

WIND ASSISTANCE: A REQUIREMENT FOR MIGRATION OF SHOREBIRDS?

ROBERT W. BUTLER,^{1,2,6} TONY D. WILLIAMS,² NILS WARNOCK,^{2,3,7} AND
MARY ANNE BISHOP^{4,5}

¹*Pacific Wildlife Research Center, Canadian Wildlife Service, 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada;*

²*Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada;*

³*Environmental and Resource Sciences, University of Nevada, Reno, Nevada 89512, USA;*

⁴*Pacific Northwest Research Station, U. S. Forest Service, P. O. Box 1460, Cordova, Alaska 99574, USA; and*

⁵*Department of Fisheries, University of Washington, Seattle, Washington 98195, USA*

ABSTRACT.—We investigated the importance of wind-assisted flight for northward (spring) migration by Western Sandpipers (*Calidris mauri*) along the Pacific Coast of North America. Using current models of energy costs of flight and recent data on the phenology of migration, we estimated the energy (fat) requirements for migration in calm winds and with wind-assisted flight for different rates of fat deposition: (1) a variable rate, assuming that birds deposit the minimum amount of fat required to reach the next stopover site; (2) a constant maximum rate of 1.0 g/day; and (3) a lower constant rate of 0.4 g/day. We tested these models by comparing conservative estimates of predicted body mass along the migration route with empirical data on body mass of Western Sandpipers at different stopover sites and upon arrival at the breeding grounds. In calm conditions, birds would have to deposit unrealistically high amounts of fat (up to 330% of observed values) to maintain body mass above absolute lean mass values. Fat-deposition rates of 1.0 g/day and 0.4 g/day, in calm conditions, resulted in a steady decline in body mass along the migration route, with predicted body masses on arrival in Alaska of only 60% (13.6 g) and 26% (5.9 g) of average lean mass (22.7 g). Conversely, birds migrating with wind assistance would be able to complete migration with fat-deposition rates as low as 0.4 g/day, similar to values reported for this size bird from field studies. Our results extend the conclusion of the importance of winds for large, long-distance migrants to a small, short-distance migrant. We suggest that the migratory decisions of birds are more strongly influenced by the frequency and duration of winds aloft, i.e. by events during the flight phase, than by events during the stopover phase of migration, such as fat-deposition rate, that have been the focus of much recent migration theory. Received 3 September 1996, accepted 14 February 1997.

THEORETICAL APPROACHES TO BIRD MIGRATION have focused on the rate at which energy reserves are obtained or replenished during migratory stopovers, i.e. the rate of fat deposition (Alerstam and Lindström 1990, Alerstam 1991, Gudmundsson et al. 1991). Individual birds are assumed to adopt one of two different strategies during migration, either (1) minimizing the time spent on migration (i.e. migrating as fast as possible), or (2) minimizing energy expenditure during migration (i.e. keeping flight costs low by storing only as much fat as

is needed to reach the next stopover site; Alerstam and Lindström 1990). Both hypotheses predict that rates of fat deposition will determine speed of migration and, therefore, that events during the stopover phase of migration are fundamental in determining successful migration. Many birds store large quantities of energy in the form of fat, and to a lesser extent protein, before and during migration to power flights between stopover sites (Helms and Drury 1960, Biebach 1985, Blem 1990, Klaassen et al. 1990, Lindström and Piersma 1992, Berthold 1996). Despite this, few studies have found a significant relationship between fat reserves and the time spent at stopover sites (Post and Browne 1976, Lank 1983, Dunn et al. 1988, Lindström and Alerstam 1992, Holmgren et al.

⁶ E-mail: rob.butler@ec.gc.ca

⁷ Present address: Forest and Rangeland Ecosystem Science Center, U. S. Geological Survey, 3200 SW Jefferson Way, Corvallis, Oregon 97331, USA.

1993, Lyons and Haig 1995, Skagen and Knopf 1994, Iverson et al. 1996). Although there have been several studies of energy costs of flight (e.g. Masman and Klaassen 1987, Castro and Myers 1988, Pennycuick 1989), much less attention has been focused on the importance of variation in rates of energy utilization *during* long-distance migratory flight.

