Pomeroy, A. C., D. A. Acevedo Seaman, R. W. Butler, R. W. Elner, T. D. Williams, and R. C. Ydenberg. 2008. Feeding–danger trade-offs underlie stopover site selection by migrants. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* **3**(1): 7. [online] URL: http://www.ace-eco.org/vol3/iss1/art7/

Research Papers

Feeding–Danger Trade-Offs Underlie Stopover Site Selection by Migrants

Compromis alimentation-prédation sous-tendant la sélection d'une halte migratoire par des migrateurs

Andrea C. Pomeroy [1,2], *Dana A. Acevedo Seaman* [1], *Robert W. Butler* [1,3], *Robert W. Elner* [1,3], *Tony D. Williams* [1], and *Ronald C. Ydenberg* [1]

Fig. 1. The Georgia Basin/Puget Sound region of British Columbia, Canada and Washington, USA.

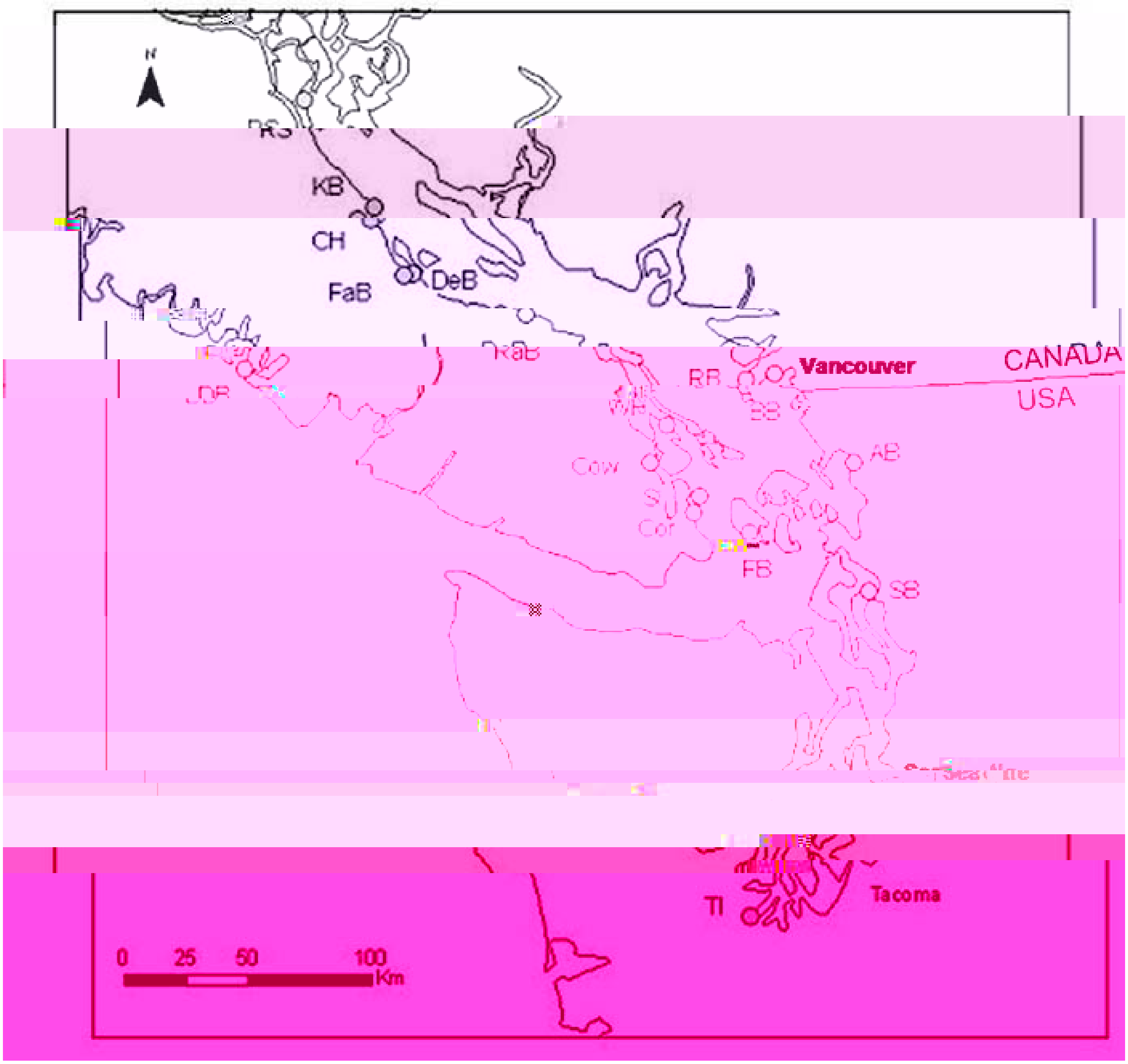


Table 1. The name and location of stopover sites sampled in the Georgia Basin/Puget Sound region, sample sizes for invertebrate cores and body-mass samples, and usage data for each migratory stage (N = northward, SA = southward adult, SJ = southward juvenile, *n* = number).

Site	Site Name	Location	Invertebrate core (*n*)	Body mass (*n*)	Usage	Peak Record	Migratory stage
AB	Alice Bay	Edison, WA	30	13	Used (Seaman 2003)	500	SA
BB	Boundary Bay	Delta, BC	146	N=63 SA=18 SJ=34	Used (Butler 1994)	>100 000	N, SA, SJ
CH	Comox Harbor	Comox, BC	15	N/A	Not used (BSC, unpublished data, 2005)	24	SA
