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MODELS AND REALITY: TIME–ENERGY TRADE-OFFS IN PECTORAL SANDPIPER (*CALIDRIS MELANOTOS*) MIGRATION

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Abstract. We used a combination of modeling and field studies to determine the spring migration strategy of Pectoral Sandpipers (*Calidris melanotos*). We developed a dynamic programming model to predict patterns that should be detected along the migratory route if Pectoral Sandpipers use a strategy of early arrival at the breeding grounds (time minimization) or arrival at the breeding grounds with excess energy reserves (energy maximization). The predictions were then compared to data collected at stopover sites in the mid-continent of North America and at the breeding grounds in Alaska over a 5-yr period (1992–1996).

During spring migration to their Arctic breeding grounds, Pectoral Sandpipers stop periodically to feed. The length-of-stay at such stopovers, for both time minimizers and energy maximizers, was predicted to vary inversely with date and body fat, and to vary directly with invertebrate abundance. We observed that: (1) length-of-stay was negatively correlated with capture date in Missouri and Nebraska, but not in Texas; (2) length-of-stay was not correlated with body fat at any site; and (3) length-of-stay was positively related to invertebrate abundance at the Nebraska and Missouri sites. As the population moves northward in the spring, three regional patterns are diagnostic of migration strategy. Length-of-stay was predicted to be bimodal (energy maximizer) or constant (time minimizer) with respect to latitude, but neither pattern was observed. The migration window, or period of time during which spring migrants occur, was predicted to decrease with increasing latitude for time minimizers, a pattern that was seen for both males and females. Body fat was predicted to increase with latitude for energy maximizers, a pattern that was seen for females but not males.

The evidence suggests that males and females differ in their spring migration strategies. Both sexes attempt to arrive in the Arctic as early as possible after ice breakup in the spring. Additionally, females gain significantly higher fat loads than males (up to 60% body fat for females) during migration, and these energy reserves may later enhance female reproductive success. However, females gained large fat loads only during 1993 and 1995, which had above normal spring precipitation along the migration route. We believe that the correlation between female body fat and precipitation reflects an abundance of high-quality stopover habitat during wet springs. This view is supported by model sensitivity analyses showing that the spacing and quality of stopover habitat can strongly influence observed migration patterns. Our results suggest the need to focus additional research on the landscape-level features of the flyway through which shorebirds migrate.

Key words: Calidris melanotos; *dynamic programming; landscape; migration strategy; model; Pectoral Sandpiper; shorebird; stopovers.*

INTRODUCTION

Hypotheses about migration strategies of birds have emphasized time of arrival and energy reserves as likely correlates of survival and reproductive success. It may be advantageous for a migrating bird to arrive on the breeding grounds as early as possible to compete for preferred breeding sites (Myers 1981*a*, *b*, Oring and Lank 1982) or to increase the time available to renest if initial attempts fail (Reynolds et al. 1986). Conversely, it may be advantageous to accumulate energy reserves, even if this means arriving on the breeding grounds later, because reserves can buffer uncertainties during migration (Davidson and Evans 1988, Gudmundsson et al. 1991), allow an individual to withstand periods of adverse weather during incubation (MacLean 1969), or meet the energetic demands of reproduction (Ricklefs 1974, Blem 1980). In addition, other resources such as water (Yapp 1962, Biesel and Nachtigall 1987) or processes such as predation (Alerstam and Lindström 1990) may also be important determinants of migration strategies. Such single-resource hypotheses are useful constructs for research, but a migrating bird's survival and reproduction may actually depend jointly on time of arrival, energy reserves, and the availability of other resources during migration.

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Ecologists have generally approached the study of migration strategies in two ways. Some have taken an exploratory approach, searching for patterns that might provide clues about migratory adaptation (e.g., Page and Middleton 1972, Post and Browne 1976, Lank 1983, Dunn et al. 1988, Holmgren et al. 1993, Dinsmore 1994, Skagen and Knopf 1994, Lyons and Haig 1995, Iverson et al. 1996). Other have followed a more hypothetico-deductive approach, using mathematical models to predict migration patterns that should be observed if a particular strategy has been adopted by a species (e.g., Alerstam and Lindströ 1990, Gudmundsson et al. 1991, Lindström and Alerstam 1992, Weber et al. 1994, Clark and Butler 1998, Weber et al. 1998*a*).

We used the latter approach to develop a computer model of spring shorebird migration (Farmer and Wiens 1998) to formulate and test hypotheses in our study of the affects of global change on migration stopover habitat. Because we were interested in the effects of stopover spacing on migration patterns, we modeled migration through a two-dimensional landscape containing stopovers at specific north-south, east-west coordinates. Additionally, we modeled latitudinal and temporal gradients in temperature and photoperiod because these variables directly influence a shorebird's time-energy budget, migration schedule, physical state and, ultimately, its fitness.

Models such as ours may be useful tools for exploring various "what-if" scenarios and for predicting patterns that should be observed in the field for shorebirds using different migration strategies. Our first objective in this paper was to use the model to generate such predictions for three migration strategies: (1) early arrival at the breeding grounds (time minimizer), (2) arrival with excess energy reserves (energy maximizer), and (3) random (no strategy). However, the value of a modeling approach must be gauged in terms of the insights it provides about reality. Accordingly, our second objective was to compare model predictions to field observations of Pectoral Sandpipers (*Calidris melanotos*) made over a 5-yr period in the Great Plains of North America. We compared observations to patterns that were predicted to occur at individual stopovers (local) and across the flyway (regional), and our third objective was to assess how the scale (local vs. regional) affects one's ability to make accurate inferences about adaptive strategies.

Study System

Pectoral Sandpipers migrate through the midcontinent of North America enroute from their wintering grounds in the Neotropics to their breeding grounds in the Arctic. During spring migration, Pectoral Sandpipers pace themselves to arrive on the breeding grounds within the small window of time when conditions are suitable for successful reproduction. However, to complete migration successfully, they must stop periodically to replenish their energy reserves.

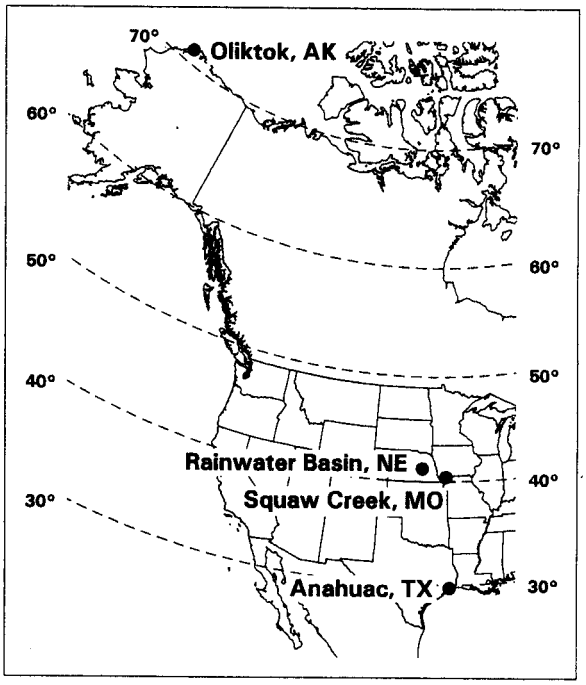

FIG. 1. Location of study areas.

Pectoral Sandpipers feed in a variety of migration habitats. They were called the "grass bird" by Bent (1927) because of their preference for wet, grassy areas, but they also use wet fields, pastures, mudflats along rivers and lakes, and moist-soil areas. Such stopover habitats are widespread in the mid-continent of North America; however, the abundance and distribution of suitable habitat varies markedly within and among years depending on the timing and amount of precipitation. Confronted by such landscape dynamics, Pectoral Sandpipers tend to be opportunistic in stopover usage. They do not concentrate at a few, large stopover sites but instead use many stopover sites and make several feeding stops that are punctuated by short migratory hops, in the same manner reported for Semipalmated (*C. pusilla*) and White-rumped (*C. fuscicollis*) Sandpipers (Skagen 1997).