Two factors that might affect energy costs of flight, and therefore the energy or fat-deposition rates required for migration, are wind speed and direction. Wind has long been recognized as an important variable to migrating birds (Parslow 1969; Able 1973; Alerstam 1979, 1990b; Richardson 1978, 1990; Elkins 1988; Piersma et al. 1990; Dau 1992; Piersma and van de Sant 1992; Marks and Redmond 1994). With a constant air speed, wind will affect ground speed and thus flight duration (time spent in migration). Conversely, if birds adjust air speed to maintain ground speed in variable winds, then wind speed will affect power output (energy cost of migration; Richardson 1990). In general, following winds (i.e. tailwinds) should minimize the energetic cost of migration. Most studies have mainly considered the effect of wind conditions on the number of birds taking off or departing from a site each day, or the number of birds aloft (Piersma et al. 1990, Gauthreaux 1991, Hall et al. 1992, Tulp et al. 1994). The relative importance of wind-assisted flight in determining energy reserves required by species that make long-distance, nonstop flights has been estimated (Stoddard et al. 1983, Piersma and Jukema 1990). Several authors suggested that favorable tailwinds are essential for large-bodied shorebirds to complete long, nonstop flights (Bar-tailed Godwit [*Limosa lapponica*], Piersma and Jukema 1990; Great Knot [*Calidris tenuirostris*], Tulp et al. 1994; Bristle-thighed Curlew [*Numenius tahitiensis*], Marks and Redmond 1994). However, the requirement of winds for small-bodied shorebirds that make relatively short flights has not been assessed, and the relative importance of wind-assisted flight has been largely unquantified in all studies (Piersma et al. 1990, Holmgren et al. 1993). As Richardson (1990) pointed out, the interaction between wind conditions and the physiological readiness to migrate (i.e. fat status and fat-deposition rate) is poorly understood. It is important to consider these issues over large geographical scales be-

cause a bird's decision to depart or stay is a complex interaction of the position of the individual along the migration route, the time remaining before the commencement of the breeding season, the body condition of the individual, and the frequency and duration of favorable winds (Piersma and Jukema 1990). For an individual to minimize its use of time and energy (Alerstam and Lindström 1990), it should match its energy levels with the frequency and duration of favorable winds. However, the frequency (but not duration) of favorable winds for migration has low predictability (Richardson 1979, 1990). In this situation, an individual should maintain its energy reserves at a high level (vs. a minimum level; cf. Alerstam and Lindström 1990) so that it can depart as soon as winds become favorable, fly for the entire duration of favorable winds, and arrive at the next stopover site prepared for rapid departure at the arrival of the next favorable wind event.

In this paper, we consider the importance of upper atmospheric winds to migrating Western Sandpipers (*Calidris mauri*) along the Pacific Coast of North America. We use current models of energy costs of flight (Castro and Myers 1988, Pennycuick 1989) and recently obtained data on the phenology of spring migration in Western Sandpipers (Iverson et al. 1996, N. Warnock and M. A. Bishop unpubl. data) to estimate energy requirements for migration in calm wind and with wind-assisted flight, and for different rates of fat deposition. We test these models by comparing predicted body-mass changes along the migration route with empirical data from Western Sandpipers captured at different stopover sites and upon arrival at their breeding grounds.

METHODS

Study species.—The Western Sandpiper is a small (body mass 23–36 g) shorebird that migrates along the Pacific Coast of North America, breeding in western Alaska and eastern Siberia and wintering along the Pacific Coast from southern Canada to Peru and on the Atlantic and Gulf coasts from the southeastern United States to Suriname (Wilson 1994, Butler et al. 1996). On average, females are about 10% larger in structural size and body mass than males (Butler et al. 1987). Prior to migration, Western Sandpipers increase their lean body mass of about 23 to 25 g by an average of about 5 g by storing mostly lipids that