Cor	Cordova Bay	Victoria, BC	15	N/A	Not used (BSC, unpublished data, 2005)	75	SA
Cow	Cowichan Bay	Duncan, BC	15	N/A	Not used	0	SA
DB	Doug Banks	Tofino, BC	25	28	Used (Butler et al. 1992)	5000	SJ
DeB	Deep Bay	Vancouver Island, BC	15	N/A	Not used (Dawe et al. 1998)	12	SA
FaB	Fanny Bay	Vancouver Island, BC	15	N/A	Not used (Dawe et al. 1998)	0	SA
FB	False Bay	San Juan Island, WA	25	7	Used (K. O’Reilly, unpublished data)	200	SJ
KB	Kye Bay	Comox, BC	15	N/A	Not used (BSC, unpublished data, 2005)	25	SA
RaB	Rathtrevor Beach	Parksville, BC	15	N/A	Not used (BSC, unpublished data, 2005)	20	SA
RB	Roberts Bank	Delta, BC	29	N=57 SA=18 SJ=66	Used (Butler 1994)	>100 000	N, SJ
RS	Rebecca Spit	Quadra Island, BC	15	N/A	Not used	0	SA
SB	Skagit Bay	Utsalady, WA	60	N=38, SA=25	Used (Evenson and Buchanan 1997)	10 000	N, SA
SI	Sidney Island	Sidney Island, BC	15	24	Used (Ydenberg et al. 2004)	1000	SJ
TI	Totten Inlet	Shelton, WA	31	27	Used (Evenson and Buchanan 1997)	2000	N
WH	Walker’s Hook	Saltspring Island, BC	15	N/A	Not used (J. Booth, pers. comm.)	0	SA

Safety

Peregrine Falcons (*Falco peregrinus*), Merlins (*F. 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, Cresswell 1994, Whitfield 2003b, Dekker and Ydenberg 2004). As the shoreline poses a great deal of danger for foraging sandpipers, stopover sites that are small and have 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 (Pomeroy et al. 2006).