To study migration strategies in this system, we analyzed data that were collected throughout the Great Plains of North America by several investigators. Additionally, we collected data at three stopover sites (Farmer and Parent 1997) and on the breeding grounds in Alaska (Fig. 1). The Anahuac, Texas site, located ~50 km northeast of Galveston, Texas, USA (29°40′ N, 94°30′ W), is one of the first stopovers used by Pectoral Sandpipers when they arrive in North America in the spring. This site is part of a tallgrass prairie ecosystem that has been extensively converted to rice fields, which are now the dominant landscape feature and shorebird habitat. The Squaw Creek site, in north-

west Missouri (40°10′ N, 95°15′ W), is near the physiographic boundary between the southern plains and the prairie pothole region to the north. This site, located in the Missouri River floodplain, contains manmade wetlands managed specifically for waterfowl and shorebirds, and agricultural "sheetwater" areas (LaGrange and Dinsmore 1989) that are abundant during periods of above normal precipitation. The Rainwater Basin site, in southeastern Nebraska (40°30′ N, 97°45′ W), is at roughly the same latitude, but it contains different wetland types than the Missouri site. This rolling landscape once contained about 4000 depressional wetlands; however, agricultural drainage since the early 1900s has reduced the number to <400. The Oliktok, Alaska site is on the breeding grounds in the Kaparuk oil field, west of Prudhoe Bay, Alaska, USA (70°20′ N, 149°50′ W). The Arctic tundra in this region contains many shallow lakes, drained lake basins, wetlands, and patterned ground-forms created by frost heaving (Walker et al. 1980), and the variety of wetland habitats attracts many species of nesting waterfowl and shorebirds.

Methods

Model development and prediction

Model concepts.—Here, we describe the general conceptual framework for our modeling approach. Details of the model structure are provided in Appendix A and by Farmer and Wiens 1998.

In our model, individual female sandpipers begin spring migration through North America at an initial stopover on the Gulf Coast of Texas (29° N latitude) with an initial state defined by two variables, energy reserves and latitude (Fig. 2). At the start of each day ($t = 1, 2, 3, \ldots$) a bird makes a decision to (1) remain at the current stopover or (2) initiate migration to one of $m - 1$ more northerly stopover sites. This decision depends on the bird's current energy reserves, its current latitude, and the date, t. For each decision, there is a daily time budget comprised of time spent in migratory flight, feeding, and resting. Migratory flights are initiated at sunset, and the time required to fly to the next stopover is dependent on a bird's flight speed. After a migratory flight is terminated, the remaining time is allocated to resting (during nonflight hours of the night) and feeding (during daylight hours).

A bird's daily energy budget is a function of its time budget, habitat quality (i.e., rate of energy ingestion), and the physical environment. While feeding, a bird has a gross rate of energy gain, which may vary among stopovers but is limited to a maximum value by physiological constraints (Kirkwood 1983). A bird also incurs metabolic losses, the rate of which depends upon whether it is feeding, resting, or migrating. The daily balance between energy gains and losses is influenced by ambient temperature and photoperiod. Ambient temperature affects metabolic rates and may influence the availability of food and thus the gross rate of energy gain. Photoperiod constrains the daily feeding time and, thus, the daily energy gain. Temperature and photoperiod, in turn, are influenced by feedback from the bird's latitude d and the date t.

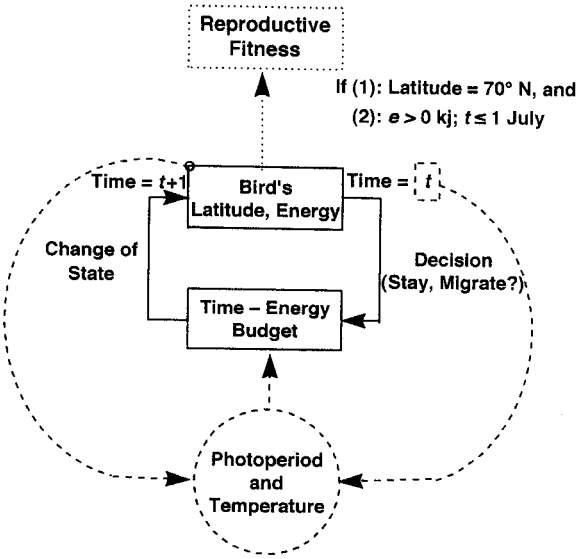

FIG. 2. Conceptual model of spring migration. Solid arrows represent the flow of time, measured in days. Dashed lines represent feedbacks from latitude and time (t) that affect the time–energy budget. Reproductive fitness is determined when the bird reaches the breeding grounds (70° N latitude), subject to two constraints: energy reserves during migration must have remained above a critical level (0 kJ), and the bird must arrive by 1 July.

A bird's state changes daily, depending on its time and energy budgets. If the daily energy balance is positive, new energy reserves are stored as tissue; if negative, a shorebird catabolizes body tissue to make up the difference. When a bird initiates a migratory flight, the actual location of its next stopover is subject to uncertainty because the location of suitable habitats is not predictable from year to year.

A bird repeats this daily cycle until it reaches its breeding grounds at 70° N latitude. During the trip, it must not allow its energy reserves to drop to a critical level (0 kJ), or it will die or otherwise be unable to continue migration and reproduce during the current year. Also, Arctic-nesting shorebirds must be present on the breeding grounds within a specified window of time (Holmes 1972, Piersma 1987) to reproduce successfully. Pectoral Sandpiper females begin nesting as early as 1 June (Pitelka 1959), but must begin by ~1 July or there will not be sufficient time for rearing young before the onset of winter. Even for birds arriving within the proper time window, there may be wide variation in expected reproductive success. By definition, time minimizers will have higher reproductive success if they arrive early in the window, and energy

maximizers will have higher reproduction if they arrive with extra energy reserves.

There are several key assumptions in this migration model: (1) a bird's daily allocation of time to migratory flight affects its migration schedule, (2) a bird's migration schedule influences its energy reserves and time of arrival on the breeding grounds, and (3) its energy reserves and time of arrival on the breeding grounds influence its expected reproductive success. Such linkages are the basis for selection and evolution of migration schedules, and for the predictions tested in this paper.

Making predictions.—To develop predictions, we first used a dynamic programming (Mangel and Clark 1988) version of our model to identify stopover decisions that would maximize fitness of shorebirds beginning at an initial stopover on the Gulf coast of Texas (29° N latitude), between 1 April and 1 May, with energy reserves of e, and bound for breeding grounds located at 70° N latitude (Appendix A, Farmer and Wiens 1998). Each dynamic model run was conducted for an ad hoc, one-dimensional flyway containing a uniform stopover spacing and habitat quality. Stopover spacing and habitat quality were systematically varied in value to assess the sensitivity of optimal decisions to changes in the landscape (Appendix B). We identified optimal stopover decisions for three different strategies based on the following fitness relationships (function $\phi(e, t)$ as used in Appendix A):

1. *Time minimizers.*—Females that arrived at the breeding grounds by 1 June had a relative fitness of 1.0. For arrival thereafter, fitness declined linearly to 0.1 for arrival on 1 July. Females arriving later than 1 July had a fitness of zero. Energy reserves did not affect fitness so long as females maintained a minimum reserve (>20 kJ) during migration.

2. *Energy maximizers.*—Females with a high level of reserves (≥593 kJ; equivalent to 30% body fat) upon arrival at the breeding grounds (or on 1 June, if they arrived before that date) had a relative fitness of 1.0. Fitness declined linearly with lower energy reserves to a relative fitness of 0.1 for birds with 20 kJ of reserves. Birds with <20 kJ were assigned a fitness of zero. Arrival time did not affect fitness so long as females arrived on or before 1 July.

3. *Random (null).*—Females made random time budget decisions subject to only one constraint: they could not choose to fly to stopovers beyond their flight range (i.e., they did not make decisions resulting in the exhaustion of energy reserves during flight).

For each migration strategy, we then simulated the migration of 200 females that: (1) arrived in Texas between 1 April and 1 May, uniformly distributed over the range of energy reserves observed at the Texas study site, and (2) made optimal stopover decisions as they migrated northward from Texas to the breeding grounds. For each individual in the population, we recorded daily values of body fat and location, and computed residence time at each feeding stop. For the population, we computed the length of the migration window (the time span during which birds occurred) at different latitudes. We then identified correlations between body fat, length-of-stay, date, latitude, stopover quality, and the migration window that might be detected in the field if one were studying such an optimal population. Differences in the predicted correlations were used to discriminate between the three migration strategies

Data collection and analysis

We captured Pectoral Sandpipers in mist nets at stopovers in Texas (1992–1993), Missouri (1993–1996), and Nebraska (1994). Pectoral Sandpipers exhibit sexual dimorphism in body size, and flattened wing length (♀ ≤ 140 mm; ♂ > 140 mm) was used to determine sex in the field (Johnsgard 1981).

