

SPRING MIGRATION OF WESTERN SANDPIPERS ALONG THE PACIFIC COAST OF NORTH AMERICA: A TELEMETRY STUDY¹

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Abstract. We studied the migratory movements of radio-equipped Western Sandpipers (*Calidris mauri*) along a 4,000 km stretch of the west coast of North America from California to Alaska during the 1992 spring migration. A total of 77 shorebirds were radio-tagged at San Francisco Bay, CA; Bolinas Lagoon, CA; Fraser River Delta, British Columbia; and the Stikine River Delta, AK. Daily aerial and ground monitoring from mid-April to late May at banding sites as well as the Copper River Delta provided data on length of stay of individual shorebirds and migration times between study areas. Fifty-eight shorebirds were detected beyond banding sites for a 74% net relocation rate. The proportion of birds detected along the migration route increased with latitude: Grays Harbor, WA (3.4%); Fraser River, British Columbia (8.6%); Stikine River, AK (28.6%); and Copper River, AK (62.3%). Length of stay averaged three days per site. We failed to detect differences in length of stay among sites or between sexes. A condition index calculated as body mass standardized for body size was a poor indicator of length of stay at a site or migration time among sites. An estimated 26% of radio-equipped birds were never relocated suggesting that migrant birds use smaller dispersed wetlands as well as the major intertidal wetland complexes we studied. We conclude that most spring migrant Western Sandpipers use a short-flight hopping migration strategy rather than a few sustained long flights. The short-flight strategy emphasizes the importance of maintaining a continuous complex of intertidal wetland habitats along the migration route to ensure shorebird conservation.

Key words: *Western Sandpiper*; *Calidris mauri*; migration; telemetry; Pacific Coast; length-of-stay.

INTRODUCTION

Shorebirds breeding in the Arctic undertake long migrations, often crossing large stretches of ocean, deserts or other geographic barriers (Alerstam

1990, Piersma and Jukema 1990). Long-distance flights require energy reserves that are accumulated at stopover sites to complete migration (Piersma and Jukema 1990, reviewed by Zwarts et al. 1990). These stopover sites are essential habitats for successful migration by shorebirds unable to shift to alternate foraging areas (Myers 1983, Senner and Howe 1984, Davidson and Piersma 1992, Myers et al. 1987), although use of specific sites may differ among individuals of a species (Gudmundsson et al. 1991).

The development of a general theory of mi-

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gration by shorebirds is based largely on dynamics of energy reserve deposition and use (Alerstam and Lindstrom 1990, Gudmundsson et al. 1991). Many individuals carry larger reserves than are necessary to make flights between stopover sites and some individuals may bypass available sites (Gudmundsson et al. 1991, Davidson and Wilson 1992). Similarly, length of stay of individuals at stopover sites is not always positively related to their body mass at departure (Page and Middleton 1972, Lank 1983, Morrison 1984, Dunn et al. 1988, Holmgren et al. 1993, Skagen and Knopf 1994). The advancement of migration theory and shorebird habitat conservation is hampered by a shortage of information on how individuals make use of successive stopover sites along migration routes (Gill et al. 1994).

Large numbers of Western Sandpipers (*Calidris mauri*), spend the winter in the Americas from Peru to California (Butler et al. 1992, Morrison et al. 1992), with small numbers overwintering as far north as southern British Columbia (Butler and Campbell 1987, Wilson 1994). Populations that winter in the Americas largely migrate to their breeding grounds up the Pacific Flyway of North America with smaller numbers migrating along the Central Flyway (Senner and Martinez 1982, Wilson 1994). During spring migration, the Western Sandpiper is the most abundant shorebird on the west coast of North America (Kjelmyr et al. 1991). In California, spring migration begins in late March and ends in mid-May (Shuford et al. 1989). Farther north in southern British Columbia, migration extends from mid-April to mid-May (Butler 1994) and 20 April to late May in Alaska (Senner 1979, Bishop and Green 1994). The Western Sandpiper breeds along coastal western Alaska, eastern Siberia, and occasionally on the North Slope of Alaska (American Ornithologists' Union 1983).

