

SPRING STOPOVER ECOLOGY OF MIGRANT WESTERN SANDPIPERS¹

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Abstract. We describe stopover ecology for 132 migrant radiomarked Western Sandpipers (*Calidris mauri*) relocated repeatedly along the Pacific Flyway of North America. Eighty-eight percent of radiomarked birds were detected at 1–5 sites north of their banding sites, at distances ranging from 240–4,000 km away. We compare length of stay and physical indices of Western Sandpipers banded at coastal sites (San Francisco Bay, California and Grays Harbor, Washington), and an interior, western Great Basin site (Honey Lake, California). Western Sandpipers radiomarked at the interior site had significantly shorter length of stays than birds radiomarked at coastal sites, and they had significantly lower fat scores. The ephemeral nature of Great Basin stopover sites and an increased risk of predation may explain some of this variation. Fat and body condition indexes explained little of the observed variation in length of stay of Western Sandpipers at banding and other stopover sites. Length of stay of birds radiomarked at Grays Harbor were significantly longer compared to birds radiomarked to the south that also stopped at Grays Harbor, suggesting a potential capture effect on length of stay of birds at banding sites. Mean length of stays at seven sites other than banding sites ranged from 1.1–3.3 days and were not significantly affected by sex of bird, year of study, or banding location. Length of stay of male Western Sandpipers at the Copper River Delta, Alaska became significantly shorter later in the migration period, but not for females. Coastal sites along the Pacific Flyway from San Francisco to the breeding grounds generally function as stopovers for Western Sandpipers instead of staging areas.

Key words: *body condition, Calidris mauri, migration, Pacific Flyway, radiotelemetry, shorebirds, Western Sandpiper.*

INTRODUCTION

Natural selection has led to a variety of migration strategies within the Scolopacidae of North American shorebirds (Morrison 1984, Boland 1990). Some species such as Rock Sandpiper (*Calidris ptilocnemis*) may carry out their entire annual cycle within sub-Arctic and Arctic regions, whereas other species such as White-rumped Sandpiper (*C. fuscicollis*) may move over 14,000 km between Arctic breeding grounds and South American wintering grounds. An equally complex array of migration strategies may be seen within species of shorebirds (Myers et al. 1990, Gratto-Trevor 1994). Common to most migrating birds is the use of intermediate resting and feeding sites between win-

tering and breeding areas. Subsequently, the stopover ecology of migrating birds is an important factor in explaining variability in avian migration behavior between and within species (Lindström 1995).

Current stopover ecology theory hypothesizes that stopover behavior has been shaped by three major selective forces on migration: time, energy, and predation (Alerstam and Lindström 1990). In spring, time and energetic considerations are perhaps most important for sub-Arctic and Arctic breeding shorebirds because their optimal breeding window is relatively brief (Johnson and Herter 1990). Birds arriving too early at northern stopover and breeding grounds will likely encounter frozen foraging habitat, resulting in loss of critical body reserves needed for further migration and breeding (MacLean 1969), as well as increased probabilities of death (Green et al. 1977). Birds prolonging stays at southerly sites risk not breeding or hatching young so late that the fledglings miss the brief

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period when their invertebrate food base is abundant (Holmes 1972).

Advances in the miniaturization of radiotransmitters have resulted in more accurate estimates of length of stay at banding and stopover sites (Skagen and Knopf 1994, Iverson et al. 1996) and have improved probabilities of detecting birds at more than one site (Iverson et al. 1996, Farmer and Parent 1997, Johnson et al. 1997). We report on stopover ecology of 132 radiomarked Western Sandpipers (*C. mauri*) relocated along a 4,000-km stretch between San Francisco, California and the Yukon-Kuskowkim Delta, Alaska. Western Sandpipers winter primarily south from California, along the southern Atlantic Coast, and the Gulf of Mexico to Central and South America. Breeding grounds are primarily in western and northern Alaska (Iverson et al. 1996).

Our two-year study expands on Iverson et al.'s (1996) single-year study of spring migration of Western Sandpipers between San Francisco, California and the Copper River Delta, Alaska. Their study found that these birds typically used a rapid, short-flight migration strategy and had short lengths of stay at stopover sites. We include length of stay information on new banding and stopover sites. For the first time, we describe the stopover ecology of Western Sandpipers migrating through the western Great Basin. Because migration cannot occur without sufficient fuel supplies, and fuel for birds is stored mainly in the form of fats (Blem 1990), we test for relationships between fat scores (Scott et al. 1994) and length of stay at banding and stopover sites of radiomarked Western Sandpipers. We also test for the same relationships using a size-independent body condition index for comparative purposes with Iverson et al. (1996). Additionally, we test for differences in length of stay at stopover sites by sex of radiomarked bird, year of study, and banding location. These data are critical, as the conservation of migratory stopover sites for birds relies not only on knowing how and when different areas of their migration landscape are used, but also on knowing what influences the use of and time spent at different areas of their landscape.