Body fat.—We estimated body fat for individual birds using regression models that incorporated body measurements as independent variables. Several measurements were made on each bird: mass (±0.01 g); flattened wing length (±0.1 mm); exposed culmen length (±0.1 mm); tarsus length (±0.1 mm); and headbill length (±0.1 mm). Additionally, five replicate conductivity (TOBEC) measurements (Castro et al. 1990) were taken on each bird using an EM-SCAN, Model SA-2 Small Animal Body Composition Analyzer (EM-SCAN Inc., Springfield, Illinois). Soxhlet extraction data were obtained from 42 birds (25 females, 17 males) collected in Texas and Missouri during the spring of 1993. Fat was extracted using petroleum ether in a modified Soxhlet apparatus (Wheaton Science Products, Millville, New Jersey; Dobush et al. 1985). Using estimated total fat as the dependent variable (Morton et al. 1991), regression models were developed with all combinations of body and TOBEC measurements, first-order interaction terms, and quadratic mass. Standard error of the estimate (SE) was used to select the best models:

Females ($N = 25$; SE = 1.988; $R^2 = 0.96$; $P < 0.001$):

$$L = -1.854 - 0.095E + 0.005M^2 \quad (1)$$

Males ($N = 17$; SE = 1.807; $R^2 = 0.86$; $P < 0.001$):

$$L = 2.407 - 0.079E + 0.003M^2 \quad (2)$$

where L is estimated body fat (g); E is the mean of TOBEC measurements; and M is total mass (g). Body fat was also estimated for museum specimens with the best models that included only M as an independent variable:

Females ($N = 25$; SE = 2.311; $R^2 = 0.94$; $P < 0.001$):

$$L = -7.619 + 0.005M^2 \quad (3)$$

Males ($N = 17$; SE = 1.989; $R^2 = 0.83$; $P < 0.001$):

$$L = -1.831 + 0.002M^2. \quad (4)$$

Length-of-stay.—We estimated length-of-stay by attaching 1.5-g radio transmitters to 20 female sandpipers per year at each stopover site. We attached radios to about four females per week over a 5-wk period, and we selected these females to span the observed range of body fat. We monitored the daily movements of each radio-tagged female while it was within 50 km of its capture site (Farmer and Parent 1997). The length-of-stay at a stopover was described by two statistics. Radio time was measured as the elapsed time between radio tagging and the time that a female's radio signal was last detected in the area. Residence time, the mean time between arrival and departure from the study area, was estimated using concepts from encounter sampling (Otis et al. 1993). Using program DISTANCE (Laake et al. 1994) we fitted a probability density function (pdf) to the radio times for females that were tagged at a given site. Residence time (and its 95% confidence limits) was estimated by taking the inverse of $f(0)$, the y intercept of the empirical pdf. Likelihood ratios were used to test for differences in residence time among study areas and dates.

Stopover quality.—We compared the floodplain wetlands of Missouri to the depressional wetlands of Nebraska with respect to length-of-stay and habitat quality. The model defined habitat quality as the rate of ingestion of metabolizable energy. However, we were unable to measure ingestion rate directly, so instead we used invertebrate abundance as a surrogate measure. Core samples were taken at 5-m intervals along randomly located, 25-m transects in wetland-edge microhabitats (moist soils and saturated soils with water depths $\leq$2.5 cm) where Pectoral Sandpipers feed. To reduce error due to previous bird-use having depleted invertebrate populations (Helmers 1991), we sampled only in habitats that had recently become available due to decreasing water levels. We sampled early (25 April–1 May) and late in migration (19–21 May), and from multiple wetlands within each study area. We used a 10.2-cm diameter PVC core sampler with a depth of 10 cm. Cores were placed in plastic bags, kept on ice in a cooler, and wet sieved through a number 30 standard test sieve. Organisms were separated from debris and placed in vials with 80% ethyl alcohol. Preserved organisms were sorted, identified, and counted by taxa. Organisms were placed on aluminum drying pans, dried in an oven at 70°C for 24 h, and then weighed to the nearest 0.01 mg using a Mettler balance. Differences in invertebrate abundance between sites were assessed using a t test.

Length of migration window.—The length of the migration window (i.e., the span of time Pectoral Sandpipers were present during spring migration) was estimated at different latitudes using a scatter plot of capture/sighting date vs. latitude for all birds trapped at our sites, collected by museums, or captured/sighted by other investigators.

The length of the migration window at a given latitude (±1°) was estimated by the number of days spanned by the central 95% of birds. To test whether the length of the window varied with latitude, we determined whether variance in dates was homogeneous across latitude using Glejser's (1969) test for heteroskedasticity. Because the data set contained records from many years, we also tested for heteroskedasticity within individual years.

TABLE 1. Predicted patterns, expressed as signs of correlations, that should be seen if Pectoral Sandpipers are time minimizers or energy maximizers in their spring migration.

Correlation	Time minimizers	Energy maximizers
Local Patterns		
Length-of-stay vs. date	−	−
Length-of-stay vs. energy reserves	−†	−†
Length-of-stay vs. ingestion	+	+
Regional patterns:		
Migration window vs. latitude	−	0
Length-of-stay vs. latitude	0	+‡
Body fat vs. latitude	0	+

Note: Predicted correlations for random decisions (the null model) are all zero.

† A negative relationship is predicted only early in the spring.

‡ Bimodal length-of-stay; higher times at southern and northern latitudinal extremes.

Fitness relationships.—We captured nesting females on the breeding grounds near Oliktok, Alaska, and measured body mass, flattened wing length, exposed culmen length, tarsus length, head-bill length, and TOBEC. Thereafter, we recaptured each female at approximately weekly intervals during incubation for additional body mass and TOBEC measurements. The series of body mass and TOBEC readings was used to compute rates of change in mass and body fat during the incubation period.

For nesting females, each egg in the clutch was weighed and its length (L) and breadth (B) measured to the nearest 0.1 mm with vernier calipers. Egg volume (V) was estimated with Hoyt's (1979) equation ($V = K_v \cdot LB^2$) assuming a value of 0.450 for the coefficient K_v, based on egg measurements from other Charadriiforms (Galbraith 1988, Grant 1990). On the first visit to a nest, we floated the eggs to estimate likely hatch date (Alberico 1995). We visited nests on the hatch date and weighed the dried chicks to the nearest 0.1 g using a Pesola scale. During one trip to a nest, we attached a 1.5-g radio transmitter to the female. Subsequently, we used the radio signal to locate females and obtain daily check counts for estimating chick survivorship.

RESULTS

Model predictions

We identified six patterns that were diagnostic of a bird's migration strategy and that could be reliably measured in our field study (Table 1). The three local

patterns were generally similar for time minimizers and energy maximizers, although there were some differences (e.g., the negative relationship between length-of-stay and date was much stronger, and perhaps more easily detectable in the field for time minimizers than for energy maximizers). Therefore, the local patterns were useful only to test for nonrandomness. However, the three regional patterns (migration window, length-of-stay, and energy reserves vs. latitude) that were predicted differ and provide one with a much stronger ability to distinguish between time and energy strategies.

Some of the patterns were predicted to occur only under certain circumstances. Length-of-stay was predicted to vary inversely with energy reserves, but only early in migration. After ~1 May at latitude 40° N, a bird's body fat has little effect on its predicted length-of-stay because at that time an Arctic-breeding bird must put a high priority on flying to the breeding grounds or it will miss the time window for successful reproduction. Length-of-stay for energy maximizers was predicted to be relatively high at lower (≅30° N) and at higher (≅60° N) latitudes because such an allocation of time would allow birds to gain extra fat just before arrival at the breeding grounds. This bimodal pattern was predicted in landscapes wherein stopovers were assumed to be of equal habitat quality, however, and such an assumption may not be an appropriate approximation of reality.

Apart from the above, the model predictions are generally robust with regard to model parameters. However, a sensitivity analysis, varying stopover spacing, stopover quality, and other model parameters (Appendix B), shows that in landscapes with closely spaced stopovers of high quality, the predicted local patterns might not be observed even if birds were behaving optimally. In such rich landscapes there might be little selection on stopover decisions because birds could follow a wide range of migration schedules and still maximize their fitness. Furthermore, in limiting landscapes, with widely spaced stopovers, poor quality stopovers, or high uncertainty, the adaptive response for both time and energy strategists, is to gain body fat early in migration. In such a landscape, the predicted regional patterns may be similar for time minimizers and energy maximizers.

