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Fitness components of avian migration: A dynamic model of Western Sandpiper migration

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ABSTRACT

Western Sandpipers, *Calidris mauri*, one of the world's most abundant shorebird species, migrate from winter sites in the southern USA and Central and South America to breeding grounds in Western Alaska and Eastern Siberia. We describe a dynamic state variable optimization model for these migrations, assuming that individual female sandpipers employ migration strategies that maximize their expected lifetime reproduction. The principal environmental factors assumed to affect migration decisions are variable wind speeds, site-specific predation risks, and the timing of food availability on the breeding grounds and at the two most northerly stopover sites. The model's predictions, which agree closely with data collected in the field, are most sensitive to changes in wind conditions during the flight phase, rather than foraging opportunities at stopover sites en route. We also show how the model can be used to assess potential impacts of habitat degradation on the fitness of this species.

Keywords: avian migration, dynamic optimization models, habitat degradation and fitness loss, predation risk, Western Sandpipers.

INTRODUCTION

Many environmental factors affect avian migration, including spatial and temporal variations in food availability, winds and weather, predator abundance, and breeding opportunities (Alerstam, 1990). Natural selection has presumably moulded migratory patterns so as to maximize individual fitness. Optimization models can help to assess our understanding, for particular species, of the relative importance of these multiple environmental factors.

Early optimization models of avian migration addressed isolated aspects of migration, such as flight speed and direction (Alerstam, 1979, 1991; Hedenström and Alerstam, 1995; Liechti, 1995) and fuel loads (Weber *et al.*, 1994; Weber and Houston, 1997). The need for more inclusive models has also been recognized (Alerstam and Lindström, 1990; Ens *et al.*, 1994).

The technique of stochastic dynamic programming (Mangel and Clark, 1988) allows the inclusion of multiple factors in a single model (Weber *et al.*, 1998; Farmer and Wiens,

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1998). For a well-studied species, such a model can help to evaluate our understanding of the selective forces that determine observed migratory behaviour. Sensitivity tests of the model can be used to assess the relative importance of different environmental factors. In practical terms, these sensitivity tests may help to identify critical conservation requirements, or to estimate the implications of environmental or climatic perturbations in terms of the productivity of the species.

In the present study, we modelled the spring migration of Western Sandpipers, *Calidris mauri*, an abundant shorebird species of the New World (Butler *et al.*, 1996). We wished to explain the timing and variation in annual migration patterns, from a typical subtropical wintering site to the species' Alaskan breeding grounds. Among the features of this pattern assumed to be fixed were the principal stopover sites (Northwestern Mexico, San Francisco Bay, Fraser River Delta, Stikine River Delta, Copper River Delta) and the breeding site (Western Alaska). These sites were treated in a sequential manner, so that birds visited each site in turn, although if wind conditions were favourable a bird could continue to the next site without refuelling. Net rates of fuel (fat plus protein) deposition at each site were also assumed to be fixed; we did not model micro foraging decisions at stopover sites (Weber *et al.*, 1994, 1998). Finally, a fixed breeding 'window' was assumed for the Alaska site. These assumptions are discussed in more detail later.

Given that feeding rates, flight speeds, distances between sites, average wind speed and direction, and the timing of the Alaskan breeding window were all assumed known, it may seem that predicting the timing of the migration would be little more than an accounting exercise: the birds should remain at a stopover site long enough to build up fuel reserves for the next stage, and should time the sequence of migration stages to arrive in Alaska at the right time to breed. But this description tacitly assumes that it is not advantageous to arrive at any stopover site earlier than the date predicted from this accounting.

Our model incorporates variable winds, which the birds are able to assess while on the ground, to a limited extent on a day-to-day basis. Long-term forecasts are not feasible. Because maximum wind speeds exceed the birds' flight speed, waiting for favourable winds may be an important aspect of migration strategy for these small birds (Butler *et al.*, 1997). As future wind conditions are unpredictable, there is an advantage in being at a given stopover site in advance of the date predicted by the accounting procedure. In fact, unless some countervailing effect is presumed, the model will predict that birds should advance to each stopover site (utilizing favourable winds) as soon as sufficient food becomes available there. But it appears that food is in fact available at the stopover sites throughout the winter – at least we have no information to the contrary. The slightly larger Dunlin (*C. alpina*) regularly overwinters as far north as the Fraser River Delta (latitude 49°5′ N) in considerable numbers. Most Western Sandpipers do not arrive at the North American sites much before April, however (see Table 1).

It would appear, therefore, that Western Sandpipers prefer southern to northern sites outside the breeding season. It might be conjectured that food is more abundant at tropical and subtropical sites, although measurements taken in Mauritania (Zwarts *et al.*, 1990; Sutherland, 1991) showed that this was not the case for similar species in the Old World. Here we hypothesize that risks of predation are generally lower at southern than at northern sites. Direct evidence for this hypothesis is weak, but if one assumes that food availability is more variable at high-latitude locations, the differential predation-risk hypothesis makes sense. Any birds wintering at a site subject to occasional interruptions of the food supply owing to storms or ice conditions must hedge against these events by maintaining a high

level of fat reserves. But maintaining high fat reserves reduces a bird's manoeuvrability (Metcalfe and Ure, 1995), thereby increasing its risk of being caught by a predator (Lima, 1986; Bednekoff, 1996). For this reason, predation risks may be relatively lower at low-latitude sites than at high-latitude sites. If the predation-risk hypothesis is correct, it provides the mechanism for a trade-off between early and late migration to stopover sites. Early migration hedges against persistent unfavourable wind conditions, but increases predation risk.