METHODS

Western Sandpipers were captured and radiomarked at two Pacific coast sites, San Francisco Bay, California and Grays Harbor, Washington,

and at a western Great Basin wetland, Honey Lake, California (Fig. 1). Capture dates at San Francisco Bay ranged from 14 April–3 May 1992 (birds used in weight analyses), 17–23 April 1995 and 18–23 April 1996; at Honey Lake from 27–30 April 1995, and on 26 April 1996; and, at Grays Harbor from 24–28 April 1995, and 28 April–4 May 1996. Measurements (mm) taken on all captured birds included exposed culmen, flattened wing, and tarsus length. Birds were weighed to the nearest 0.5 g within 30 min of capture. Sex was determined by length of the exposed culmen; extensive pre-alternate molt prevented aging birds (Page et al. 1972).

Each bird was assigned a fat score value ranging from 0–5 based upon the amount of fat visible in the furculum of the clavicle (tracheal pit), where 0 = no visible fat in the tracheal pit and 5 = fat overflowing the tracheal pit (Krementz and Pendleton 1990). The majority of fat scores were assigned by the senior author. For each Western Sandpiper, we calculated another size-independent body condition index (C) using the following equation (Iverson et al. 1996): $C = \log(M)/\log(W^{\text{exp}})$, where M = mass (g), W = flattened wing (mm), and exponent (exp) = 0.991 for males and 1.679 for females. The exponent was the slope of the simple regression between the $\log(M)$ and $\log(W)$ for birds captured at San Francisco Bay in the springs of 1992, 1995, and 1996 (359 males, 112 females).

For the periods 17–28 April (San Francisco, 1995 and 1996) and 21 April–3 May (Grays Harbor, 1996), we calculated a mean daily fuel deposition rate for males and females. We used the slope of the estimated linear equation obtained by regressing the mean body mass of single day catches of Western Sandpipers against Julian Date (cf. Gudmundson et al. 1991), weighted by the number of individuals in each daily catch ($\bar{x} \pm \text{SD} = 21 \pm 17$ birds, range = 3–68). Because we had only seven capture days at Grays Harbor, we also regressed Julian Date against masses of individual birds weighted by the number of individuals in each daily catch (6 ± 5 birds, range = 1–13). We had insufficient data for Honey Lake to calculate mean daily gains in body mass of Western Sandpipers.

A total of 132 Western Sandpipers (Table 1) were radiomarked and monitored during their north migration. Radiomarked birds had 0.9 g radiotransmitters (Holohil Systems Ltd., Wood-

TABLE 1. Numbers of Western Sandpipers radiomarked and detected at areas north of banding sites: Spring 1995, 1996. Total detected = number of individual birds heard at least once past banding site.

	Banding location							
	San Francisco		Honey Lake			Grays Harbor		
	Male	Female	Male	Female	Unknown	Male	Female	Unknown
Banded								
1995	16	13	12	6	—	7	7	—
1996	15	15	7	5	1	21	6	1
Total detected								
1995	15	9	10	4	—	7	6	—
1996	14 ^a	13	5	5	0 ^a	20	6	0

^a One bird dropped from detection estimates because its radio frequency overlapped with a caribou frequency in Alaska causing us to prematurely stop monitoring for that radio.

lawn, Ontario, Canada) glued to their lower backs using methods described by Warnock and Warnock (1993). Monitoring was conducted using methods described by Iverson et al. (1996). We monitored transmitters from the ground and from fixed-wing aircraft at known or suspected stopover sites from San Francisco Bay to the Yukon-Kuskokwim Delta, Alaska (Table 2, Fig. 1). Monitoring began north of banding sites as soon as the radiomarked birds' signal was no longer detected at the banding site. All monitoring at a site ceased when either all radiomarked birds had departed, or when minimal migratory activity was observed, unless otherwise indicated.

We assumed that all radiomarked birds at a banding or monitoring site were detected on a given day. Length of stay was measured in one day increments, unless a bird was seen at two sites in one day in which case we assigned 0.5 days for each site. At the Copper River Delta, high winds prevented monitoring on 6 May 1995. For the Copper River, we assumed that birds detected 5 May departed 5 May ($n = 2$), and birds detected 7 May arrived 6 May ($n = 7$).

STATISTICAL ANALYSES

Statistical analyses were performed using STATA (Computing Resource Center, Santa Monica, CA 1992), unless otherwise noted. Significance was set at $P \leq 0.05$. Data were examined for departures from normality and homogeneity by preliminary graphing and testing of data. If needed, we normalized data using a log transformation. We used analysis of variance (ANOVA) to test for significant differences between means and interactions between variables. We

used analysis of covariance (ANCOVA) to control for the potentially confounding effect of banding date in some analyses. Where parametric assumptions were not met, we tested for overall group differences with the Kruskal-Wallis test (KW test) and then tested for between group differences holding our groupwise error rate constant (Siegel and Castellan 1988).

