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Gone with the Wind? A Comment on Butler et al. (1997)

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Because wind speed and flight speed of migratory birds generally are of the same magnitude, wind direction has a significant effect on the ground speed of birds. Consequently, migrants should prefer days of favorable tailwinds for commencing migratory flights, or at least they should avoid strong headwinds. These predictions generally are the case as revealed by radar studies (Richardson 1990). Based on estimated flight costs of shorebirds, Butler et al. (1997) concluded that tailwinds are necessary for successful spring migration of Western Sandpipers (*Calidris mauri*). Butler et al. (1997) proposed that the migration strategy for Western Sandpipers consists of maintaining relatively large fuel reserves and departing on migratory flights when tailwinds are present. This strategy was put forth as an alternative to the strategy of time minimization of migration (*sensu* Alerstam and Lindström 1990). We think it is premature to reject time minimization as a migration strategy for Western Sandpiper on the basis of the data presented by Butler et al. (1997), and we outline our arguments below. First, we show that new information concerning the aerodynamic drag of bird bodies indicates that Western Sandpipers may complete their spring migration without wind assistance. Next, we provide a critical discussion of the assumptions, methods, and conclusions put forward by Butler et al. (1997).

Flight costs: They can do it.—Butler et al. (1997) calculated that when using Pennycuick's (1989) model of bird flight performance, the arrival mass will be 17.5 g for a male Western Sandpiper in the absence of wind assistance. Two amendments to the theory of bird flight may change this conclusion. First, the default value for the body-drag coefficient (C_{par}), which determines the magnitude of parasite drag (i.e. drag of the body), has been overestimated previously. The old default value ($C_{par} = 0.4$) was based on measurements using frozen bird bodies in a wind tunnel (Pennycuick et al. 1988), although the experiments were suspected to overestimate C_{par} . Based on new wind-tunnel experiments on live birds, Pennycuick et al. (1996) found that C_{par} is much lower than previously measured on frozen birds, and they rec-

ommended a new default value of $C_{par} = 0.1$. For streamlined bird bodies, such as seabirds and shorebirds, Pennycuick et al. (1996) even suggested a value as low as $C_{par} = 0.05$, i.e. eight times lower than the default value in Pennycuick (1989). Pennycuick (1995) also introduced a minor change to the calculation of profile power to depend on aspect ratio.

We made the same sort of analysis as that conducted by Butler et al. (1997), i.e. calculating fat consumption during flight, but using the revised Pennycuick model and allowing refueling at 0.4 g per day at stopovers. This rate of fat deposition was the lowest used by Butler et al. (1997). To make our calculations conservative with respect to arrival mass, we used the rate of energy consumption of flight at departure mass of each flight, hence overestimating the total flight cost because flight power should decline as fuel is consumed during long flights. We also calculated flight costs for low-altitude flights (air density = 1.23 kg/m³), which gives higher flight costs compared with higher-altitude flights. Biometrics, departure mass (32.7 g), and lengths of stopover were taken from Butler et al. (1997).

The results of our calculations are shown in Figure 1 for the same spring migration stages considered by Butler et al. (1997). Using $C_{par} = 0.1$ and an initial departure mass of 32.7 g, the arrival mass was 22.8 g, which is 0.1 g more than the average lean mass of a male Western Sandpiper. If $C_{par} = 0.05$, which perhaps is more realistic for shorebirds, the mass loss during spring migration is lower, and the arrival mass becomes 26.3 g (Fig. 1), which is close to the observed arrival mass of Western Sandpipers (Butler et al. 1997). Hence, new aerodynamic assumptions actually allow Western Sandpipers to complete their spring migration without the aid of tailwinds. Flight in flock formation will improve the situation further (e.g. Lissaman and Shollenberger 1970).

Modeling assumptions.—In simulating the changing level of fat during the journey, Butler et al. assumed that stopover lengths were fixed. This makes the calculations straightforward, but such an assumption is not consistent with their claim that the frequency and duration of winds aloft are shaping departure decisions. What if favorable winds occur on the first day of a stopover? In their introduction, Butler et al.

