RELATIONSHIP BETWEEN STOPOVER SITE CHOICE OF MIGRATING SANDPIPERS, THEIR POPULATION STATUS, AND ENVIRONMENTAL STRESSORS

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ABSTRACT

Measures of animal behavior can be used in a variety of situations to make inferences about the environment and population status. Work by our research group shows that migratory shorebirds adjust their usage of, and behavior at, stopover sites in response to environmental conditions. Motivated by this, we built an individual-based model of migrating shorebirds moving through a sequence of alternating small and large stopover sites. Birds at larger sites are safer from predators, but we assumed that less food is available than at small sites. In the model, both predation risk and food intake are density-dependent, and the behavior of migrants is controlled by two rules: one that determines whether a bird will depart a stopover site, and one that controls the individual's foraging versus vigilance intensity. The optimal behavior is calculated by maximizing a payoff function that depends on arrival date and arrival energy stores at the final site. We used this model to predict mass gain, foraging intensity, and usage by migrants of small and large sites under various conditions. We examined the effects of a flyway-wide reduction in the amount of food, a flyway-wide increase in predation danger, and the effects of lowering the overall population size. The mass action of many individuals, each optimizing its migration timing and routing, leads to the emergence of distinctive patterns of behavior and site choice under these differing environmental conditions. When food availability is reduced throughout the flyway, our model predicts that foraging intensity increases at every stopover site, thereby forcing birds to accept greater danger to maintain the fitness benefit of a timely arrival to the breeding area. A flyway-wide increase in predation danger results in fewer migrants choosing (and/or migrants staying a shorter time at) small stopover sites, balanced by a higher usage of large sites. These effects contrast with what is observed under true population declines, when the usage of both small and large sites declines.

Keywords: bird migration, genetic algorithm, behavior, optimization, departure rules, stopover ecology, shorebirds, *Calidris mauri*

INTRODUCTION

Census data give ample reason for concern about the population trends of many migrant bird species (e.g., Morrison et al., 2001). Unfortunately, migrants are, by their nature, hard to count, and the inherent uncertainties often make it difficult to assign much confidence to estimates of population trends. While in some cases direct counts can be made when individuals are concentrated at a few breeding or nonbreeding sites (e.g., Morrison et al., 2004), many migrant species are censused only at stopover sites, where census changes may be caused by mechanisms other than changes in the size of the population. For example, the site may have declined in quality, or sites elsewhere improved, causing migrants to alter their distribution; or migrants may change behavior in ways that make them more difficult or easier to see. Of course, a remedy is to census at many sites (Haig et al., 1998), but this is correspondingly more demanding of time and resources, and even intensive census efforts can yield ambiguous results. Bart et al. (2007), for example, used a data set comprised of 32,782 surveys from 168 sites to estimate population trends of North American shorebirds, but even this massive effort was not conclusive, and confidence intervals were large.

Reliance on intensive census efforts in conservation has two further drawbacks. First, census declines are trailing indicators, becoming evident only after declines have already occurred (Rosenzweig, 2007). Second, censuses often contain little information about the causes of decline. For example, the loss or degradation in the quality of stopover sites is suspected as a prime cause in alleged shorebird population declines, but the evidence supporting this hypothesis is no stronger than that for other possible causes. Easily-applied methods that can be leading rather than trailing indicators, and that would indicate the causes for decline, would be vastly preferable. But do such methods exist?

Behavioral measures have been used in a variety of situations to make inferences about the environment. Recently, for example, it was widely reported that the walking speed of pedestrians in several cities had increased over the past 30 years. The interpretation given in the press was that cities are more stressful places that require more hurried lives than before. While many readers will doubtless identify with this plausible conclusion, it must be acknowledged that there are other possible explanations for the higher walking speed. For example, city dwellers might now be fitter, sidewalks may have been improved, and the composition of the pedestrian population may have changed, for example as more people obtained cars and ceased walking. Before we could confidently conclude that increased stress is indeed the underlying cause, we need good knowledge of pedestrian ecology, and, more importantly, we would need a theoretical basis to explain why increasing stress levels should step up the walking pace.

Behavioral ecology provides a framework for understanding the relationships between behavior and the environment. One of its central tenets is that organisms assess the state of their environment and make adaptive behavioral adjustments. The idea that we can interpret behavior to make inferences, and hence testable predictions about the state of the environment, rests on this concept.

Migrants have evolved mechanisms to deal with a large set of contingencies that can arise during migration, and are nothing if not flexible (Sutherland, 1998). They integrate

experience accumulated along the route with innate knowledge to evaluate where and how intensively to feed, the fat load to accumulate, when to depart, and the route to take. The parts of this process that take place at stopover sites are to some extent accessible to human observers, and, to the extent that we understand the ecology and evolutionary history of migrants, we can try to infer from behavioral measures the prevailing environmental conditions.