We used simple linear regression analyses and report the Pearson product-moment correlation coefficient (r). We used Spearman's rank correlation test (r_s) if assumptions of normality were not met. We tested for effects of capture by randomly pairing birds radiomarked at Grays Harbor with radiomarked birds from San Francisco or Honey Lake arriving within one day of the Grays Harbor bird being banded. We compared their length of stays using a Wilcoxon matched-pairs signed ranks test. Data are reported as $\bar{x} \pm SD, n$.

RESULTS

BANDING SITES

Body measurements. Controlling for banding date, mean body masses of male and female Western Sandpipers differed between banding locations (ANCOVA; males, $F_{2,356} = 86.1, P < 0.001$; females, $F_{2,109} = 24.9, P < 0.001$). We detected significant differences between mean body masses of male and female Western Sandpipers at all banding locations, but significant year effects only at Honey Lake and Grays Harbor (Table 3). Banding date, the covariate, explained significant variation in mean body masses of birds at San Francisco (birds banded later in date were heavier), and there also was a significant year-by-sex interaction at San Francisco.

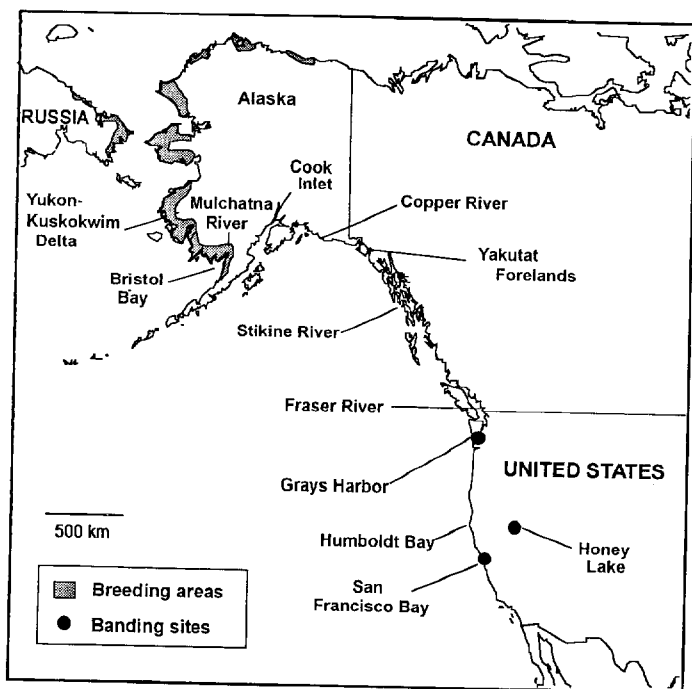


FIGURE 1. Banding and stopover sites of Western Sandpipers during the 1995 and 1996 spring migration.

At Grays Harbor, we detected a significant year-by-date of banding interaction (Table 3). Except for females in 1995, mean body masses of Western Sandpipers banded at San Francisco were

higher than those of Honey Lake and Grays Harbor (Table 4).

For birds banded at San Francisco, body mass (log transformed) was positively related to date

TABLE 2. Daily effort at each site where length of stay of radiomarked Western Sandpipers was monitored. Included is the range of days sites were monitored as well as total number of days sites were monitored from the ground and by aircraft.

Location	1995			1996		
	Range	Ground days	Aerial days	Range	Ground days	Aerial days
California						
San Francisco Bay	18 April–8 May	18	5	18 April–8 May	21	5
Honey Lake	29 April–9 May	11		25–28 April	4	
Humboldt Bay	28 April–3 May	5		23 April–9 May	17	4
Oregon						
Malheur NWR				30 April–10 May	1	3
Washington						
Gray Harbor	24 April–9 May	15	7	24 April–15 May	2	20
Willapa Bay				21 April–11 May	20	9
British Columbia						
Fraser River Delta	25 April–18 May	24		24 April–16 May		23
Tofino Beach	21 April–8 May	18				
Alaska						
Stikine River Delta	27 April–15 May	2	15	25 April–20 May	3	23
Yakutat Forelands	4–19 May		23	26 April–22 May	27	25
Copper River Delta	28 April–22 May		23	27 April–20 May		24
Cook Inlet	29 April–18 May		19	24 April–17 May	9	18

TABLE 3. Analysis of covariance to determine the effects of year, sex, and interactions on body mass of Western Sandpipers at banding sites, with banding date as a covariate. Body mass data for San Francisco Bay collected in 1992, 1995, and 1996, and for Honey Lake and Grays Harbor 1995 and 1996.

