Large and consistent body mass differences of migrant *Calidris* sandpipers at adjacent stopover sites: phenomenon and possible explanations

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Lissimore, D., Lemon, M.J.F., Lank, D.B., Butler, R.W & Ydenberg, R.C. 1999. Large and consistent body mass differences of migrant *Calidris* sandpipers at adjacent stopover sites: phenomenon and possibilities. *Wader Study Group Bull.* 88: 55-58.

Current theory emphasises the importance of time and energy strategies over a whole migration in explaining patterns of variation in mass levels of migratory birds at individual stopover sites. These models predict similar masses for migrant populations at a given stage of their journey. Data from three species of calidrid sandpipers over several years show that body masses are consistently 9-12% higher among birds caught on a large, open mudflat versus those caught at a small island lagoon nearby. The differences occur within all age/gender classes, and the birds do not differ in structural size between sites. We present several possible explanations for this difference, emphasising the possibility that migrants are making state-specific short-term settlement decisions with respect to site-specific differences in local food and predator regimes.

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INTRODUCTION

The study of avian migration from an evolutionary perspective has expanded greatly over the past two decades. Shorebird migration has attracted special attention in this regard; questions of interest have ranged across wintering distributions (Myers 1981a, Hockey *et al.* 1992), mating systems (Myers 1981b), timing and stopover site usage (Alerstam & Lindström 1990) and mass gain patterns of different populations of the same species (Drent & Piersma 1990). The dominant theme in this research is that tight time and energy budgets drive major decisions in migratory strategy, with the need for obtaining energy and nutrient reserves to fuel flights between successive stopover sites setting the migratory agenda (e.g., Piersma & Jukema 1993). In this note we draw attention to an observation that sits somewhat uneasily within this framework, and raise questions about its significance.

STUDY SITES, POPULATIONS, AND METHODS

As part of an ongoing program started by the Canadian Wildlife Service in 1977, Western *Calidris mauri*, Least *C. minutus*, and small numbers of Semipalmated Sandpipers *C. pusilla* have been captured on southward migration through the southern part of the Strait of Georgia, between Vancouver Island and mainland British Columbia. Migrants have been studied at two sites (Figure 1, Butler *et al.* 1987, Butler & Kaiser 1995). Along the edge of the Fraser River delta is an expansive open mudflat (ca. 250,000 ha at low tide) which is used by hundreds of thousands of migrant shorebirds on northward and southward migration, as well as by 10-30,000 wintering shorebirds. Approximately 35km across the Strait of Georgia to the south-west is Sidney Island, which has a small mudflat within a ca.100 ha lagoon that is used by several thousand migrant shorebirds. The lagoon is enclosed by forest on the east and dune ridges and a saltmarsh on the west and south and has a narrow opening to the Strait. Other small mudflats used by migrant sandpipers are scattered throughout the Strait of Georgia.

Western Sandpipers, and the Semipalmated Sandpipers that pass through our study sites breed in western Alaska. They likely arrive in the Strait of Georgia after a long flight over the Gulf of Alaska (Butler *et al.* 1996). In contrast, the Least Sandpipers passing through our sites breed in south and central Alaska and northern British Columbia and appear to fly south along the coast of British Columbia. Most adults of both species pass though southern British Columbia in July, and juveniles in August, with individuals spending several days (range 1-5d) at the sites before continuing southward (Butler *et al.* 1987, Butler & Kaiser 1995). The next largest stopover site for calidrids is Gray's Harbor, Washington, 280 km to the south.

