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Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger

Andrea C. Pomeroy,[a] **Robert W. Butler,**[a,b] **and Ronald C. Ydenberg**[a]
[a]Centre for Wildlife Ecology and Behavioural Ecology Research Group, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada and [b]Pacific Wildlife Research Centre, Canadian Wildlife Service, 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada

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 with 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 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. *Key words:* food abundance, migration, predation danger, stopover site usage, trade-off hypothesis, western sandpiper. *[Behav Ecol 17:1041–1045 (2006)]*

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, whereas 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, whereas 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 (Sih 1980; Lima 1988; Laundre et al. 2001). Under dangerous conditions, foragers become more vigilant, join larger flocks, or move to safer (but poorer) feeding sites (see reviews in Lima and Dill 1990; Brown and Kotler 2004).

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 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, whereas Burns and Ydenberg (2002) show that more heavily wing-loaded 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 (Lindström 1990; Cresswell 1994; Ydenberg et al. 2002, 2004; Schmaljohann and Dierschke 2005; Pomeroy 2006). However, experimental work to confirm that migrants are sensitive to predation danger is scant. Cimprich et al. (2005) found that blue–gray 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

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Address correspondence to A.C. Pomeroy. E-mail: apomeroy@sfu.ca.

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and Symonds 1992). Peregrine falcons (*Falco peregrinus*), merlins (*Falco columbarius*), and other raptors hunt shorebirds, including western sandpipers (Page and Whitacre 1975; Whitfield 1985; Buchanan et al. 1988; Dekker 1988; Cresswell 1994, 1996), and achieve greatest hunting success using cover to conceal their approach (Whitfield 1985, 2003; Cresswell 1994; Dekker and Ydenberg 2004). 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 with 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.

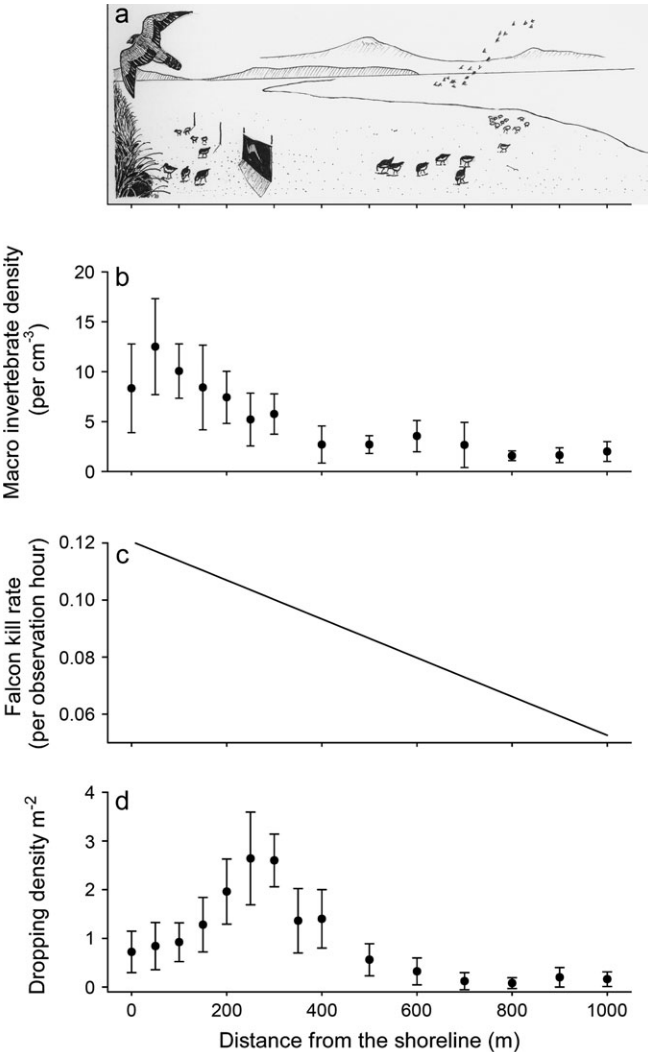

Figure 1
(a) Experimental design with location of control and treatment transects relative to the shoreline at Boundary Bay, (b) the distribution of macroinvertebrates at the study site as sampled in 2002 (adapted from Pomeroy 2006), (c) the kill rate of peregrine falcons hunting dunlin in winter at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

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, (49°4.13′N, 122°58.05′W) twice annually while travelling between tropical nonbreeding 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- to 200-m-wide strip of salt marsh. 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 (Sutherland et al. 2000; Mathot and Elner 2004). Peregrine falcons and merlins hunt sandpipers there (Ydenberg et al. 2002; Lank et al. 2003).

