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Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*

Andrea C. Pomeroy

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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 tradeoff 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.

A. C. Pomeroy, Centre for Wildlife Ecology, Simon Fraser Univ., 8888 University Drive, Burnaby, British Columbia, Canada, V5A 1S6 (apomeroy@sfu.ca).

Tradeoffs 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 (Elgar 1989, Bednekoff and Lima 1998, Downes and Hoefer 2004) 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 et al. 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

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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 (Cresswell 1994b, Barbosa 1997, Whitfield 2003) despite potential costs of interference competition that can occur between foragers at high densities (Yates et al. 2000), and decrease feeding rates to increase vigilance (Cresswell 1994b, Barbosa 1997). 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 1994a, Ydenberg et al. 2002, Yasué et al. 2003), furthermore they can alter their usage within a site to optimize this tradeoff.

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 et al. 2005a, 2005b).

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 tradeoff 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 tradeoff 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 et al. 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 et al. 2003). Conversely, danger is low for sandpipers as they migrate southward (July) through the Fraser Estuary since falcons do not pass through the study site in high abundance until August (Lank et al. 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, Whitfield 2003, Dekker and Ydenberg 2004). 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 (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 et al. 2000). Each taxa sampled has been shown to be consumed intentionally (Wolf 2001) or unintentionally (Sutherland et al. 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 h 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 40× 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 (20 April–15 May). 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 25–60× 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 (reviewed by 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 (Cresswell 1994b, Barbosa 1997).

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.) 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 m^{-2} 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 of the results, 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 two and nine 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.

JMPIN 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 (Fig. 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 (Fig. 1, 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 six times greater at the shoreline than at the 1 km mark. The average invertebrate density was

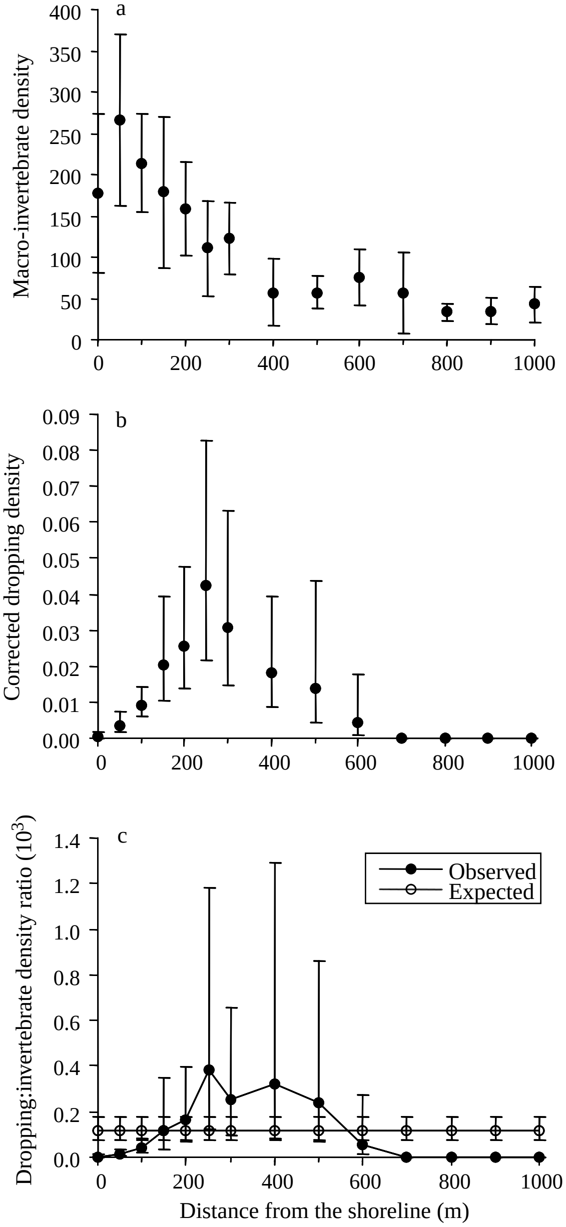

Fig. 1. Northward migration: the mean density of macro-invertebrates (invertebrates $core^{-1}$) (a) and sandpiper droppings (droppings m^{-2} min^{-1}) (b) as distance from the shoreline increases. The observed ratio of dropping to invertebrate densities (c) does not closely match the expected ratio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