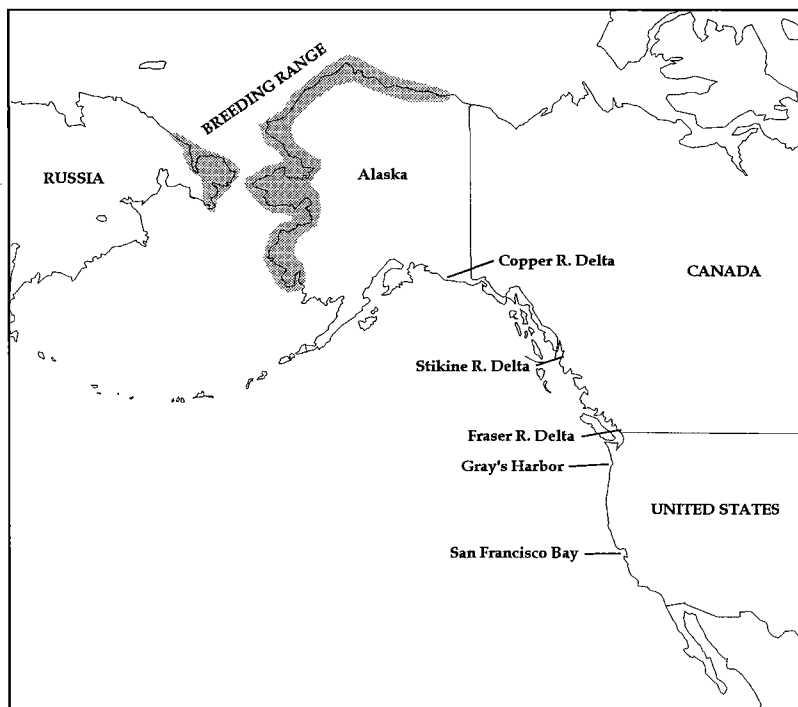


FIG. 1. Map showing migratory route of Western Sandpipers along the Pacific coast, with the five major stopover sites.

they replenish at stopover sites along the migration route (Senner 1979). Major stopovers include San Francisco Bay, California; Grays Harbor, Washington; Fraser River delta, British Columbia; and the Stikine and Copper River deltas, Alaska (Butler et al. 1996, Iverson et al. 1996; Fig. 1). Most migrants move northward along the Pacific Coast of North America from early April to mid-May and arrive on the breeding grounds in western Alaska between mid- to late May (Holmes 1971).

Timing of migration and body-mass estimates.—Body mass data from each of the stopover sites and at arrival on the breeding grounds were assembled from published and unpublished sources (Senner 1979, Butler et al. 1987, S. Warnock unpubl. data, B. K. Sandercock unpubl. data). Because most of the mass change associated with migration in Western Sandpipers is due to fat storage and utilization (cf. lean mass change; C. Guglielmo and T. D. Williams unpubl. data), body mass is a good index of fat status (see also Johnson et al. 1989). Mean body mass did not differ significantly ($P > 0.05$) among years at four sites for which we have three years of data, so we used mean body mass per site pooling data over years. We estimated the departure mass in grams (M_d) at each site using the formula:

$$M_d = M_i + (F_i \cdot L_i), \quad (1)$$

where M_i is the arrival mass at site i , F is the fat-deposition rate, and L is the length-of-stay duration. The arrival mass at each stopover site was estimated using the formula:

$$M_i = M_d - [(D/(S + W))E/c], \quad (2)$$

where M_d is the mass (g) at departure from the previous stopover site, D is the distance (km) from stopover site $i - 1$ to stopover site i , S is the average ground speed (km/h) over distance D , W is the average wind speed (km/h) during the flight from site $i - 1$ to stopover site i , E is the energy cost (kJ) required to fly distance D , and c is the energy from fat available for flight. Each of these terms is described below.

Departure mass.—We estimated departure mass from 24 males captured at San Francisco and fitted with radio transmitters (Iverson et al. 1996) by adding to their mass at capture the product of the number of days between capture and departure, assuming an average mass gain of 0.34 g/day (Butler and Kaiser 1995). This resulted in an estimated departure mass of $32.7 \pm \text{SE of } 0.5 \text{ g}$ (range 27.0 to 37.6 g). Predicted body mass at each subsequent stopover site was then calculated by subtracting the fat mass required for each flight leg from the departure mass at the previous site (equation 2). Departure mass from

TABLE 1. Wind speeds (km/h; $\bar{x} \pm SE$ with n in parentheses) favorable to migration along the Pacific Coast of North America during April and May 1992.^a Wind speeds used in the present analysis are shown in bold.

Altitude (m) ^c	Stage of migratory flight ^b			
	SF-GH	GH-FR	FR-SR	SR-CR-AK
10	13.7 ± 4.8 (4)	12.6 ± 1.4 (24)	16.6 ± 1.8 (43)	25.6 ± 1.8 (51)
100	32.4 (1)	32.0 ± 3.6 (26)	Calm	41.8 ± 2.9 (55)
1,000	25.2 ± 10.8 (2)	27.4 ± 4.0 (28)	41.0 ± 3.2 (23)	45.4 ± 3.6 (47)
1,500	18.4 ± 3.2 (10)	31.3 ± 7.6 (11)	Calm	45.4 ± 4.0 (33)
3,000	22.3 ± 2.9 (10)	7.2 (1)	Calm	47.5 ± 5.4 (26)
5,550	33.5 ± 3.2 (11)	32.4 (1)	No data	58.7 ± 7.2 (21)

^a Wind conditions measured at Oakland, California; Quillamette, Washington; Port Hardy, British Columbia; Annette Island, Alaska; and Anchorage, Alaska.