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 1b,c). 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 (Reise 1985; Kennish 1986), and high macroinvertebrate 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, 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 1c). The natural pattern of western sandpiper usage across the mudflat peaks at intermediate distances (Figure 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 the 3 treatment transects in Boundary Bay during northward migration in 2003 (Figure 1a). The 3 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 macroinvertebrate abundance [invertebrates/cm^3 ± 95% confidence interval (CI)] on the shoreward side of the obstruction (50–150 m along the transect) was almost twice that on the oceanward side (150–250 m; shore side: 11.28 ± 1.39; ocean side: 6.31 ± 0.96, based on data in Pomeroy 2006; see Figure 1b).

The tidal rhythm at Boundary Bay is semidiurnal, with the time of the highest tide shifting later by approximately 45 min/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 is 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 h, and was removed between replicates. The procedure was replicated 3 times on 2 transects and 4 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 6-h 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 ± 95% CI = 0.48 ± 0.10, $N = 66$). These are washed away with each tidal inundation (AC Pomeroy, unpublished data) and hence provide a sensitive measure of use since the previous high tide. We counted droppings in 1-m^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 of transects.

Dropping densities (droppings/m^2) at each station were adjusted to account for the total duration of tidal exposure (droppings/m^2/min) 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 nonlinearity) and all interactions between the 3 main factors as dependent variables. All variables were included in the model, and nonsignificant variables were removed sequentially ($P > 0.05$) until the minimum adequate model was derived. The change in deviance, which approximates a chi-square (χ^2) distribution, was used to determine the significance of changes made to each model. Means ± 95% CIs are presented throughout. Genstat V. 8.2 (GenStat, 2005) was used for all statistical analyses.

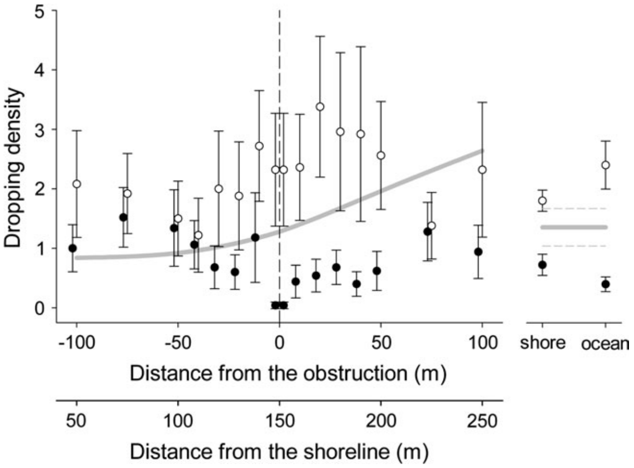

Figure 2
The effect of an experimental obstruction at 150 m (indicated by dashed vertical line) on usage of western sandpipers at a stopover site during northward migration. Open circles are mean dropping densities on control, whereas closed circles are densities on treatment transects. The gray line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

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 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 2; matched pairs, $t = 2.30$, degree of freedom (df) = 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 3; $\chi^2 = 4.7$, df = 1, $P = 0.03$, $N = 160$).