Effects	San Francisco			Honey Lake			Grays Harbor		
	F	df	P	F	df	P	F	df	P
Year	1.3	2, 304	0.27	26.9	1,41	<0.001	8.6	1, 117	<0.01
Sex	24.1	1, 304	<0.001	11.3	1,41	0.002	13.3	1, 117	<0.001
Banding Date	53.8	1, 304	<0.001	0.1	1,40	0.80	0.1	1, 117	0.82
Year*Sex	2.7	4, 304	<0.05	0.1	1,38	0.72	0.0	1, 111	0.89
Year*Banding Date	1.4	2, 301	0.25	—	—	—	16.0	2, 117	<0.001
Sex*Banding Date	0.5	1, 301	0.47	0.5	1,38	0.50	0.2	1, 111	0.66

(male, $r = 0.73$, $P = 0.001$, $n = 16$ days; female, $r = 0.74$, $P = 0.002$, $n = 14$ days). Slopes of these lines were not significantly different (ANCOVA, $F_{1,26} = 0.6$, $P = 0.44$), so we pooled males and females to calculate the population mean daily gain in body mass for San Francisco Western Sandpipers. Mean daily gain in mass was 0.40 g day^{-1} . For birds banded at Grays Harbor, body mass was positively related to date for males (1996 using individual birds, insufficient data for 1995, $r = 0.59$, $P < 0.001$, $n = 45$ males), but no relationship was detected for females. The mean daily gain in body mass of males at Grays Harbor was 0.98 g day^{-1} . Using the mean body masses of daily catches instead of body masses of individual birds to regress against Julian date, we found approximately the same mean daily gain in body mass of males at Grays Harbor (0.99 g day^{-1}), but the relationship

was not significant ($r = 0.73$, $P = 0.06$, $n = 7$ days).

Body condition indexes were significantly correlated with our empirically derived fat scores (males, $r = 0.65$, $P < 0.001$, $n = 281$; females, $r = 0.83$, $P < 0.001$, $n = 65$). We failed to find differences in fat scores between sexes at any of the banding locations (KW test; San Francisco, $\chi^2_1 = 0.5$, $P = 0.49$; Honey Lake, $\chi^2_1 = 0.5$, $P = 0.58$; Grays Harbor, $\chi^2_1 = 0.0$, $P = 0.84$). However, fat scores of Western Sandpipers were significantly different between banding locations (KW test, $\chi^2_2 = 70.7$, $P < 0.001$). Fat scores of birds banded at San Francisco were significantly higher than those banded at Honey Lake or Grays Harbor, and Grays Harbor birds had higher fat scores than Honey Lake birds (Table 4).

Length of stay. Length of stay was not signif-

TABLE 4. Mean body mass (g) and fat scores (on scale of 0–5) of Western Sandpipers banded at San Francisco Bay, Honey Lake, and Grays Harbor.

		Male			Female		
		$\bar{x} \pm \text{SD}$	n	Test ^a	$\bar{x} \pm \text{SD}$	n	Test ^a
Mass							
	1992	San Francisco	27.9 ± 3.4	78	32.6 ± 4.3	48	
	1995	San Francisco	29.3 ± 3.0	74	30.5 ± 4.1	15	A
		Honey Lake	26.7 ± 1.5	16	28.8 ± 2.0	6	A
		Grays Harbor	24.7 ± 2.0	58	27.3 ± 3.2	9	A
	1996	San Francisco	29.1 ± 3.0	72	33.1 ± 4.0	24	A
		Honey Lake	23.5 ± 2.2	17	26.2 ± 2.3	5	B
		Grays Harbor	28.1 ± 3.8	45	29.1 ± 2.6	6	B
Fat ^b							
		San Francisco	3.6 ± 1.1	197			A
		Honey Lake	1.8 ± 1.2	45			B
		Grays Harbor	2.8 ± 1.2	127			C

^a Multiple comparison tests comparing body masses between banding locations (within sexes and years) based on results of separate analysis of covariance tests with date of banding as a covariate, using sequential Bonferroni test to maintain table-wide significance level (Rice 1989). Multiple comparison tests comparing fat scores between banding locations based on KW test for overall differences between groups (Siegel and Castellan 1988). Different letters (i.e., A vs. B) within the same column and year indicate significant differences at $P \leq 0.05$.

^b Sexes and years combined. Fat scores between sexes not significantly different (KW test: SF, $\chi^2_1 = 0.2$, $P = 0.65$; HL, $\chi^2_1 = 0.6$, $P = 0.45$; $\chi^2_1 = 0.1$, $P = 0.77$).

icantly correlated with banding date of Western Sandpipers at San Francisco and Grays Harbor ($r = 0.10$, $P = 0.26$, $n = 99$) or Honey Lake ($r_s = 0.06$, $P = 0.74$, $n = 31$). We failed to detect any significant effects of two and three-way interactions of sex, year, and banding location on length of stay at banding sites (all P s > 0.25). Testing only the main effects, we failed to detect any significant effects of sex ($F_{1,124} = 2.9$, $P = 0.09$) or year ($F_{1,124} = 0.2$, $P = 0.67$), but we did detect a significant banding location effect ($F_{2,124} = 31.0$, $P < 0.001$). The length of stay of birds banded at Honey Lake was 2.6 ± 1.9 days ($n = 31$), whereas length of stay for birds at San Francisco and Grays Harbor was approximately three times longer (SF, $\bar{x} = 9.1 \pm 4.6$ days, $n = 58$; GH, $\bar{x} = 8.5 \pm 3.7$ days, $n = 42$). We detected no significant difference between length of stay of San Francisco and Grays Harbor birds (KW test; $\chi^2_1 = 0.2$, $P = 0.68$).