METHODS

Our optimization model of Western Sandpiper spring migration covers the annual time period from Julian dates 90 (31 March) through 151 (31 May). The sites (s) considered are: 0: last subtropical stopover site, in Northwestern Mexico (ME); 1: San Francisco Bay (SF); 2: Fraser River Delta (FR); 3: Stikine River Delta (ST); 4: Copper River Delta (CR); 5: breeding site in Western Alaska (AK) (see Fig. 1). (The site at Gray's Harbor, Washington was not included separately, because of its proximity to the Fraser River Delta site.) These sites are known to support the largest number of Western Sandpipers during spring migration (Iverson *et al.*, 1996). The model does not specify any particular wintering area; Western Sandpipers in winter disperse over a large area, including the coasts of the Southern USA, Central America, and South America from Venezuela to Peru. In the model we account for this winter dispersion by assuming staggered arrivals of birds from further south and east at the stopover site 0. The basic time interval treated by the dynamic model is one day; at the start of each day the bird, if located at a stopover site s ($0 \le s \le 4$), chooses one of three options: (1) remain at the current site s, spending the day feeding; (2) initiate migration to the next site $s + 1$; (3) initiate return migration to the wintering grounds.

A bird's daily decision (stay, migrate northwards, return) is allowed to depend on the current date t, the bird's current location s, its current energy reserves x, and current wind conditions w. Wind conditions were defined as favourable if winds (as observed from the stopover site) were of such strength and direction as to assist the bird in its flight to the next stopover site. We considered two extreme cases of wind predictability:

1. *Predictable winds*: birds are able to tell whether or not winds are favourable for the next migration segment (but birds cannot foretell the exact wind velocity to be encountered during the flight), and to choose a flight altitude that maximizes ground speed in the desired direction (this case is henceforth referred to as the 'basic model').
2. *Unpredictable winds*: birds have no ability to detect or optimize winds, but can adjust their flight direction appropriately when winds allow forward progress.

Wind speed vectors were obtained from meterological data, for each intersite segment, and used to calculate a distribution of ground speeds (see Appendix). Table 3 specifies the parameters used in the basic model.

The bird's energy reserves are depleted while flying, and replenished while on the ground at any stopover site $s = 0$ to 4. Daily rates of energy gain were treated as constants throughout the season, except for the last two stopover sites (3 and 4: ST and CR), which were assumed to be unavailable or unproductive owing to ice or snow conditions before date 110.

The Alaskan breeding grounds were assumed to provide a window of breeding opportunity between dates 133 and 151 inclusive, with expected reproduction $\varphi(x,t)$ depending on

the date of arrival t, and on energy reserves x upon arriving (later arrivals have reduced breeding success, as do birds with very low reserves: see below). The model pertains to female breeders, so that reproduction counts only female offspring.

Finally, birds were assumed to be subject to a daily predation risk $\mu_0(s)$ depending on site s; while in flight between sites there is no predation risk, but birds will perish if they exhaust their energy reserves en route.

The dynamic programming algorithm determines the migration strategy that maximizes a bird's expected lifetime reproductive fitness. Specifically, fitness $F_s(x,t)$ for a bird located at site s, and having energy reserves x, at the beginning of date t, is defined as the sum of current and future years' expected total reproduction. For the breeding site $s = 5$ we assume that, for a bird that arrives on day t with reserves x,

$$F_5(x,t) = \varphi(x,t) + \sigma R_0 \tag{1}$$

where $\varphi(x,t)$ is expected reproduction in the current year, σ is the probability of surviving from day $t_1 = 151$ in the current year to day $t_0 = 90$ in the next year, and R_0 is expected future lifetime reproduction, assessed by day t_0. Current reproduction is given by

$$\varphi(x,t) = W_1(x)\,W_2(t)\,r_{\mathrm{AK}} \tag{2}$$

where r_{AK} is the expected reproduction of a bird arriving in Alaska on day $t_{\mathrm{AK}} = 133$, with adequate reserves, and where $W_1(x)$ and $W_2(t)$ are penalty factors given by

$$W_1(x) = \min(k_1 x, 1)$$

$$W_2(t) = 1 - k_2(t - t_{\mathrm{AK}}) \tag{3}$$

Here k_1 and k_2 are parameters, the assumption being that reproductive success is reduced linearly by inadequate energy reserves, and by late arrival. As explained later, R_0 in equation (1) is simultaneously an input to, and an output from, the model; an iterative procedure was used to reconcile these two values.