Observations at a local scale

Length-of-stay vs. date.—Length-of-stay estimates were based on 110 females that were radio-tagged in Texas (n = 36), Missouri (n = 54), and Nebraska (n = 20). Mean radio time (and 95% confidence limits) in Texas was 2.5 d (0.7–5.7 d), in Missouri was 5.8 d (4.6–7.0 d), and in Nebraska was 8.5 d (5.7–11.2 d). Radio time was not significantly correlated with capture date in Texas (r = 0.15, P = 0.38), but it was negatively correlated with capture date in Missouri (r = −0.39, P = 0.004) and in Nebraska (r = −0.86, P < 0.001) (Fig. 3).

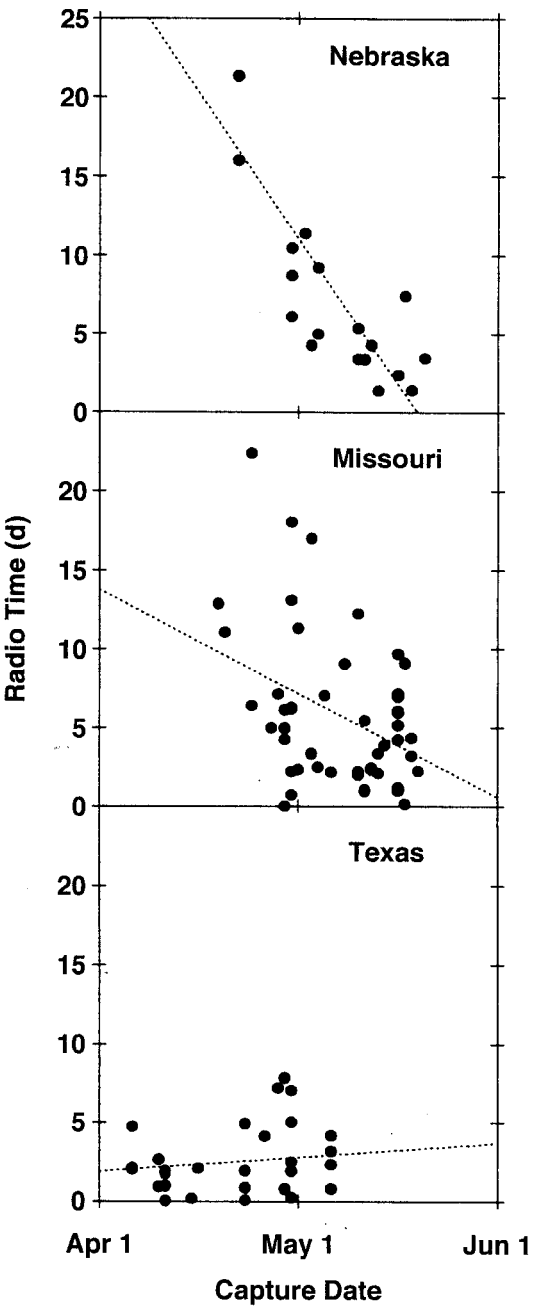

FIG. 3. Scatterplots and linear regressions of radio time vs. capture date for female Pectoral Sandpipers at migration stopovers in Texas, Missouri, and Nebraska.

Mean residence time (and 95% confidence limits) was 4.5 d (3.8–5.4 d) in Texas, 11.5 d (10.8–12.5 d) in Missouri, and 14.2 d (10.2–19.7 d) in Nebraska. To test whether residence time varied with date, Missouri and Nebraska females were partitioned into early and late subgroups delineated by the median capture date for females at that site. In both Missouri and Nebraska,

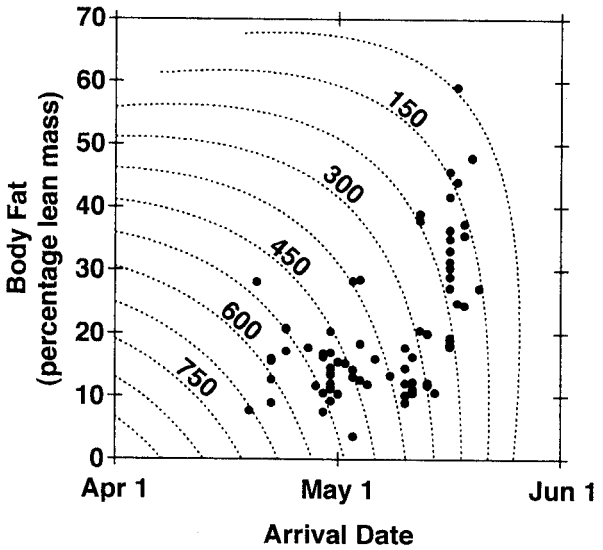

FIG. 4. Predicted residence time (h) vs. body fat and arrival date for time-minimizing females at 40° N latitude in a flyway with stopovers spaced at 1000 km. Contours of predicted residence time (dashed lines) are overlaid with field data on body fat and capture date of female Pectoral Sandpipers in Missouri and Nebraska (solid circles).

the mean residence time for early females was significantly higher (likelihood ratio test, $P < 0.001$) than for late females (12.8 d vs. 6.8 d in Missouri, 21.3 d vs. 9.2 d in Nebraska). Thus, at two of three sites both radio time and residence time varied inversely with date, as predicted by the model.

Length-of-stay vs. body fat.—After the effects of date were taken into account, body fat did not explain any of the remaining variation in radio time in Texas ($P = 0.98$), Missouri ($P = 0.45$), or Nebraska ($P = 0.81$). However, a relationship between length-of-stay and fat was most likely to be detected only early in the season. To illustrate this, predicted residence times were overlaid with data points representing the capture date and body fat of females from Nebraska and Missouri (Fig. 4). Early in the season, when residence time was predicted to be most sensitive to differences in body fat, only lean birds were captured. Later in the season, captured birds exhibited a wider range of body fat but residence time was not predicted to be sensitive to changes in body fat at that time. Thus, the spread of our data was not sufficient to test for this pattern.

Length-of-stay vs. stopover quality.—We collected 89 cores from three wetlands in Missouri and 90 cores from five wetlands in Nebraska. The density of organisms was significantly higher in Nebraska ($\bar{X} = 5508/m^2$, SD = 5576) than in Missouri ($\bar{X} = 1414/m^2$, SD = 2807) (separate variance t test, $P < 0.001$). Biomass was also higher in Nebraska samples ($\bar{X} = 1457$ mg/m^2, SD = 3194) than in Missouri ($\bar{X} = 769$ mg/m^2, SD = 1696) (separate variance t test, $P = 0.024$). Nebraska and Missouri samples contained similar invertebrate taxa, although Nebraska samples were dominated by midge larvae (Chironomidae; 97% of individuals, 58% of biomass), and Missouri samples were dominated by Tubifex worms (Tubificidae; 74% of individuals, 68% of biomass). The gross energy content of Chironomids (McCauley and Tsumura 1974) is similar to that of Annelids (Golley 1961) and Oligochaetes (Griffiths 1977), and Castro et al. (1989) found that assimilation efficiency by birds was ~75% for many invertebrates. Moreover, shorebirds are opportunistic feeders during migration (Baldassare and Fischer 1984, Skagen and Oman 1996). Therefore, it seems likely that the wetlands we sampled in Nebraska provided a greater food base than did those in Missouri.

During 1994, when the invertebrate data were collected, radio time was significantly greater in Nebraska ($\bar{X} = 8.5$ d, SD = 1.4) than in Missouri ($\bar{X} = 5.3$ d, SD = 0.97) (pooled variance t test, $P = 0.05$). Also, mean residence time in 1994 was significantly higher in Nebraska (14.2 d) than in Missouri (9.4 d) (likelihood ratio test; $P = 0.006$). Thus, the rank order of the two sites determined by length-of-stay was the same as that for invertebrate abundance. Although the sample size is small, this pattern is consistent with model predictions for both time and energy strategies (Table 1).

Clearly, the preceding observations made at individual stopovers are inconsistent with random decision making, but we cannot distinguish between time minimizers and energy maximizers—both are supported by the field observations. What do the regional patterns suggest?