Habitat of known stopover sites for large numbers of Western Sandpipers includes tideflats and salt ponds in bays and estuaries along the coast of California, Washington, British Columbia and Alaska (Page et al. 1979; Senner et al. 1981; Butler and Campbell 1987; Butler 1994; Gill et al. 1994; Warnock and Takekawa, in press). It is unclear if and how individual Western Sandpipers use successive sites during the migration journey. Gill (1978), Senner (1979) and Senner et al. (1981) suggested that Western Sandpipers made frequent short flights during migration along the Pacific Coast, adopting a relatively low-risk

"hopping" migration strategy (Piersma 1987). Shorebird habitat conservation requires an understanding of the relative ecological contribution of individual stopover sites to migrant shorebirds.

The purpose of this paper is to describe the use of stopover sites and length of stay at successive sites along the migration route, and examine factors that may affect the rate of migration of individual Western Sandpipers during spring migration along the Pacific Coast of North America. We evaluate Western Sandpiper migration strategies and implications for the conservation of important habitats.

METHODS AND STUDY AREAS

We studied the movements of Western Sandpipers during April and May 1992 from California to Alaska (Table 1). The principal study sites in Table 1 have been described for San Francisco Bay, CA (SF) (Warnock and Takekawa, in press); Bolinas Lagoon, CA (BL) (Page et al. 1979); Grays Harbor, WA (GH) (Herman and Bulger 1981); Fraser River Delta, British Columbia (FR) (Butler et al. 1987); Stikine River Delta, AK (SR) (del Moral and Watson 1978); and Copper/Bering River Deltas, AK (Isleib and Kessel 1973) hereafter referred to as Copper River Delta (CR).

Sandpipers were captured with mist nets in intertidal areas and salt ponds within two hours either side of high tide (Butler et al. 1987; Warnock and Takekawa, in press). We measured body mass (live weight) to the nearest 0.5 g, exposed culmen to the nearest 0.1 mm, and flattened wing length to the nearest 0.1 mm. Each bird was sexed using culmen measurements (females > 24.8 mm, males < 24.2 mm, Page and Fearis 1971). One bird with an intermediate culmen length was not assigned a gender. Age classes were not assigned because they are nearly indistinguishable during late spring (Page et al. 1972). Structural size differences were standardized by calculating the slope (1.714) of the least-squares regression between the logarithm of body mass and logarithm of wing length. A condition index, representing a size-independent nutrient reserve mass, was derived for each individual by dividing the logarithm of body mass by the logarithm of wing length raised to the exponent 1.714.

A radio-transmitter weighing 0.8–1.1 g (Model BD2, Holohil Systems Ltd., Ontario) was glued with waterproof epoxy to clipped feathers on the lower back about 5 mm anterior to the uropygial

TABLE 1. Banding locations, and telemetry monitoring methods and schedule for studying movements of Western Sandpipers during spring migration, 1992.

Location	Banding dates	Telemetry method	Monitoring dates
California			
San Francisco (SF)	Apr 13–15, 22–24	daily ground, 6 flights	Apr 14–May 9 Apr 24, 27, 30 May 1, 4, 10 Apr 14–May 3
Bolinas Lagoon (BL)	Apr 19, 24	daily ground	
Washington			
Grays Harbor (GH)	none	daily ground	Apr 23–May 14
British Columbia			
Fraser River Delta (FR)	Apr 24, 29	daily flights	Apr 17–May 6
Alaska			
Stikine River Delta (SR)	Apr 27, May 5, 6	daily flights	Apr 27–May 20*
Copper River Delta (CR)	none	daily flights	Apr 29–May 24
Upper Cook Inlet			
Susitna–Redoubt Bay	none	2 flights	May 13, 15
Lower Cook Inlet			
Kachemak Bay, Homer	none	daily ground	Apr 29–May 17
Kamishak Bay	none	4 flights	May 4, 8, 11, 15
Kuskokwim Bay			
Chagvan Bay	none	daily ground	Apr 30–May 21
Yukon–Kuskokwim Delta			
Kigigik Island	none	daily ground	May 19–28, Jun 1–2

* No flights were conducted 3 May and 10 May due to severe weather.

gland (Warnock and Warnock 1993). Transmitters averaged 2–3% of total shorebird body mass. Retention time using this method of attachment was at least seven weeks (Warnock and Warnock 1993). Battery life of four reference transmitters averaged 42.5 days (range 39–45 days, SE = 1.3) and detection distances ranged from 2–5 km on the ground and 9–10 km in the air.