^b SF = San Francisco Bay, California; GH = Grays Harbor, Washington; FR = Fraser River delta, British Columbia; SR = Stikine River delta, Alaska; CR = Copper River delta, Alaska; AK = Alaskan breeding grounds (see Fig. 1).

^c Approximately 1,000, 950, 850, 750, 650 and 550 millibars, respectively.

the next site was calculated from equation 1. Lean body mass for male Western Sandpipers was assumed to be 22.7 g (derived from body composition analysis; R. W. Butler and T. D. Williams unpubl. data).

Flight distance and flight speed.—Flight distances were measured as straight-line distances (km) between stopover sites, i.e. they represent conservative or minimum estimates. Total flight time (h) was estimated by dividing the flight distance by the maximum range speed. Maximum range speed for a male Western Sandpiper flying in calm air, weighing 27.7 g (the midpoint between lean mass and departure mass) and having a wing length of 257 mm was estimated to be 38.5 km/h (Pennycuik 1989).

Wind speed.—Wind speed was equal to zero in calm conditions. Wind speeds for each stage of migration were obtained from data on average upper-atmosphere (0 to 5,500 m altitude) winds collected every 12 h from weather stations near each stopover site in April and May 1992, corresponding with the migration tracking data (Anonymous 1993; see Table 1). Favorable winds were defined as those with a direction of $\pm 45^\circ$ of the bird's required straight-line heading of $315^\circ N$. We used the maximum wind speed available at any altitude up to 5,500 m based on the assumption that Western Sandpipers sought out the most favorable altitude for migration (see Piersma and Jukema 1990, Richardson 1990, Bruderer et al. 1995).

Energy requirements and energy available for flight.—Energy cost of flight was 10.2 kJ/h using equation c of Castro and Myers (1988), and 10.8 kJ/h using Masman and Klaassen's (1987) formula. We used Castro and Myers' (1988) estimate because it was the most conservative. Total energy cost (kJ) for each flight stage was then estimated by dividing the total flight time by the energy cost per hour, and this value was converted to mass of lipid required for each stage of migration assuming an energy value for lipid of 39 kJ/g (Blem 1990). Although premigratory mass gain

has both a lipid and a protein component (Lindström and Piersma 1992), we assumed that 100% of the energy for flight was derived from fat catabolism (Blem 1990, Berthold 1996).

Length of stay and fat-deposition rates.—Data on length of stay at stopover sites other than Grays Harbor, and overall timing of migration, were taken from a radio-telemetry study of male Western Sandpipers migrating from San Francisco Bay to the Copper River delta in April/May 1992 (Iverson et al. 1996) and 1995 (N. Warnock and M. A. Bishop unpubl. data). At all sites except Grays Harbor, we used the midpoint between the 1992 and 1995 data. Iverson et al. (1996) reported a length of stay of one day for a male at Grays Harbor in 1992. In 1995, the length of stay was estimated to be 3.7 days, also from a small sample ($n = 7$; N. Warnock and M. A. Bishop unpubl. data). As a consequence of these small samples, we conservatively estimated the length of stay to be 4.0 days for Grays Harbor. We considered three different patterns and rates of fat deposition in estimating mass gain at stopover sites: (1) a variable deposition rate in which birds gained the minimum amount of fat at each site, over the known length of stay, sufficient to complete the next stage of migration ("variable rate" model; Dunn et al. 1988, Alerstam and Lindström 1990, Alerstam 1991); (2) a maximum constant rate of fat deposition of 1.0 g/day (estimated from Zwarts et al. 1990, Lindström 1991; "maximum constant rate" model); and (3) a lower constant rate of fat deposition of 0.4 g/day based on field data on mass gains of Western Sandpipers and morphologically similar Semipalmated Sandpipers (*Calidris pusilla*) ("mean constant rate" model; Morrison 1984, Butler and Kaiser 1995).

RESULTS

The magnitude of potential energy savings of wind-assisted flight was estimated to be be-

TABLE 2. Flight distances, length of stay (LOS), flight time, energy expenditure, fat requirement, and average flight speed for migrating Western Sandpipers with and without wind-assisted flight.