USAGE OF STOPOVER SITES AS A BEHAVIORAL INDICATOR

Our research group has studied the migratory and stopover ecology of western sandpipers (*Calidris mauri*) in some detail (Lank and Nebel, 2006). Using the conceptual context of "danger management"—the idea that migrants must manage the danger posed by predators as carefully as they manage their energy budgets (Ydenberg et al., 2007)—we have shown that an assortment of behavioral measures can be used to indicate environmental change. Western sandpiper migrations cover the ~9–12,000 km between Alaskan breeding grounds and Neotropical nonbreeding areas in successive "legs" of 500–3000 km, interrupted by stopovers, during which birds build reserves of fat and protein to power the next leg. The main predators of western sandpipers are falcons, particularly peregrines (*Falco peregrinus*) and merlins (*Falco columbarius*). Because these predators use cover for effective surprise attacks (Dekker and Ydenberg, 2004), the size and shape of stopover sites affects the danger level. Stopover sites also vary in the availability of food and hence in the rate at which migrants are able to fatten (Ydenberg et al., 2002).

At Boundary Bay, British Columbia, food abundance for western sandpipers declines with increasing distance from the shoreline, while safety from predators increases. Birds are sensitive to this feeding–danger tradeoff and adjust their feeding intensity and habitat usage accordingly (Pomeroy, 2006a,b). Sandpipers avoid using dangerous habitats close to shore despite an abundance of food, and those birds that do feed there heighten their level of vigilance to further compensate for increased risk. Similarly, they avoid feeding in the low food habitats farthest from shore, despite the safety, and consequently, their usage is concentrated between 100 and 300 m from the shoreline, where levels of food and safety are intermediate (Pomeroy, 2006a,b). We have also shown that sandpipers adjust this behavior in response to annual variation in danger. Birds spent far less time close to shore when the attack rate of falcons was high (0.45 attacks/h in 2004) than when it was low (0.17 attacks/h in 2005; Pomeroy, unpubl. data; Fig. 1).

At Sidney Island, another intensively-monitored stopover site in British Columbia, we measured a steep decline in the numbers of western sandpipers censused; the annual rate of decline between 1992 and 2001 was 18%. Sidney Island is a small and dangerous site. Over the past three decades, peregrine populations have recovered, and western sandpipers (at stopover sites and times that are independently categorized as dangerous) have steadily lowered the amount of reserves they carry, and they have shortened stopover durations. Taking these effects into account revealed that the total number of birds stopping over at Sidney Island had not changed, but that the shortened stopover time lowered the total census (Ydenberg et al., 2004).
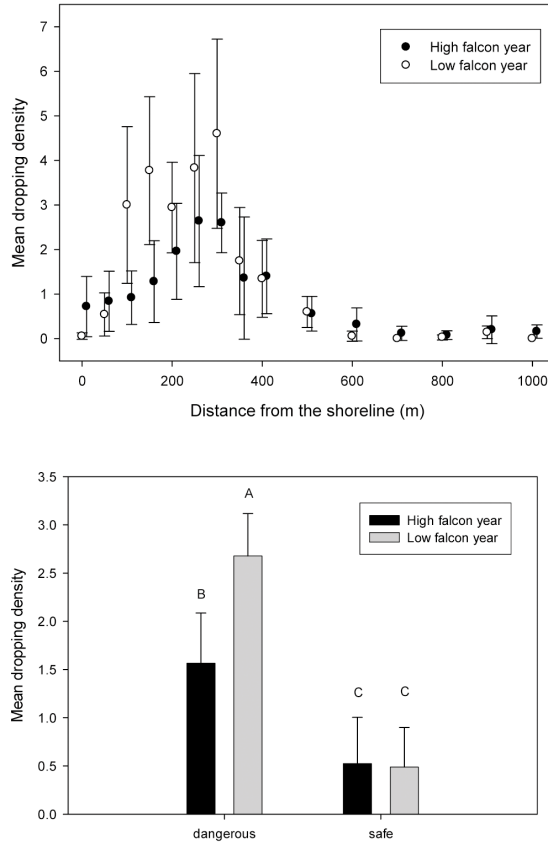
Fig. 1. Mean dropping density indicating intensity of usage by western sandpipers at Boundary Bay, British Columbia, as distance from shore varies. Overall usage is greater in the dangerous habitat (≤300 m) than the safe habitat. When falcon attack rates were low, usage was greater in the dangerous habitat; however, there was not a corresponding decrease in usage in the safe habitat (adapted from Pomeroy, 2006a).

In these examples, an assortment of behavioral measures indicated that there was an ongoing environmental change, and the theory of danger management provided a framework for understanding why these changes were adaptive in the face of increased environmental danger. But what behavior would we expect to see if some other environmental change had been taking place, or if the population had truly been falling? A method for addressing this question begins with two premises. The first is that avian migrants have optimized their behavior for early arrival time and high energy reserves at arrival on the breeding ground. This premise is supported by the evidence that, in many bird species, higher reproductive success and survival are correlated with earlier time of arrival and better condition at arrival (see references in Drent et al., 2006; Newton,

2006). The second premise is that migratory timing and routing by individual migrants is flexible, and that individual migrants are able to use experience to adjust their migrations. These adjustments have consequences in that changes in migrant behavior at one site must affect other sites. Birds shortening their stopover time at one site must spend some additional stopover time elsewhere. The mass action of many individuals, each adjusting to its experience, will lead to changes in migration that can be measured by observing a number of stopover sites with different properties.