We monitored transmitters from the ground and from aircraft at 11 known stopover sites between San Francisco and western Alaska (Table 1, Fig. 1). Cooperators communicated daily about departures and arrivals of radio-marked birds at each site and monitoring was generally initiated when the first bird had departed locations immediately to the south. Flights were conducted at 150–1,000 m above ground level within 1–2 hours of diurnal high tide at FR and SR and daily between 09:00 and 12:00 at CR. Aircraft were equipped with paired Yagi or H antennas fixed to both wing struts. Flights covered the entire intertidal portions of each delta.

Ground monitoring was conducted daily at SF and BL from vantage points, and monitoring from aircraft over SF was conducted approximately every five days. Daily ground monitoring was done at Bowerman Basin in GH where over 50%

of Western Sandpipers stopping there roost around high tide (Herman and Bulger 1981, Wilson 1993). Monitoring ceased at SF and BL two days after no radio-marked birds were detected and large numbers of migrants were no longer present. At FR, aerial monitoring ceased after migratory numbers had diminished to <ca. 2,000 birds, and ceased at SR and CR when no radio-marked birds had been detected for two days and no radio-marked birds were present at sites to the south. In addition, twice daily flights were conducted at SR to more precisely estimate daily arrival and departure times. Population estimates were also obtained from FR, SR, and CR during aerial monitoring efforts. Occasional aerial and ground monitoring was conducted at five sites west of CR (Table 1).

We used the number of days between first and last detections at sites other than banding sites to estimate length of stay (LOS) at a site. We assumed that a bird remained at a site for the entire day that it was detected (e.g., $LOS \geq 1$ day) and that it remained at the site from the first to last detection day. Migration time was the interval between successive sites that a bird remained undetected in full one-day increments. Because we detected varying nocturnal and di-

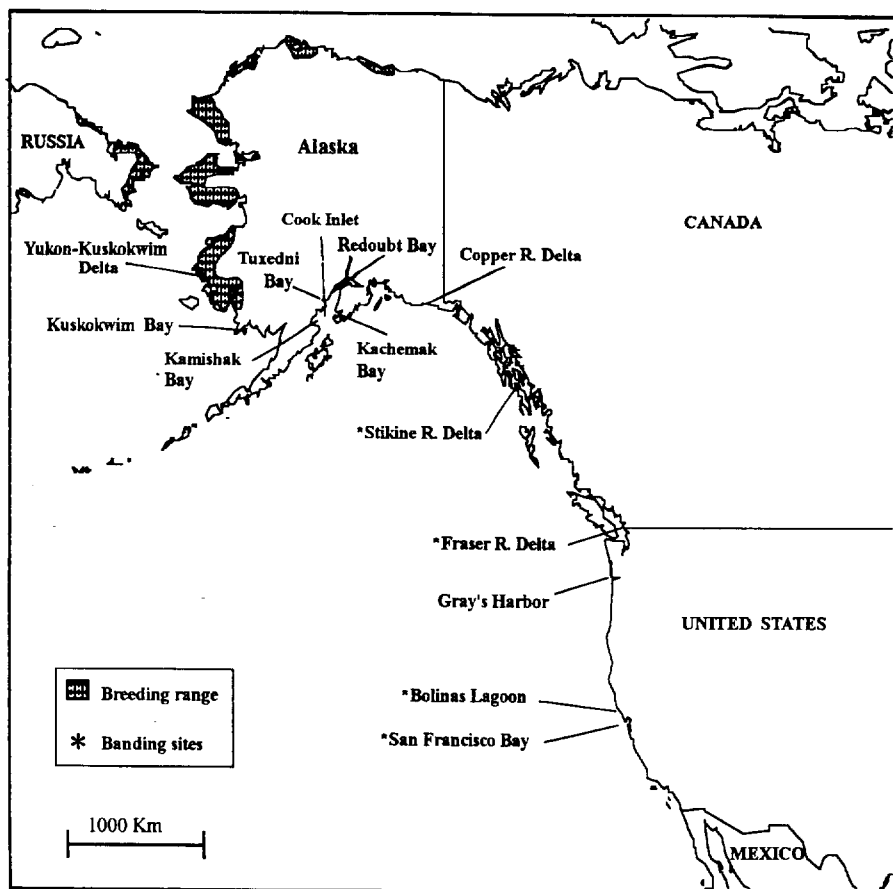


FIGURE 1. Banding and telemetry monitoring study sites to examine Western Sandpiper migration along the Pacific Coast of North America.

urnal travel patterns, we could not assume nocturnal migration (Lank 1989) to establish bounds for developing finer scale (e.g., <24 hr) estimates of LOS and migration time. A turnover rate, the probability that a bird present on the current day was present the next day, was estimated using the method of maximum likelihood (Butler et al. 1987). Relocation rate refers to the proportion of banded birds that were detected at least one time beyond the banding location and can be specific to a banding location, a stopover area, or a net rate among all locations. We use CA to refer to birds captured in California (e.g., BL and SF).