Next, $F_s(x,t)$ is calculated for the last stopover site $s = 4$ by an optimization procedure (for details, see Appendix), and this process is repeated for $s = 3$ down to $s = 0$. Each calculation also determines the optimal decision matrix $D_s(x,t,w)$ at each site. These decision matrices (for favourable winds) are depicted in Fig. 1. These results, as well as results corresponding to other cases, are discussed later.

To compare the predictions of the model with field observations, we ran 100 Monte Carlo simulations of optimal migrants using the decision matrices $D_s(x,t,w)$ to generate time-trajectories of optimally migrating birds initially located at site 0. These trajectories are stochastic, being influenced by random winds. We simulated differences in the timing of migration from different wintering grounds by spreading the birds' arrival dates at site 0 over a 20-day span, $t = 90$ to 119; all birds arriving at site 0 on a given day, with adequate reserves, follow identical migration schedules thereafter in any given year. One hundred simulations were used to generate long-run population-level statistics of migratory behaviour (see Fig. 2).

RESULTS

The optimal decision matrices $D_s(x,t,w)$ for the basic model, and for favourable wind conditions, are shown in Fig. 1. For example, a bird located at the initial site ($s = 0$)

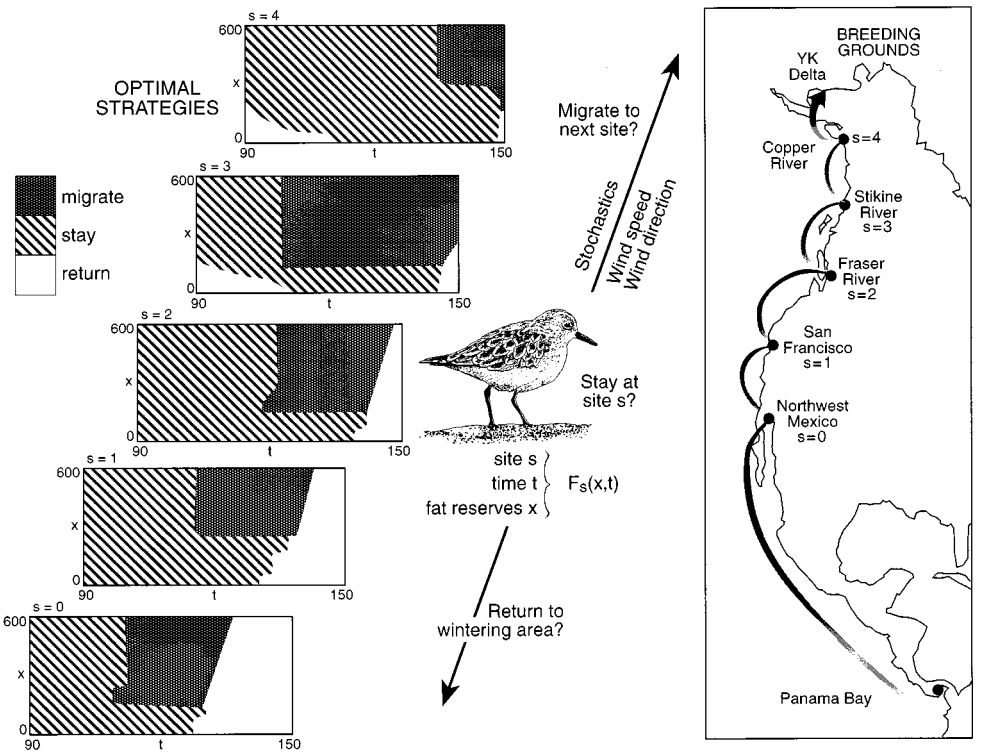

Fig. 1. Optimal migration strategy for Western Sandpipers under favourable wind conditions, for the case of predictable winds. The optimal decision (stay on site, migrate to next site, return to winter site) is a function of time t, fuel load x and location s. The optimal strategy was computed by dynamic programming, based on the assumption that migration strategy maximizes the expected lifetime reproductive success of individual birds.

should initiate migration to San Francisco Bay ($s = 1$) as soon after date 113 as winds are favourable, up to date 135, unless its energy reserves are very low (< 150 kJ). Birds that have not departed by date 135 should return to the winter site. Similar migration 'windows' (shaded areas in Fig. 1) apply to each site. For the last two sites ($s = 3$ and 4), birds arriving prematurely with low reserves should return, since they will starve if they remain at these sites. Of course, no optimal migrant will encounter this situation. The migration pattern indicated in Fig. 1 is qualitatively realistic; the location and shape of the various regions in the graphs depend on model parameters. Figure 2 is a combined histogram of predicted peak dates of Western Sandpiper numbers at each stopover site, resulting from the Monte Carlo simulations. The predicted and observed modal peak dates at each site are listed in Table 1, lines (a) and (b). The predicted peak dates are within the range of observed values for each site.