Observations at the regional scale

Length of the migration window vs. latitude.—We plotted capture/sighting date vs. latitude for our data ($n = 548$ birds), museum data ($n = 47$ birds), and data from other investigators ($n = 1504$) (Fig. 5a). Based on these data, the length of the migration window, as measured by variance of date, decreased at higher latitudes (Glejser's test; $P < 0.001$).

However, these data were collected over multiple years and the longer migration window at lower latitudes may simply reflect greater year-to-year variation in arrival dates at those latitudes. We analyzed the data separately for each of 14 yr (1981 through 1994 inclusive) during which there were sufficient observations to span at least 20° of latitude. There was significant heteroskedasticity each year (Glejser's test, $P \leq 0.05$). Moreover, there was little interannual variation; the median capture/sighting dates at 29° and 40° N varied <7 d over the 14-yr period. Thus, the latitudinal decrease of the migration window (Fig. 5a) cannot be attributed to between-year effects, but instead reflects within-year effects consistent with model predictions.

Some data points from other investigators represented more than one bird sighted on that date and latitude, and many of these points represented birds of

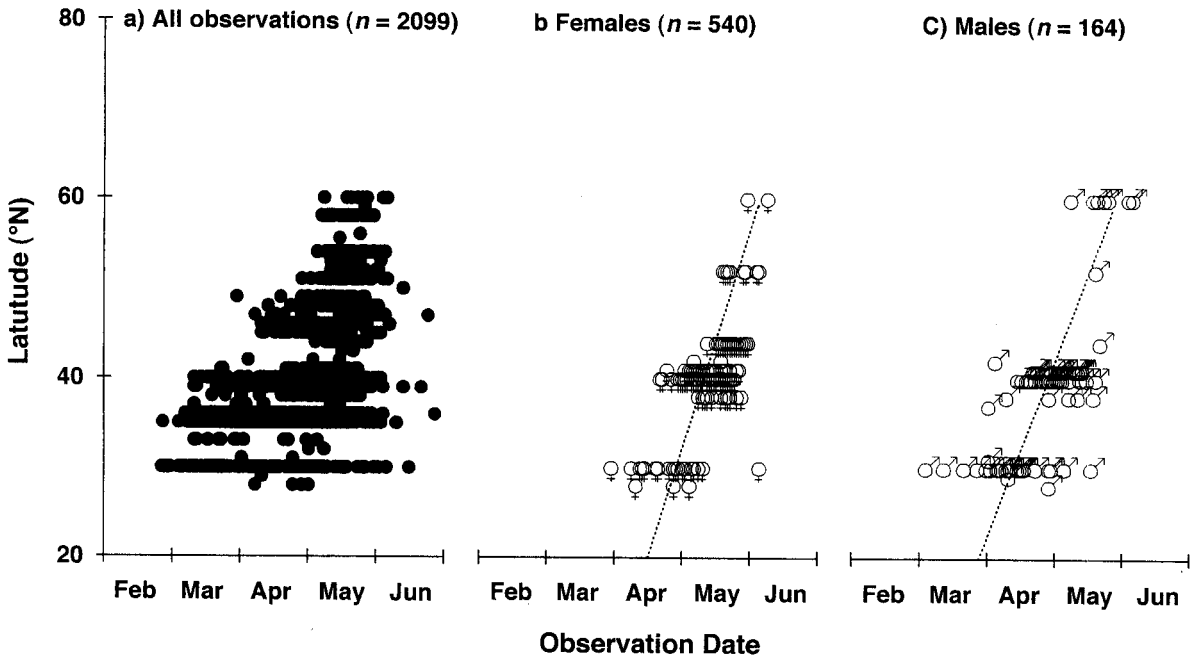

FIG. 5. Latitudes vs. date for Pectoral Sandpiper observations during spring migration: (a) all observations; (b) females (DATE = 83.61 + 1.17LAT; $P < 0.001$); and (c) males (DATE = 58.42 + 1.48LAT; $P < 0.001$).

unknown sex. When considering only data points representing individuals, the migration window varied with latitude as follows: in Texas (29° N), the central 95% of individuals were observed over a 32-d period; in Missouri and Nebraska (40° N), the central 95% of individuals were observed in 25 and 23 d, respectively; and at 55° N, the central 95% window decreased to ~14 d.

When known-sex individuals were considered, we found two trends. First, the migration window for females decreased with increasing latitude (n = 540, Glejser's test, $P < 0.001$) (Fig. 5b), as did the window for males (n = 164, Glejser's test, $P = 0.05$) (Fig. 5c). These results coincide with the pattern predicted for time selection (Table 1). Additionally, we also found that the differences among sexes in the mean capture/sighting date decreased with increasing latitude, as measured by testing for differences between the slopes of their respective regressions (weighted least squares, $P = 0.002$) (Figs. 5b, c). The decrease in the time lag between the sexes provides additional evidence that Pectoral Sandpipers are time minimizers.

Length-of-stay vs. latitude.—Based on our model, length-of-stay is predicted to be constant with latitude for the null and time minimizer cases. Energy maximizers, however, are predicted to have a bimodal pattern: relatively long length-of-stay at southern (i.e., Texas) and northern ends of the flyway, and a shorter length-of-stay at mid-latitudes (i.e., Missouri/Nebraska). Neither of these patterns was observed. Mean radio time in Texas (2.5 d) was significantly shorter than in Missouri (5.8 d) and Nebraska (8.5 d). Moreover, mean residence time in Texas (4.5 d, 95% CI of 3.8–5.4 d) was significantly shorter than in Missouri (11.5 d, 95% CI of 10.8–12.5 d) or in Nebraska (14.2 d, 95% CI of 10.2–19.7 d)

Body fat vs. latitude.—We estimated body fat for 533 birds (416 females, 117 males) captured in our study and 296 birds (245 females, 51 males) from museum collections and other investigators (Fig. 6). Data from both sources suggest the same trend. In Texas (29° N, ±5°), males and females were relatively lean, although males ($\bar{X}$ = 13.7%, SD = 3.2) were significantly fatter than females ($\bar{X}$ = 10.2%, SD = 8.9) (separate variance t test, $P = 0.002$). However, by latitude 40° N (±5°) females doubled their fat reserves ($\bar{X}$ = 20.4%, SD = 11.6), and were significantly fatter than males ($\bar{X}$ = 16.6%, SD = 4.7) ($P < 0.001$). Females remained significantly higher in body fat between 40° N and the breeding grounds. Moreover, between 40° N and the breeding grounds many females exceeded 40% body fat (and some exceeded 50%), but males rarely exceeded 25% body fat. Thus, females increased their fat reserves quickly as they moved north and reached peak body fat by ~40° N.

Females were also more variable in body fat than were males. The relatively high variance among females had both within-year and between-year components. There were significant within-year variations in the body fat of females arriving at the Missouri site. The earliest arriving females at that latitude were always lean, averaging ~10% body fat. Females arriving

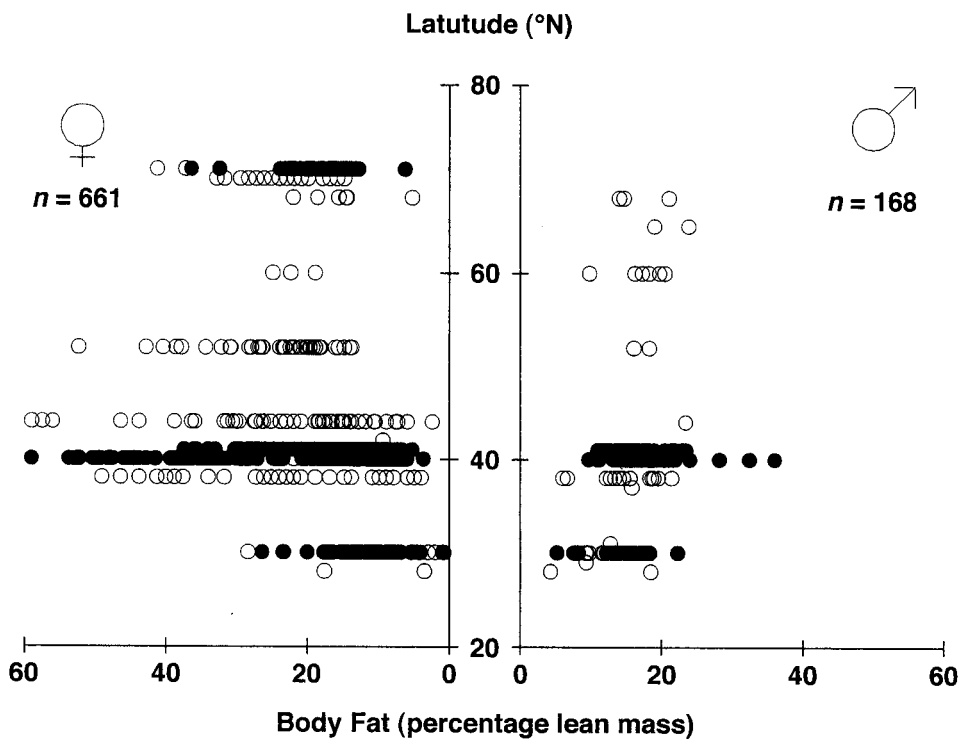

FIG. 6. Latitude vs. body fat for all females and males. Solid circles are our data; open circles are data obtained from museums and other investigators.