Regressing length of stay at the banding site against the body condition index and the fat score for each banding site and sex separately, we failed to detect any significant relationships (body indexes, all P s > 0.24 ; fat scores, all P s > 0.08). Because length of stay of birds at banding sites at San Francisco and Grays Harbor did not differ, we pooled the two sites and looked to see if the body condition indexes explained variation of length of stay with the larger data set, and then repeated the analyses using the fat scores. There were no significant differences using the body indexes (males, $r = 0.17$, $P = 0.22$, $n = 58$; females, $r = 0.02$, $P = 0.89$, $n = 39$), and fat scores for males ($r_s = -0.24$, $P = 0.06$, $n = 58$) or females ($r_s = -0.12$, $P = 0.43$, $n = 40$).

STOPOVER SITES AND POTENTIAL CAPTURE EFFECTS

Relocations. In 1995, 51 of the 61 Western Sandpipers (84%) were relocated at 8 areas beyond their banding sites for a total of 85 relocations (Table 1). In 1996, 63 of the 69 Western Sandpipers (91%); 2 birds were dropped from detection estimates because their radio frequencies overlapped with caribou radio frequencies in Alaska causing us to prematurely stop monitoring for those radios) were relocated at one or several of 10 areas beyond their banding sites for a total of 140 relocations.

Length of stay. Mean length of stay of radiomarked Western Sandpipers relocated away

TABLE 5. Mean length of stay (days) of radiomarked Western Sandpipers at stopover area, 1995 and 1996 combined.

	$\bar{x} \pm SD$	n
Humboldt Bay, California	3.3 ± 3.0	9
Grays Harbor, Washington	2.3 ± 2.3	23 ^a
Fraser River, British Columbia	2.2 ± 1.2	25
Stikine River, Alaska	2.8 ± 1.5	21
Yakutat Forelands, Alaska	1.1 ± 0.3	21
Copper River, Alaska	2.2 ± 1.1	90
Cook Inlet, Alaska	1.7 ± 1.2	3

^a Not including birds banded there.

from their banding sites varied significantly among stopover sites (KW test; $\chi^2_6 = 13.0$, $P = 0.04$, each bird used only once) from 1.1–3.3 days (Table 5). At Grays Harbor, we found no significant effect of sex or banding location (KW test; P s > 0.16 , $n = 23$) on length of stay, but length of stays in 1996 were significantly shorter than those in 1995 (KW test; $P = 0.05$; 1995, $\bar{x} = 3.7 \pm 2.9$ days, $n = 7$; 1996, $\bar{x} = 1.7 \pm 1.8$ days, $n = 16$). There was no significant effect of sex, year, or banding location on length of stay at any other stopover site.

We used data from the Copper River Delta to test whether body condition at the banding site subsequently affected length of stay at a stopover site. For male Western Sandpipers, there was a significant relationship ($r = 0.28$, $P = 0.05$, $n = 54$). In females, no significant relationship was detected ($r = 0.01$, $P = 0.90$, $n = 34$). Using fat scores, we failed to explain significant variation in length of stay for males ($r_s = 0.15$, $P = 0.28$, $n = 55$) or females ($r_s = 0.07$, $P = 0.68$, $n = 34$). Length of stay at the Copper River Delta, for males, was significantly related to arrival date ($r^2 = 0.25$, $P < 0.001$, $n = 54$), but not for females ($r^2 = 0.09$, $P = 0.12$, $n = 34$). For males, the later the date, the shorter their length of stay was at the Copper River Delta (Fig. 2).

Potential banding effect. Mean length of stay at Grays Harbor was significantly longer for birds banded at Grays Harbor ($\bar{x} = 7.6 \pm 3.4$ days, range = 1–7 days) than for birds banded at San Francisco and Honey Lake ($\bar{x} = 1.9 \pm 1.9$ days, range = 1–12 days; Wilcoxon matched-pairs signed ranks test, $z = -3.27$, $P = 0.001$, $n = 14$).