Two important model parameters, for which we were unable to obtain empirical estimates, were tuned to achieve this fit. The first tuned parameter, q_w, specifies the bird's ability to locate and utilize the most advantageous winds aloft. The base case, with $q_w = 1.0$, assumes that this ability is perfect. Line (e) in Table 1 shows that changing to $q_w = 0.8$ moves

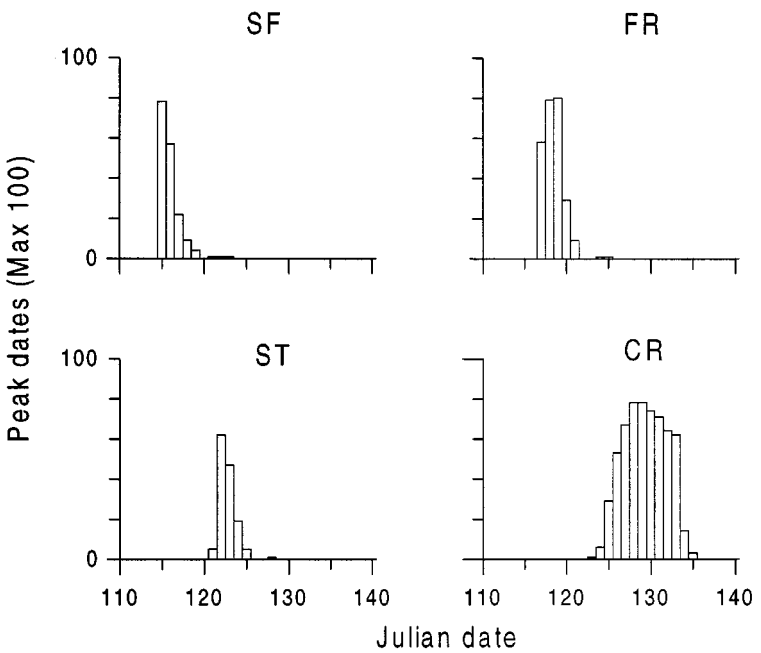

Fig. 2. Histograms of predicted peak dates for migratory Western Sandpipers at each stopover site: SF, San Francisco Bay; FR, Fraser River Delta; ST, Stikine River Delta; CR, Copper River Delta. One hundred Monte Carlo simulations of optimal migrants.

Table 1. Modal predicted peak dates for migrating Western Sandpipers (100 Monte Carlo simulations of 20 birds) for (a) basic model, (b) observed data and (c–e) alternative values of tuned parameters α and q_w, as described in the text

Parameters	San Francisco Bay (SF)	Fraser River Delta (FR)	Stikine River Delta (ST)	Copper River Delta (CR)
(a) Basic	115	119	122	128–129
(b) Observed	111–118	118–121	123–126	129
(c) $\alpha = 1.5$	111	118	122	130
(d) $\alpha = 2.5$	121	123	124	129
(e) $q_w = 0.8$	108	115	118	130

the predicted peak dates forward by 7 days at San Francisco Bay, 4 days at the Fraser and Stikine River Deltas, and backward 1–2 days at the Copper River Delta.

The second tuned parameter, α = (flight cost at maximum fuel load) ÷ (flight cost at half-fuel load), specifies the shape of the Pennycuick flight-range curve of equation (A11) below. As shown in Table 1, increasing or decreasing the value of α by 25% from its base value $\alpha = 2.0$ also alters the predicted modal peaks by several days. The sensitivity of quantitative predictions of fuel departure loads in optimal migration models, to the assumed shape of the flight-range curve, has been considered by Weber and Houston (1997). These authors

stress the importance of such sensitivity tests, given that the flight range equations are among the most uncertain relationships used in the analysis of bird migration.

The quantitative predictions obtained from an optimization model are typically quite sensitive to assumed parameter values (Mangel and Clark, 1988, p. 188). For a model of such complex behaviour as long-range migration, some parameters are inevitably not accurately known. It is therefore important to test the model's sensitivity to these parameters, and to check whether there are reasonable specifications of parameter values that will yield successful predictions. The latter requirement seems to be met by our model, although alternative parameter values led to predictions of migration patterns that differed typically by up to a week at the southern sites (SF, FR), but much less at the northern ones (ST, CR). We next discuss two changes to the model that lead to completely erroneous predictions.

The ability to respond to winds

Our basic model assumes that Western Sandpipers possess the ability to detect favourable wind conditions, while on the ground, and to select flight altitudes that optimize wind assistance. We also considered an alternative ('null') version of the model, in which it was assumed that the sandpipers possess no such abilities. The birds were assumed simply to take off and fly to the next site in whatever winds exist at the time, correcting for wind speed and direction if possible. Subject to this limitation, the birds were assumed to use a migration strategy that maximizes fitness. Under this alternative, our model indicates that such behaviour would be strongly maladaptive: the calculated fitness $F_0(x_0,t_0)$ of a bird located initially at site 0, with fuel reserves x_0, was less than 0.1 under any realistic assumptions about reproductive rates on the breeding ground (compared to $F_0(x_0,t_0) = 1.0$ for the basic model). In retrospect, this result is not surprising. Western Sandpipers that fail to respond to existing wind conditions (other than flying so as to track the desired migratory direction) would have a low probability of successfully completing the spring migration. We conclude that strong selection pressure must exist for small, long-distance migrants such as the Western Sandpiper, to utilize the assistance of winds, a finding also reported by Butler *et al.* (1997) for this species using a simpler model. In spite of inevitable difficulties in modelling the influence of winds, future models of avian migration need to take account of this factor.

