrate abundance ± 95% C.I. = 26.33 ± 5.8) the data were pooled because the scale of Skagit Bay is more relevant to the regional scale used for this analysis.

Safety

Peregrine falcons (*Falco peregrinus*), merlins (*F. columbarius)* and other raptors hunt shorebirds, including western sandpipers (Buchanan et al. 1988; Cresswell 1994; Cresswell 1996; Dekker 1988; Page & Whitacre 1975; Whitfield 1985), and achieve greatest hunting success using cover to conceal their approach (Cresswell 1994; Dekker & Ydenberg 2004; Whitfield 1985, 2003b). Since the shoreline poses a great deal of danger for foraging sandpipers, stopover sites that are small with a large proportion of available foraging habitat close to cover are more dangerous than stopover sites that are large where sandpipers can spend large amounts of time feeding on the open mudflat far from the danger lurking along the shoreline.

As an index of safety we used the distance tool in ArcMap (ESRI 2005) to measure the furthest distance from the shoreline (as indicated by the upper water mark on marine charts (N.D.I 2005; N.O.A.A. 2005)) in the intertidal zone at each of the sites. For a large open mudflat or beach, this measure is the distance (m) between the shoreline (upper water mark) and the waterline (low water mark) at the widest point. For an enclosed bay surrounded by shoreline, the index of safety is measured as the distance from the shoreline to the midpoint of the widest distance across the bay.

Site usage

Usage of each study site by sandpipers on migration was assessed from a variety of sources including the published and non-published literature, the Bird Studies Canada Coastal Waterbirds Survey (BSC 2005) database, and local knowledge (Table 5-1). Sites were considered used by sandpipers if there were single day records of 100 or more birds at the site during migration. Sandpipers use these sites on stopover during migration on a regular and annual basis (Acevedo Seaman et al. 2006; Buchanan 1988; Butler et al. 1992; Butler et al. 1987; Evenson & Buchanan 1997; Iverson et al. 1996; Warnock & Bishop 1998). Sites with records of fewer than 100 western sandpipers at the site during migration were considered unused. These sites are used infrequently, when used at all. In addition to information on usage in the literature, the used sites were visited during this study and peak numbers of birds observed were recorded (Seaman 2003).

At sites that were used during migration, we captured sandpipers using mist nets to measure the state (fuel load) of individuals using the site (for sample sizes see table 5-1). Western sandpipers were removed from the mist nets immediately after capture and weighed within 10 minutes. Tarsus and culmen were measured using callipers (to the nearest 0.1 mm) and tarsus was included in analysis as a covariate to account for the effect of body size on mass.

Statistical analysis

We tested for differences between sites in food abundance using analysis of variance (ANOVA). T-tests were used to test if food abundance and safety differed between used and unused sites. Separate logistic regressions were used to test if food abundance, safety, and food abundance and safety affected stopover site usage by sandpipers.

For analysis of body mass, we used analysis of covariance (ANCOVA) including tarsus length as a covariate to account for body size differences between individuals. Since northbound migrants were significantly heavier (0.8 g) than southbound migrants ($P = 0.05$), we also included migratory period in the analysis. Body mass values are therefore reported as least squares means. To investigate the relationship between site safety and state of individuals using a site, we then used these least square means of body mass at each site. Means and 95% confidence intervals are used throughout. JMP*IN* V. 4.04 (SAS 2001) was used for all statistical analyses.

Results

Of the 17 sites surveyed, 8 were used by 100 or more sandpipers on migration (Table 5-1). Food abundance and safety from predators varied widely between study sites. Food abundance for sandpipers differed between the sites (Figure 6-2. ANOVA: $F_{16, 479} = 16.3$, $P < 0.0001$) ranging from sites with mean invertebrate abundances of 8 to 204 invertebrates core^{-1}. Invertebrate densities were over three times greater at the sites that were used by sandpipers than at sites that were not used (ANOVA: $F_{1, 15} = 9.26$ $P = 0.008$). The sites ranged in safety index from 75 m to 4560 m (Figure 6-3). Sites that were used were, on average, 3 times safer (i.e. larger distance from shore (m)) than unused sites (ANOVA: $F_{1, 15} = 5.4$, $P = 0.03$, $N = 17$).