late in the season had as much as 60% body fat (Fig. 4), but this did not occur in all study years. During the 4-yr period (1993–1996), we measured significant year-to-year variation in female body fat in Missouri. In 1993 and 1995, late arrivals averaged ~50% fat (all 1993 and 1995 females, $\bar{X}$ = 31%). However, in 1994 and 1996, females were relatively lean (all 1994 and 1996 females, $\bar{X}$ = 12%) throughout the season. Over the 4-yr period, female body fat was correlated with January–May precipitation (r = 0.80), as measured at 63 weather stations distributed uniformly between 29° and 40° N latitude (Farmer 1997). Museum birds that were collected in the Great Plains between 1981 and 1994 showed a marginally significant relationship (P = 0.055) between female body fat and spring precipitation, providing additional evidence of a linkage between precipitation and female body condition.

Observations on the breeding grounds

We made repeated fat measurements from 1 to 14 d apart ($\bar{X}$ = 7.8 d) during the period 9 June to 16 July 1992 on 16 incubating females. Incubating females were highly variable in the rate of change in body fat, ranging from −1.73 g/d to +0.91 g/d. The mean value, −0.077 g/d, was not significantly different from zero (t test, P = 0.51). The mean rate of change in lean mass (−0.114 g/d) was also not significantly different from zero (t test, P = 0.10).

We obtained fat measurements on 53 females with four-egg clutches during egg laying and incubation. Female body fat ranged from 6.25 to 23.9% ($\bar{X}$ = 16.9%), and mean egg volume per clutch varied from 9.89 to 13.17 cm^3 ($\bar{X}$ = 11.77 cm^3). There was a significant relationship between a female's body fat and egg volume (P = 0.027). We obtained body-mass measurements on chicks from seven of these nests. The mean chick weight per brood varied from 7.82 to 9.20 g ($\bar{X}$ = 8.60 g) and was positively related to mean egg volume (n = 7, $P < 0.001$). Our sample size on daily chick counts was too small to draw conclusions about chick survivorship.

DISCUSSION

Pectoral sandpiper migration strategy

Comparison of field observations to the model predictions clearly indicates that Pectoral Sandpipers employ a nonrandom migration strategy. Four of six predicted patterns indicative of optimal decision making were observed in the field. Furthermore, males and females differ in their strategies during spring migration. Females display migratory patterns suggesting that they are both time minimizers (decreasing migration window with increasing latitude) and energy maximizers (increasing fat reserves with increasing latitude). Males, on average, do not gain mass, have a

decreasing migration window with increasing latitude, and thus appear to be strictly time minimizers in spring migration. Differences among males and females observed in recent migration studies of Semipalmated Sandpipers (*C. pusilla*) (Lyons and Haig 1995) and Western Sandpipers (*C. mauri*) (Warnock and Bishop 1998) suggest a similar differentiation of strategies.

Our results are consistent with the breeding system of Pectoral Sandpipers. Males arrive on the breeding grounds first, establish territories, and attempt to mate with females that enter their territory (Pitelka et al. 1974). In such a system, males benefit by arriving as early as possible to compete for the best breeding sites (Myers 1981*a*, *b*, Oring and Lank 1982). Males take no part in incubation, however, and this places additional energetic burdens on the female to maintain both her clutch and her own body condition. Therefore, a female's expected reproduction may be enhanced by having extra energy reserves upon arrival at the breeding grounds.

There are two alternative hypotheses relating a female's energy reserves to her expected reproductive success. First, females may increase their fat reserves during migration to provide a buffer during incubation (MacLean 1969). Our data did not support this hypothesis; 16 incubating females showed no significant decline in either body fat or lean mass during incubation. However, our data were collected during one year (1992) that had normal weather, and energy reserves may be most critical to incubating females during abnormally cold periods such as described by Pitelka (1959) for one of his study years. Second, females may increase their fat reserves during migration because such reserves may enhance their production of fledglings. The data showed that fatter females produced larger eggs and that larger eggs produced larger hatchlings. We were unable to determine if larger chicks had higher survivorship; however, other studies have shown a positive relationship between egg size and chick survivorship in Charadriiforms (Galbraith 1988, Grant 1990). Therefore, there appears to be an opportunity for fecundity selection, and females may increase their fat reserves during migration to enhance their reproductive success through linkages between fat reserves, egg size, and chick viability.

On the other hand, model analyses identified two other explanations for the increase in female body fat that have little to do with fecundity selection. First, females may increase their fat reserves as a hedge against environmental uncertainty during migration (Davidson and Evans 1988, Gudmundsson et al. 1991). If environmental uncertainty were the motivation for increased lipid reserves, however, one would expect males to show this response because they migrate earlier than females and stand a greater chance of encountering unseasonable weather. But males do not significantly increase their body fat as they migrate northward, suggesting that environmental uncertainty is not a valid explanation for the pattern seen in females. Second, late-migrating females may be fatter simply because that is an adaptive response to a lower quality landscape than was available to the males earlier in migration. We cannot rule out this explanation, but we would expect that, as spring progresses, wetlands would become more productive of invertebrates, not less so. However, such increases in wetland quality may be offset by decreases in the number of ephemeral wetlands as the weather becomes warmer in late spring.

Based on the collective evidence, it seems that the migration strategy of female Pectoral Sandpipers is to arrive on the breeding grounds as early as possible and, if possible, to arrive with excess energy reserves. A female's top priority is early arrival on the breeding grounds; to accomplish this, females migrate at a consistent average rate from year to year. Our analyses showed that the median capture/sighting dates at 29° and 40° N varied <7 d over the period 1981–1994. Moreover, it seems likely that females attempt to maintain this consistent rate of migration independent of the habitat conditions, or their perception of the conditions, any single year.

However, females also increase their energy reserves as they move north, if habitat conditions in a given year allow it. During 1993–1996, we measured significant year-to-year variation in female body fat in Missouri. We suspect that this interannual variation in body fat was related to stopover habitat south of the Missouri site, which was likely more abundant in years of above-normal spring precipitation (LaGrange and Dinsmore 1989). During wet springs, when there are abundant, high-quality habitats in the flyway, females find more stopover options, perhaps spend less time searching for food, and as a consequence, have a higher average rate of energy gain as they move northward through the plains. In good habitat years, females arrive on the breeding grounds early and they also obtain a fitness bonus by arriving with additional energy reserves.

The scale of observation and inference

Our modeling results lead to the conclusion that one's ability to discriminate between alternate migration strategies depends on the scale of observation. The predicted local patterns concerning length-of-stay vs. date and energy reserves have been investigated by many migration studies. However, our modeling results (Table 1) show that these patterns do not discriminate between time minimizers and energy maximizers and, if detected in the field, provide evidence only that stopover behavior is nonrandom. Local patterns lack diagnostic power because the expected fitness of Arctic-nesting migrants, as we defined it, is a function of both time and energy. Time minimizers must acquire energy reserves to buffer uncertainties and avoid exhaustion and death during migration, and energy maximizers must still arrive on the breeding grounds within narrow tight time constraints to reproduce successfully. Fur-

thermore, the time-window constraint for Arctic breeding can have an overriding influence on a bird's time-budget decisions. Late in spring and south of the breeding grounds, a female's highest priority, regardless of her strategy, must be on migratory flight, or this year's reproductive opportunity will be lost.