Predation-risk differential

Returning to the basic model, we next altered the assumption that predation risks are lower at the wintering site than at stopover sites, assuming instead equal predation rates at the winter site and all stopover sites, namely 0.001 day^{-1}. This change completely altered the model's predictions: with no differential predation risk, all birds migrate immediately (when winds are favourable) from northern Mexico to San Francisco Bay, and then continue on to the Fraser River Delta. The predicted dates of first arrival at stopover sites, for the model with no predation-risk differential, were advanced by 21 days at SF, 16 days at FR, 13 days at ST and 6 days at CR. (These dates would have been advanced further if we had initiated the simulations earlier than day 90.) Differential predation risks (lower at more southern locations) are thus potentially an important factor determining Western Sandpiper migration strategies. This question is discussed further in the concluding section.

Table 2. Percent reduction in fitness resulting from a 50% decline in food availability at separate stopover sites, and from the same decline at all sites simultaneously[a]

Site	No adaptive response (%)	New optimum (%)
San Francisco	0.2	0.2
Fraser River	4	2
Stikine River	5	2
Copper River	20	8
All sites	35	17

[a] See Appendix for technical details.

Implications of environmental changes

By altering certain parameters in the basic model, we can assess the potential effects on the fitness of Western Sandpipers that could result from various kinds of environmental changes. These results may provide insight into conservation requirements for this species. In carrying out the computations, the ability of the birds to adapt to the changed environment needs to be considered. At one extreme, individuals might not change their migration strategies at all, continuing to use the originally (but no longer) optimal strategy. At the opposite extreme, individuals might adapt or evolve modified strategies that optimize fitness in the changed environment. Our model is capable of assessing the fitness consequences of both extreme cases.

In practice, the birds might be expected initially to show an intermediate plastic response to the changed environment, which could then evolve through natural selection to an improved response. Our method is not capable of predicting such evolutionary dynamics, however.

Table 2 shows the percent reduction in fitness (i.e. expected reproductive success per female), for the basic model, resulting from a 50% decline in food availability at each of the stopover sites considered separately, and for all sites simultaneously. These results suggest that each separate stopover site is fairly unimportant, except for the final site, Copper River, to the Western Sandpiper population. Degradation of all sites simultaneously has a more pronounced deleterious effect than the sum of the separate effects. Also, by evolving new migratory strategies, the birds can compensate for environmental change to a limited extent.

DISCUSSION

A body of theory has arisen to explain how migratory birds might make decisions on the basis of events occurring at staging sites (Alerstam, 1990; Alerstam and Lindström, 1990; Gudmundsson *et al.*, 1991). In the present paper, following Ens *et al.* (1994), we describe migratory behaviour as the outcome of individual decisions in which behaviours are determined by the expected fitness rewards, fitness being defined in terms of lifetime reproductive success. Our model, in which birds use daily information on winds, energy reserves and the time remaining until the start of the breeding season, generated predictions that closely matched field data. These predictions were fairly insensitive to assumed parameter values,

with two notable exceptions. First, when site-specific predation risks were altered to remove the latitudinal differential, a completely different, unrealistic pattern of migration emerged. This result supports the hypothesis that small shorebirds may experience lower levels of predation risk at tropical winter sites, as a result of requiring less fat reserves to hedge against variation in food supply, relative to temperate sites. The model's predictions were also greatly altered by changing the assumption that the birds can detect and respond to wind conditions. Our findings support the conclusion of Butler *et al.* (1997) that migratory behaviour of the Western Sandpiper is strongly influenced by upper atmospheric wind conditions during the flight phase. In addition, we show that refuelling rates at individual stopover sites provide a small contribution to the fitness of the Western Sandpiper. Whether this conclusion can be extended to other migratory birds is unclear. However, there is a growing body of evidence to suggest that winds aloft are very important for successful migration of large and small birds. Arctic breeding Brant Geese (*Branta bernicla*) reproductive success is positively correlated with favourable tail winds during migration (Ebbinge, 1989). Moreover, there is a growing body of evidence to indicate that winds are an important component of migration for many small birds (e.g. Liechti, 1995; Butler *et al.*, 1997). The potentially large saving in energy and flight time in favourable winds, the large cost of flying against the wind (Liechti, 1995), and the fitness consequence of decisions (this paper) provide a mechanism for the selection of appropriate behaviours. Selecting the optimal time to initiate migrations between stopover sites requires that the birds are capable of detecting variable wind conditions. It seems highly likely that Western Sandpipers use weather cues at a given stopover site for this purpose; future work should consider correlations between the departure of flocks and local meterological data. Our computations suggest a strong selection pressure in favour of such forecasting abilities.