Statistical analyses were performed using the Statistical Analysis System (SAS Institute 1989). We used nonparametric statistics to test hypotheses because data were not normally distributed. We compared LOS and migration time between

sexes and study areas using the Wilcoxon two-sample test or the Kruskal Wallis Test for more than two comparisons. Spearman's rank correlation (r_s) analysis was used to evaluate the strength and significance of the relationship between variables. The *Chi-square* goodness of fit was used to test differences in relocation rates.

RESULTS

USE OF SITES

Of 87 Western Sandpipers fitted with transmitters, 77 departed the banding site and 57 were detected at least once beyond the point of banding for a net relocation rate of 74% (Table 2). Relocation rates from individual banding sites ranged from 50% (FR) to 90% (BL). The proportion of overall relocations and relocations between sexes did not vary significantly among

TABLE 2. Number and location of Western Sandpipers equipped with transmitters and number recovered along the west coast of North America. Some individuals were detected at multiple sites and are tabulated together under Relocation by Stopover Area. Total Relocation Rate represents the proportion of recoveries made at individual staging sites among all possible at that point (e.g. divisor for GH and FR = 58 sandpipers banded at SF and BL).

Banding location		Banded (n)	Relocated ^{a,b}		Individual Western Sandpiper relocation by stopover area			
			(n)	%	GH	FR	SR ^c	CR ^d
SF	male	27	23		1	4	10	16
	female	20	13		1	0	4	13
	total	48*	37*	77	2	4	15*	30*
BL	male	6	5		—	1	1	5
	female	4	4		—	0	0	4
	total	10	9	90	—	1	1	9
FR	male	12	6		—	—	4	4
	female	0	0		—	—	0	0
	total	12	6	50	—	—	4	4
SR	male	3	2		—	—	—	2
	female	4	3		—	—	—	3
	total	7	5	71	—	—	—	5
Combined	male	48	36		1	5	15	27
	female	28	20		1	0	4	20
	total	77*	57*	74	2	5	20*	48*
Total relocation rate (%)					3.4	8.6	28.6	62.3

* Unknown Sex (n = 1).

^b Among sites, sexes combined: $\chi^2 = 0.82$, df = 3, $P > 0.05$.

^c Between sexes, among sites: $\chi^2 = 4.15$, df = 3, $P > 0.05$.

^d Between sexes, among banding sites: $\chi^2 = 1.39$, df = 2, $P > 0.05$.

^e Between sexes, among banding sites: $\chi^2 = 1.91$, df = 3, $P > 0.05$.

banding locations (Table 2). Twenty (26%) radio-equipped sandpipers that departed banding sites were never relocated.

The relocation rate including all banded birds nearly doubled with each successive site farther north starting with 3.4% at GH and ending at 62.3% at CR (Table 2). The proportion of relocations of birds banded only in CA increased significantly with increasing distance northward from GH (3.4%) to CR (67%) ($r^2 = 0.98$, df = 3, $P < 0.01$). Number of stopovers at which the same individual was relocated varied with 31 birds detected at only one site, 12 at two sites and three birds at three different sites. Relocations at GH and SR represent conservative estimates. Monitoring at GH was conducted from the ground only and birds may have been missed that otherwise may have been relocated with aerial monitoring. At SR, flights could not be conducted on two dates due to severe weather conditions, and monitoring began on 27 April when three birds had already departed CA and bypassed FR (one each on 24, 25, and 26 April).

There was no preference for specific sites for either sex. The overall proportion of males and females relocated did not vary significantly among

the four study areas regularly monitored ($\chi^2 = 6.4$, df = 3, $P > 0.05$) for birds banded at all locations or for birds banded only within the largest sample at SF ($\chi^2 = 3.6$, df = 3, $P > 0.05$). Within the SR and CR study areas, sexes were detected in proportion to their frequency within the banded sample from all banding locations (Table 2). For each banding location, there was no difference in the proportion of overall detections between sexes ($\chi^2 = 5.8$, df = 3, $P > 0.05$).