Stage ^a	Distance (km)	LOS (days)	No wind			Wind assistance			Speed (km/h)
			Time (h)	Energy (kJ)	Fat (g)	Time (h)	Energy (kJ)	Fat (g)	
SF-GH	1,180	4.0	30.6	312	8.0	16.4	167	4.3	72.0
GH-FR	250	3.1	6.5	66	1.7	3.5	36	0.9	70.5
FR-SR	1,180	3.3	30.6	312	8.0	14.8	151	3.9	79.5
SR-CR	900	2.5	23.4	239	6.1	9.3	94	2.4	97.2
CR-AK	1,200	—	31.2	318	8.2	12.3	126	3.2	97.2

^a See Table 1 for abbreviations.

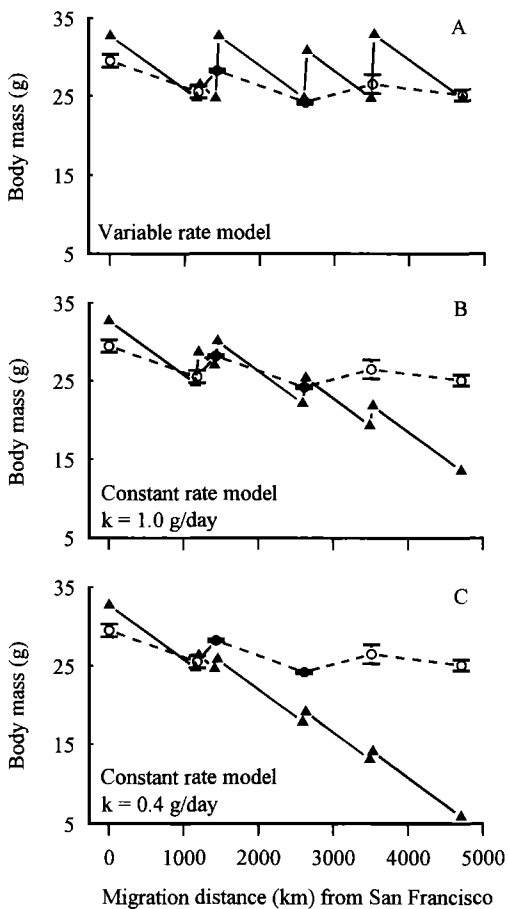


FIG. 2. Predicted (closed triangles) and observed (open circles) body masses of Western Sandpipers during migration in calm conditions (no wind assistance), assuming (A) birds gain enough fat mass at each site sufficient to complete the next stage of migration (variable rate of fat deposition), (B) constant rate of fat deposition = 1.0 g/day, and (C) constant rate of fat deposition = 0.4 g/day. Observed values are presented as means \pm 95% confidence limits.

tween 46–61%, depending on the stage of migration. The mean speed of favorable winds increased from south to north (Table 1). As a result, the estimated flight time, and subsequent energy reserves compared with those under calm wind conditions, decreased by about 1.9 times between San Francisco, Grays Harbor, and the Fraser River delta; 2.1 times between the Fraser and Stikine River deltas; and 2.5 times between the Stikine River delta, Copper River delta, and the breeding grounds (Table 2).

Calm-wind model.—For all three rates, predicted mass changes during migration in calm winds declined compared with observed body masses at each stopover (Fig. 2). For the variable rate model (Fig. 2A), the rank order of predicted versus observed body mass was not significantly different (Wilcoxon test, $P > 0.05$), i.e. the overall pattern of mass change was similar. However, in order to maintain the observed body masses at successive stopovers, a male Western Sandpiper flying in calm air would have to achieve a daily mass gain of 2.6 g/day at the Fraser River delta, 1.8 g/day at the Stikine River delta, and 3.3 g/day at the Copper River delta. These estimates are 180–330% higher than the predicted and observed maximum fattening rates reported in the field (Zwarts et al. 1990, Lindström 1991). The constant rate models (assuming fat-deposition rates of 1.0 and 0.4 g/day) with calm air conditions both resulted in a steady decline in predicted body mass over the course of the migration (Fig. 2B–C). These models predict average arrival masses for birds on the Alaskan breeding ground of only 60% (13.6 g) and 26% (5.9 g) of average lean mass (22.7 g), which are far below the lightest body masses reported in the field and clearly would be impossible for birds