Our conclusions are based on several assumptions, including that there is a fixed refuelling rate at each site, that the breeding window of opportunity is fixed and that birds can assess winds from the ground. We are not entirely confident that refuelling rates are fixed at each site. We consider this conservative modelling assumption, in the sense that our model is capable of predicting realistic migration schedules without the additional assumption that these schedules are influenced by the timing of food supplies at stopover sites. Moreover, Butler *et al.* (1997) showed that refuelling rates were relatively unimportant compared with winds in predicting the body masses at stopover sites. Our assumption that the breeding window is fixed seems reasonable. Kessel (1989) reported that egg-laying by this species was fairly synchronized during the last week of May in most years. Although we have no empirical evidence that Western Sandpipers can assess upper atmospheric wind conditions from the ground, it is possible that they might use some simple cues. Increased wind from the east and southeast accompanied by increased cloud cover and rain are cues for a building low pressure system that generates favourable winds for migration in the northeast Pacific. The movement of clouds also indicates the direction of winds in the upper atmosphere.

Recent telemetry studies (Iverson *et al.*, 1996) have shown that Western Sandpipers sometimes migrate non-stop between remote sites, presumably taking advantage of favourable winds. Our model does not directly allow for this possibility, but assumes at least a part-day sojourn at each stopover site. Under persistent favourable winds, however, the model predicts immediate resumption of migration to the next site.

The potential impacts of environmental changes on wildlife populations have been studied previously using a life-history modelling approach (e.g. Sandercock and Gratto-Trevor,

1997). Dynamic programming models, which are an extension of life-history models (Clark, 1993) allowing for the detailed consideration of micro decisions, seem particularly appropriate for the case of migratory species. But both approaches overlook processes of population regulation and dynamics. Including these processes to obtain quantitative predictions regarding environmental impacts on population size is a major undertaking, however (Goss-Custard *et al.*, 1995). The more modest approach followed in this paper can assess the relative impacts on population productivity that might result from such environmental changes.

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APPENDIX: MODEL AND COMPUTATIONS

Here we describe the dynamic state variable model of Western Sandpiper migrations, and discuss computational details. The parameters used in the model are listed in Table A1.

The fitness of a (female) bird located at site s with energy reserves x, at the beginning of date t (Julian), is denoted by $F_s(x,t)$. Thus $F_s(x,t)$ represents total expected future lifetime reproduction of a bird that uses the optimal migration strategy. The decision whether to migrate is assumed to be made once a day. The bird first assesses current wind conditions (w); if favourable, she may elect to 'migrate' – that is, fly to the next stopover site ($s+1$) – depending on her current state x and the date t. If she decides not to fly on, she can choose between spending the day at the current site

Table A1. Model parameters

Symbol	Meaning	Base-case values
Global parameters		
t_0, t_f	initial and terminal dates (Julian)	90, 151
E_{max}	maximum energy reserves (kJ)	600
Δx_1	average energy gain while feeding ($kJ \cdot day^{-1}$)	39.0
Δx_2	metabolic cost if not feeding ($kJ \cdot day^{-1}$)	10.0
v	average flight speed ($km \cdot h^{-1}$)	38.5
c_f	average flight cost ($kJ \cdot h^{-1}$)	12.2
R_0	expected future reproduction	1.0
α	flight cost coefficient	2.0
q_v	wind optimization ability	1.0
Site-specific parameters ($s = 0, 1, 2, 3, 4$)		
$t_{open}[s]$	site-opening date	{90, 90, 90, 110, 110}
$\Delta d[s]$	distance to next site (km)	{960, 1540, 1180, 900, 1180}
$p_w[s]$	probability of favourable winds	{0.65, 0.65, 0.80, 0.78, 0.78}
$\mu_0[s]$	predation risk (day^{-1})	{0.0005, 0.002, 0.003, 0.003, 0.003}
$\mu_1[s]$	return migration mortality risk	{0.0, 0.02, 0.05, 0.06, 0.08}
$t_m[s]$	return migration time (d)	{0, 3, 8, 12, 15}
Breeding-window parameters		
t_{AK}	opening date, Alaska site	133
r_{AK}	maximum expected reproduction (females)	0.297 (see text)
k_1	low energy reserves penalty coefficient	$1/(0.2E_{max})$
k_2	late arrival penalty coefficient	0.025

('stay') or initiating return migration to the wintering site ('return'). Values of t range from t_0 (earliest migration date) to t_f (last date for reaching the breeding ground).

Let $f_s(x,t,w)$ denote the bird's fitness after wind conditions w have been observed on day t. Since $F_s(x,t)$ applies before this information becomes available, we have

$$F_s(x,t) = E_w(f_s(x,t,w)) \tag{A1}$$

where E_w denotes mathematical expectation with respect to the random variable w. We considered just two wind states, $w = +1$ indicating favourable winds and $w = -1$ indicating unfavourable winds. Then for $t < t_f$ we have

$$f_s(x,t,-1) = \text{maximum of 'stay', 'return'} \tag{A2}$$

$$f_s(x,t,+1) = \text{maximum of 'stay', 'return', 'migrate'} \tag{A3}$$

These actions are specified as follows: 'Stay' means that the bird spends the day t at the current site s, obtaining a net increase Δx in reserve level provided it survives predation. 'Return' means that the bird abandons northward migration for the current year and returns to the wintering grounds. The return option is needed in the model for logical completeness: a bird located at site s too late in the season to successfully complete its northward migration is assumed to return to the wintering site, where predation is reduced. In running the model, optimally migrating birds never encounter this possibility. 'Migrate' means that the bird takes off for the next site, $s + 1$. The terms in quotation marks have the following mathematical expressions:

$$\text{'stay'}: (1 - \mu_0(s))F_s(x + \Delta x, t + 1) \tag{A4}$$

$$\text{'return'}: \sigma(s,t)\cdot R_0 \tag{A5}$$

$$\text{'migrate'}: E_\tau(F_{s+1}(x'_\tau, t'_\tau)) \tag{A6}$$

These expressions are explained in greater detail below. The terminal value of F_s on date $t = t_f$ is given by

$$F_s(x,t_f) = \sigma(s,t_f)\cdot R_0 \tag{A7}$$

In the above expressions, $\mu_0(s)$ represents daily predation risk at site s, and $\sigma(s,t)$ is the probability that a bird initiating return migration from site s on day t survives to day t_0 of the following year. This is given by

$$\sigma(s,t) = (1 - \mu_1(s))(1 - \mu_0(0))^{365 - (t - t_0 - t_m(s))} \tag{A8}$$

where $\mu_1(s)$ is the mortality risk on the return migration (e.g. resulting from the risk of predation at stopover sites), and $t_m(s)$ is the time required to complete the return trip. Both $\mu_1(s)$ and $t_m(s)$ were assumed to be proportional to the total distance travelled on the return migration to site 0 (see Table A1; details of this return migration, and of further migration from site 0 to the bird's wintering grounds, are not explicitly modelled). Equation (A4) is self-explanatory. In equation (A5), R_0 represents future expected reproduction for a bird situated at site 0 on date t_0 of the following year. We assume that R_0 is the same for all birds, regardless of age. We discuss the specification of R_0 further below.

In equation (A6), τ denotes travel time between sites s and $s + 1$. This is a random variable determined by stochastic wind speeds encountered during migration. The values of x'_τ and t'_τ, which represent energy reserves and time of arrival at site $s + 1$, are calculated from the flight equation described below.

For the breeding grounds ($s = 5$) we have

$$F_5(x,t) = \varphi(x,t) + \sigma(5,t_f)\cdot R_0 \tag{A9}$$

as in equation (1).

Equations (A1)–(A9) constitute the dynamic programming algorithm for our model. Computer solution of these equations, calculating backward from site 4 to site 0, and also calculating backwards in time t from t_f to t_0 at each site, yields the values of $F_s(x,t)$ as well as the optimal strategy matrices $D_s(x,t,w)$. Specifically, we begin with site $s = 4$, calculating $F_4(x,t)$ in turn for $t = t_f - 1$ down to $t = t_0$ for all values of x. The procedure is then repeated for $s = 3, 2, 1, 0$. Figure 1 displays the resulting strategy matrices when winds are favourable, that is $D_s(x,t,1)$.

Our model of flight dynamics is standard (e.g. Pennycuick, 1989; Weber *et al.*, 1994). Let x denote fuel reserves (kJ) during a flight, and let $\mathrm{d}x = J(x)\mathrm{d}s$ denote the amount of fuel required to fly a distance $\mathrm{d}s$ (in still air). For a bird that initiates a flight with reserves x_0 and flies a distance D, we then have

$$D = \int_0^D \mathrm{d}s = \int_{x_1}^{x_0} J(x)^{-1}\mathrm{d}x \tag{A10}$$

where x_1 = fuel reserves remaining. The maximum flight range, given initial reserves x_0, is:

$$D_{\max} = \int_0^{x_0} J(x)^{-1}\mathrm{d}x$$

In our model, we assumed, following Pennycuick (1975), that

$$J(x) = c_1(1 + c_2 x)^{3/2} \tag{A11}$$

where c_1 and c_2 are constants.

Flight speed v in still air was assumed to be constant. For a given wind vector $\vec{w}$, the bird was assumed to employ a flight vector $\vec{v}$ (of magnitude v) such that the resultant ground speed vector $\vec{v} + \vec{w}$ points in the direction of the next stopover site, if this is possible. Specifically, let θ_w be the angle between the desired track and $\vec{w}$, and let θ_v be the corresponding angle for $\vec{v}$. If $w|\sin \theta_w| > v$, the bird is unable to follow the desired track. In the case that the birds cannot detect favourable wind conditions, we assumed that a bird encountering such winds would be blown off course and would perish; this situation does not arise under the alternative case of predictable winds.

If $w|\sin \theta_w| \leq v$, the compensating angle θ_v is given by

$$v \sin \theta_v = w \sin \theta_w$$

and the ground speed in the desired direction is

$$v_1 = v \cos \theta_v + w \cos \theta_w$$

Winds were defined to be favourable if $v_1 \geq v$; in the basic model, birds attempt to migrate only when winds are favourable.