As an index of safety, we used the distance tool in ArcMap v.9.1 (ESRI 2005) to measure the furthest distance from the shoreline (as indicated by the upper water mark on marine charts (Nautical Data International 2005, National Oceanic and Atmospheric Administration (NOAA) 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

Sites were classified as “used” or “unused” based on the intensity and frequency of use, using as sources published literature, unpublished reports, the Bird Studies Canada Coastal Waterbirds Survey (Bird Studies Canada, unpublished data, 2005) database, and local knowledge (Table 1). Sites were classified as “used” if hundreds or thousands of sandpipers on stopover are recorded there on a regular and annual basis (Butler et al. 1987, 1992, Buchanan 1988, Iverson et al. 1996, Evenson and Buchanan 1997, Warnock and Bishop 1998, Acevedo Seaman et al. 2006). Sites were considered “unused” if there are no records of Western Sandpipers there. A few sites (see Table 1) had single-day records up to 75 birds, but the sites are in fact visited only rarely by western sandpipers, and were therefore classified as “unused.”

At sites that were used during migration, we used mist nets to capture sandpipers to measure the body mass of individuals using the site (for sample sizes see Table 1). Western Sandpipers were removed from the mist nets immediately after capture and weighed within 10 min. Tarsae were measured using callipers (to the nearest 0.1 mm).

Statistical Analysis

We tested for differences between sites in food abundance and safety 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 whether food abundance, safety, or 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. As northbound migrants were significantly heavier (0.8 g) than southbound migrants (P = 0.05), we also included migratory stage (northward, southward adult, southward juvenile) in the analysis. Body-mass values at each site are reported as the least-squares mean. To investigate the relationship between site safety and state of individuals using a site, we then used these least-squares means of body mass at each site. Means and 95% C.I. are used throughout. JMP*IN* V. 4.04 (SAS 2001) was used for all statistical analyses.

RESULTS

Of the 17 sites surveyed, eight were classified as “used” and nine as “unused” according to our criteria (Table 1). Food abundance and safety measures both varied widely between study sites. Food abundance ranged from means of eight to 204 invertebrates core^{-1} (ANOVA: $F_{16, 479} = 16.3$, $P < 0.0001$). Invertebrate densities were on average three times greater at used than at unused sites (mean invertebrate density/core ± 95% C.I.; used sites = 99.4 ± 32.2; unused sites = 31.9 ± 30.4, ANOVA: $F_{1, 15} = 9.26$, $P = 0.008$). The relative abundance of invertebrate taxa sampled at each site is provided in Appendix 1. The safety index ranged from 75 m to 4560 m, with used sites on average three times safer (mean distance from shore ± 95% C.I. = 1932.5

± 845.9 m) than unused sites (mean distance from shore ± 95% C.I. = 581.7 ± 797.5 m, ANOVA: $F_{1, 15} = 5.4$, $P = 0.03$, $N = 17$).

In a logistic regression model including food as the only independent variable, usage of 12 of the 17 sites was predicted correctly (Table 2. $\chi^2 = 8.51$, d. f. = 1, $R(U)^2 = 0.36$, $P = 0.0035$). The logistic regression model including safety as the only independent variable also correctly predicted usage of 12 of 17 sites ($\chi^2 = 5.78$, d.f. = 1, $R(U)^2 = 0.25$, $P = 0.02$), although the identity of the 12 sites differed (Table 2). The logistic regression including both food abundance and safety as explanatory variables performed better than either of these models, correctly predicting the usage of 14 of 17 sites (Fig. 2. $\chi^2 = 10.24$, d.f. = 2, $R(U)^2 = 0.44$, $P = 0.006$).

The body mass of individuals (controlled for structural size and migratory stage) was greater at stopover sites with greater safety (Fig. 3. Nonlinear Regression: LS mean body mass = 26.6 * (1 - e $^{(-0.0061*safetyindex)}$), $R^2 = 0.55$, $P = 0.03$), but was not significantly related to food abundance ($P = 0.41$).

