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Trade-offs, condition dependence and stopover site selection by migrating sandpipers

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Western sandpipers *Calidris mauri* on southward migration fly over the Gulf of Alaska to the Strait of Georgia, British Columbia, where they stop for a few days to replenish reserves before continuing. In the Strait, individuals captured on the extensive tidal mudflats of the Fraser estuary (~ 25000 ha) are significantly heavier (2.71 g, or > 10% of lean body mass) than those captured on the small (< 100 ha) mudflat of nearby Sidney Island. Previous work has shown that the difference cannot be attributed to seasonal timing, size, age or gender effects, and here we compare predictions made by six hypotheses about a diverse set of data to explain why, partway through a migratory journey of ~ 10000 km, birds have such different body masses at two stopover sites within 40 km of each other. The 'trade-off' hypothesis – that the large Fraser estuary offers safety from predators, but a lower fattening rate, while the small Sidney Island site is more dangerous, but offers a higher fattening rate – made six successful predictions, all of which were upheld by the data. All other hypotheses failed at least one prediction. We infer that calidrid sandpipers arriving in the Strait of Georgia with little fat remaining (and therefore low body mass) choose to take advantage of the high feeding rate at small sites like Sidney Island because they are less vulnerable to avian predators than are individuals with higher fat reserves, who instead elect to feed at large open sites like the Fraser estuary mudflats.

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Recently, we reported (Lissimore et al. 1999) that among western sandpipers *Calidris mauri* migrating southward through the Strait of Georgia in British Columbia, Canada, those captured on the extensive tidal mudflats of the Fraser estuary were 2.71 g heavier (difference in overall average of annual means) than those captured on the small mudflat of Sidney Island, located only 35 km to the southwest (Fig. 1). Even larger differences occur within each of the two years (1996: 3.13 g; and 1997: 7.65 g) for which we have good samples from both sites.

These birds were on stopover after a long (~ 2500 km) flight over the Gulf of Alaska from their breeding area in western Alaska (Butler et al. 1996), and individual birds spent only a few days in the Strait of Georgia before continuing southward. In this context, the observed weight difference is large and significant: if 80% fat, it represents a non-wind assisted flight range of those feeding at the same time on an inland meadow only 100 km away (Piersma and Jukema 1993). Also, western sandpipers on northward migration are lighter at inland than at coastal sites (Warnock and Bishop 1998).

Such weight differences between nearby sites could be due to various biases, such as the seasonal timing (e.g. Lindström 1998) or the age/gender composition of samples from different sites. However, the difference we measured is found within every age and gender class, and holds throughout the summer-long passage period (Lissimore et al. 1999). A different idea is that the birds on the different sites could be from different populations and on different migratory routes or schedules (e.g. Dick et al.Dicbut3utesu.1(n)-5like-441356sum-463.2(al.)pp-44T*[(tion463583withern)-380583wandpipers