We model here how the following change under different types of environmental change and population decline: (i) the usage of stopover sites in different safety categories; (ii) the fuel load accumulated; and (iii) the intensity of feeding observed on these sites. Our results show that some of these changes leave characteristic "signatures" written in behaviors of migrants across these types of stopover sites that one can easily measure at stopover sites.

AN INDIVIDUAL-BASED MODEL

We model 10,000 shorebirds moving through a flyway consisting of a set of ten alternating large and small sites. At large sites, birds are relatively safe from predation and experience weaker interference competition for food. Small sites are more dangerous because birds are forced to forage closer to cover. For shorebirds foraging on a mudflat, cover provides avian predators with the opportunity for surprise attacks, which have higher success rates (Dekker and Ydenberg, 2004). In this model, the sites are equally spaced (600 km apart). Each site has an associated food quality (maximum daily intake rate) and danger (maximum probability of mortality). Both fuel deposition and predation mortality are reduced by the number of conspecifics at the site, and both depend also on the foraging intensity of the individual bird. Each individual has a fuel load, x, ($0 < x \leq 100$) expressed as the percentage of lean body mass. A bird's initial fuel load is a random variable drawn from a normal distribution with mean 5 and standard deviation 1.0. If x falls to zero or below, the bird dies of starvation.

In one day, a bird foraging at intensity, u, ($0 < u \leq 1$) at site i and time t will gain $f_{i,t}$ fuel units and be subject to a mortality risk of $m_{i,t}$, where

$$f_{i,t} = gu\left(\frac{1}{1 + \frac{q}{A_i}(N_{i,t} - 1)}\right) - g_{daily} \tag{1}$$

and

$$m_{i,t} = (mmax_i)u^2\left(\frac{1}{1 + p(N_{i,t} - 1)}\right) \tag{2}$$

$N_{i,t}$ is the number of birds at the site, g_i is the density-independent rate of fuel gain, and $mmax_i$ is the maximum mortality at the site. q is the strength of interference and p is the dilution rate; the rate at which individual mortality decreases as the number of birds

increases. Both p and q are assumed to be the same at all sites, although interference strength is modified by the area of the site (A_i). g_{daily} is the daily fuel necessary for normal activity.

The fuel, x, needed to fly a given distance, Y, is calculated from the most commonly used range equation (Alerstam and Lindstrom, 1990; Weber and Houston, 1997; Weber et al., 1998)

$$x(Y) = \left(\frac{c^2}{(c-Y)^2} - 1 \right) 100 \tag{3}$$

where c is a constant with units of km that depends on species morphology. We assume that one full day is needed to fly between two adjacent sites.

The behavior of each individual is at the core of the model. Behavior is determined by optimization for reproductive success, which is assumed to be a function of arrival time and arrival fuel (Clark and Butler, 1999). The effects of arrival time and fuel load are assumed to be multiplicative, so the reproductive success F derived from arriving at time t_a with fuel load x_a is given by:

$$F(x_a, t_a) = R(x_a)k(t_a) \tag{4}$$

where $k(t_a)$ is the component of fitness that depends on arrival time t_a, and is given by:

$$k(t_a) = \begin{cases} \dfrac{t_a}{t_{opt}} & \text{if } t_a \leq t_{opt} \\ 1 - d_1(t_a - t_{opt}) & \text{if } t_a > t_{opt} \end{cases} \tag{5}$$

and $R(x_a)$ is the component of fitness that depends on arrival fuel load x_a, and is given by:

$$R(x_a) = \begin{cases} 1 - d_x(x_a - x_{opt}) & \text{if } x_a \leq x_{opt} \\ 1 & \text{if } x_a > x_{opt} \end{cases} \tag{6}$$

Each individual has two behavioral rules; one rule determines whether a bird will depart a stopover site on each day (or skip the site if it never foraged there), and the other controls the bird's foraging intensity (u) at a site. We assume that birds have access to four pieces of information (inputs) described below. A more detailed description for calculation and normalization of these inputs is given in Appendix 1.

(1) *Timing (I_T):* whether the bird is early or late; this depends on time and how far the bird is along the migration route.
(2) *Range (I_R):* how far the bird can expect to fly. This depends on the individual's fuel load.
(3) *Fuel deposition (I_F):* the expected daily fuel gain. This depends on the food available at the site and the density of birds.
(4) *Predation risk (I_P):* the expected mortality due to predation for an individual bird. This depends on the intrinsic danger of the site and the number of birds currently at the site.