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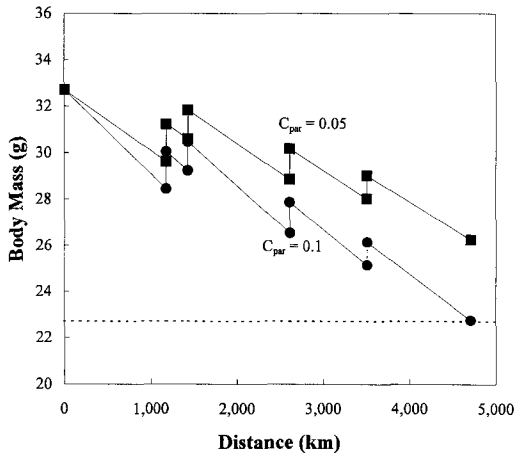


FIG. 1. Calculated body-mass changes of Western Sandpipers during spring migration in calm conditions (no wind assistance) based on a modified version of Pennycuik (1989) to estimate flight costs. The initial departure mass (32.7 g), wing span (25.7 cm), flight stages, and stopover lengths are the same as in Butler et al. (1997). The two curves refer to body-drag coefficients of $C_{par} = 0.05$ (squares) and $C_{par} = 0.1$ (circles), respectively; fat-deposition rate is 0.4 g per day. The dotted line represents lean body mass.

imply that the birds should depart, but they disregard this possibility in their calculations. To arrive at the expected changes in fat load under different assumptions about fuel-deposition rates and different decision rules, a Monte Carlo simulation using individual migrants (or flocks of migrants) would have been appropriate.

Furthermore, the graphs presented in Butler et al. are somewhat misleading in that they show the mass loss of birds as if only fat were catabolized during flight, even when the mass of the birds drops below fat-free mass. When the birds start using up lean mass, i.e. protein, body mass should decline at a much higher rate than when fat is the main fuel.

In defense of time minimization.—Two of Butler et al.'s facts undermine their claim for the near-exclusive importance of wind in shaping migration decisions. First, the authors identify rather constant stopover periods at each stopover site. Unless a favorable wind always occurs after such a fixed stopover duration, other factors must be involved in the decision to depart. Such a minimum stopover length is a prediction of a model of time minimization by migrants that take wind conditions into account (Weber et al. 1998). Second, Iverson et al. (1996) show that most birds bypass one or more stopover sites on this particular route. The skipping of sites is an exclusive prediction of time-minimization models (Gudmundsson et al. 1991, Weber et al. 1994).

Butler et al. (1997) also maintain that the observed

lack of a relationship between length of stay and fat reserves speaks against the importance of time minimization. It must be realized, however, that the expected relationship is very shallow and thus could easily be confounded by uncontrolled variation among individuals with respect to flight costs and fueling rates and also could be deflated by small sample sizes. In fact, the decision rule suggested by Butler et al. to leave with the first favorable wind could also detect a negative relationship between length of stay and departure load, or alternatively, to a positive relationship between fattening rate and departure fat load; i.e. with a high fattening rate, migrants will have accumulated high fat loads on the day a favorable wind finally occurs, and birds with low fattening rates will have accumulated low fat loads (Weber et al. 1998). This demonstrates that purely verbal arguments can be misleading. When suggesting that a "new" factor is important in the evolution of migration strategies, while simultaneously dismissing another factor, it is necessary to formulate clear, exclusive, and, if possible, quantitative predictions.

Simple time-minimization models produce a number of qualitative and robust predictions, and a general agreement between predictions and data has been found in experimental studies of migrating passerines during stopover. For example, time-minimization models predict that migrants should be sensitive to variation in fattening rates, and this prediction has been confirmed in several studies (see Lindström and Alerstam 1992).

The cost of flight is a critical aspect in any quantitative analysis of a particular migratory system (Weber and Houston 1997, Alerstam and Hedenström 1998), and it is risky to base wide-ranging conclusions about the evolution of migration on such a shaky foundation. Butler et al. (1997) based their conclusion on both aerodynamic (Pennycuik 1989) and empirical estimates of flight costs (e.g. Masman and Klaassen 1987, Castro and Myers 1988). However, we prefer the aerodynamic approach, because the empirical estimates based on mass loss during migratory flights will include possible effects of wind encountered during the flight. Empirical estimates of flight cost are therefore inadequate as a wind-neutral reference value.

Conclusions.—Contrary to Butler et al. (1997), our calculations show that Pennycuik's model allows Western Sandpipers to complete spring migration without wind assistance. However, in stressing the importance of time, we do not claim that sandpipers do not use tailwinds during migration. All migrating birds would benefit by using tailwinds, but the issue is whether they depart with the first tailwinds, or whether they are time or energy minimizers that take current wind conditions into account. Recently, wind has been incorporated into the theory of optimal migration (Weber et al. 1998). This work shows

that wind-sensitive migrants will always remain for a minimum number of days at a stopover site regardless of favorable wind conditions, and only after this period will they depart on the first day with favorable winds. If the probability of favorable winds is low, migrants eventually will depart, even if the winds are unfavorable, after a few days of waiting for good conditions.

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