Additionally, even if birds are making optimal stopover decisions, the local patterns may not be detected in the field. First, the inverse relationship between length-of-stay and body fat was predicted to occur only early in migration. The early spring arrivals at our study sites were relatively lean, however, and the spread of the data was not sufficient to detect a relationship. Later arrivals spanned a range of body fat, and included some individuals with very high fat loads, but our model predicted no relationship between body fat and length-of-stay during that period. Studies of other shorebird species have reported similar dynamics in body fat at stopover sites (e.g., Dunn et al. 1988, Lyons and Haig 1995). Thus, it may be no coincidence that a relationship between body fat and length-of-stay has been detected in only one recent migration study (Skagen and Knopf 1994). Second, in relatively rich landscapes, length-of-stay patterns at individual stopovers can be highly variable among individuals because a wide range of schedules is possible without loss of fitness (Appendix B). In such situations, shorebirds could appear to be following multiple individual strategies (Iverson et al. 1996) or to be more random and opportunistic (Skagen and Knopf 1994) even if all were following a single, optimal strategy.

The predicted regional patterns (Table 1) reflect the cumulative results of decisions made at several stopovers and apparently provide more diagnostic power. However, these patterns are not infallible indicators of adaptive strategies. It seems to be a truism that making of broadscale predictions requires simplifying assumptions about fine-scale phenomena, but such assumptions may be so simplistic that the credibility of the predictions is undermined. In our study, the predicted bimodal pattern of length-of-stay vs. latitude for energy maximizers is based on a modeled landscape with stopovers of uniform quality, an assumption that is unlikely to be correct. Even if fine-scale assumptions were correct, however, sensitivity analyses (Appendix B) showed that similar regional patterns can develop from entirely different processes; there are at least four hypotheses that could explain a latitudinal increase of fat reserves. Consequently, detecting one of the regional patterns in the field does not necessarily confirm that migrating birds attempt to maximize fitness as assumed in a model.

Inferences based on observations at either the local or regional scale of observation have their own limitations. Therefore, much can be gained by integrating observations of migratory populations over a wide range of stopover latitudes as exemplified by recent studies of Western Sandpiper (*Calidris mauri*) migration (Iverson et al. 1996, Warnock and Bishop 1998), and by looking also for regional patterns across the same flyway.

Models and reality

No model, whether residing in someone's mind or represented by computer code, is a perfect copy of reality. In the present study, our model is based on simplifying assumptions. Some parameter values are rough estimates, and potentially influential variables (e.g., predation) are excluded due to a lack of data. Further, some of the field data, collected from numerous sources over many years, bear only indirectly on the predicted patterns. Recognizing such imperfections, an early reviewer of this paper went so far as to recommend that we throw out the model and let the field data stand on their own. But field data do not stand alone. They are interpretable only in the light of some concept, or model, of the system being studied.

The dynamic programming model helped us to formulate a self-consistent set of testable hypotheses and to identify limits to the validity of these hypotheses. Model analyses led to the insight that diagnostic patterns (Table 1) might be detected only at selected times, places, or under certain landscape conditions (Wiens and Farmer 1996, Farmer and Wiens 1998). This insight, to a degree, undermines the strength of our study conclusions because, as with most migration studies, we also lacked specific knowledge about landscape conditions. On the other hand, the insight that heterogeneous environments might affect one's ability to detect and to interpret migratory patterns is valuable because it identifies a focus for future research. Our results suggest, for example, that the interplay between fat deposition, stopover spacing and quality, and regional precipitation merits explicit research effort.

A formal model can have the added benefit that it allows one to incorporate newly gained information that, in turn, leads to new insights. In this regard, dynamic programming seems particularly suited to the study of migration. A key process in migration is the exchange of energy between a bird and its environment. The rate of exchange varies temporally and spatially and, consequently, a bird's net energy balance depends on where and when it chooses to stop and feed during migration. But its choices are constrained because stopover habitats occur only at discrete locations. Thus, the interaction of stopover location (and stopover quality) with environmental gradients influences a bird's survival and reproduction. Dynamic programming can be used to model the complex interactions among these factors and can be a useful tool to help guide research on the landscape-level features of the flyway through which shorebirds migrate.

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APPENDIX A

Dynamic Programming Model

State variables.—A female shorebird's state during spring migration is defined by its energy reserves e and latitude d, which are constrained as follows:

$$29° \text{ N} \leq d \leq 70° \text{ N} \qquad 0 \text{ kJ} \leq e \leq 1580 \text{ kJ}. \qquad \text{(A.1)}$$

Spring migration through North America begins at a stopover in coastal Texas at 29° N. A bird's flight path may zigzag through the landscape as it moves between stopovers, but breeding cannot occur until it reaches the breeding grounds, at 70° N latitude. A theoretical maximum fat load for birds the size of Pectoral Sandpipers is ~120% (Hedenström and Alerstam 1992). However, the data show that migrating Pectoral Sandpipers rarely exceed 60%, therefore we set the upper limit slightly above this observed value, at 80% body fat (=1580 kJ), so as not to constrain model predictions.

Decision variable.—Flying time is the single decision variable. Daily, a bird chooses from among m options: (1) remain at the current stopover or (2) initiate migration to one of $m - 1$ stopovers at an equal or greater latitude and within the bird's flight range. This decision is allowed to depend on the bird's current energy reserves e, its current latitude d, and the date t.

Time and energy budgets.—For a possible decision, there is a unique daily time budget, computed with the following assumptions. The total required flight time (t_m) is estimated assuming a flight (ground) speed of 50 km/h and is divided into two portions: the number of whole days and the remaining time on the last day of flight (e.g., a 36-h flight is comprised of one whole day and a remaining 12 h on day 2). Then the following assumptions are used to compute the time budget: (1) migratory flights begin at sunset (Evans 1968, Grimes 1974, Richardson 1979); (2) resting occurs during

nonflight hours of the night; and (3) feeding occurs only during daylight (A. Farmer, *unpublished data*):

a) if remaining time > NIGHT,

$$t_r = 0$$

$$t_f = 24 - t_m$$

b) or, if remaining time ≤ NIGHT,

$$t_r = \text{NIGHT} - t_m$$

$$t_f = \text{DAY} \qquad \text{(A.2)}$$

where t_f is feeding time (h), t_r is resting time (h), NIGHT is the number of nighttime hours, and DAY (equal to 24 − NIGHT) is the photoperiod, estimated with an algorithm from McCabe et al. (1985). For each time budget there is a corresponding energy budget, which is a function of the bird's daily ingestion rate, its metabolic rates while feeding, resting, and flying. Farmer and Wiens (1998) give equations used to compute the daily energy budget.

Change of state.—A bird's state changes daily depending on its time and energy budgets. When the daily energy budget is positive, the new energy is stored as tissue (39 kJ/g of lipid, 18 kJ/g of protein) with an assimilation efficiency $\rho = 0.75$ (Ricklefs 1974). New energy reserves are not necessarily converted to fat. Up to 30% of mass gain by migrating shorebirds may be protein (Lindström and Piersma 1992). However, the assumed proportion of lipid in the energy reserve has little effect on model results (Farmer and Wiens 1998). When the energy budget is negative, tissue is catabolized, but some of the energy stored in tissue is lost as the heat increment of feeding; thus $\rho = 0.85$.

If a bird initiates a migratory flight, the location of the next stopover is subject to uncertainty. When a migratory flight begins, a bird sets out for a particular destination that will be found with probability λ, but will not be found with probability $(1 - \lambda)$. If the destination stopover is not found, the next most northerly stopover will be found with probability $\lambda(1 - \lambda)$, the next one beyond that with probability $\lambda(1 - \lambda)^2$, etc. (a geometric distribution, $p(i) = \lambda(1 - \lambda)^i$). The parameter λ incorporates two sources of uncertainty: habitat dynamics (individual stopovers may not be available in all years) and navigational error.

Fitness relationships.—A female's fitness is operationally defined as an index of the number of young fledged during the current year. A female will not reproduce during the current year if energy reserves during migration drop to the critical level (0 kJ). The window of arrival time for successful breeding is assumed to be 1 June through 1 July. A female can arrive on the breeding grounds earlier than 1 June, but must survive until that date to initiate a nest. However, it must arrive on the breeding grounds and initiate nesting by 1 July, or its fitness will be zero because there will not be sufficient time for rearing young before the onset of winter. Within these time constraints, reproductive fitness is defined by the function $\phi(e, t)$, which generally may vary with arrival time, energy reserves, or both (Clark and Butler 1998). However, to obtain unambiguous predictions for time minimization and energy maximization, we assumed in this paper that the function ϕ was a univariate function of either time or energy reserves, as defined in the *Methods* section.