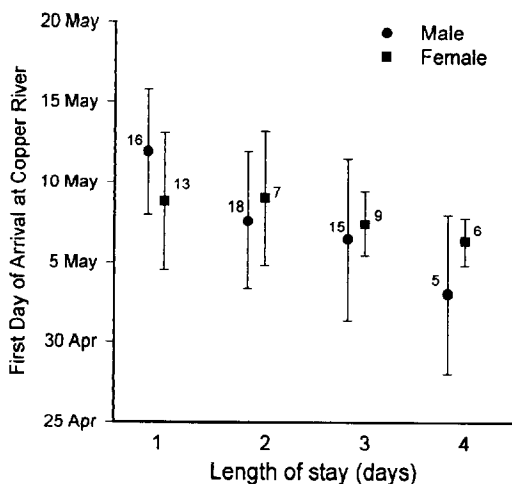


FIGURE 2. Mean length of stay of male and female Western Sandpipers at the Copper River Delta, Alaska as a function of their arrival date at the Copper River Delta. Bars and adjacent numbers indicate SD and sample size, respectively.

DISCUSSION

CHANGES IN BODY MASS

Migration is an energetically expensive undertaking, fueled primarily by fat (Blem 1990). Depending upon what conditions a bird faces during migration, and where to and when a bird is migrating, a diversity of strategies in maintaining optimal body masses should be evident (Alerstam and Lindström 1990, Weber and Houston 1997). For instance, of two subspecies of Dunlin (*Calidris alpina*) stopping at the Wadden Sea during spring migration, the one with the longest migration had the largest mean body mass (corrected for size differences) and most rapid gain in body mass day^{-1} (Goede et al. 1990).

We found that Western Sandpipers from San Francisco were heavier than Grays Harbor birds, although birds from these two sites appear to use the same breeding areas (Bishop and Warnock, unpubl. data). The higher body masses of San Francisco Western Sandpipers may reflect their longer migration distances to the breeding grounds compared to Grays Harbor birds (who are 1,000 km farther north). At the same time, interior migrating Western Sandpipers, represented by Honey Lake birds, traveled lean compared to San Francisco birds even though the two banding sites are within 3° latitude. One possible explanation is that the breeding grounds of Western Sandpipers passing through Honey

Lake are closer than the breeding grounds of San Francisco birds. However, our relocations of radiomarked Western Sandpipers suggest that, if anything, Honey Lake birds breed farther north in Alaska than San Francisco birds (Bishop and Warnock, unpubl. data).

An intriguing alternative explanation for the low body masses we observed in Honey Lake birds is that these birds maintain lighter body masses in response to high predation pressure by raptors. Theoretical work (Lima 1986), experimental studies (Witter et al. 1994) and field research (Gosler et al. 1995) have predicted and demonstrated that birds in an environment characterized by increased risk of predation by raptors should and will maintain lower body masses. It may be that individual Western Sandpipers passing through Honey Lake are more likely to encounter a raptor than birds passing through San Francisco or Grays Harbor, and preliminary data suggest that this may be true (N. Warnock, unpubl. data). This deserves further investigation. Other scenarios are possible. Skagen and Knopf (1994) suggested that the ephemeral nature of wetlands at interior sites in the Great Plains may result in rapid movement. Rapidly changing conditions at interior wetlands coupled with quick turnover rates could preclude birds from gaining much mass compared to mass gains at more stable wetlands on the coast.

How fast birds are able to deposit fat and other fuel at stopovers may be an important component to understanding their length of stay (Alerstam and Lindström 1990). At San Francisco, male and female Western Sandpipers had positive daily mass gains (0.40 g day^{-1}), similar to the daily mass gain of 0.34 g day^{-1} calculated from repeat measurements of four Western Sandpipers at Sidney Island, British Columbia (Butler and Kaiser 1995). At Grays Harbor, male Western Sandpipers gained almost 1 g day^{-1} , whereas we detected no significant daily gains in body mass for females. However, our estimates of daily body mass gain are based on gains of the population, not on gains of individuals measured repeatedly, and caution must be used in the interpretation of these data. At San Francisco Bay, we may be capturing some Western Sandpipers not yet in a state of premigratory fattening, so that inclusion of these birds would depress the actual rate of body mass gain at the site (Zwarts et al. 1990). Western Sandpipers

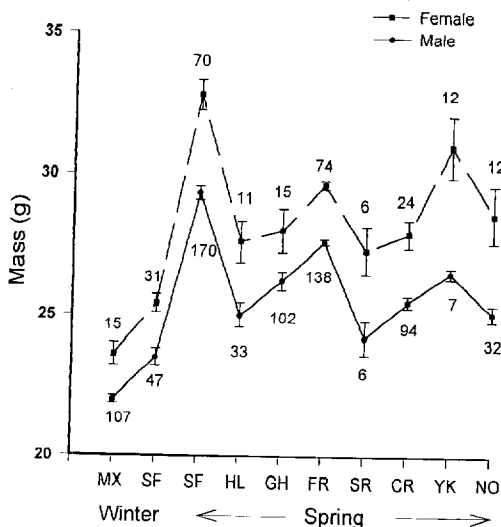


FIGURE 3. Mean masses (\pm SE, n) of male and female Western Sandpipers along the Pacific Flyway. Winter masses from January, spring masses from mid-April to mid-May. MX = Ensenada, Mexico; SF = San Francisco, CA; HL = Honey Lake, CA; GH = Grays Harbor, WA; FR = Fraser River Delta, BC (Butler et al. 1987); SR = Stikine River Delta (C. Iverson, unpubl. data); CR = Copper River Delta (O'Reilly 1995); Yukon-Kuskokwim Delta, Alaska (Holmes 1972); Nome, Alaska (O'Reilly 1995).