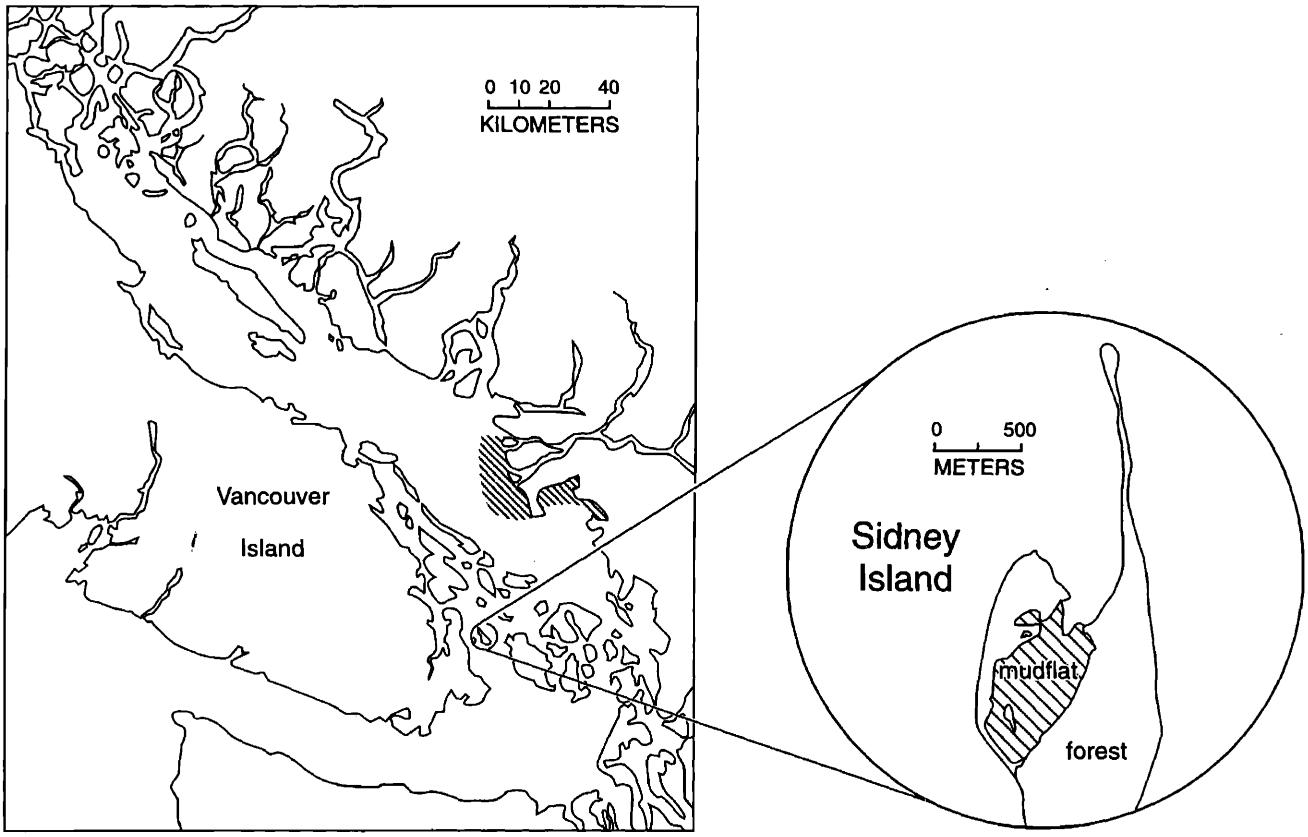

Figure 1. Map of the southern Strait of Georgia, showing sites used by migrant sandpipers. The extensive mudflats adjacent to the Fraser River delta, south-west of the city of Vancouver, are shaded in the main map, with Boundary Bay to the south and Roberts Bank to the west. Sidney Island, off the south-east coast of Vancouver Island, is circled on the main map, and its mudflat shown in the inset map.

All three species feed on small benthic animals seized from the surface or pulled from the mud. Western Sandpipers feed almost exclusively in flocks on exposed mudflats. Both Least and Semipalmated Sandpipers readily flock with Western Sandpipers, but Least Sandpipers also often feed solitarily in the saltmarsh vegetation fringing the mudflats.

Following procedures outlined in Butler *et al.* (1987), sandpipers at both study sites were captured in mist nets, weighed (+/- 0.1g), wing length (flattened wing cord) and culmen measured (+/- 0.1mm) with wing ruler and callipers, and assigned an age class (juvenile or adult) based on plumage (Haymen *et al.* 1986). Gender was subsequently assigned to Western Sandpipers based on culmen length (Page & Fearis 1971). We include data from birds captured from mid-June through September, including 12,426 Western Sandpipers caught between 1977 and 1997, 725 Least Sandpipers and 42 Semipalmated Sandpipers.

RESULTS

The phenomenon of interest is shown in Figure 2. All three species of sandpipers caught at the Fraser Delta site were consistently and substantially heavier than those caught on Sidney Island. The overall average annual difference in mass for Western Sandpipers, for which we have the largest samples, is 2.3g, meaning that Fraser Delta birds are 9.4% heavier. As data from the two sites were, for the most part, not obtained in the same year, the mass differences might be attributed to inter-annual effects or a long-term change. However, concurrent captures throughout the season at both sites in 1996 and 1997 confirmed that this difference occurs within years. The only apparent exception was 1990, but we attribute an unusually low value for the Fraser Delta to having a sample of only 9 Western Sandpipers that year. A strikingly similar mass difference was observed in Least Sandpipers and Semipalmated Sandpipers, for which our smaller samples were pooled over all years.