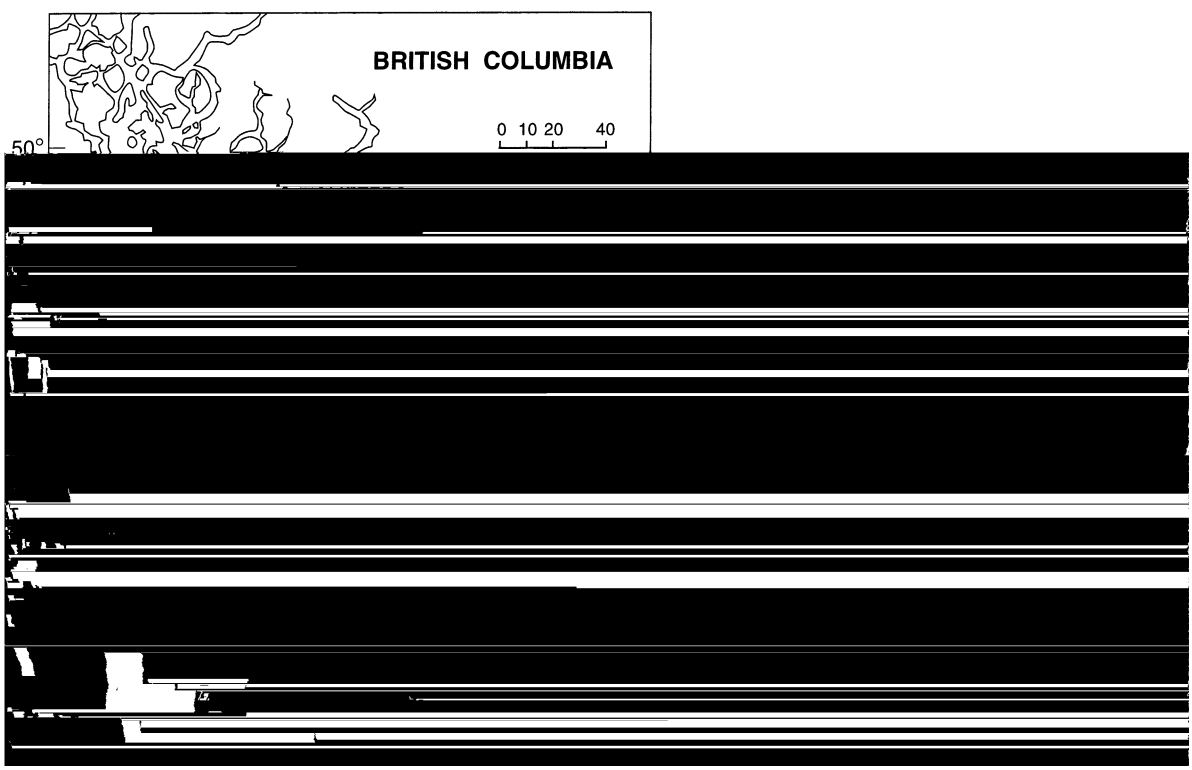


Table 1. Comparisons of the body mass of southward migrating calidrid sandpiper species captured at large (Fraser estuary FE, Gray'

Testing six hypotheses

Six hypotheses could potentially explain the different body weights of western sandpipers at the two sites. In this section we deduce and test (with the data described above) predictions made by these six hypotheses, aiming to generate a set of tests that together discriminate between the hypotheses.

The population-structure hypothesis

The first hypothesis is that different populations, wintering groups or ecotypes of western sandpipers use the two sites (cf. Morrison 1984, Dick et al. 1987). This seems unlikely to apply to western sandpipers as no subspecies or races are recognized. Moreover, our study sites are only 35 km apart, and both are used continuously over the extended southward migration period (late June–early September), as are a large number of other nearby sites. Also, the telemetry study of Iverson et al. (1996) showed that migrating western sandpipers use both large and small stopover sites. Nevertheless, groups of western sandpipers seem to be highly philopatric to specific wintering sites (P. D. O'Hara unpubl. data), and it is possible that they could have different migration routes and schedules, with different body weights. Under this hypothesis, members of one western sandpiper group should not be seen at both our Strait of Georgia study sites.

In three different and independent samples of marked birds, individuals have been located on both our study sites. (i) Twelve sightings have been made of birds flagged on the wintering areas at Chitré, in Panamá: eight were on the Fraser estuary, three at Sidney Island, and one at False Bay, another small mudflat site located in the Strait. (ii) Of western sandpipers marked on the breeding grounds near Nome, Alaska, two were located at Sidney Island and three on the Fraser estuary (Butler et al. 1996). (iii) Five birds banded at Sidney Island were later sighted on the Fraser estuary, and one of these was seen at both locations in the same year. Local movement is also demonstrated by two other same-season resightings of sandpipers banded at Sidney Island at other small sites in Georgia Strait, one at Cowichan Bay 27 km west; and one at Cordova Bay, 5 km south. These observations do not support the hypothesis of differential use of the sites by separate groups or populations, and are entirely consistent with use of both sites by birds from the same areas.

A second test of the population structure hypothesis concerns the body weights of other, related species at our two study sites. It seems unlikely *a priori* that other sandpiper species should have population structures leading them to use these sites in the same way and so demonstrate similar body mass differences. Least sandpipers, for example, have a breeding range and southward migration route quite different from western sandpipers, making parallel population differentiation exceedingly unlikely. Evidence of a similar body weight difference in other species would support an explanation common to small sandpiper species, rather than one peculiar to western sandpipers. Data on the body masses of other species prove that both least ($n = 2667$) and semipalmated sandpipers ($n = 41$) show a pattern of body masses across the two sites identical to that of western sandpipers (Table 1).

By the same logic, if the body mass difference is intrinsic to our two particular sites, there is no reason to suppose that similar sites at other locations should show the same pattern. Data from O'Reilly (1995) show that the body masses of southward migrating western sandpipers are significantly higher at Gray's Harbor ($n = 65$), a large stopover site, than at False Bay ($n = 18$, Table 1), a small site. The body masses are strikingly similar to those we measured at corresponding large (Fraser estuary) and small (Sidney Island) Strait of Georgia sites, and though involving only a single paired set of other sites, this does not support the population structure hypothesis.