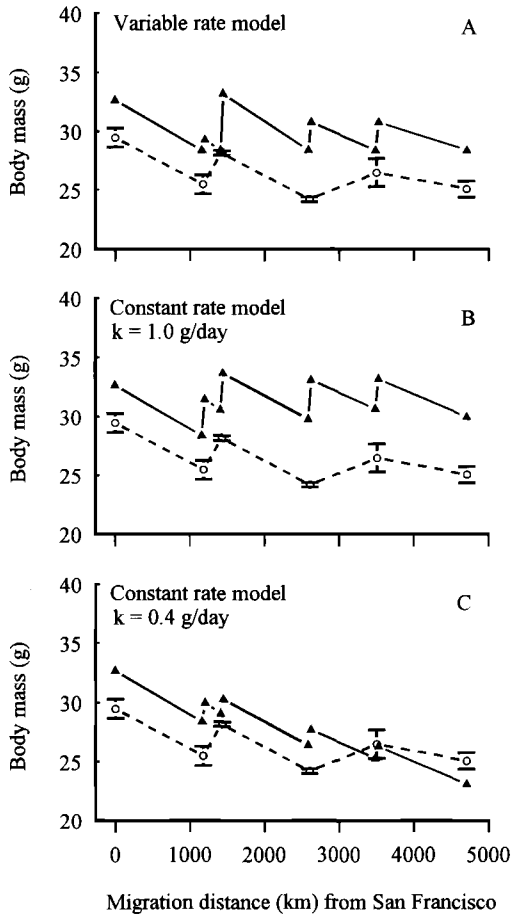


FIG. 3. Predicted (closed triangles) and observed (open circles) body masses of Western Sandpipers during migration with wind-assisted flight (favorable tailwinds), assuming (A) variable rate of fat deposition, (B) constant rate of fat deposition = 1.0 g/day, and (C) constant rate of fat deposition = 0.4 g/day. Observed values are presented as means \pm 95% confidence limits.

to survive. With a fat-deposition rate of 0.4 g/day, predicted body mass is lower than lean mass (22.7g) by the time birds reach the Stikine River (when they are still 2,100 km from the breeding grounds; Fig. 2C).

Wind-assisted models.—The three models that assume wind-assisted flight generally showed a much closer fit between the overall pattern of mass change for predicted and observed body masses (Fig. 3A-C). However, with the addition of favorable tailwinds, the variable rate model predicted body masses that were greater than those observed in the field (Wilcoxon test, $P =$

0.009; Fig. 3A). Moreover, this model still requires an average fat-deposition rate of 1.6 g/day on the Fraser River delta, which is near or higher than maximum estimated values for shorebirds the size of Western Sandpipers (Lindström 1991). The two wind-assisted, constant rate models predicted a slow decrease in body mass during migration relative to observed masses (Fig. 3B-C). With a fat-deposition rate of 1.0 g/day (Fig. 3B), predicted body masses again were significantly higher than observed masses at all stages of migration (Wilcoxon test, $P = 0.009$). The model with wind-assisted flight and a fat-deposition rate of 0.4 g/day provided the best fit with the empirical data, both in terms of absolute body mass and the pattern of mass change during migration (Wilcoxon test, $P = 0.34$; Fig. 3C).

DISCUSSION

Our analysis showed that: (1) observed body masses of male Western Sandpipers at stopover sites along the Pacific Coast of North America in spring could not be attained using conservative cost estimates of migration and, (2) the force of average favorable tailwinds during migration is sufficient to provide a cost savings during flight that would explain the observed body masses. Birds migrating in calm conditions would have to achieve unrealistically high rates of fat deposition (up to 330% of observed values) during each stopover in order to maintain body mass above absolute lean-mass values. Conversely, birds migrating with wind-assisted flight would be able to complete migration with fat-deposition rates as low as 0.4 g/day, similar to values reported for similar-sized birds from field studies (see below).

Our conclusion that wind-assisted flight is important for successful spring migration in male Western Sandpipers is dependent on several key assumptions about length of stay at stopover sites, fat-deposition rates, flight speeds, and energy costs of flight. However, we believe that our conclusion is robust because we used conservative estimates of length of stay, energy expenditure, and mass gain. Some authors have suggested that length-of-stay estimates always underestimate the number of days a bird is present at a site because birds may arrive days before first capture and remain after the day they are last observed (e.g.

Dunn et al. 1988). However, in Western Sandpipers some individuals remained at stopover sites for less than 24 h (M. A. Bishop and N. Warnock, unpubl. data), and if these birds went undetected, then length-of-stay estimates from captured birds would have overestimated true residence times. Our estimates of average length of stay of three to four days for male Western Sandpipers as reported for the Fraser, Stikine, and Copper River deltas by Iverson et al. (1996) are similar to those reported for other species of shorebirds (Pienkowski and Dick 1975, Isleib 1979, Holmgren et al. 1993). If length of stay is overestimated, then the required fat-deposition rate would in turn have to be greater, increasing (vs. decreasing) the importance of wind-assisted flight.