DISCUSSION

Our analysis shows that including both food abundance and safety as factors improved our ability to predict which stopover sites were used by migrating sandpipers and which were not. Either factor on its own was also able to predict stopover-site usage, but migrant sandpipers used sites that were dangerous only if food abundance there was high, and used sites with low food abundance only if they were very safe. To our knowledge, no other study has investigated the usage of stopover sites by migrants or compared multiple site attributes at both used and unused sites on a regional scale. Our results also confirm that, on this scale, the usage of stopover sites depends on the fuel load of individual sandpipers, previously shown in a comparison of just two sites by Ydenberg et al. (2002). Sandpipers on dangerous stopover sites carry on average less fuel than those on safer sites. We hypothesize that this occurs because sandpipers with adequate fuel loads do not need to risk feeding in dangerous places.

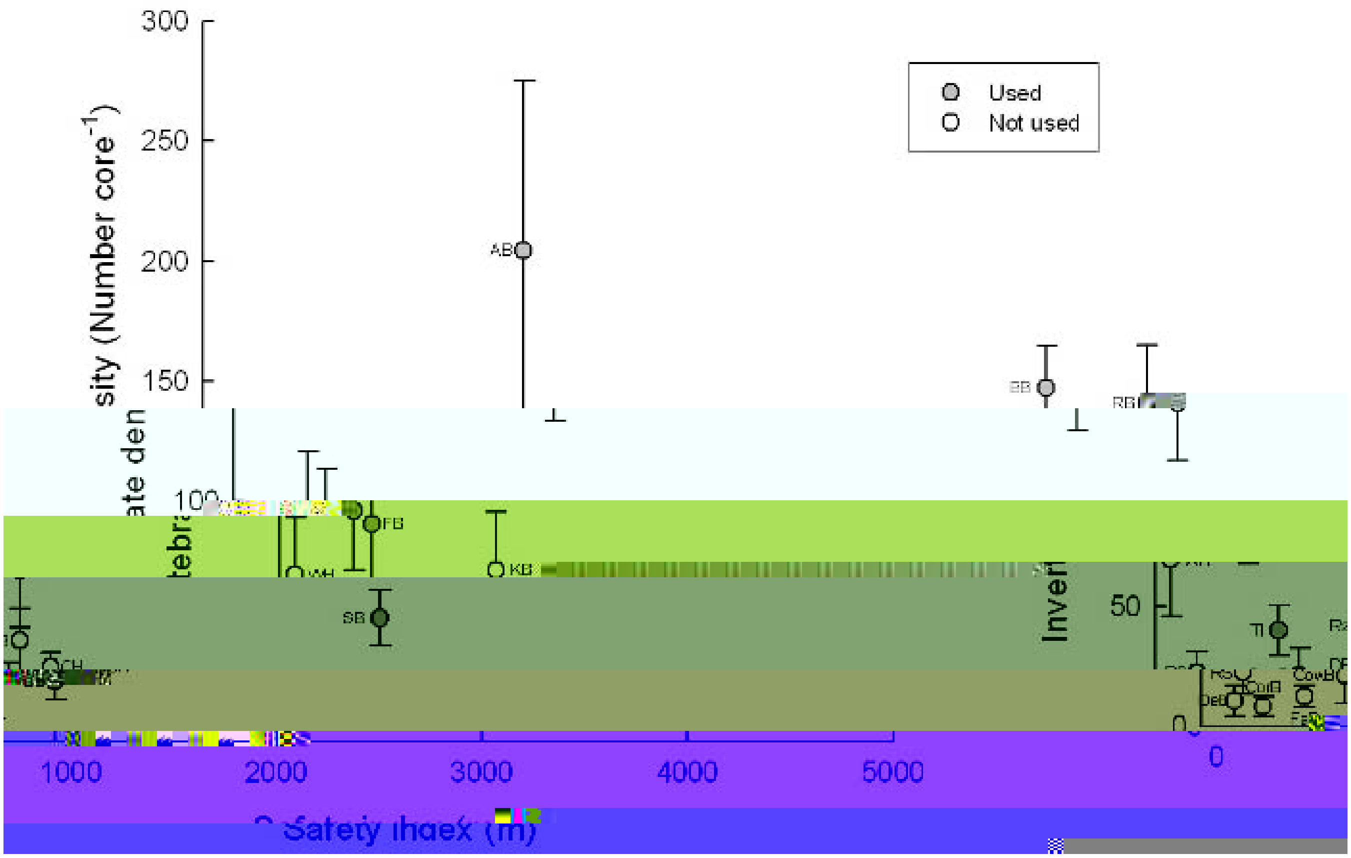
Our best model incorrectly predicted usage of three of the 17 sites, and an examination of their characteristics can help to understand these assignment errors. Two sites (Doug Banks and Totten Inlet) were classified by the model as “unused,” but are in fact used regularly by sandpipers on stopover. The cover surrounding these two sites differs from that lining the shoreline of the other six “used” sites, which consists of low marsh grasses whereas Doug Banks and Totten Inlet are surrounded by tall coniferous trees. From the perspective of a migrant sandpiper, these sites may be functionally safe, as falcons do not appear to use these trees for attack cover, but hunt by attacking over the open mudflat, much like the attack strategy they employ at larger sites (J. Buchanan, pers. comm.). This difference suggests that cover type might be an important factor influencing stopover-site usage by migrants and may be used, in addition to distance from cover, to remotely asses the danger of a potential site.