Habitat segregation by gender and/or age class could be a simple explanation for the differences. However, site differences of similar magnitudes within years occurred for all age/gender classes of Western Sandpipers in 1996 and 1997 (Figure 3). Thus overall mass differences are not accounted for by differential usage of the sites by age or gender classes

A second possibility is that structural body size differs among birds at the two sites. However, wing lengths of Western Sandpipers did not differ between the two sites for any of the four age/gender classes ($p > 0.05$). The non-significant difference is positive for two classes and negative for the other two, and the overall mean difference is a negligible 0.012 mm, or about 0.01%. Finally, residuals of body mass, removing the effects of year, time of capture, age, and gender, show that birds of a given culmen length were significantly heavier at the Fraser Delta ($p < 0.001$). Thus, the mass difference was not caused by differential use of the sites by birds of varying structural size.

DISCUSSION

Despite differences in migratory strategies between Western

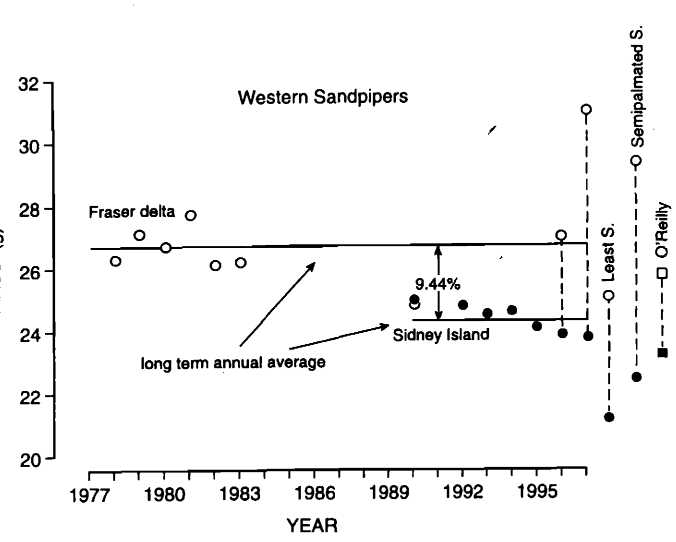

Figure 2. Mean body masses of three species of calidrid sandpipers captured on southward migration are consistently heavier at Fraser Delta (open dots) than at Sidney Island (solid dots). Horizontal lines show the means of annual means of Western Sandpiper mass at each site. Weights of Western Sandpipers recorded by O'Reilly (1995) at the small site False Bay (solid square, n = 18) and the large site Gray's Harbor (open square, n=160) are also displayed. Vertical lines connect site means within particular years. Sample sizes: Western Sandpipers at Fraser Delta 1977-1983: 14, 630,1915, 2551, 1014, 2621, 2046; 1990: 9; 1996-1997: 334, 72. Western Sandpipers at Sidney Island: 1990: 238; 1992-1997: 52, 161 100, 178, 191, 299. Least and Semipalmated Sandpipers, 1996 and 1997: pooled 127, 32 at Fraser Delta; 598 and 10 at Sidney Island. 95% confidence intervals for most values are on the order of 0.1g or less and not displayed.

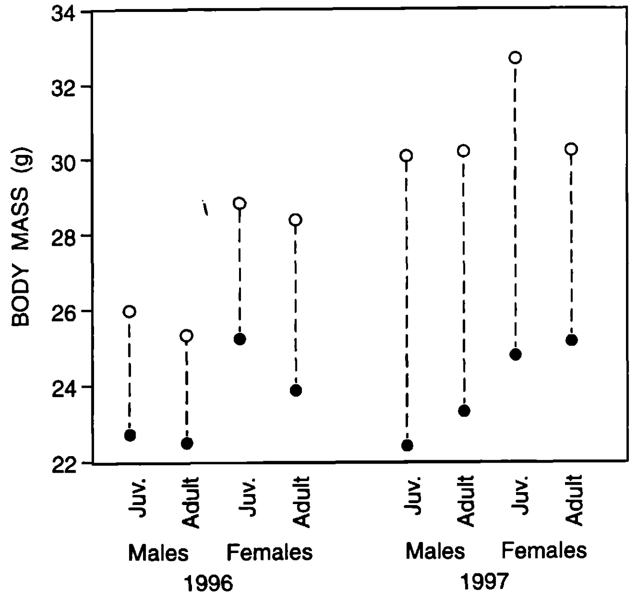

Figure 3. Western Sandpipers of all four age/gender classes are consistently heavier at Fraser Delta (open dots) than at Sidney Island (solid dots) in both 1996 and 1997. Vertical lines connect site means within each year. Sample sizes, left to right: Fraser Delta: 17, 126, 73, 117, 7, 35, 13, 16; Sidney Island: 6, 87, 14, 84, 54, 83, 50, 99. 95% confidence intervals are generally small and not displayed.

and Semipalmated Sandpipers, which make a long jump from Alaska prior to land fall in our area, and Least Sandpipers, which are believed to hop down the coast from less distant breeding areas, we find large and consistent differences in masses of birds caught at the two sites. We present five hypotheses that might explain these observations.