Zwarts et al. (1990) summarized data on fat deposition from 42 studies of shorebirds. The five studies that considered species that weigh 20 to 30 g (i.e. similar to Western Sandpipers) reported fat-deposition rates during spring of 0.2 to 0.4 g/day for "population" estimates, and 0.2, 0.4, and 0.4 g/day for "individual" estimates (Morrison 1984, Pearson 1987, Dunn et al. 1988). Butler and Kaiser (1995) reported average deposition rates of 0.34 g/day for four Western Sandpipers. Zwarts et al. (1990) concluded that maximum rates of increase in body mass must be 4 to 5% of "winter" mass per day, or 1.1 g/day for a 22.7-g Western Sandpiper. Lindström (1991) gave a range of maximum fat-deposition rates of 2.6 to 4.3% of lean mass, or 0.59 to 0.98 g/day, for a 22.7-g Western Sandpiper. Similarly, maximum rates reported for congeneric Semipalmated Sandpipers were 1.1 to 1.26 g/day (Lank 1983, White 1985). The available data therefore confirm our assumption that a fat-deposition rate of 0.4 g/day, which provided the best fit with our models (Fig. 3C), is not unreasonable for Western Sandpipers during spring. Although we recognize that some individuals may achieve mass gains greater than 0.4 g/day, they do not represent the "average" sandpiper; rates of 1.0 g/day likely represent maximum rates, and deposition rates of 2 to 3 g/day are unlikely to be attainable in a bird of this size.

We assumed that the maximum range speed of Western Sandpipers is 38.5 km/h and that wind assistance and flight speed are additive. Our estimate of maximum range speed is reasonable for Western Sandpipers because it is

close to estimates for birds of similar body mass (Alerstam 1990a: table 27). However, our assumption that flight speed and wind speed are additive is an oversimplification. In theory, birds that reduce their flight speed when flying in tailwinds will reduce flight costs (Alerstam 1990a). However, the estimated savings of adjusting flight speed in a tailwind are not large. Alerstam (1990a) estimated the energy savings of a 36-km/h tailwind to a Common Wood-Pigeon (*Columba palumbus*) would be only 3%. Although our approach is oversimplified, other studies have shown that shorebirds can attain very high flight speeds, e.g. 51 to 91 km/h (Lane and Jessop 1985), 105 km/hr (Johnson et al. 1989), and 22 to 87 km/h (Tulp et al. 1994). In support for our contention that Western Sandpipers achieve high flight speeds, we compare the sum of stopover time and flight time in Table 2 from departure at San Francisco to departure at Copper River. In calm conditions, the estimated flight time would be 16.7 days, but with wind-assisted flight, migration time drops to 14.7 days, which is closer but still above the average of 12.1 days reported by Iverson et al. (1996). It is unlikely that sandpipers can depend on tailwinds to assist them for their entire flight. The vector and strength of winds will change, resulting in birds expending additional amounts of time and energy compensating for winds blowing them off course (Liechti 1995). At least in some situations, however, compensating for drift due to crosswinds has only a small effect on energy requirements and estimated flight ranges (Bruderer et al. 1995) and, in any case, this would increase our estimate of energy costs for migration. We stress that our analysis compared values for the average flock member along the entire journey, whereas in reality, individuals experience a range of conditions during migration.

Two potential cost savings not accounted for in our analysis were increased migration speed at higher altitudes and reduced drag by flying in flock formation. Because air density declines with altitude, birds could increase their speed by about 5% per 1,000 m altitude (Alerstam 1990a). Flocks of 20 Red Knots (*Calidris canutus*) and Dunlins (*C. alpina*) increased their flight speed by about 5 km/h over that of solitary individuals (Alerstam 1990a). Western Sandpipers probably are like Semipalmated

Sandpipers (Richardson 1979) that migrate in flocks at high altitude.

We conservatively assumed that Western Sandpipers used every stopover site along the migration route to replenish fat reserves, whereas Iverson et al (1996) showed that most birds (93.5%, $n = 46$) bypassed one or more stopover sites. For example, they reported that 28.6% of the birds from San Francisco were detected in the Stikine River delta, a nonstop flight of 2,610 km. A flight of this distance would require 67.8 h of flying at a maximum range speed of 38.5 km/h in calm air and cost 691.6 kJ (10.2 kJ/h \times 67.8 h). The fuel payload required to make this flight would increase the departure mass of a male Western Sandpiper to about 40.4 g. Rarely do individual Western Sandpipers attain so large a body mass. With wind assistance, however, the cost of flight drops so that the estimated departure mass from San Francisco is 31.9 g, a value very close to our estimated departure mass of 32.7 g (see Methods).