In a logistic regression model including only food as an independent variable the usage of 12 of the 17 sites was predicted correctly (Table 5-2. $\chi^2_{1, 15} = 8.51$, $R(U)^2 = 0.36$,

$P = 0.0035$). Similarly, the logistic regression model including only safety as an independent variable correctly predicted usage of 12 of 17 sites ($\chi^2_{1,15} = 5.78$, $R(U)^2 = 0.25$, $P = 0.02$). The 12 correctly predicted sites differed between the food only and safety only models (Table 5-2). The best model was a logistic regression including both food abundance and safety as explanatory variables, which correctly predicted the usage of 14 of 17 sites, improving our ability to predict usage by 12% (Figure 6-4. $\chi^2_{2,15} = 10.24$, $R(U)^2 = 0.44$, $P = 0.006$). The food*distance interaction term was not significant ($P = 0.55$).

The body mass of individuals (controlled for structural size) captured at stopover sites was greater at stopover sites with greater safety (Figure 6-5. Nonlinear Regression: LS mean body mass $= 26.6\left(1-e^{(-0.0061 * safetyindex)}\right)$, $R^2 = 0.55$, $P = 0.03$), but was not related to food abundance ($P = 0.41$). There was no difference in structural body size (tarsus; ANOVA: $F_{7,410} = 0.67$, $P = 0.64$) or the culmen length (ANOVA: $F_{7,410} = 1.03$, $P = 0.41$) of sandpipers between the stopover sites, suggesting that the fuel load of individual migrants also influences stopover site selection.

Discussion

Migrant western sandpipers in this study consider both food abundance and safety from predators in their usage of stopover sites. Although measures of food and safety alone can predict stopover site usage at some sites, including both factors in our analysis was the best predictor. Migrant sandpipers only used sites that were dangerous if food abundance there was high and only used sites with low food abundance that were very safe. Furthermore, these results support the hypothesis that usage of stopover sites is affected by the state of individual sandpipers. Lean sandpipers, for which the benefit might be greater, used dangerous stopover sites, while heavy sandpipers that do not need to risk feeding in dangerous places, used relatively safer sites. To our knowledge this is one of the first studies to investigate regional scale usage of stopover sites by migrants and to compare multiple site attributes at both used and unused sites.

This study indicates that the food and danger attributes of a site strongly influence stopover site usage by migrants. Stopover site selection by migrants is thought to be hierarchical (Hutto 1985). To avoid the costs of sampling potential stopover sites, migrants likely use features of the environment to approximate levels of food abundance and predation danger at the site level to decide whether or not to use the site. For example, high densities of macro-invertebrates, on which many shorebirds feed, are often associated with fine-grained sediments (Kennish, 1990, Yates et al., 1993). It is possible that migratory shorebirds can visually assess food abundance of potential stopover sites from the air, for example by the reflectance or sediment properties of a beach or mudflat (Pomeroy and Butler 2005, Rainey et al., 2003).

Proximity to cover may be used by migrants to remotely assess the predation danger at a site. Large mudflats with a vast expanse of foraging habitats many kilometres from the shoreline is indicative of a relatively safe site for a migrant shorebird, whereas a small mudflat surrounded by marsh grass would be deemed a potentially dangerous place to stop. Upon selecting a stopover site, migrants can more accurately assess the levels of food abundance, and gauge the level of danger there based on their encounters with predators, then they can make appropriate adjustments to anti-predator behaviours to carefully balance food and danger over short temporal and small spatial scales. This work provides rare evidence that food and danger attributes are considered in site selection on the landscape scale.

Although the model including both food abundance and safety from predators performed better than those using either food or safety alone, the model incorrectly predicted usage of 3 of the 17 sites. According to the model, Doug Banks and Totten Inlet should not be used (but are in fact used regularly) by sandpipers on stopover since measures of both food abundance and safety there are comparatively low. A striking difference between these and the other stopover sites in our study is that the cover lining most of the shore there are tall coniferous trees, unlike the marsh grasses on the shores of other stopover sites. At Totten Inlet, falcons hunt by attacking over the open mudflat, much like the attack strategy they employ at some larger sites (J. Buchanan, pers. comm.). From the perspective of a migrant sandpiper these sites may functionally act as a safe site since the cover there is not used by falcons to mount surprise attacks. This unexpected difference actually supports our hypothesis that sites where falcons can mount surprise attacks are the most dangerous to shorebirds. Cover type, and its affect on safety, might also be an important factor influencing stopover site usage by migrants.