First, different sub-populations of sandpipers might use the sites and their masses could reflect different migration schedules (e.g., Dick *et al.* 1987; see below). Several lines of evidence indicate that this is unlikely. Western Sandpipers from a wintering group at Chitré in Panama have been sighted at both sites (Butler *et al.* 1996), and individual birds marked at Sidney Island have been sighted at the Fraser Delta within a few days (R. Butler pers. obs.). This indicates local movement between these sites. Moreover, the same pattern of body mass differences is evident in Least and Semipalmated Sandpipers, and it seems unlikely that there are sub-populations of all three species that use these sites in just the same way. Finally, O'Reilly (1995) has observed a similar mass difference between Western Sandpipers caught at False Bay, a small, enclosed site in Washington State topographically similar to the Sidney Island lagoon, versus migrants caught at Gray's Harbor, a large coastal site similar to Fraser Delta (Figure 2). These facts suggest that the explanation is more likely to have something to do with the general migration biology of all three species and general attributes of the sites themselves, rather than with different migration schedules of sub-groups or populations.

Second, the nature of our activities at the sites might bias mist-net captures toward lower mass birds at Sidney Island and heavier individuals at the Fraser Delta. At Sidney Island, an influx of new arrivals was easily observed during population surveys, and our capture effort often intensified, and/or our capture success increased, with more birds at the site. Thus, on average, migrants at Sidney Island may have been captured sooner after their migratory arrival, and thus at a lighter mass, than those at the Fraser Delta, where netting effort was less variable from day to day and not obviously correlated with population changes. However, with fat deposition rates of the order of 0.3 gd^{-1} (Butler & Kaiser 1995), birds would have to be captured about 7.7 days (2.3g /0.3 gd^{-1}) sooner to account for the difference. With residence times of 1-5 days measured for Western and Least Sandpipers at Sidney Island (Butler *et al* 1987, Butler & Kaiser 1995), this seems an unlikely explanation for the mass difference. Because the fattening rate estimates are based on small samples, however, this possibility is open to further evaluation.

The remaining ideas hypothesise that upon arrival in the Strait of Georgia, birds facultatively choose one site over the other in response to aspects of their condition, excluding gender and age, and attributes of the sites. Hypothesis three is that the distribution of the sandpipers reflects a phenotype-limited or some other ideal free distribution (Sutherland & Parker 1985). The sheer size of the Fraser Delta site relative to the number of birds, and the almost daily changes in the numbers of migrants, make this an unlikely explanation. A fourth hypothesis is that the mass difference reflects a risk-sensitive choice (e.g. Guillemette *et al.* 1992) with birds in poor condition birds choosing Sidney Island. Finally, there may exist a feeding rate predation risk trade-off (Lima & Dill 1990). For example, Sidney Island might be better for feeding, but at the same time more dangerous, which attracts individuals more in need of better food, whereas the Fraser Delta might attract heavier individuals prioritising a lower risk from predators. Considerable work has been done examining the food base on the Fraser Delta (e.g., Sewell *et al.* 1996), but we have no comparative work from Sidney Island. Avian predators are conspicuous at both sites, but we thus far lack comparative measures of predation risk or perceived predation risk.

We are as yet unable to test these ideas, but we raise the issue here because there may be other similar observations that could shed light on this puzzle. For example, Dick *et al.* (1987) attribute the differences in body mass of Red Knots *Calidris c. canuta* stopping over at estuaries hundreds of kilometres apart in western Europe to their usage by knots from different wintering areas (West Africa versus South Africa). They assert that the differential site usage results from the altered time and energy scheduling forced on the South African birds by the large extra migration distance. Piersma & Jukema (1993), however, report that Bar-tailed Godwits *Limosa lapponica* on spring migration from the Afro-Siberian population differ in mass by 30-40g (8-13%) at two sites only 97 km apart in the Dutch Wadden Sea, but they do not consider this in detail. If this and the difference we report here is real, some factor(s) other than the tight scheduling of mass and energy will be necessary to account for the large disparity in masses of these migrating birds at sites that lie so close together in migratory journeys of thousands of kilometres. More detailed inspection of this phenomenon may further illuminate the evolutionary ecology of migration.

ACKNOWLEDGEMENTS

We thank the many persons who gathered or assisted us in gathering these data, particularly Gary Kaiser, who provided data from the Fraser Delta (1977-1983), Katie OReilly for providing a breakdown of her data, Terry Sullivan, Rhys Bullman, Holly Butler, Myrica Butler, Horacio de la Cueva, Brett Sandercock, Chris Guglielmo, Tony Williams, Chris and Tina Schmidt and many others. Financial support has been provided the Canadian Wildlife Service, NSERC grants to R. Ydenberg, F. Cooke, and D. Lank, and the Chair in Wildlife Ecology at Simon Fraser University.

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