The probability of departure and the foraging intensity (u) are the outputs of two rules that depend on a weighted sum of inputs and use a sigmoid logistic transfer function to normalize the output to be between 0 and 1. For each rule,

$$output = \frac{1}{1 + \exp\left(-100 \sum_{x} W_x X - 0.5\right)} \tag{7}$$

where X is the set of inputs. Each input X has an associated weight, W_x, that controls how steeply the resulting probability depends on input X, and therefore the relative importance of input X with respect to the other inputs. The inputs to the departure rule are (I_T, I_R, $1-I_F$, and, I_P). We use $1-I_F$ instead of I_F because we assume that the rule's output, the probability of departure, decreases with increasing fuel deposition rates and increases with the other three variables. Using similar logic, the inputs to the foraging intensity rule are (I_T, $1-I_R$, $1-I_F$, and $1-I_P$).

The behavior of each individual is, therefore, controlled by a string of 8 numbers: 4 weights for the departure rule and 4 weights for the foraging intensity rule. Each number can take 8 possible values. Weights vary from 0 to 1.0 as described above. Initial rules for individuals are generated randomly and we use a genetic algorithm to find the behavior that maximizes fitness as given by eqs 4–7. The details of the optimization procedure are described in Appendix 2. We generated optimal behavioral rules for a flyway in which conditions at every site are generated randomly for each iteration of the algorithm. Maximum mortality rates for each site were drawn randomly from a uniform distribution between 0.01 and 0.15. Maximum intake rates were drawn randomly from a truncated normal distribution (mean = 8, sd = 2, minimum value = 4, maximum values = 12). This generates optimal behavioral rules that are flexible enough to deal with a large range of possible conditions. A summary of all parameters and their default values used in this model is given in Table 1.

MODEL PREDICTIONS

We applied our model with the optimal behavior generated as described above to a flyway with two types of sites that alternated along the birds' route. Large sites have low relative predation risk but also lower food availability, but birds are less subject to interference. Small sites are more dangerous, with higher food availability, but a given number of birds at the site will experience stronger interference than at a large site. Comparison of behavioral indicators at the two types of site gives us information about what the current status of the population is, whether conditions are difficult during migration or relatively easy. Furthermore, trends in environmental conditions lead to characteristic trends in behavior.

The following indicators are presented here: (a) relative usage of different types of sites, (b) relative foraging intensity at different types of sites, and (c) mass gain at different types of sites. We also examine trends in these indicators as signals of trends of increasing predation or population decline. Results are summarized in Table 2.

Table 1
Parameters used in the model with values

Parameter	Baseline value	Description
S	11	number of sites
D	600 km	distance between sites
T	100 days	length of the migration period
A_i	1 if i is even (small sites)	foraging area available at each site i
	3 if i is odd (large sites)	
q	0.00001	strength of interference
p	0.001	strength of dilution effect
t_{opt}	75	optimal arrival time at the breeding ground
x_{opt}	20	optimal fuel load at arrival to breeding ground
d_t	0.02	rate of decrease of fitness with time later than t_{opt}
d_x	0.004	rate of decrease of fitness with arrival fuel lower than x_{opt}
g_i	4 for large sites and 6 for small sites or	maximum daily fuel gain
	6 for large sites and 10 for small sites	from foraging at site i
g_{daily}	1	daily fuel necessary for normal activity
c	14000 km	Constant used to determine flight range
$mmax_i$	0.03 if i is even (small sites)	Maximum mortality due to
	0.01 if i is odd (large sites)	predation for site i

Table 2
Summary of predicted effects

Effect	Less food	More danger	Population decline
Large sites	Increase in foraging intensity. May result in increased length-of-stay but this depends on relative values of food and danger parameters	Usage increases	Usage decreases
Small sites	Increase in foraging intensity and therefore decrease in individual safety. May result in decrease in usage but this depends on relative values of food and danger parameters	Usage decreases	Usage decreases