There are two possible sources of bias in this study, 1) the selection of sites to include in the study and 2) our measurements of food abundance at each site. Sites that were selected for inclusion in this study were either known, or suspected, to be used by western sandpipers, or other shorebirds, during migration. These sites were known coastal mud or sandflats in the region that from initial visits appeared to be potential stopover sites for shorebirds. These sites then were biased to include attributes, which from our perspective, would be selected by migrant sandpipers. A complete survey of possible stopover sites might have included coastal sites with gravel or cobble substrate, or inland sites such as agricultural fields and wetlands. Although our study is biased toward coastal mud and sandflats the underlying finding that food and danger attributes affect usage of sites by migrants remains clear.

Another possible source of bias in this study is from our measure of food at each site. We measured invertebrate abundance from core samples extracted within 500 m of the shoreline at each site; however, this methodology might not accurately represent food abundance across entire sites. At Boundary Bay, for example, there is a strong declining gradient in food abundance as distance from the shoreline increases (Pomeroy 2006). For large sites where these gradients are likely to occur (Kennish 1986; Reise 1985; Swennen et al. 1982), we might be overestimating food abundances, where as our measures of food abundance at smaller sites are likely more accurate. Despite this possible bias, our analyses remain powerful.

This study highlights the importance of considering the effects of predators on the behaviour of birds to understand and predict stopover site usage by migrants. As danger from predators increases, migrant birds have been shown to alter their behaviour at stopover sites by decreasing length of stay at the site (Ydenberg et al. 2004), allocating more feeding time to vigilance (Cimprich et al. 2005; Pomeroy 2006) and carrying lower fuel loads (Schmaljohann & Dierschke 2005; Ydenberg et al. 2002; Ydenberg et al. 2004). Danger management theory also predicts that as danger increases on the landscape, migrants should shift usage from small dangerous sites to larger, safer ones. If danger from predators is not considered in the study of migrants on stopover, each of these behavioural adaptations to avoid mortality by predation could be instead attributed to declines in food abundance at a site or as population decline (see Butler et al. 2003; Ydenberg et al. 2004).

This model is also useful as applied to other migrant birds. For example, though migrant landbird populations are known to be affected by forest fragmentation via edge effects while nesting (Burke & Nol 1998; Robinson et al. 1995), at stopover sites migrants also face greater danger from predators when foraging near the edge of forest patches (Cimprich et al. 2005). Migration presents a significant threat to adult survival (Sillett & Holmes 2002) and so as danger increases on the landscape, landbirds should also respond by behaving more cautiously.

We show here evidence that migrant western sandpipers select stopover sites according to tradeoffs between food abundance and predation danger. Furthermore, usage of these sites depends on the state of an individual. This study suggests that migrants use features of the habitat such as proximity to cover as a measure of predation danger, and that they mediate their probability of mortality by predation by adjusting habitat usage on a landscape scale. Results such as these can be applied to predict the behaviour of migrants at stopover sites, and usage of stopovers if food and/or danger attributes at a site change. According to this study, usage of stopover sites by migrants will change if levels of food and/or danger change depending on a) the magnitude of the change, and b) the level of the other attribute. For example, if food abundance declines at a safe site, usage by migrants might not change, whereas if the site is dangerous the site might no longer be used. Furthermore, usage of stopover sites by migrants depends on state. As danger from predators changes on the landscape the state of the birds that use those sites might also change (Ydenberg et al. 2004). This study indicates that to identify migration stopover sites for conservation both the food and danger attributes must be considered.