The third incorrectly classified site was Kye Bay, which, according to the model, should be used by sandpipers due to its high food abundance; however, there is no record of usage by Western Sandpipers. A noticeable difference between this and all other used stopover sites is the relatively high percentage (60%) of nematodes (Phylum Nematoda, Class Adenophorea) among the potential prey items, compared with a maximum of 46% and an average of 25% nematodes among used sites (Appendix 1). Although all prey taxa presented here have been documented as Western Sandpiper prey (Wolf 2001), there is evidence that nematodes are less preferred by Western Sandpipers than other prey items such as polychaetes (Sutherland et al. 2000). It is possible that prey type may also be an important factor influencing stopover-site selection by migrants and may be used, in addition to prey abundance, to remotely assess the food availability of a potential site.

One 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 (Swennen et al. 1982, Reise 1985, Kennish 1986), we might be overestimating food abundances, whereas our measures of food abundance at smaller sites are

Table 2. Actual usage at sample sites on migration by sandpipers, and usage as predicted by each logistic regression model. (Y = yes; N = no.)

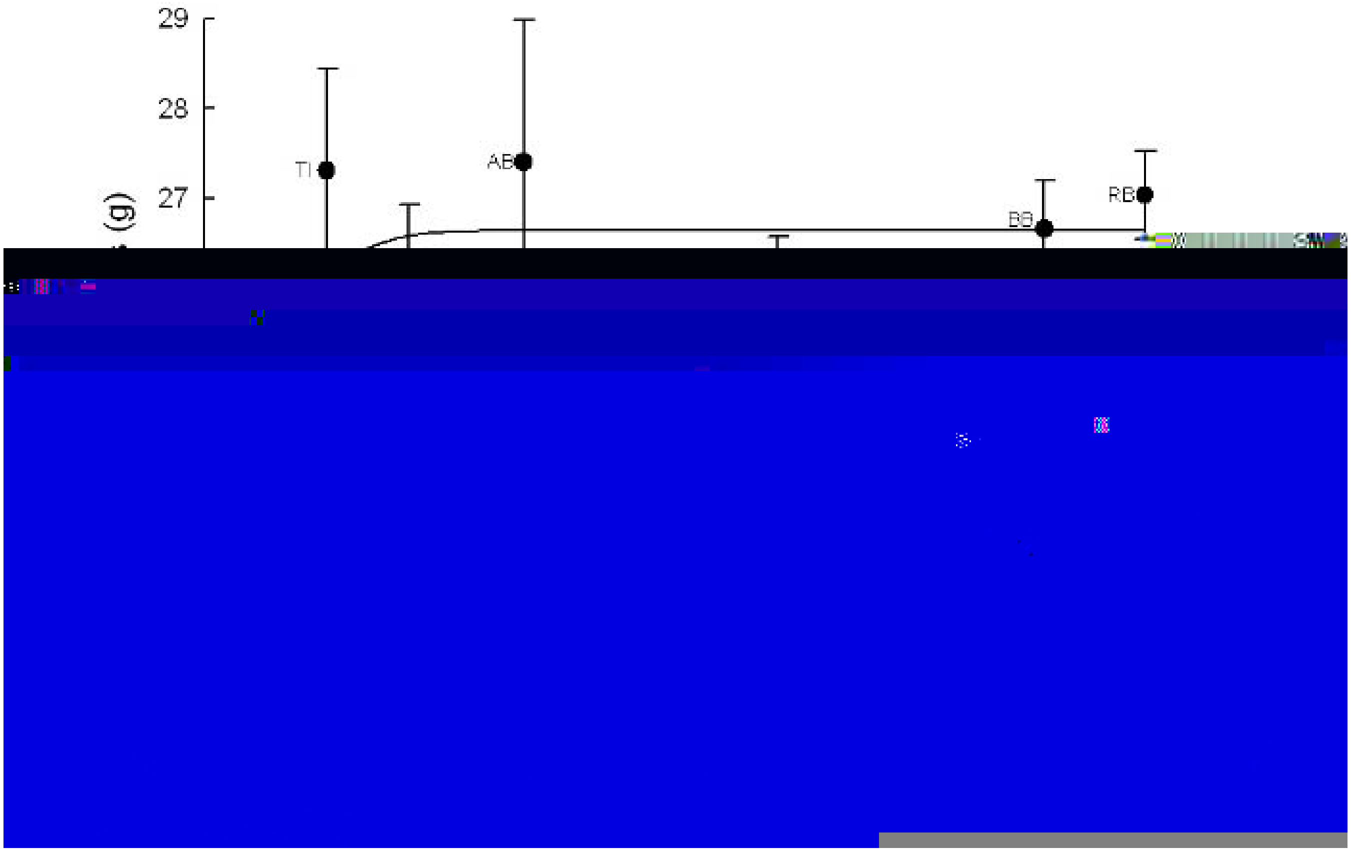
Fig. 2. The mean invertebrate density (± 95% C.I.) and safety index for sites that are used and not used by Western Sandpipers on migration.



the levels of food abundance, and gauge the level of danger there based on their encounters with predators, and they can make appropriate adjustments to anti-predator behaviors to carefully balance food and danger over short temporal and small spatial scales. This work suggests that migrants assess food and danger attributes of stopover sites remotely and that these attributes affect which sites they will use.

Assessment of the conservation value of stopover sites for migrants should evaluate measures of both food and danger. As migration is energetically expensive, stopover-site quality is often associated with the quantity or quality of food resources (Yong et al. 1998, Baker et al. 2004, Placyk and Harrington 2004, Battley et al. 2005, Stillman et al. 2005a, van Gils et al. 2005, Smith et al. 2007). However, migration is also dangerous. As danger from predators increases, migrant birds have been shown to alter their behavior 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 (Ydenberg et al. 2002, 2004, Schmaljohann and Dierschke 2005). Predation danger influences habitat usage by migrants within and between stopover sites. Assessments of stopover-site quality then must include both food and danger attributes of sites. Furthermore, stopover-site quality is condition dependent. Whereas heavy individuals with ample fuel reserves may prefer safe sites with

Fig. 3. The relationship between the safety index measured at stopover sites and the least-squares mean body mass (± 95% C.I.) of sandpipers captured. The line is that predicted from the nonlinear regression (LS mean body mass = 26.6 * (1-e(-0.0061*safety index))).



high bird densities despite few food opportunities, lean birds would be more likely to consider a high-quality site as one where it could fatten quickly, despite the added danger. Our results suggest that a variety of site types (i.e., both high food and high safety) need to be conserved.