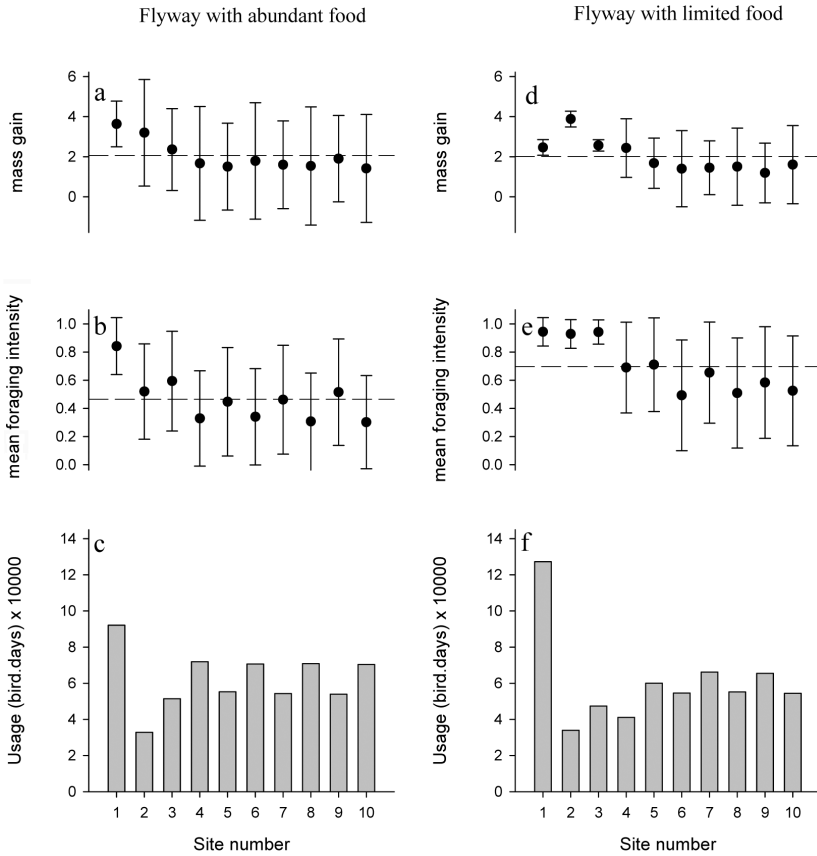Flyway with abundant food

Flyway with limited food

Fig. 2. Model predictions of patterns of usage of the ten sites in the flyway when food is abundant, $g_i = 6$ and 10 at large and small sites, respectively, (a–c), and when food is less abundant, $g_i = 4$ and 6 at large and small sites, respectively, (d–f). Large and small sites alternate in the flyway so that odd-numbered sites are large and even-numbered sites are small. (a) and (d) show the mean daily mass gain of all birds at each site. (b) and (e) show the mean foraging intensity of all birds at each site. (c) and (f) show the total usage of each site. The dashed lines on a, b, d, and e show the mean across all sites.

INDICATORS OF OVERALL FOOD CONDITIONS

We compared the case when there is abundant food in the flyway ($g_i = 6$ and 10 at large and small sites) to the case where food is more limited ($g_i = 4$ and 6 at large and small sites).

Our model predicts that when there is abundant food in the flyway, the small food-rich sites are used slightly more than the large sites, except for the first two sites (Fig. 2c). The first site has a higher usage than other comparable sites as birds use it for

initial fueling, which occurs whether the first site is large, as shown in Fig. 2, or small (results not shown). Birds compensate for higher danger at small sites by having a lower foraging intensity (Fig. 2b). When the maximum intake rate is lower, i.e., there is less food available at all sites, foraging intensity increases (compare Fig. 2b,e), so that the birds achieve the same daily intake rate (Fig. 2a,d). This increases danger at all sites, and usage of small sites drops while usage at large sites increases, especially at the first site (Fig. 2f). This pattern remains if the first site encountered is small, but the usage does not increase as much (results not shown).

Some of these results are likely to be sensitive to parameter values. We have not conducted an extensive sensitivity analysis, but explorations with different parameter values suggest that the changes in foraging intensity are robust, but the usage patterns depend sensitively on the relative food levels between the different site types and on the strength of interference competition (results not shown).

INDICATORS OF INCREASING PREDATION

Abundance of avian predators, such as peregrines, has been increasing in the last few years and it is expected that this trend will continue. It has been suggested that observed trends in small shorebirds could be attributed to danger management.

In our model, we increase the predation the same proportionally at all sites ($mmax_i$ is increased from 0.01 to 0.05 at large sites and from 0.03 to 0.15 at small sites), so that the maximum mortality at a small site is always three times the maximum mortality at a large site. The changes in total usage are shown in Fig. 3a. Increased predation always causes an increased use of large sites and decreased use of small sites. Foraging intensity is adjusted so that the mean daily mass gain does not change. This does not lead to obvious trends in foraging intensity as predation changes.

INDICATORS OF DECLINING POPULATION

We get a different result if we model the case where the entire population is in serious decline (Fig. 3b). We set the total population size to values between 10,000 and 2000 and, as expected, we found that usage declines at all sites. No changes in foraging intensity or mass gain at different sites are predicted.

DISCUSSION

Our model focused on the mass gain, foraging intensity, and usage by migrants of small (and, therefore, dangerous) and large (and, therefore, safer) stopover sites under various conditions. We examined the effects of two sorts of "stressors" on environmental conditions: (i) a flyway-wide reduction in the amount of food and (ii) a flyway-wide increase in predation danger. We also examined the effects of lowering the overall population size. The mass action of many individual migrants each optimizing its migration timing and routing under these differing environmental conditions leads to the emergence of distinctive patterns of behavior and site choice.