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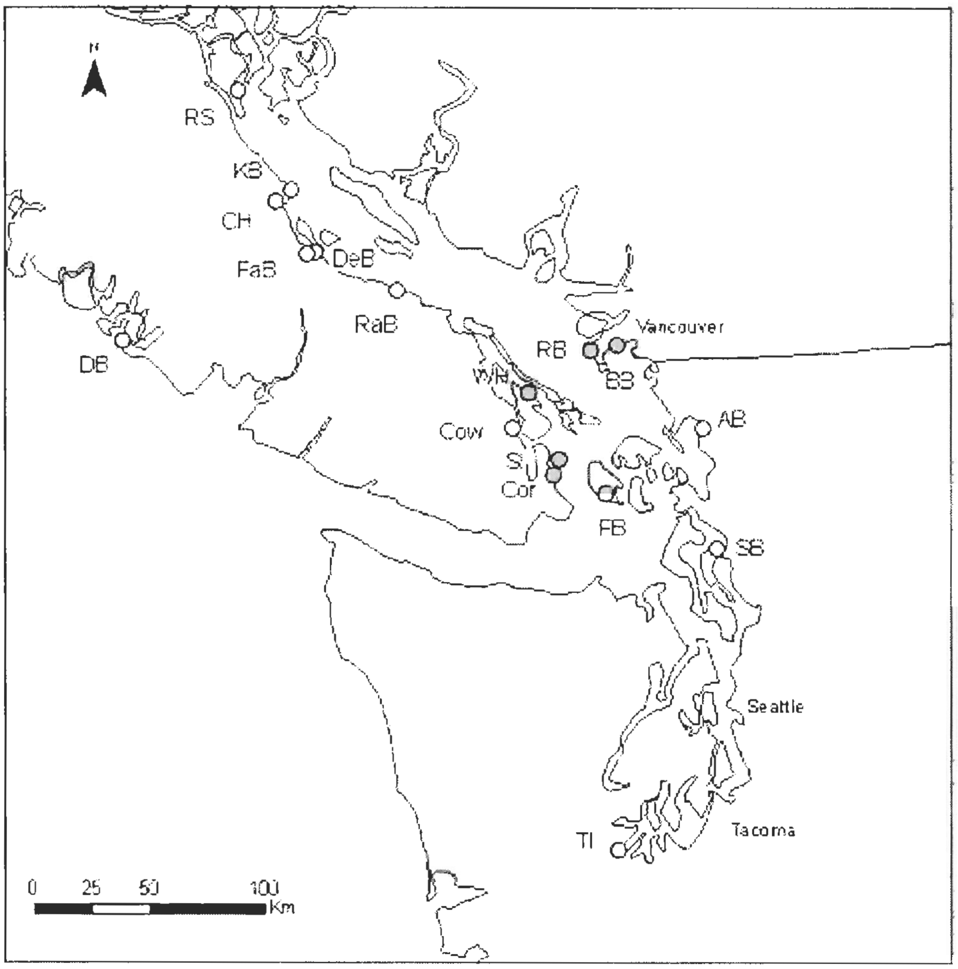

Figure 6-1: The Georgia Basin/Puget Sound region of British Columbia, Canada and Washington, USA.

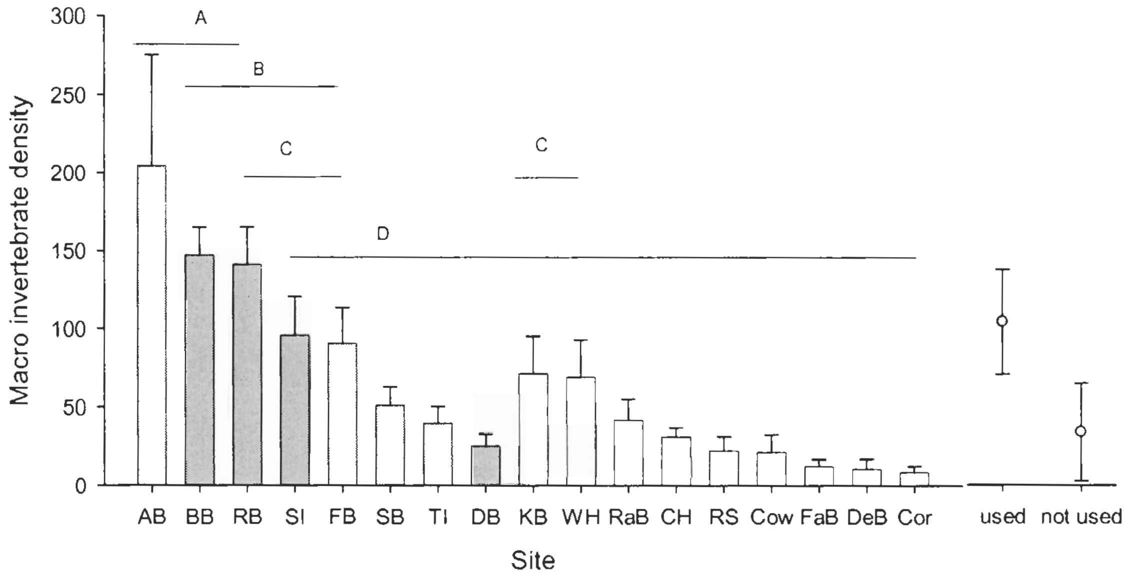

Figure 6-2: Mean macro invertebrate densities sampled at each site (± 95% CI). Sites that are labelled with different letters are significantly different from one another (Tukey HSD P<0.05). Grey filled bars and circles indicate values for sites that are used, white filled bars and circles represent sites that are unused. The offset panel provides the mean invertebrate densities (± 95% CI) of used and unused sites.