The absolute difference between predicted and observed body mass is dependent on initial departure mass at San Francisco (estimated to be 32.7 g). A lower departure mass would result in a better fit between estimated and observed data for the wind-assisted models with either the variable rate or 1.0 g/day of fat deposition. However, in calm conditions a lower departure mass would result in even lower predicted body masses earlier in migration. This assumption, therefore, does not affect our conclusion about the importance of wind-assisted flight.

We have less confidence in our ability to estimate the flight speed and energy cost of migration. We estimated maximum range speeds and energy costs of flight from widely used equations derived from comparison of interspecific data (Castro and Myers 1988). These models often provide a good statistical fit to the data. Castro and Myers (1988) model relating cost of flight to body mass has an r^2 value of 0.80. Moreover, our estimated flight cost of 10.2 kJ/h derived from Castro and Myers' (1988) formula was very close to the 10.8 kJ/h cost we derived from Masman and Klaassen's (1987) equations from interspecific data. However, Pennycuick's (1989) formula yielded an estimated flight cost of 8.6 kJ/h for a Western Sandpiper with a wing span of 25 cm, which is

substantially lower than the estimate we derived from Castro and Myers (1988) formula. It is unclear which estimate best approximates true flight costs because none has been critically tested due to the difficulties in obtaining direct measurements of energy expenditure of shorebirds in flight (see Blake et al. 1990). When we used the flight-cost estimate from Pennycuick's (1989) formula, the predicted body mass of Western Sandpipers declined through the migration so that the average male arrived on the breeding ground with a mass of 17.5 g. Therefore, our conclusion that wind is essential during at least part of the migration is robust. Between San Francisco and the Alaskan breeding grounds, strong southeasterlies and northwesterlies are generated by the Aleutian low-pressure system in the Gulf of Alaska that dominates the weather systems of the North Pacific Coast from January to July (Favorite et al. 1976). The westward progression of this low-pressure system results in strong inflow winds generated along the Pacific Coast every few days during the spring migration period.

Several authors have suggested that large shorebirds (e.g. Bar-tailed Godwit, Great Knot, and Bristle-thighed Curlew) require favorable tailwinds to complete their long-distance migrations (although these studies did not consider the effects of wind on fat loads or fat-deposition rates; Piersma and Jukema 1990, Marks and Redmond 1994, Tulp et al. 1994). That we arrived at the same conclusion for a small-bodied, short-distance migrant such as the Western Sandpiper suggests that the frequency and duration of favorable winds are important variables shaping the migration strategy of many birds migrating at high altitudes. Although many researchers have alluded to the importance of winds for migrating birds, much of the current theory of migration deals with the rate at which fat is accumulated at stopover sites (Alerstam 1991, Lindström and Alerstam 1992, Williams and Webb 1996).

Our view differs from these other studies in one fundamental way. We suggest that the evolution of migration strategies by birds is largely determined by the frequency and duration of winds aloft during the migration. Western Sandpipers migrating with the assistance of wind are able to conserve energy (often arriving with fat reserves remaining) and thus are able to rapidly prepare to depart with the next

favorable wind event. This would explain why the relationship between arrival mass and duration of stopover in many species of shorebirds either is poor or absent (e.g. Lindström and Alerstam 1992, Holmgren et al. 1993, Skagen and Knopf 1994, Lyons and Haig 1995). It would also explain why many birds depart with fat reserves in excess of that required to reach the next stopover site, allowing them to take advantage of favorable winds if they are encountered aloft (Post and Browne 1976, Summers and Waltner 1979, Piersma and Jukema 1990, Zwarts et al. 1990, Barter and Wang 1991, Harrington et al. 1991, Skagen and Knopf 1994). A bird's departure mass would therefore be established mostly by the expected duration and frequency of favorable winds and less by the distance between stopover sites (cf. Alerstam and Lindström 1990). These reserves also might serve as an insurance should conditions suddenly deteriorate, as proposed by Alerstam and Lindström (1990), but we do not believe that this is the primary reason that birds carry large fat reserves. Although Alerstam and Lindström (1990) recognized that wind conditions will modify optimal migration strategies, they suggested that this would affect fat loads and/or stopover duration only "to a small degree." Our study, and those of Piersma and Jukema (1990), Marks and Redmond (1994), and Tulp et al. (1994), suggest that weather patterns are a much more important selective force in the evolution of bird migration and should be included in future theories of optimal migration (e.g. Holmgren et al. 1993, Williams and Webb 1996).

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