Comparing the changes in usage and foraging intensity of small and large sites under
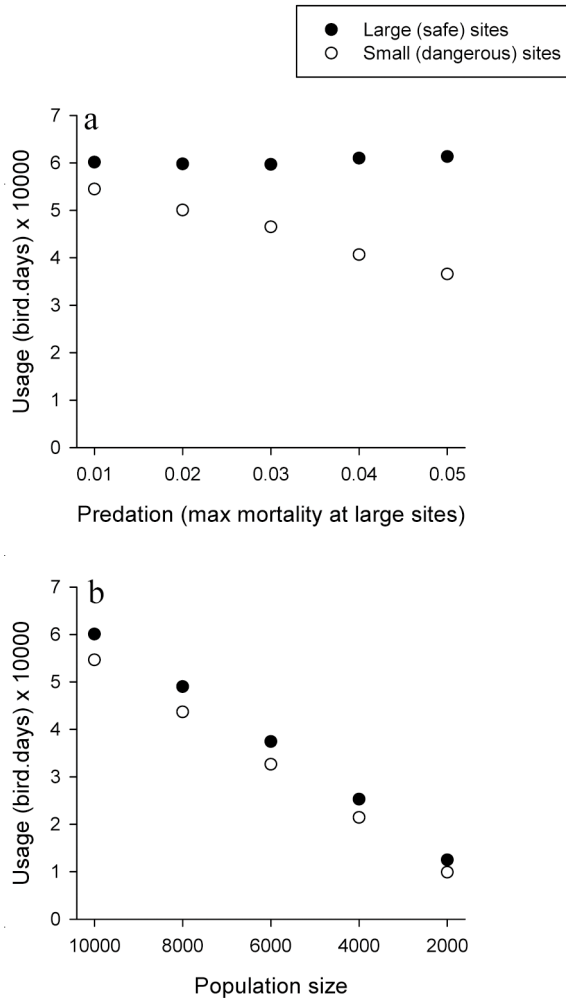
Fig. 3. Model predictions of trends in mean usage of small sites (open circles) and large sites (solid circles) when (a) predation is increased at all sites and (b) overall population declines.

these three environmental circumstances provides a set of unique signatures (Table 2). We examined the effect of food availability by lowering the intake rate attainable on every stopover site on the flyway. As a consequence, foraging intensity increased everywhere on the flyway, thereby forcing birds to accept greater danger in order to be able to maintain the fitness benefit of a timely arrival to the breeding area (see eq 5) with some reserves (see eq 6). Foraging intensity in this model represents all types of behavior that birds manifest within a site that result in higher fuel deposition rates but lower danger or

vice versa. Some examples of the types of behavior that have been documented for small shorebirds of the types modeled here are: flocking behavior in response to increased threat (Cresswell, 1994; Cullen and Robertson, 1999), choice of feeding location within a site (Pomeroy, 2006b; Pomeroy et al., 2006), vigilance rates during foraging (e.g., Pomeroy, 2006b), roost selection, in cases where safer roosts are farther from foraging areas (Rogers et al., 2006), and time of day when foraging occurs (Sitters et al., 2001). The consequence of altering food availability in terms of site usage changes is highly sensitive to parameter values. With the parameter set we chose, we saw a decrease in usage of small sites and an increase in the usage of large sites. Usage incorporates both number of individuals using the site and the length of stay of each bird. Birds stayed much longer at the first site in order to build up initial fuel supplies (Fig. 2).

A flyway-wide increase in predation danger has a clear effect on usage patterns, leading to fewer migrants choosing (and/or migrants staying a shorter time) at small stopover sites, balanced by a higher usage of large sites (Fig. 3a). In effect, migrants under these circumstances can afford to forego the higher density of food available on small sites and use the higher safety on large sites to increase their fitness payoff. We argue that this effect underlies the decline in western sandpiper usage measured on Sidney Island (Ydenberg et al., 2004). How animals respond to predators appears to be a valuable indicator of their conservation status. Macleod et al. (2007) used a large data set of weights of nonbreeding birds in Europe to show that bird species that respond to increased danger from predators by decreasing their mass are associated with declining populations, whereas species that increase their mass instead are likely foraging in higher quality habitats and have stable or increasing populations. Variation in mass gain in response to predators may be another useful behavioral indicator.

These effects contrast with what is observed when the population truly declines (see Fig. 3b), under which the usage of both small and large sites decreases, although this may depend on the strength of the different density-dependent processes and conditions on the flyway. In the case shown here, the choice of parameters is such that the decline is approximately the same at small and large sites.

The patterns of site usage suggested by our model are one sort of indicator, but the model also showed that foraging intensity is adjusted so that the birds achieve almost the same average daily mass gain (e.g., Fig. 2d,e). This intensification can be easily revealed by behavioral observations of feeding rates. At Boundary Bay, the choice of how close to shore western sandpipers feed is an example of foraging intensity, and the annual variation in this pattern is an indicator of annual variation in local danger (Fig. 1, Pomeroy, 2006a). Studies of the behaviors of migrants within sites (e.g., Pomeroy, 2006a) or comparing behavioral shifts between safe and dangerous sites (e.g., Ydenberg, et al., 2004) is certainly informative and less expensive than studies on the flyway scale.