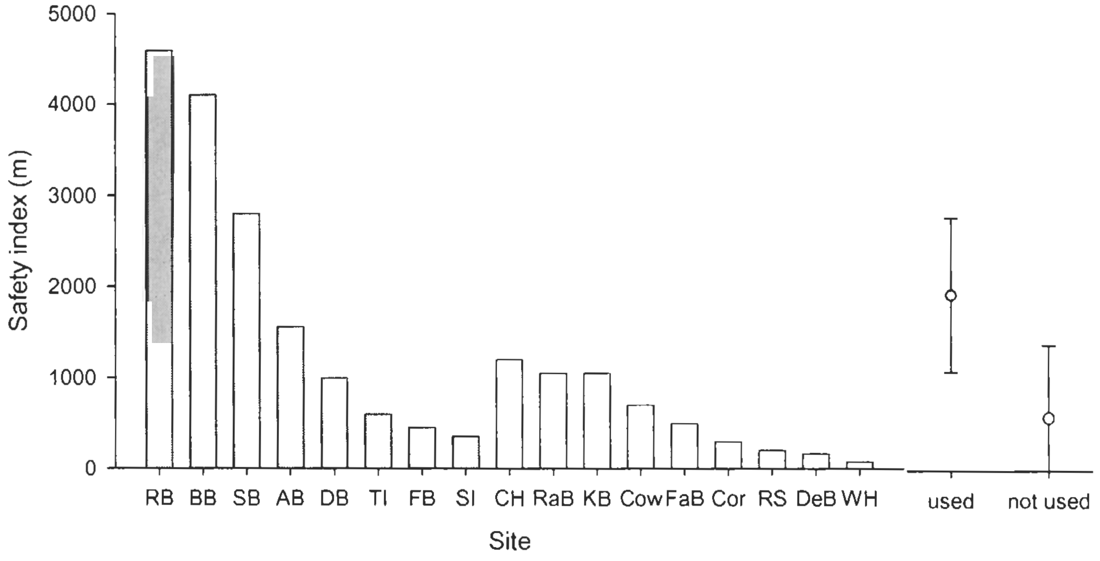

Figure 6-3: The safety index measured for each site. Grey filled bars and circles indicate values for sites that are used, white filled bars and circles represent sites that are unused. The offset panel provides the mean index of safety (± 95% CI) of used and unused sites.