Food abundance also affects the usage pattern as predicted. The difference in dropping density between treatment and

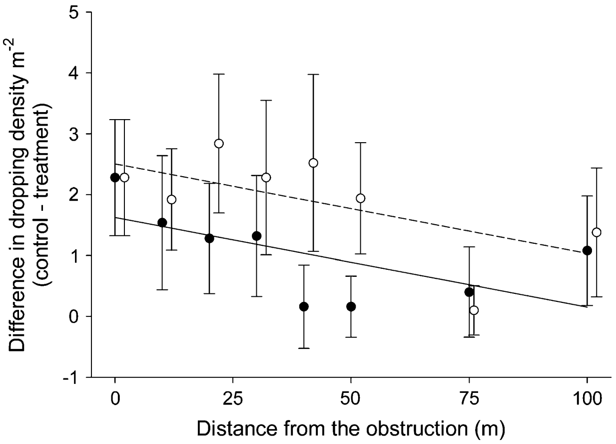

Figure 3
The difference in usage (droppings/m^2) between matched control and treatment transects on high- (shore, filled circles) and low-food (ocean, open circles) sides as distance from the obstruction increases. The lines are those predicted from the statistical model. Error bars are 95% CIs.

control transects was greater on the low-food oceanward side of the obstruction than on the high-food shoreward side (Figure 3; $\chi^2 = 4.5$, df = 1, $P = 0.03$, $N = 160$). Nonsignificant 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. 1991; Kotler et al. 2004), have ample reserves (Kotler 1997), and when predators are abundant (Kotler 1992; Kotler et al. 1991, 2004), 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 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 (Cresswell 1994; Makino et al. 2003; Kamenos et al. 2004; Sapir et al. 2004; Apollonio et al. 2005; Cimprich et al. 2005; Dussault et al. 2005; Heithaus 2005; 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. Because 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 macroinvertebrates, 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 (Rainey et al. 2003; Pomeroy and Butler 2005). 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 kilometers from the shoreline are 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. On 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 and then they can make appropriate adjustments of antipredator 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 trade-offs 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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REFERENCES

Apollonio M, Ciuti S, Luccarini S. 2005. Long-term influence of human presence on spatial sexual segregation in fallow deer (*Dama dama*). J Mammal 86:937–46.

Brown JS. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobiol 22:37–47.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014.

Buchanan JB, Schick CT, Brennan LA, Herman G. 1988. Merlin predation on wintering dunlins; hunting success and dunlin escape tactics. Wilson Bull 100:108–18.

Burns JG, Ydenberg RC. 2002. The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). Behav Ecol Sociobiol 52: 128–36.

Butler RW, Kaiser GW, Smith GEJ. 1987. Migration chronology, length of stay, sex ratio, and weight of western sandpipers (*Calidris mauri*) on the south coast of British Columbia. J Field Ornithol 58:103–11.

Cimprich DA, Woodrey MS, Moore FR. 2005. Passerine migrants respond to variation in predation risk during stopover. Anim Behav 69:1173–9.

Cresswell W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? J Anim Ecol 63:589–600.

Cresswell W. 1996. Surprise as a winter hunting strategy in sparrowhawks *Accipiter nisus*, peregrines *Falco peregrinus* and merlins *F. columbarius*. Ibis 138:684–92.

Dekker D. 1988. Peregrine falcon and merlin predation on small shorebirds and passerines in Alberta. Can J Zool 66:925–8.

Dekker D, Ydenberg RC. 2004. Raptor predation on wintering Dunlins in relation to the tidal cycle. Condor 106:415–9.

Dussault C, Ouellet JP, Courtois R, Huot J, Breton L, Jolicoeur H. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–28.

GenStat. 2005. GenStat V. 8.2. Hemel Hempstead: VSN International.

Greenberg R, Marra PP. 2005. Birds of two worlds: the ecology and evolution of migration. Baltimore, MD: Johns Hopkins University Press.

Heithaus MR. 2005. Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. Mar Biol 147:27–35.

Kamenos NA, Moore PG, Hall-Spencer JM. 2004. Maerl grounds provide both refuge and high growth potential for juvenile queen scallops (*Aequipecten opercularis L.*). J Exp Mar Biol Ecol 313:241–54.

Kennish MJ. 1986. Ecology of estuaries: physical and chemical aspects. Volume I. London: CRC Press.

Kennish MJ. 1990. Ecology of estuaries: biological aspects. Volume II. London: CRC Press.

Kotler BP. 1992. Behavioral resource depression and decaying risk of predation in two species of coexisting gerbils. Behav Ecol Sociobiol 30:239–44.