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 it might no longer be used. At the landscape scale, increases in predator abundance would likely cause migrants to shift usage from small, dangerous sites to larger, safer ones (e.g., Ydenberg et al. 2004, Taylor et al. 2007). Moreover, changes in stopover-site usage will be condition dependent (Ydenberg et al. 2002, 2004). A decrease in food abundance at a dangerous site will have a greater effect on lean birds, whereas increasing danger at safe sites will have a greater effect on heavy birds. If we neglect the role of predators and the effect they have on stopover-site usage, the behavioral adaptations used by migrants to avoid mortality by predation, including increasing vigilance, decreasing length of stay, and adjusting habitat usage, could instead be attributed to declines in food abundance at a site or to population decline (Ydenberg et al. 2004). Efforts to conserve habitat for migrants must consider the role of food abundance and predation danger in stopover-site usage.

Stopover-site conservation is essential to maintain populations of migratory birds. The importance of identifying, prioritizing, and protecting stopover habitat for birds is gaining increasing recognition (Myers et al. 1987, Donovan et al. 2002, Mehlman et al. 2005, Skagen 2006). Many bird conservation programs identify and prioritize sites of importance based on the number of individuals (or proportion of a population) using a particular site (e.g., Western Hemispher Shorebird Reserve Network (WHSRN), Important Bird Area (IBA)). However, this approach may overemphasize the importance of large (safe) sites that can support significant numbers of birds. Mehlman et al. (2005) assert that efforts to conserve stopover habitat for landbirds should target a mosaic of different types of stopover habitats. The authors suggest three categories of stopover sites representing points on a continuum of their capacity to meet the needs of migrants. These categories range from fire escapes (infrequently used with few available resources, but vital in emergencies) to convenience stores (mid-quality stopover sites that are used for rest, and replenishment of some fuel, but where food resources might be low and/or predation danger high), to full-service hotels (high-quality sites with abundant resources where migrants can safely rest and refuel for the next leg of migration). In our study system, the sites with ample food and safety would be considered full-service hotels, and sites that are high in either food or safety could be thought of as convenience stores, whereas sites that are low in food and safety may be potential fire escapes. Within each of these categories, the sites can then easily be ranked based on their food and safety attributes, and prioritized accordingly for conservation.

We show here evidence that migrant Western Sandpipers select stopover sites according to trade-offs between food abundance and predation danger. Furthermore, usage of these sites depends on the state of an individual. This study suggests that migrants use habitat features, such as cover, to assess predation danger, and that they mediate their probability of mortality from predation by adjusting habitat usage on a landscape scale. Results such as these can be applied to predict the behavior of migrants at stopover sites, and usage of stopovers if food and/or danger attributes at a site change. Furthermore, stopover-site usage 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 food and danger attributes must be considered.

Responses to this article can be read online at:
http://www.ace-eco.org/vol3/iss1/art7/responses/

Acknowledgments:

The Centre for Wildlife Ecology at SFU, Environment Canada's Science Horizons program, and The SeaDoc Society (grant to T.D.W., C.G.G., and R.W.E.) through the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis, provided funding for this project. Thanks are owed to C. Ames, M. Evanson, P. S. Kretz, D. Lissimore, J. Macnair, K. J. Mathot, H. Middleton, W. Stein, L. Takahashi, and R. Worcester for assistance in the field and lab. Also thanks to J. Buchanan, R. Cannif, P. Clarkson, M. Lemon, L. Leschner, S. Murphy, Padilla NEER, S. Pearson, Samish Bay Sports Club, University of Washington, and Washington DNR for logistical support and site access. We thank Bird Studies Canada for supplying British Columbia Coastal Waterbird Survey data, and all the volunteer participants who gathered data for the project, and thanks to Tasha Smith and Peter Davidson of Bird Studies Canada for providing this data set for use in this study. Thanks to E. A. Krebs, W. Cresswell, N. Warnock, R. I. G. Morrison, and

LITERATURE CITED

Acevedo Seaman, D. A., C. G. Guglielmo, R. W. Elner, and T. D. Williams. 2006. Landscape-scale physiology: site differences in refueling rates indicated by plasma metabolite analysis in free-living, migratory sandpipers. *Auk* **123**:563–574.

Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. d. L. S. d. Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in red knots:

Battley, P. F., D. I. Rogers, J. A. van Gils, T.

Pomeroy, A. C. 2006. Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*. *Oikos* **112**:629–637.

Pomeroy, A. C., and R. W. Butler. 2005. Color infrared photography is not a good predictor of macro invertebrate abundance on mudflats used by shorebirds. *Waterbirds* **28**:1–7.

Pomeroy, A. C., R. W. Butler, and R. C. Ydenberg. 2006. Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. *Behavioral Ecology* **17**:1041–1045.

Rainey, M. P., A. N. Tyler, D. J. Gilvear, R. G. Bryant, and P. McDonald. 2003. Mapping intertidal estuarine sediment grain size distributions through airborne remote sensing. *Remote Sensing of the Environment* **84**:480–490.

Reise, K. 1985. *Tidal flat ecology: an experimental approach to species interac.2(P)Td [(irMTf 2.5(:rMTf4 -12 Td [(iluem71.-Verlag,(Mapping 2.5(:y)]TJ 0 Berlin, Ger* *of Ecology and Evolution* **53**: 245–261.

van Gils, J. A., P. F. Battley, T. Piersma, and R. Drent. 2005. Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proceedings of the Royal Society of London: Series B* **272**:2609–2618.

Warnock, N., and M. A. Bishop. 1998. Spring stopover ecology of migrant western sandpipers. *Condor* **100**:456–467.

Weber, T. P., B. J. Ens, and A. I. Houston. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. *Evolutionary Ecology* **12**:377–401.

Whitfield, D. P. 1985. Raptor predation on wintering waders in southeast Scotland. *Ibis* **127**:552–558.

Whitfield, D. P. 2003a. Predation by Eurasian sparrowhawks produces density-dependent mortality of wintering redshanks. *Journal of Animal Ecology* **72**:27–35.

Whitfield, D. P. 2003b. Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *Journal of Avian Biology* **34**:163–169.

Wilson, W. H. J. 1994. The effects of episodic predation by migratory shorebirds in Grays Harbor, Washington. *Journal of Experimental Marine Biology and Ecology* **177**:15–25.

Wolf, N. 2001. Foraging ecology and stopover site selection of migrating Western Sandpipers (*Calidris mauri*). Thesis, Biological Sciences Department, Simon Fraser University, Burnaby, British Columbia, Canada.

Yates, M. G., J. D. Goss-Custard, S. McGrorty, K. H. Lakhani, S. E. A. L. Durell, R. T. Clarke, W. E. Rispin, I. Moy, T. Yates, R. A. Plant, and A. J. Frost. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology* **30**:599–614.

Ydenberg, R. C., R. W. Butler, D. B. Lank, C. G. Guglielmo, M. Lemon, and N. Wolf. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. *Journal of Avian Biology* **33**:47–55.

Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith, and J. Ireland. 2004. Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proceedings of the Royal Society of London: Series B* **271**:1263–1269.

Yong, W., D. M. Finch, F. R. Moore, and J. F. Kelly. 1998. Stopover ecology and habitat use of migratory Wilson's warblers. *Auk* **115**:829–842.

Zanette, L., P. Doyle, and S. M. Trémont. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* **81**:1654–1666.

Appendix 1. The percentage of each taxon represented at each site.

Please click here to download file 'appendix1.doc'.