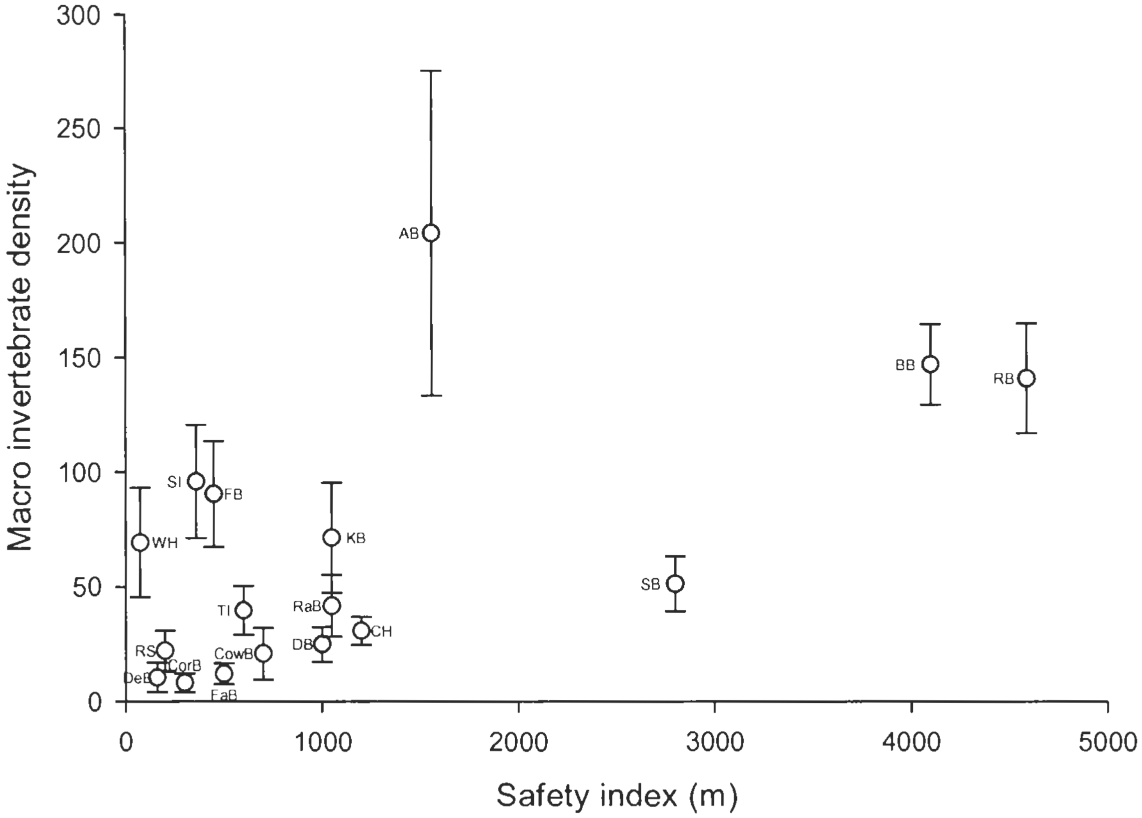

Figure 6-4: The mean macro invertebrate density (± 95% CI) and safety index for sites that are used (grey circles) and not used (white circles) by western sandpipers on migration.

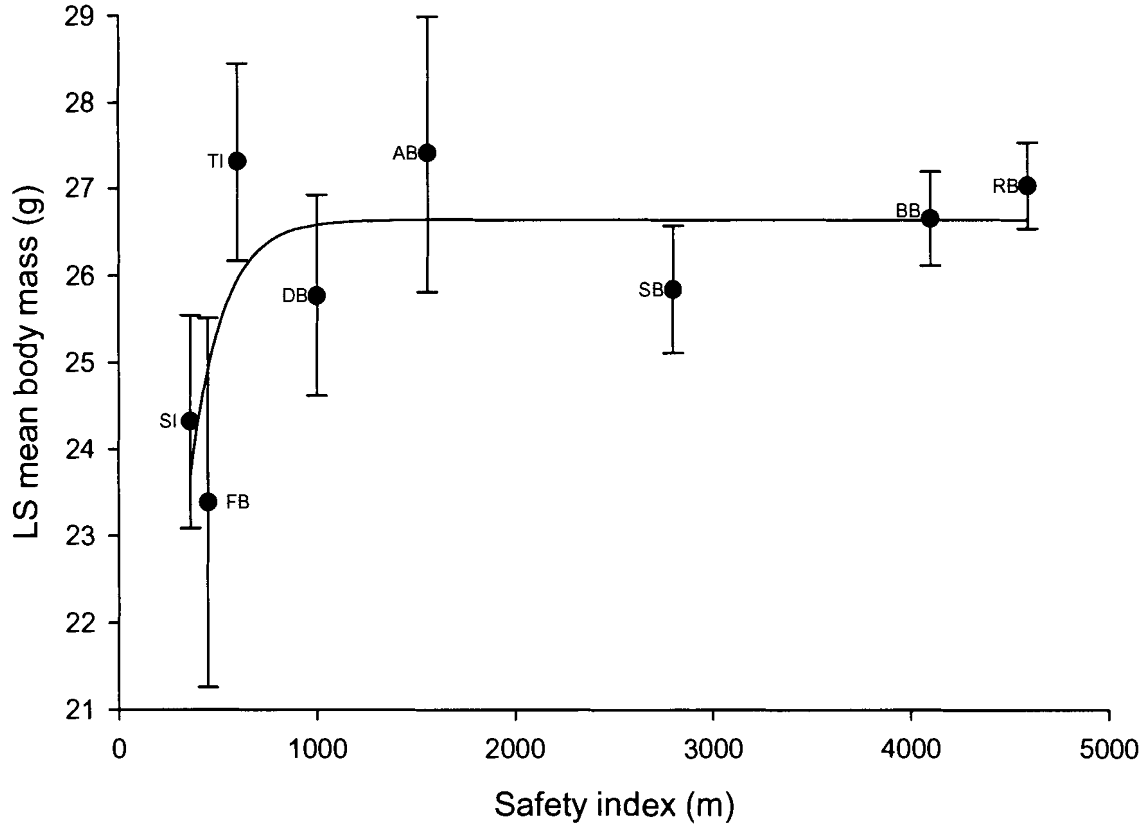

Figure 6-5: The relationship between the safety index measured at stopover sites and the least square mean body mass (± 95% CI) of sandpipers captured. The line is that predicted from the Nonlinear regression (LS mean body mass=26.6 * $(1\text{-}e^{(-0.0061*\text{safety index})})$.

