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Reply to Hedenström and Weber

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It has long been recognized that birds take advantage of tailwinds during migration. In our paper, we proposed that the relative importance of wind has been underestimated in small shorebirds. We provided as an example the northward migration of the Western Sandpiper (*Calidris mauri*) and showed that body mass of individuals captured at stopover sites along the migration route could not be explained based on current estimates of flight and refueling costs unless the assistance of winds aloft were included in the model (Butler et al. 1997). Hedenström and Weber (1999) showed that Western Sandpipers theoretically could complete the flights without the assistance of winds if new values of aerodynamic drag are used in the calculation of flight costs. They also stated that we proposed our model as an alternative strategy to time minimization (sensu Alerstam and Lindstrom 1990).

We believe that Western Sandpipers maintain large fuel reserves to depart on favorable winds, but we did not explicitly state that individuals depart on the first favorable wind, nor did we propose this strategy as an alternative to time minimization (sensu Alerstam and Lindstrom 1990), as Hedenström and Weber contend. Instead, we indicated that individuals can minimize the time on migration if they are prepared to take advantage of favorable winds. Our purpose was to point out the relative importance of wind assistance as a component of time minimization.

Flight costs: Can they do it?—We premised our argument on flight costs by using estimates widely used by other researchers (Pennycuick 1989). However, we pointed out that we were less confident about the estimates of the flight phase than of estimates of refueling at stopover sites. Therefore, we were pleased that Hedenström and Weber have been able to refine these estimates of flight costs. Their argument is based on new estimates of flight costs derived from wind-tunnel experiments. Hedenström and Weber indicate that previous estimates of the body-drag coefficient, C_{par} derived from frozen birds were too high. Pennycuick et al. (1996) revised

their previous estimates using live birds, which showed that C_{par} should be about 0.1 or “as low as 0.05 for streamlined birds, such as seabirds and shorebirds.” We are not sure why seabirds or shorebirds should be more streamlined than other volant birds, but we will not quibble about that here.

Hedenström and Weber recalculated flight costs using our data and $C_{par} = 0.1$ to show that Western Sandpipers flying in calm conditions would arrive on the Alaskan breeding grounds with a body mass close to the average lean mass. Because Western Sandpipers actually arrive in Alaska heavier than lean mass, either the flight-cost estimates are still too high, or Western Sandpipers receive some assistance from winds, as we contend. Hedenström and Weber then used the lower value of $C_{par} = 0.05$ to show a close fit between estimated and observed data. We concede that their calculation suggests that Western Sandpipers theoretically could make the flight without the assistance of winds, but only if the lowest value of C_{par} is used. However, there is no clear guidance on which estimate most closely reflects parasite drag for this species. Nevertheless, if Pennycuick’s lower estimate of C_{par} is accurate, we still have to reconcile the large body mass attained by some Western Sandpipers at stopover sites and the empirical data that show that at least some individuals fly at rates well above the maximum-range speed.

During capture in spring, the body mass of some individuals is 10 to 15 g above lean mass; yet, Hedenström and Weber’s model (their fig. 1) shows that the most efficient fat mass would be about 5 g. By design, our model was conservative in that we allowed each individual to stop at all stopover sites in sequence, when in reality many individuals bypass stopover sites (Iverson et al. 1996, Warnock and Bishop 1998). Therefore, some individuals are capable of using fuel loads to go beyond what we estimated was a minimum flight with wind assistance. Second, we know that some individuals fly much faster than their predicted maximum-range speed in calm winds (38.5 km/h; sensu Butler et al. 1997). Iverson et al. (1996) presented data on migration speeds of three individuals that made direct flights between stopover sites. In the first case, an individual flew at least 77 km/h over an 1,850-km flight, and in the sec-

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ond case, two individuals traveled 840 km in 20 h (at least 42 km/h). These are *minimum* estimates based on the time elapsed between detections that were taken once each day (Iverson et al. 1996).

Modeling assumptions.—We concur with Hedenström and Weber's that our assumption that stopover duration is fixed is unrealistic considering that decisions are based on the frequency and duration of favorable winds (see Iverson et al. 1996, Warnock and Bishop 1998). However, in a more sophisticated analysis of the same data, Clark and Butler (1999) allowed birds to alter their departure times in accordance with winds. They found that estimates of arrival and departure times at stopover sites were consistent with field data. More important, their model showed that when birds were allowed to depart without taking the wind into consideration, such behavior was strongly maladaptive. We also agree with Hedenström and Weber that our assumption that mass loss occurs only from the catabolism of fat is probably not true. However, if our calculations had also included protein as a source of energy, as Hedenström and Weber suggest, arrival masses would have been even lower than we showed, which would have strengthened our conclusion that wind is an important element in the migration of sandpipers.

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