Dynamic programming equation.—We denote the expected future fitness of a bird with reserves e at latitude d on date t by $F(e, d, t)$, and assume that the bird will maximize its fitness by making the proper choice from the decision space m of possible migratory flights on date t. The first possible decision is to stay at the current stopover, in which case $\lambda = 1$ because there is no uncertainty inherent to this decision. Each of the other possible decisions involves flight to a new stopover site, and we assume that a bird would find this destination stopover at latitude d_0 with probability λ, in which case it would have e_0 energy reserves and a future fitness of $F(e_0, d_0, t + 1)$. The destination would not be found, however, with probability $1 - \lambda$. In this case, a bird would continue flying until it found the ith more northerly stopover at latitude d_i with probability $\lambda(1 - \lambda)^i$. Upon finding a suitable stopover at d_i, it would have remaining energy reserves of e_i and a future fitness of $F(e_i, d_i, t + 1)$. Combining these expectations of future fitness across $n + 1$ stopovers, we obtain the dynamic programming equation:

$$F(e, d, t) = \begin{cases} \max\limits_{m} [(1 - \beta_t) \times [\lambda F(e_0, d_0, t + 1) + \lambda(1 - \lambda)F(e_1, d_1, t + 1) + \lambda(1 - \lambda)^2 F(e_2, d_2, t + 1) + \cdots + \lambda(1 - \lambda)^n F(e_n, d_n, t + 1)]] & \text{if } d < 70°, \quad t \le 1 \text{ July} \\ \phi(e, t) & \text{if } d = 70°, \quad t \le 1 \text{ July} \\ 0 & \text{if } d < 70°, \quad t > 1 \text{ July} \end{cases} \qquad \text{(A.3)}$$

where $\max_m$ implies the maximum over the decision space m of migratory destinations that are reachable from the current stopover. The parameter β_t is the probability of predation mortality on date t. Conceptually, the value of β_t might vary spatially, temporally, by habitat type, by activity, or as a function of the bird's state. However, no data were found to support the assignment of probabilities for any of these hypotheses. Thus, we assigned β_t a value of zero in all model runs and include it here only for completeness.

APPENDIX B

Sensitivity Analysis

Model predictions are influenced by changes in two landscape parameters, stopover spacing and stopover quality (i.e., ingestion rate). To investigate these influences, we systematically varied stopover spacing (from 50 to 250, 500, 1000, 1250, and 1666 km) and ingestion rate (from 0.6 to 1.0 times Kirkwood's [1983] maximum rate, in 0.01 steps) while holding uncertainty constant ($\lambda = 1.0$). At each combination of stopover spacing and ingestion rate we (1) ran the dynamic programming model to solve for optimal time budgets, (2) conducted a forward simulation of birds at 29° N latitude with 15% body fat on 1 April, and (3) plotted their expected reproductive fitness in that particular landscape.

These model analyses delineate three types of landscapes with respect to fitness (Fig. B1) (Farmer and Wiens 1998). In "rich" landscapes, optimally behaving shorebirds could achieve maximum fitness ($W = 1.0$) by following many different time budgets. In these landscapes, there may be little selective advantage in following any particular time budget and patterns observed in the field might be quite variable even if shorebirds were acting optimally. As stopovers are spaced farther apart or reduced in quality, the landscape eventually becomes "limiting". In such a landscape, usually there is a unique, optimal time budget; however, even if a shorebird follows this time budget, the highest fitness it can achieve ($0 < W < 1$) is lower than that attainable in a rich landscape. As stopover spacing increases or ingestion rate decreases even

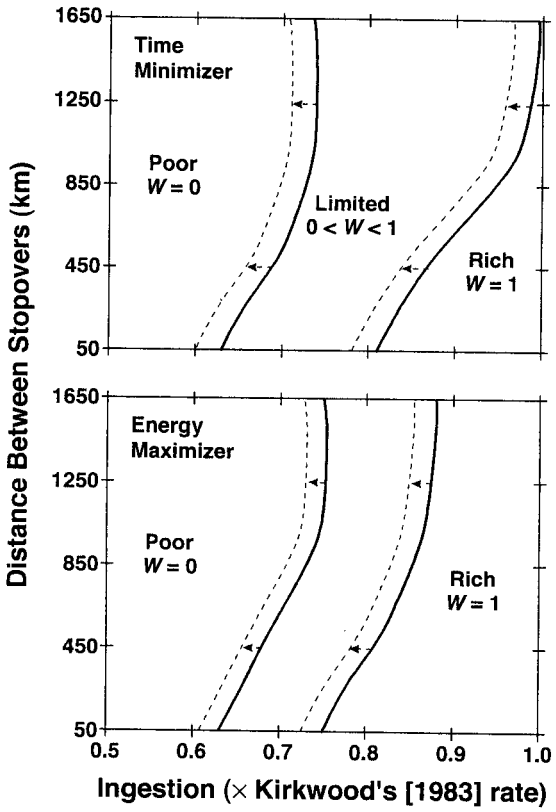

FIG. B1. Fitness (W) is a function of stopover spacing and ingestion rate. Landscapes are either "Rich" ($W = 1$); "Limited" ($0 < W < 1$); or "Poor" ($W = 0$). Dashed lines indicate the extent that the fitness surfaces would shift (−0.03 units for time minimizers, −0.025 units for energy maximizers) if the flying metabolic rate were 10% less than the assumed value (Farmer and Wiens 1998).

more, the landscape becomes "poor" and no longer provides resources sufficient for a bird to complete migration ($W = 0$).

The effective richness of a landscape is influenced not only by stopover spacing and quality, but also by parameters that influence a shorebird's energy balance as it moves through that landscape (Farmer and Wiens 1998). Generally, varying any model parameter causes the fitness surface to shift laterally to the left or to the right, parallel to the x-axis as shown for a 10% decrease in flying metabolic rate in Fig. B1. However, changing the value of uncertainty (λ) has a different effect (this action also causes the fitness surface to rotate with respect to the axes) because the consequences of uncertainty are more severe in landscapes with widely spaced stopover sites. For example, reducing the value of λ from 1.0 to 0.9 shifts the fitness contours ~0.01 units to the right at a stopover spacing of 50 km, but >0.05 units to the right at a stopover spacing of 750 km. The fitness surface would also be affected by incorporating other variables into the model. For example, we did not include wind speed and direction in our model, although tailwinds can be important aid to migrating birds (Butler et al. 1997). In the mid-continent of North America, however, Skagen and Knopf (1994) found no patterns of departure vs. wind direction and speed, and our radio telemetry data show no patterns for Pectoral Sandpipers, although such patterns could be complex and difficult to detect (Weber et al. 1998*b*). Pectoral Sandpipers likely encounter both tailwinds and headwinds during migration that, on average, modify the effective richness of the landscape to an unknown extent. Moreover, wind and other model parameters are additive in their effects; e.g., a 10% increase in flying metabolism would be offset by a 10% increase in the assumed flying (ground) speed, and thus have little effect on the fitness surface (Fig. B1). Thus, the effective richness of a landscape is determined by the collective, net effect of all parameters.

Of course, we did not know the actual stopover spacing or stopover quality during our study, nor did we know the magnitude and direction of errors in our parameter estimates. Therefore, we had no way of knowing which type of landscape was being studied in any given year: rich, limiting, or poor (Fig. B1). In lieu of having such knowledge, our study was more susceptible to potential errors of inference because some of the diagnostic patterns (Table 1) are predicted to occur only in certain landscape conditions. In rich landscapes associated with a range of optimal decisions, the local patterns (Table 1) are predicted only for some of the time budgets that individuals might follow (an exception is length-of-stay vs. date, which is predicted to show a negative relationship over a wide range of landscape conditions). Consequently, interpretation of local patterns is particularly susceptible to increased odds of making Type I errors because optimal behavior can be quite variable and difficult to detect in very rich landscapes. In very limiting landscapes the predicted regional patterns may be more similar for time minimizers and energy maximizers than Table 1 indicates. In particular, time minimizers may increase fat reserves early in migration (and at lower latitudes), similar to the prediction for energy maximizers, to buffer low quality or uncertain conditions that lie ahead (Farmer and Wiens 1998). Thus, interpretation of observed regional patterns is particularly susceptible to Type II errors, especially for latitudinal increases in energy reserves, which can occur for reasons that have little to do with fitness as we define it.