Table 6-1: The name and location of stopover sites sampled in the GB/PS, sample sizes for invertebrate cores and body mass samples, and usage data for each migratory period (N=northward, SA=southward adult, SJ=southward juvenile).

Site	Site Name	Location	Invertebrate core (N)	Body mass (N)	Usage	Migratory period
AB	Alice Bay	Edison, WA	30	13	Used (G. Bletsch unpubl data cited in (Seaman 2003)	SA
BB	Boundary Bay	Delta, BC	146	N=63 SA=18 SJ=34	Used (Butler 1994)	N,SA,SJ
CH	Comox Harbour	Comox, BC	15	N/A	Not used (BSC 2005)	SA
Cor	Cordova Bay	Victoria, BC	15	N/A	Not used (BSC 2005)	SA
Cow	Cowichan Bay	Duncan, BC	15	N/A	Not used	SA
DB	Doug Banks	Tofino, BC	25	28	Used (Butler et al. 1992)	SJ
DeB	Deep Bay	Vancouver Island, BC	15	N/A	Not used (Dawe et al. 1998)	SA
FaB	Fanny Bay	Vancouver Island, BC	15	N/A	Not used (Dawe et al. 1998)	SA
FB	False Bay	San Juan Island, WA	25	7	Used (K. O'Reilly unpubl. data)	SJ
KB	Kye Bay	Comox, BC	15	N/A	Not used (BSC 2005)	SA
RaB	Rathtrevor Beach	Parksville, BC	15	N/A	Not used (BSC 2005)	SA
RB	Roberts Bank	Delta, BC	29	N=57 SA=18 SJ=66	Used (Butler 1994)	N, SJ
RS	Rebecca Spit	Quadra Island, BC	15	N/A	Not used	SA
SB	Skagit Bay	Utsalady, WA	60	N=38, SA=25	Used (Evenson & Buchanan 1997)	N, SA
SI	Sidney Island	Sidney Island, BC	15	24	Used (Ydenberg et al. 2004)	SJ
TI	Totten Inlet	Shelton, WA	31	27	Used (Evenson & Buchanan 1997)	N
WH	Walker's Hook	Saltspring Island, BC	15	N/A	Not used (J. Booth pers. comm.)	SA

Table 6-2: Actual usage at sample sites on migration by sandpipers and usage as predicted by each logistic regression model.

Site	Used	Predicted used by food only	Predicted used by danger only	Predicted used by food and danger
AB	Y	Y	Y	Y
BB	Y	Y	Y	Y
CH	N	N	Y	N
CorB	N	N	N	N
CowB	N	N	N	N
DB	Y	N	N	N
DeB	N	N	N	N
FaB	N	N	N	N
FB	Y	Y	N	Y
KB	N	Y	N	Y
RaB	N	N	N	N
RB	Y	Y	Y	Y
RS	N	N	N	N
SB	Y	N	Y	Y
SI	Y	Y	N	Y
TI	Y	N	N	N
WH	N	Y	N	N

Appendix 6-1: The percentage of each taxon represented at each site.

				Site Migratory Period					
				AB	BB	BB	BB	CH	CorB
				SA	N	SA	SJ	SJ	SJ
Phylum	Class	Order		(N=30)	(N=49)	(N=56)	(N=41)	(N=15)	(N=15)
Sarcomastigophora	Granuloreticulosea	Foraminifera		0	0.2	0.2	0.2	0.2	2.4
Nematoda	Adenophorea			15.4	16.1	12.4	10.9	14.7	80.8
Mollusca	Bivalvia			0	0	0	0	0.9	0
	Gastropoda			0	0.1	0.1	0.7	0	0.8
Annelida	Polychaeta			69.7	64.1	60.1	48.6	9.1	2.4
Arthropoda	Ostracoda			13.4	5.3	9.2	12.1	2.2	0
	Copepoda			1.2	13.7	5.9	2.1	14.0	13.6
	Malacostraca	Amphipoda	*Corophium*	0.1	0	6.1	10.4	23.9	0.0
			Gammaridae	0	0	0	0	0	0
		Cumacea		0	0.1	0.1	0	0.9	0
		Tanaidacea		0	0.2	5.6	14.7	33.4	0
	Insecta	Diptera		0.2	0.2	0	0.1	0	0
Other				0.1	0	0.1	0	0.9	0
		Mean invertebrate density		204	136	168	132	31	8