In nature, migrating western sandpipers always have a choice between fast/dangerous fueling and slow/safe fueling behavior. They can choose between safe or dangerous sites on a landscape scale (Ydenberg et al., 2002), can select safe or dangerous locations within stopover sites (Pomeroy, 2006b), and in addition, can feed rapidly with little vigilance, or slowly but much more circumspectly, at any location. Our approach of

alternating large and small sites in the model was chosen because it is a computationally tractable method that reasonably offers model migrants the choice between fast/dangerous and slow/safer fueling. Some details of the migration strategy that our approach yields depend on the sequence of large and small sites along the flyway. In general, however, whether large or small sites are encountered first has little impact on our predictions. Model migrants load heavily at the first site, regardless of whether it is small or large. This occurs because fuel loads acquired there can subsidize the acquisition of fuel at later sites (see Gudmundsson et al., 1991). The exact order of subsequent sites would affect the migration strategy, but so long as small and large sites are available along the entire route, the model we have used here will be a reasonable approximation. Similarly, while we believe that the patterns reported here are generally robust, some of our results may be sensitive to changes in parameter values, particularly the relative food levels at different types of sites and the strength of interference competition. A full sensitivity analysis is outside the scope of this paper, though we admit that such an analysis would be useful.

On an annual scale most stopover site usage by migrant shorebirds is concentrated on relatively few large sites. However, the use of small sites appears more sensitive to changes in environmental conditions than does the use of large sites, and, of course, small sites are easier to oversee and generally easier to work on. The value of study at these sites is made clear by this model, which indicates that by comparing shifts in the behavior of migrants between different types of sites we can evaluate changes in site condition and population status. This result emphasizes that studying smaller sites may be valuable to conservation efforts, even if relatively small numbers of individuals use such sites.

We developed this model to examine the idea that the mass action of many individual migrants, each optimizing its migration timing and routing under these differing environmental conditions, would result in the emergence of distinctive patterns of behavior and site choice. Our results suggest that this would be a profitable approach. Our model is, of course, limited, and some of the patterns that emerge are highly sensitive to choices of parameter value that are notoriously difficult to obtain for real species. The real value of the model is in making clear the logic underlying why these patterns emerge.

Our most basic conclusion is that the type of stopover site (safe versus dangerous and high versus low food abundance) has a strong effect on its usage by migrating shorebirds, and, moreover, that the relative usage of these types of sites changes in characteristic ways that differ with environmental circumstances and population decline. Although site type is not accounted for in most censuses of migrant shorebirds, these data exist in the International Shorebird Survey (ISS) and Maritime Shorebird Survey (MSS). Bart et al. (2007) derived from ISS a data set comprised of 32,782 surveys from 168 sites to estimate population trends of North American shorebirds. Data sets such as these should be re-examined in light of site type to test the hypothesis that North American shorebird populations are declining, based on our model predictions. Many of the stopover sites in these datasets are highly dynamic interior wetlands (Skagen, 2006). Another profitable model-based investigation might include examining usage of stopover sites that vary

in quality, danger, or size from year to year. In this work, we examined how usage and behavior of a single species should change in response to changes in site usage under various situations.

REFERENCES

Alerstam, T., Lindstrom, A. 1990. Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner, E., ed. Bird migration: the physiology and ecophysiology. Berlin, Springer, pp. 331–351.

Bart, J., Brown, S., Harrington, B.A., Morrison, R.I.G. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? Journal of Avian Biology 38: 73–82.

Clark, C.W., Butler, R.W. 1999. Fitness components of avian migration: a dynamic model of western sandpiper migration. Evolutionary Ecology Research 1: 443–457.

Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa-Tetanus*. Animal Behaviour 47: 433–442.

Cullen, S., Robertson, G.J. 1999. Temporal changes in the anti-predator flocking behavior of wintering shorebirds. Waterbirds 22: 156–159.

Dekker, D., Ydenberg, R.C. 2004. Raptor predation on wintering dunlins in relation to the tidal cycle. Condor 106: 415–419.

Drent, R.J., Fox, A.D., Stahl, J. 2006. Travelling to breed. Journal of Ornithology 147: 122–134.

Goldberg, D.E. 1989. Genetic algorithms in search, optimization, and machine learning. Reading Mass., Addison-Wesley Pub. Co.

Gudmundsson, G.A., Lindstrom, A., Alerstam, T. 1991. Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba* and turnstones *Arenaria interpres*. Ibis 133: 140–152.

Haig, S.M., Mehlman, D.W., Oring, L.W. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology 12: 749–758.

Lank, D.B., Nebel, S. 2006. Cross-cutting research on a flyway scale—beyond monitoring. In: Boere, G.C., Galbraith, C.A., Stroud, D.A., eds. Waterbirds around the world. Edinburgh, U.K, The Stationery Office, pp. 107–112.

MacLeod, R., Lind, J, Clark, J., Cresswell, W. 2007. Mass regulation in response to predation risk can indicate population declines. Ecology Letters 10: 945–955.

Morrison, R.I.G., Abry, Y., Butler, R.W., Beyersbergen, G.W., Donaldson, G.M., Gratto-Trevor, C.L., Hicklin, P.W. 2001. Declines in North American shorebird populations. Wader Study Group Bulletin 94: 39–43.