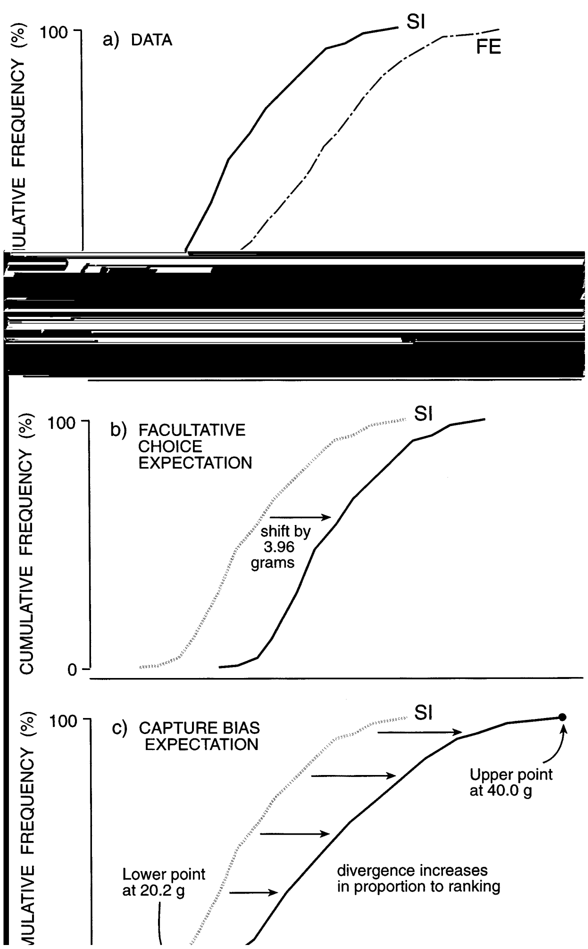
Thus, none of these data provide any support for the population structure hypothesis. Instead, they implicate a general mechanism common to all three small sandpiper species and operational on other, similar sites.

The capture-bias hypothesis

Our second hypothesis is that the nature of the sites biases mist-net captures toward low-mass birds at Sidney Island and heavy individuals on the Fraser estuary. Such a capture bias could arise by several mechanisms. For example, at small sites new arrivals may be detected or mist-netted more easily, so that they are captured sooner after their migratory arrival than at large sites. Quicker capture means that birds would have had less time to replenish reserves, and hence would be lighter. This hypothesis would apply to other small calidridines, and to other sites.

The capture bias hypothesis makes a specific prediction about the shape of the cumulative frequency distributions of body masses on the two sites (Fig. 2). Under capture bias, the distributions should start at the same point, but rise more slowly on the Fraser estuary because individuals have on average spent more time feeding prior to capture. In contrast, on any facultative choice hypothesis (see below) whereby heavy individuals choose the Fraser estuary and light individuals Sidney Island, the frequency distribution should be shifted upwards by a constant amount at the Fraser estuary, as compared with Sidney Island.

We test these predictions against data on body masses of western sandpipers measured in 1996 and 1997, when sizeable samples of birds were captured at both sites. In these two years, the mean weight difference between sites was 3.96 g. The lightest 1% of birds captured on each site differ by 2.50 g, and less than 5% of the 405 western sandpipers caught on the Fraser estuary weighed less than 22 g, compared to 25% (of 490) on Sidney Island. At the 25, 50, and 75% cumulative frequency marks, the weight differences are 3.2, 4.2, and 4.9 g, respectively. No bird caught at Sidney Island weighed more than 32.1 g, while 15% of the birds on the Fraser estuary did so. These data indicate that the body mass distribution at



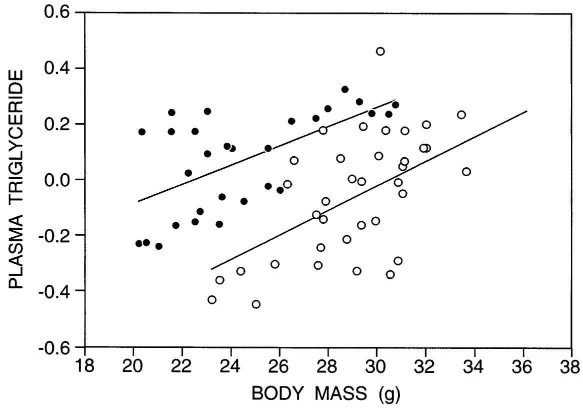


Fig. 3. Plasma triglyceride concentrations (mmol l^{-1}) of western sandpipers ($n = 66$) captured on southward migration at Sidney Island (solid dots) and on the Fraser estuary (open dots). Data are residuals of $\log_{10}$ transformed plasma triglyceride concentration correcting for bleed-time, lines are least squares regressions. As found in captive studies (Williams et al. 1999), residuals are significantly related to body mass (Sidney Island, $r^2 = 0.39$, $p = 0.0003$; Fraser estuary, $r^2 = 0.33$, $p = 0.0002$). There is no site × mass interaction ($p = 0.56$) and no time of day effect at either site ($p = 0.16$). Controlling for body mass, plasma triglyceride concentration is significantly higher at Sidney Island ($p = 0.0001$).

observation that least sandpipers (with a different migratory route) show the same body mass difference, or to explain why an unrelated pair of large and small sites also show a body mass difference. Nevertheless, it remains a logical possibility, and its main prediction is that Sidney Island site is inferior to the Fraser estuary for feeding.