Appendix (con't): The percentage of each taxon represented at each site.

				Site Migratory Period					
Phylum	Class	Order		CowB SJ (N=15)	DB SJ (N=25)	DeB SJ (N=15)	FaB SJ (N=15)	FB SJ (N=25)	KB SJ (N=15)
Sarcomastigophora	Granuloreticulosea	Foraminifera		24.1	1.9	0	0	0.4	0
Nematoda	Adenophorea			23.5	7.8	66.0	47.5	41.7	60.2
Mollusca	Bivalvia			0.3	0.6	1.3	1.1	0.1	0.2
	Gastropoda			0	0	0.6	2.7	0	0
Annelida	Polychaeta			6.7	12.9	4.4	12.6	6.4	32.2
Arthropoda	Ostracoda			2.5	2.1	6.3	4.4	20.7	0
	Copepoda			4.4	39.3	11.9	6.0	23.4	7.4
	Malacostraca	Amphipoda	*Corophium*	4.1	20.9	6.9	25.1	6.2	0
			Gammaridae	0	0	1.3	0	0	0.1
		Cumacea		0	11.0	0.6	0	0.9	0
		Tanaidacea		0	1.3	0	0	0.2	0
	Insecta	Diptera		34.3	1.9	0	0	0	0
Other				0.0	0.2	0.6	0.5	0.1	0
		Mean invertebrate density		21	25	11	12	91	71

Appendix (con't): The percentage of each taxon represented at each site.

				Site Migratory Period					
Phylum	Class	Order		RaB SJ (N=15)	RB N (N=14)	RB SJ (N=15)	RS SJ (N=15)	SB N (N=30)	SB SA (N=30)
Sarcomastigophora	Granuloreticulosea	Foraminifera		0	0.1	0.6	0	18.2	6.5
Nematoda	Adenophorea			43.2	33.9	10.6	57.1	38.8	29.4
Mollusca	Bivalvia			1.3	0	0	0.6	0.7	5.3
	Gastropoda			2.1	0	0.0	7.8	0	0
Annelida	Polychaeta			9.9	57.3	83.9	7.5	19.1	14.9
Arthropoda	Ostracoda			6.5	0.1	0.1	6.6	0.2	0.4
	Copepoda			5.4	6.1	1.0	16.8	0	25.1
	Malacostraca	Amphipoda	*Corophium*	30.6	0.9	0.8	1.5	0.2	13.8
			Gammaridae	0	0	0	0	0	0
		Cumacea		0.5	1.2	0	0	12.3	2.9
		Tanaidacea		0	0.4	2.8	0.3	6.3	1.4
	Insecta	Diptera		0	0	0.1	0	2.8	0.4
Other				0	0	0	1.8	1.4	0
		Mean invertebrate density		42	147	135	22	76	26

Appendix (con't): The percentage of each taxon represented at each site.

				Site Migratory Period		
				SI	TI	WH
				SA	N	SJ
Phylum	Class	Order		(N=15)	(N=31)	(N=15)
Sarcomastigophora	Granuloreticulosea	Foraminifera		17.6	0.6	6.0
Nematoda	Adenophorea			46.1	42.8	62.3
Mollusca	Bivalvia			0.0	0	1.1
	Gastropoda			0.1	0	0
Annelida	Polychaeta			5.2	52.6	4.5
Arthropoda	Ostracoda			1.9	0.9	4.1
	Copepoda			9.5	0.1	5.0
	Malacostraca	Amphipoda	*Corophium*	15.2	2.4	15.6
			Gammaridae	2.6	0	0.5
		Cumacea		0.2	0.6	0.3
		Tanaidacea		1.5	0	0.5
	Insecta	Diptera		0.1	0	0
Other				0	0	0.2
		Mean invertebrate density		96	40	69