Meteorological data were used to calculate the probability of favourable winds at each stopover site s, and to estimate the distribution of track speeds v_1 between adjacent sites at different altitudes (the data encompassed five different altitudes). These track speeds then determined the duration of the flight. In the basic model, the bird was assumed to choose the altitude at which v_1 is maximum, but no such ability was assumed in the computations involving lack of wind predictability.

Life-history consistency

We next comment on the concept of fitness assumed in our model, namely expected lifetime reproductive success. This datum, denoted by R_0 in life-history theory, is appropriate for stable populations. Since we know of no information suggesting long-term changes in the Western Sandpiper population, we adopted R_0 as our fitness concept. An important consistency requirement is that $R_0 = 1$; otherwise, the assumption of a stable population would be violated. But R_0 is simultaneously an input (expected future reproduction) and an output (fitness) for our model. If we assess fitness on day t_0 at the initial site $s = 0$, these two values should coincide, and equal 1:

$$F_0(x_0,t_0) = R_0 = 1 \tag{A12}$$

Here x_0 denotes the average energy reserves of a bird at site 0 on day t_0. If condition (A12) is not satisfied by the computed fitness value $F_0(x_0,t_0)$, the conclusion is that the model is numerically inconsistent. Ideally one should have a complete specification of density-dependent factors for every input parameter (Mylius and Diekmann, 1995), but this is obviously impractical. The alternative is to consider adjusting one or more input parameters so as to achieve the required consistency. We chose to adjust r_{AK}, the expected number of female offspring per year that survive to maturity, for females that reach the Alaskan breeding ground. The parameter includes juvenile survival, a poorly known quantity. For the basic parameter values, $r_{AK} = 0.297$ resulted in the desired life-history consistency.

To assess the fitness consequences of a given environmental change, we considered both the short-term, non-adaptive response (in which birds continued to use the formerly optimal strategy, $D_s(x,t,w)$), and the long-term, fully adaptive response (in which birds evolved a newly optimal strategy, $D'_s(x,t,w)$). For the first case, we ran the dynamic programming calculations, but without the maximization component, using decisions $D_s(x,t,w)$ and altered parameter values representing the modified environment. We varied R_0 to obtain $F_0(x_0,t_0) = R_0$. The new value of R_0, in relation to the original value ($R_0 = 1$), measures the change of fitness resulting from the environmental change (see Table 2, under 'no adaptive response').

For the fully adaptive response, we re-ran the full dynamic programming calculations with new parameter values, again varying R_0 until $F_0(x_0,t_0) = R_0$. As before, the new values of R_0 indicate the environmental impact (see Table 2).

Parameter values

The parameter values (Table A1) were derived from several literature sources and personal observations. Western Sandpipers begin migration from tropical areas by mid-February ($t = 50$) and complete migration on the breeding ground by the end of May ($t = 151$). We assumed that Northern Mexico, San Francisco Bay and the Fraser River Delta could support migrant sandpipers at any time, because they remain ice-free in winter. The Stikine and Copper River Deltas cannot support shorebird feeding until they are free of ice, which we assumed to occur about 20 April ($t = 110$). The earliest observed arrivals on the Seward Peninsula, Alaska, is in the second week of May ($t = 134$) (Kessel, 1989).

The greatest body mass of Western Sandpipers caught during spring migration is about 39 g, and lean mass is about 22 g, implying maximum energy reserves of about 17 g. We assumed energy reserves consisted of 85% lipids and 15% muscle protein (Lindström and Piersma, 1992). The energy contents of lipids and protein are 39 and 18 kJ·g^{-1}, respectively. Therefore, the maximum energy reserves are about 566 + 45 ≅ 600 kJ.

A 27 g shorebird could increase its mass by about 1 g, or 39 kJ·day^{-1} (Blem, 1990), which is about the maximum rate observed in the congeneric Semipalmated Sandpiper (*C. pusilla*) in coastal habitats (D. Lank, personal communication). We do not have direct measurements of resting metabolic rate, but assumed 10 kJ·day^{-1} as a reasonable value.

The body mass of a typical Western Sandpiper carrying 50% of maximum energy reserves was set at 30.5 g. The maximum flight speed for such a bird, having a wing span of 98 mm, was estimated as 38.5 km·h^{-1} (Pennycuick, 1989). We used Norberg's (1996) estimated cross-species relationship $P = 53.7W^{0.81}$ (where P is power in watts and M is body mass in kg) to estimate average flight cost for a 30.5 g Western Sandpiper as 12.2 kJ·h^{-1}.

Since we lacked data from which to estimate the two parameters c_1 and c_2 in the flight cost model (equation A11), we introduced an additional parameter α = (flight cost at $E_{max} = 600$ g) ÷ (flight cost at 300 g), and then turned α to yield the best fit between predicted and observed migration patterns. As indicated in Table 1, the predicted peak dates at SF and FR are fairly sensitive to this tuned parameter, within a range of several days about the basic value.

Wind data (Anon, 1993) were collected at 12 h intervals at altitudes up to 5500 m. Migrating birds, including sandpipers, are known to select elevations having favourable winds (Richardson, 1978, 1979, 1990; Liechti, 1995). Our basic model assumed that the birds optimized the use of winds while flying ($q_w = 1.0$).