



As a group, shorebirds in North America have experienced declines in populations over the past several decades (Morrison 2001, Morrison and Hicklin 2001). Most migratory bird species use intermediate resting and feeding sites between wintering and breeding areas, and understanding the stopover ecology of shorebirds at these sites is critical in determining the effects of factors such as habitat change on population dynamics (Skagen 1997, Warnock and Bishop 1998). Advances in radiotracer and stable-isotope technologies have resulted in considerable information being obtained for timing of migration, links between wintering and breeding areas, migration routes, and length of stay (LOS) at stopover sites (e.g., Davis et al. 1996, Marra et al. 1998, Farmer and Wiens 1999). One of the best-studied examples for shorebirds in North America is the Western Sandpiper (*Calidris mauri*; hereafter "sandpiper"), for which migratory patterns have been described in detail for the region between San Francisco, California, and western Alaska (Iverson et al. 1996, Bishop and Warnock 1998, Warnock and Bishop 1998, Bishop et al. 2005). Despite this work, factors that determine site use and LOS and the potential benefit that birds obtain at specific sites (e.g., in terms of fatening rates) remain poorly understood. As an example, simple measures of body condition (e.g., body mass or size-corrected body mass) are poor predictors of LOS

at a stopover site or migration times among sites (e.g., Holmgren et al. 1993, Skagen and Knopf 1993, Warnock and Bishop 1998).

Numerous studies have shown that changes in certain plasma metabolites, especially triglycerides, can be used to estimate physiological state and rates of mass change in birds (e.g., Jenni-Eiermann and Jenni 1994, Jenni-Eiermann and Jenni 1996, Williams et al. 1999, Acevedo Seaman et al. 2006).

Durin diet stability in the Pacific Northwest



null-peak telemetry systems were used at San Francisco Bay; hand-held, three-element Yagi antennas were used at remaining ground monitoring sites; and aerial monitoring was conducted from planes equipped with exterior, dual-mounted antennas. Flights were conducted at altitudes of 300–1,500 m, with timing of flights varying by area. When a bird was located at a site, we monitored its presence until it had not been detected for at least two days or the bird had been relocated at another site. Monitoring at a site ended either when all radiomarked birds had departed or when minimal migratory activity was observed. For analysis of metabolite levels in relation to LOS, we used data from a subsample of radiomarked birds in San Francisco Bay ( $n = 33$ ) and Punta Banda ( $n = 34$ ) from which blood samples were taken. Length of stay was the number of days from capture and transmitter attachment to the last detection at the initial banding site. We assumed that a detected bird remained on the site the entire day (i.e., LOS = 1 day) and that the



### Results

*Variation in body mass.*—Body mass of sandpipers varied markedly among sites ( $F = 27.9$ ,  $df = 8$  and  $439$ ,  $P < 0.001$ ) and with sex ( $F = 18.1$ ,  $df = 1$  and  $439$ ,  $P < 0.001$ , controlling for tarsus length because females are structurally larger than males; site\*sex interaction not significant,  $P > 0.80$ ). In general, body mass was higher in females than in males, and this sex difference was significant ( $P < 0.05$ , controlling for tarsus length) among birds caught at San Francisco during the winter and in Mexico, Oregon, Botle Beach, and Alaska, but not at other sites (Fig. 1). Among stopover sites, variation in body mass was not explained by latitude for either males ( $F = 0.24$ ,  $df = 1$  and  $7$ ,  $P > 0.80$ ) or females ( $F = 0.09$ ,  $df = 1$  and  $7$ ,  $P > 0.90$ ). We estimated the change in body mass with date (as a potential measure of fatening rate; but see below) for three stopover sites where we had robust sample sizes with sampling spread over >16 days. Body mass varied significantly with date

in San Francisco during spring ( $F = 7.10$ ,  $df = 1$  and  $119$ ,  $P < 0.001$ ,  $b = 0.381 \pm 0.054$ ) and at the Washington sites ( $F = 2.10$ ,  $df = 1$  and  $89$ ,  $P < 0.05$ ,  $b = 0.090 \pm 0.042$ ), but not at Hartney Bay ( $P > 0.80$ , controlling for tarsus length in each case).

*Effect of body mass, handling time, age, sex, time of day, and date on metabolite levels.*—Plasma triglyceride levels were positively related to body mass ( $F = 8.58$ ,  $df = 1$  and  $453$ ,  $P < 0.001$ ,  $b = 0.024$ ) and negatively related to handling time between capture and blood sampling ( $F = 4.17$ ,  $df = 1$  and  $453$ ,  $P < 0.001$ ,  $b = -0.004$ ). By contrast, plasma glycerol levels were independent of both mass and handling time ( $P > 0.25$ ). There

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LOS and any of the measured variables for this site ( $P > 0.20$  in all cases). Plasma triglyceride levels in birds at Punta Banda or San Francisco did not explain variation in the number of days of travel ( $P > 0.50$ ), or rate of travel ( $\text{km day}^{-1}$ ,  $P > 0.30$ ), between these initial banding sites and either the first stopover site where birds were relocated or between the initial banding site and H site



departed, and then were replaced by newly arriving birds of lower body mass, body mass would not change with capture date at the population level, even though individual birds were fat ening. Interestingly, the slope of mass with date for San Francisco in the present study was very similar to that reported for the same site by Warnock and Bishop (1998;  $0.4 \text{ g day}^{-1}$ ). It is possible that the greater mean LOS of birds at San Francisco ( $7.8 \pm 7.1$  days; N. Warnock et al. unpubl. data) compared with other sites (mean: 1–3 days) means that the method of analysis of mass by date provides a more accurate estimate of actual fat ening rate at this site.

Body mass of sandpipers was higher at San Francisco Bay than at any of the stopover sites farther north. Higher body mass, combined with the greater LOS, confirms previous suggestions (e.g., Warnock and Bishop 1998) that San Francisco Bay is a staging area for sandpipers (*sensu* Skagen and Knopf 1993). By contrast, most other sites where LOS is generally short (<3 days) are better classified as true stopover sites (Warnock and Bishop 1998). Interestingly, the second-highest mean body masses in 2004 were recorded at Hartney Bay, the site sampled closest to the breeding grounds in the present study. It is possible that this reflects the advantages of arriving on the breeding grounds with higher body mass or nutrient reserves (e.g., Smith and Moore 2003). Howevand



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