Morrison, R.I.G., Ross, R.K., Niles, L.J. 2004. Declines in wintering populations of red knots in southern South America. Condor 106: 60–70.

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147: 146–166.

Pomeroy, A.C. 2006a. Feeding and predation danger tradeoffs in stopover site usage by western sandpipers (*Calidris mauri*). Ph.D. thesis, Simon Fraser University, Burnaby.

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

Rogers, D.I., Battley, P.F., Piersma, T., van Gils, J.A., Rogers, K.G. 2006. High-tide habitat choice:

insights from modelling roost selection by shorebirds around a tropical bay. Animal Behaviour 72: 563–575.

Rosenzweig, M. 2007. On foraging theory, humans and the conservation of diversity: a prospectus. In: Stephens, D.W., Brown, J., Ydenberg, R.C., eds. Foraging. Chicago, University of Chicago Press, Chapter 14.

Sitters, H.P., Gonzalez, P.M., Piersma, T., Baker, A.J., Price, D.J. 2001. Day and night feeding habitat of red knots in patagonia: profitability versus safety? Journal of Field Ornithology 72: 86–95.

Skagen, S.K. 2006. Migration stopovers and the conservation of arctic-breeding calidridine sandpipers. Auk 123: 313–322.

Sutherland, W.J. 1998. Evidence for flexibility and constraint in migration systems. Journal of Avian Biology 29: 441–446.

Weber, T.P., Houston, A.I. 1997. Flight costs, flight range and the stopover ecology of migrating birds. Journal of Animal Ecology 66: 297–306.

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

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

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

Ydenberg, R.C., Butler, R.W., Lank, D.B. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. Journal of Avian Biology 38: 523–529.

APPENDIX 1
CALCULATION OF INPUT VARIABLES

Variable	Description	Calculation	Interpretation
I_T	Timing: whether the bird is early or late according to the distance traveled and time.	$I_T(i,t) = \min\left[1, \frac{1}{2}\left(1 + \frac{t}{t_{opt}} - \frac{iD}{(S-1)D}\right)\right]$	Value of 0.5 means bird is exactly on time, <0.5 bird is early, >0.5 bird is late
I_R	Range: how far individual bird can expect to fly. This is a function of individual fuel load.	$I_R(x) = Y(x)/\left(Y(x_{max})\right)$ Where $Y(x)$ is calculated from eq 3	Value of 0 means bird has zero fuel stores, value of 1 means expected range is maximum possible
I_F	Expected daily fuel gain. This depends on site characteristics, individual fuel load, and number of conspecifics at the site	$I_F(i,t) = \frac{f_{i,t} - g_{min}}{g_{max} - g_{min}}$ where f_t is the birds' expected fuel gain calculated from eq 1 with foraging intensity, $u = 1$. g_{max} and g_{min} are the maximum possible intake rates given the interference strength and the number of birds.	Values close to 0 indicate very low and negative expected fuel gain. Values close to 1 indicate high expected fuel gain
I_P	Expected mortality due to predation. This depends on site characteristics and number of conspecifics at the site	$I_P(i,t) = \frac{m_{i,t}}{M_{max}}$ mortality $m_{i,t}$ is calculated from eq 2 with foraging intensity, $u = 1$, and M_{max} is the maximum possible mortality.	Value reflects relative risk of mortality due to predation

APPENDIX 2
OPTIMIZATION PROCEDURE

We used a genetic algorithm (GA) to search through the possible rules and find the rule that maximizes the reward function described in eqs 1–3.

The GA starts by randomly generating 1000 behavioral rules, each of which is assigned to 10 individuals in the model. We then run the migration model, and at the end of the simulation, we calculate the fitness of each individual from eq 1 and the fitness of the rule, which is the mean fitness of the 10 birds using it. We rank each rule with a number from 1 to 1000. We allocate the highest ranks, according to fitness, to those rules that have non-zero fitness (i.e., those that produce birds that arrive to the breeding grounds). Rules with zero fitness (i.e., those used by individuals, none of whom make it to the breeding grounds) are assigned lower ranks, according to the mean of the product of final location achieved and number of days survived for each of the 10 birds. For each iteration, the algorithm chooses 1000 parental rules according to their ranks. The probability of choosing a parent of rank R is given by the probability distribution,

Two new rules are generated from each pair of parental rules using a simple crossover function (Goldberg, 1989). The crossover function generates a random crossover point, cp, of the two strategies to be recombined and generates new vectors by combining the first cp elements of each vector with the last $(20 - cp)$ elements of the other vector. There is also a small probability ($p = 0.005$) of mutation (to a neighboring value, +1 or –1) for each element to maintain diversity and improve the performance of the algorithm (Goldberg, 1989). The algorithm terminates after 200 iterations. We found that the GA worked well and converged on a single "optimal" rule, meaning that most of the birds in the model ended up with the same rule after 200 iterations. For each run, we repeated the algorithm at least 5 times to increase our confidence that we had found the optimal solution.