Kotler BP. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. Oikos 78:274–82.

Kotler BP, Brown JS, Bouskila A. 2004. Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. Ecology 85:917–22.

Kotler BP, Brown JS, Hasson O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249–60.

Lank DB, Butler RW, Ireland J, Ydenberg RC. 2003. Effects of predation danger on migration strategies of sandpipers. Oikos 103: 303–19.

Laundre JW, Hernandez L, Altendorf KB. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Can J Zool 79:1402–9.

Lazarus J, Symonds M. 1992. Contrasting the effects of protective and obstructive cover on avian vigilance. Anim Behav 43:519–21.

Lima SL. 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos 53:12–26.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–40.

Lindström Å. 1990. The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. Behav Ecol 1:102–6.

Makino W, Yoshida T, Sakano H, Ban SH. 2003. Stay cool: habitat selection of a cyclopoid copepod in a north temperate oligotrophic lake. Freshw Biol 48:1551–62.

Mathot KJ, Elner RW. 2004. Evidence for sexual partitioning of foraging mode in western sandpipers (*Calidris mauri*) during migration. Can J Zool 82:1035–42.

Page G, Whitacre DF. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

Pomeroy AC. 2006. Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*. Oikos 112:629–37.

Pomeroy AC, Butler RW. 2005. Color infrared photography is not a good predictor of macroinvertebrate abundance on mudflats used by shorebirds. Waterbirds 28:1–7.

Quinn JL, Cresswell W. 2004. Predator hunting behaviour and prey vulnerability. J Anim Ecol 73:143–54.

Rainey MP, Tyler AN, Gilvear GJ, Bryant RG, McDonald P. 2003. Mapping intertidal estuarine sediment grain size distributions through airborne remote sensing. Remote Sensing of the Environment 84:480–90.

Rappole JH. 1995. The ecology of migrant birds: a neotropical perspective. Washington: Smithsonian Institution Press.

Reise K. 1985. Tidal flat ecology: an experimental approach to species interactions. Berlin, Germany: Springer-Verlag.

Sapir N, Abramsky Z, Shochat E, Izhaki I. 2004. Scale-dependent habitat selection in migratory frugivorous passerines. Naturwissenschaften 91:544–7.

Schmaljohann H, Dierschke V. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears (*Oenanthe oenanthe*). J Anim Ecol 74:131–8.

Sergio F, Scandolara C, Marchesi L, Pedrini P, Penteriani V. 2005. Effect of agro-forestry and landscape changes on common buzzards (*Buteo buteo*) in the Alps: implications for conservation. Anim Conserv 8:17–25.

Sih A. 1980. Optimal behavior: can foragers balance two conflicting demands. Science 210:1041–3.

Spencer RJ, Cavanough VC, Baxter GS, Kennedy MS. 2005. Adult free zones in small mammal populations: response of Australian native rodents to reduced cover. Austral Ecol 30:876–84.

Sutherland TF, Shepherd PCF, Elner RW. 2000. Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence from dual foraging modes. Mar Biol 137:983–93.

Swennen C, Duiven P, Spaans AL. 1982. Numerical density and biomass of macrobenthic animals living in the intertidal zone of Surinam, South America. Netherlands J Zool 15:406–18.

Whitfield DP. 1985. Raptor predation on wintering waders in southeast Scotland. Ibis 127:552–8.

Whitfield DP. 2003. Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. J Avian Biol 34:163–9.

Wilson WH. 1994. The western sandpiper. The birds of North America. Volume 90. p 1–20. Ithaca: Cornell Laboratory of Ornithology.

Yates MG, Goss-Custard JD, McGrorty S, Lakhani KH, Dit Durrell SEA, Clarke RT, Rispin WE, Moy I, Yates T, Plant RA, et al. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. J Appl Ecol 30: 599–614.

Ydenberg RC, Butler RW, Lank DB, Guglielmo CG, Lemon M, Wolf N. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. J Avian Biol 33:47–55.

Ydenberg RC, Butler RW, Lank DB, Smith BD, Ireland J. 2004. Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. Proc R Soc Lond B 271:1263–9.