rarely winter at Grays Harbor, thus all birds we captured were probably migratory

The varying rates of body mass gain of Western Sandpipers we observed between stopovers and between sexes may reflect real differences between quality of stopover sites and/or variance in stopover strategies of different birds. Most studies investigating daily body mass gain combine males and females in their samples (reviewed by Zwartz et al. 1990), yet our study suggests that at least for Western Sandpipers sexes may accumulate fat and other energy at different rates while at the same stopovers. Once Western Sandpipers reach their breeding grounds, it appears that they arrive with some body reserves despite the long migration. At the Copper River Delta and at the breeding grounds body masses are lower than at San Francisco in the spring, but significantly higher than winter masses (O'Reilly 1995, Fig. 3).

FACTORS AFFECTING LENGTH OF STAY

Numerous studies have examined the relationship between indexes of body condition of migrant shorebirds to length of stay at stopover

sites (e.g., Skagen and Knopf 1994, Lyons and Haig 1995, Iverson et al. 1996). In this study, we found no relationship between length of stay and body condition of birds at their banding sites, but we detected a small but significant trend for body condition at the banding site of male Western Sandpipers to be correlated with length of stay at the Copper River Delta. Adult, male Western Sandpipers tend to arrive slightly earlier at the breeding grounds than females, just as snow begins to melt (Holmes 1971). Earliest arrivals to sub-Arctic and Arctic breeding grounds encounter greater uncertainties in weather (Green et al. 1977) and food availability (Holmes 1972), forces that will select for birds in better body condition.

However, body condition of migrating shorebirds at time of capture generally explains little of the variation in the length of stay of birds at stopovers (Skagen and Knopf 1994, Lyons and Haig 1995, Iverson et al. 1996, this study), and other factors need be considered. Wind conditions could mask effects of body condition on length of stay at stopover sites (Holmgren et al. 1993), and may be the most important influence on length of stay for some species of shorebirds (Butler et al. 1997). Skagen and Knopf (1994) failed to detect effects of wind on the departures of migrating Semipalmated Sandpipers (*C. pusilla*), but in one year they found White-rumped Sandpipers departing more often on northerly winds. Western Sandpipers appear to be unable to make the migration movement from San Francisco to Alaska given the time they do it in (Iverson et al. 1996) and their body conditions without assistance from wind (Butler et al. 1997). Winds along the Pacific Coast are variable, and favorable wind conditions are generated every few days during the spring migration period (Butler et al. 1997).

Fuel loads needed to cover given distances will differ greatly with or without wind assistance (Butler et al. 1997). Where wind conditions are stable, birds are likely to follow other energy optimization criteria. For Bluethroats (*Luscinia svecica*) migrating through Sweden during a period of constant wind conditions, birds appeared to let fuel deposition rates at current sites and expected speed of migration later on guide their stopover decisions (Lindström and Alerstam 1992, Å. Lindström, pers. comm.).

Other factors likely influence length of stay of shorebirds at stopover sites. Two such factors

are arrival date and sex. Semipalmated Sandpipers (Lyons and Haig 1995), Little Stints (*C. minuta*, Keijl et al. 1992), and White-rumped Sandpipers (in one of two years, Skagen and Knopf 1994), have shorter length of stays as the migration progresses. Male Semipalmated Sandpipers have shorter length of stay in spring than females (Skagen and Knopf 1994, Lyons and Haig 1995). We failed to detect differences in length of stay of Western Sandpipers at banding sites based on date or sex. However, at one stopover site, the Copper River Delta, the last major stopover site before the breeding grounds, the later in date a male arrived, the shorter he stayed. No pattern was detected for females.

Shorebirds migrating towards breeding grounds in the sub-Arctic and Arctic face time constraints, and males probably face tighter constraints than females the closer they get to the breeding grounds. Monogamous male Western Sandpipers must obtain breeding territories. Early arrivals may fledge more young than late arrivals as is seen with female, polyandrous Spotted Sandpipers (*Actitis macularia*, Oring and Lank 1986). Female Western Sandpipers also face time constraints. Eggs laid too early in the season face freezing (Green et al. 1977), whereas for chicks hatching too late in the short breeding season there is an increased probability of food shortages (Holmes 1972) and, in some years, greater predation (Oring and Lank 1986, Jönsson 1991). However, energetic costs for females may be equally or more important than time considerations because egg production is energetically expensive (MacLean 1969, Blem 1990).