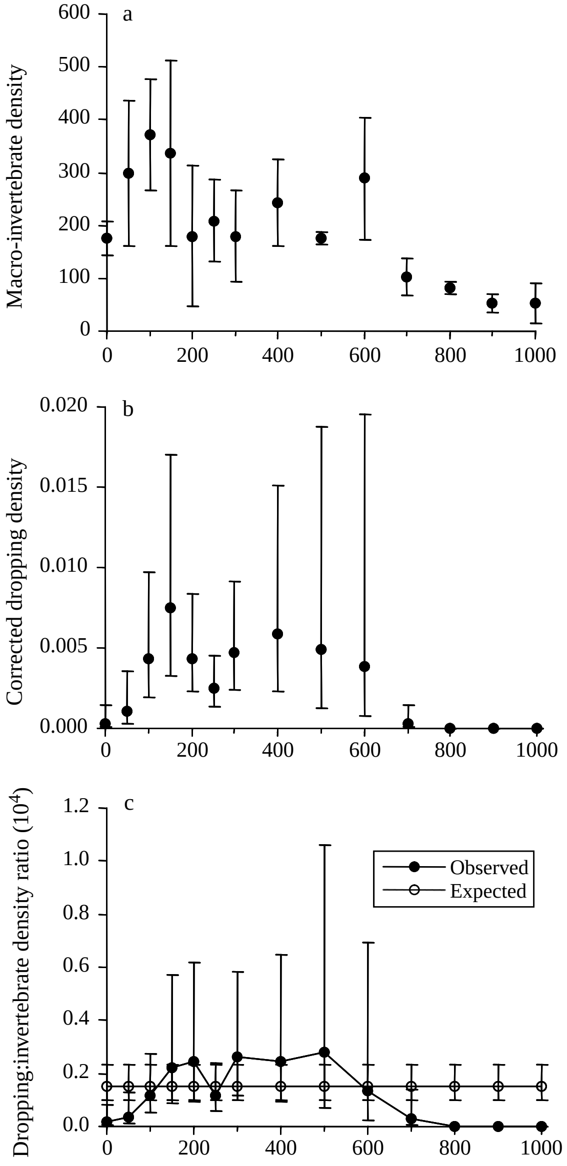

Fig. 2. Southward migration: the mean density of macro invertebrates (invertebrates core^{-1}) (a) and sandpiper droppings (droppings m^{-2} min^{-1}) (b) as distance from the shoreline increases. The observed ratio of dropping to invertebrate densities (c) does not closely match the expected ratio based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

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 (Fig. 1, 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 1). In separate regression analyses, polycheate ($F_{1,137} = 198.13$, $R^2 = 0.59$, $P < 0.0001$), nematode ($F_{1,137} = 31.04$, $R^2 = 0.10$, $P < 0.0001$), foraminefera ($F_{1,137} = 14.76$, $R^2 = 0.10$, $P = 0.0002$), 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 (Fig. 3; logistic regression: Wald $\chi^2 = 9.45$, $n = 240$, $df = 1$, $P = 0.0021$). This effect did not differ between migratory periods (logistic regression: Wald $\chi^2 = 0.094$, $n = 240$, $df = 2$, $P = 0.76$). The probability that a western sandpiper was vigilant 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.

Table 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
Polychaete	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)

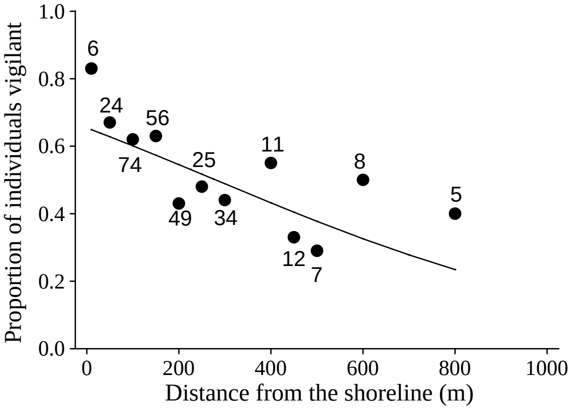

Fig. 3. The proportion of individuals vigilant (1) as distance from the shoreline increases (solid circles). The sample size for each point is shown on the figure. The logistic regression curve (solid line) shows the probability of an individual being vigilant as distance from the shoreline increases.

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 (Fig. 1, 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 (Fig. 2a) 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 (Fig. 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 (Fig. 1, 2c). The observed pattern of usage supports the hypothesis that spatial usage reflects a tradeoff 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 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 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 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 one and directly compared (Fig. 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 (Lazarus and Symonds 1992, Buchanan 1996, Cresswell 1996, Dekker 1998, Whitfield 2003, Dekker and Ydenberg 2004). 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 (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.). 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

Table 2. Differences between observed and expected ratios of dropping to invertebrate densities for northward ($\times 10^3$) and southward ($\times 10^4$) 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)

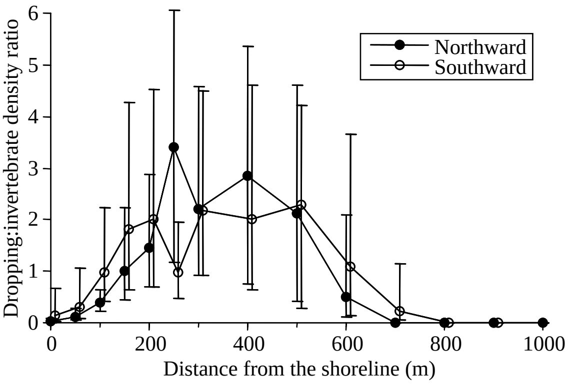

Fig. 4. The overall pattern of spatial usage of Boundary Bay between migratory periods when the ratio of dropping to invertebrate densities is scaled to unity for each migratory period. Error bars are 95% confidence limits. Data points are offset slightly for clarity.

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 (Brown 1988, Altendorf et al. 2001, Kotler et al. 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 (Fig. 4). For southbound adults food abundance at Boundary Bay is higher (Fig. 1, 2a) and predator abundance is lower (Lank et al. 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 et al. 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 et al. 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 et al. 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 (Reise 1985, Kennish 1986). 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 (Lazarus and Symonds 1992, Buchanan 1996, Cresswell 1996, Whitfield 2003). Although data on raptor predation on western sandpipers was 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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