The data refute this hypothesis. The least squares mean concentration of triglyceride in the plasma of sandpipers at Sidney Island (4.16 mmol l^{-1}) is more than twice that at the Fraser estuary (2.04 mmol l^{-1}; $n = 66$; $p < 0.0001$; Fig. 3). This analysis includes adults and juveniles at the

However, the critical prediction about variance is not supported. There is no significant difference between the standard deviations of plasma triglyceride concentrations of western sandpipers measured at the two sites (Fraser estuary $SD = 1.84$ mmol l^{-1}, $n = 37$: Sidney Island $SD = 1.42$ mmol l^{-1}, $n = 29$. $F_{14,28} = 1.66$, NS). If anything, variance is higher on the Fraser estuary.

The trade-off hypothesis

The final hypothesis postulates a trade-off between feeding rate and predation risk, with one site offering better feeding, but at the same time posing more predation danger (Lima and Dill 1990, Houston et al. 1993, Cresswell 1994). Sidney Island appears to offer better feeding, so the hypothesis requires that it be more dangerous. The hypothesis assumes that birds with smaller fat deposits are less vulnerable to predators, making the better feeding at Sidney worth the extra risk, while the Fraser estuary would be the better choice for heavier, more vulnerable, individuals.

The idea that carrying fat puts birds at risk from predators has been invoked in theoretical treatments of body-mass regulation of birds in winter (e.g. Lima 1986) and on migration (Alerstam and Lindström 1990, Houston 1999). Empirical tests of fat load on escape flight performance indicate that migrants are slowed by the fat they carry (van der Veen and Lindström 2000), and our field measurements (Burns and Ydenberg unpubl. data) show that increased wingloading reduces take-off performance of migrating western and least sandpipers. We surmise that sandpipers carrying more fat are more vulnerable to predators.

Sidney Island appears to be more dangerous. At both sites, feeding sandpipers move closer to cover on a rising tide and move further away as the tide falls (y is distance to cover (m) and x is tidal height (m), SI: $y = 157 - 66x$, $n = 30$, $r^2 = 0.66$, $p < 0.0001$; FE: $y = 4297 - 834x$, $n = 19$, $r^2 = 0.58$, $p < 0.0001$). The change in distance to cover with change in tidal height is much less at Sidney Island (66 vs. 834 m of distance per m tidal height), but the overall mean distance to cover on the Fraser estuary is more than 30 times that at Sidney Island (SI: 87.3 m; FE: 2911 m). At the mean tidal height of the observations of 1.298 m this translates to a mean distance-to-cover of 49 m at Sidney Island and 2971 m at Fraser estuary, different by a factor of 60. Moreover, the mudflat at Sidney Island is small (< 100 ha) and almost completely enclosed by forest, dune ridges and salt-marsh vegetation, and there is a forested island in the lagoon. All these features provide approach cover for hunting raptors. In contrast, the horizon-to-horizon vistas on the Fraser estuary mudflats allow sandpipers to spot predators at great distances. This contrast suggests that the Fraser estuary is a safer feeding place than is Sidney Island.

Discussion

Of the six hypotheses we considered, the trade-off hypothesis was most strongly supported (Table 2). Its predictions were all upheld, while other hypotheses failed one or more predictions. Moreover, none made a successful prediction that was not shared with the trade-off hypothesis, and the predictions that Sidney Island is a better and more dangerous feeding site were unique to the trade-off hypothesis.

Table 2. Summary of the match between observations and the predictions of six hypotheses to explain why sandpipers are lighter at Sidney Island than on the Fraser estuary. 'yes' means the hypothesis predicts the observation, 'no' means the hypothesis is not supported. '/' means that the hypothesis makes no specific prediction, or that that the observation does not violate the assumptions of the hypothesis.

Observation	Population structure	Capture bias	Fill-in	Ideal-free	Variance sensitivity	Trade-off
Individuals from same groups seen at both sites	no	/	yes	yes	yes	yes
LESA and SESA[1] show same mass difference	no	yes	no	yes	yes	yes
WESA[2] at other sites show same mass difference	no	yes	no	no	/	yes
Body mass distribution	/	no	yes	yes	yes	yes

The population-structure hypothesis failed all three of

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