A potential influence on length of stay is prey depletion at stopover sites. At some sites, shorebirds impact invertebrate populations over the migration period (Schneider and Harrington 1981, Wilson 1989). However, Wilson (1994) failed to detect a significant impact of shorebird predation on invertebrate abundance at Grays Harbor, Washington. He suspected that length of stay of birds was too short at the site to have a significant impact. Likewise, at the Fraser River Delta, British Columbia, Western Sandpipers did not appear to significantly reduce their invertebrate prey (Sewell 1996). At the Copper River Delta, Alaska, Senner (1977) suggested that shorebird predation depleted some age classes of the bivalve *Macoma balthica*, but they were not an important prey item of Western Sandpipers.

These studies combined suggest that prey depletion by Western Sandpipers at stopover sites along the Pacific Flyway is probably not important in determining length of stay at sites.

POSSIBLE EFFECTS OF CAPTURE

Birds marked at San Francisco Bay and Honey Lake and subsequently seen at Grays Harbor stayed an average of 1.9 days at Grays Harbor, significantly shorter than birds captured at Grays Harbor (over 7 days), pointing out the possibility of a capture effect. Shorebirds can lose significant body mass after capture (Lindström 1995, Warnock et al. 1997). It may be that these birds require a few extra days to acquire additional reserves to offset initial weight loss. Skagen and Knopf (1994) found no relationship between length of stay of radiomarked Semipalmated and White-rumped Sandpipers and handling time. However, if there is a minimum threshold level of disturbance that birds respond to, they would have been unable to detect a banding effect because they monitored only at banding sites. This threshold level of disturbance may be reached quickly. O'Reilly and Wingfield (1995) found that stress indicators (measured by corticosterone levels) in captured shorebirds, including Western Sandpipers, reached maximum amounts after 15 min.

Given our high recovery rates of birds past the banding sites and subsequent short length of stays at stopover sites, this capture effect appears to be temporary. In a concurrent study of the migration of radiomarked Pacific Golden-Plovers (*Pluvialis fulva*) from Hawaii to Alaska, 19 of 20 radiomarked birds left Hawaii for Alaska to breed and then came back the following winter season (Johnson et al. 1997). Wintering Western Sandpipers radiomarked at San Francisco Bay appear to acclimate to radio transmitters after the first three days (Warnock and Warnock 1993, Warnock and Takekawa 1996). However, future studies of shorebird stopover ecology, especially those interested in calculating length of stay of birds, should evaluate possible temporary capture effects.

STOPOVER VS. STAGING SITES

Recently, attempts have been made to distinguish between different types of areas shorebirds use during migration (Skagen and Knopf 1994, Farmer and Parent 1997). Expanding on Myers' (1983) use of the term staging sites to describe

single wetlands hosting large numbers of shorebirds, Skagen and Knopf (1994) further defined staging sites as migration stops with predictable and abundant feeding resources where birds have long lengths of stay, fatten significantly, and depart suddenly at a threshold date. This definition has been used to describe a coastal model of shorebird migration (Skagen 1997). Contrasting interior sites with coastal sites, Skagen and Knopf (1994) pointed out that sites in the Great Plains are more unpredictable in resources (mainly water), and they argued that shorebirds using interior wetlands exhibit low site fidelity, have shorter lengths of stay, and show little increase in body mass during their stays (Skagen and Knopf 1994, Skagen 1997). These interior wetlands have been called resting areas (Hands 1988) or more recently stopover sites (Skagen and Knopf 1994).

Our study shows that despite their predictable water resources, most coastal sites between San Francisco and the Yukon-Kuskokwim Delta, Alaska do not fit the current definition of staging sites, at least for Western Sandpipers. As defined by Skagen and Knopf (1994), there are probably few true staging areas for shorebirds in the U.S.A., although sites such as Lake Abert and Mono Lake in the Great Basin used by phalaropes in the fall function as such (Jehl 1988), as well as the Bay of Fundy for fall migrating Semipalmated Sandpipers (Hicklin 1987). Our results indicate that whereas coastal sites often host large concentrations of Western Sandpipers, length of stays of Western Sandpipers are typically short (< 3 days) with variable rates of daily gain in body mass. Based upon the short lengths of stay, most sites used during the spring migration are better classified as stopovers, and this is likely true for fall migration where similar short length of stays have been reported (Butler et al. 1987). However, for some individuals, these same sites may function as staging areas. Coastal stopover sites appear to differ from interior stopover sites in the number of birds that may stop at a given time, in the amount of body mass birds can gain day⁻¹, and predation pressure, but the differences remain to be properly tested.

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