Additional patterns in banding and relocation occurred among study sites. While 62% of the banded sample was eventually relocated at CR, seven SF banded birds that were relocated at either FR or SR were never relocated at CR. This represents up to 15% of the SF population that apparently bypassed CR in 1992. Six of these seven birds were captured during the first banding efforts at SF in mid-April, while the seventh was captured nearly ten days later. In addition, birds banded in mid-April at SF were less likely to stop at CR when only 13 of 28 (46%) birds were relocated at CR whereas 17 of 22 (77%) of birds banded in late April at SF were later relocated at CR. Of the ten birds banded at BL, nine were eventually relocated at CR. All 15 of

TABLE 3. Estimates of length of stay (LOS) for radio-equipped Western Sandpipers at stopover sites along the west coast of North America during spring migration, 1992. Turnover rate is probability that a bird present one day will be present the next. California birds were considered 'residents' and not included in the statistical tests.

Location	Length of stay estimate (days)									Turnover rate <i>P</i> (SE)
	Male ^a			Female ^b			Combined ^c			
	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	
CA ^d	31	11.22	0.81	24	13.54	1.14	56 ^e	12.21	0.67	0.91 (0.001)
GH	1	1.00	0	1	1.00	0	2	1.00	0	—
FR	5	3.60	0.93	—	—	—	5	3.60	0.93	0.73 (0.10)
SR ^e	13	4.31	1.01	4	2.75	0.63	18	3.83	0.75	0.76 (0.05)
CR ^f	27	2.85	0.30	20	3.50	0.43	48	3.13	0.24	0.68 (0.04)

^a Kruskal-Wallis Test of males between sites: $\chi^2 = 2.608$, $df = 3$, $P = 0.45$.

^a Kruskal-Wallis Test of males between sites; $\chi^2 = 2.608$, *df* = 3, *P* = 0.45.

^b Kruskal-Wallis Test of females between sites; $\chi^2 = 2.408$, *df* = 2, *P* = 0.29.

^c Kruskal-Wallis Test of combined sexes between sites; $\chi^2 = 3.805$, *df* = 3, *P* = 0.27.

^d Wilcoxon 2-Sample Test between sexes; *Z* = 1.44, *P* = 0.15.

^e Wilcoxon 2-Sample Test between sexes; *Z* = -0.23, *P* = 0.81.

^f Wilcoxon 2-Sample Test between sexes; *Z* = 1.09, *P* = 0.27.

^g LOS could not be estimated for 2 of 58 shorebirds banded and includes one bird of unknown sex.

the birds captured at FR and equipped with radios and all five of the SF or BL birds detected at FR were males.

At SR, we documented patterns of diurnal and nocturnal arrivals and departures. When morning (10:00) and late afternoon (15:00) flights were conducted on 5 May at SR, four radio-marked birds not previously detected apparently arrived during midday, and of eight birds previously detected, two departed and six birds remained. Consecutive flights were also conducted during the evening of 6 May (16:00), early morning on 7 May (07:00) and again that afternoon (17:00). During the first interval (nocturnal), one new bird arrived, three of the 12 previously detected birds departed while nine remained. During the second interval (diurnal), one previously detected bird departed and nine others remained.

Periodic monitoring conducted west of the Copper River Delta resulted in the detection of five radio-equipped sandpipers. All birds were located in Cook Inlet, including one at Redoubt Bay, two at Tuxedni Bay during aerial flights on 13 and 15 May, and two birds were located during ground surveys in Kachemak Bay. All five birds were previously detected at CR.

LENGTH OF STAY

Average LOS ranged from 1–3.8 days per site and was not significantly different among sites or between sexes (Table 3). The condition index among all birds captured at SF was not significantly related to the subsequent period the bird remained at CA (*P* > 0.15, *n* = 56), nor to LOS

at the next stopover (all *P* > 0.05). However, among males captured at SF there was a negative relationship such that birds with lower condition indices remained longer (*r_s* = -0.33, *P* = 0.06, *n* = 31). There was no similar relationship between condition index at capture among females and the time they remained at SF (*P* = 0.9, *n* = 24). Furthermore, among all birds, the earlier a bird was captured at SF, the longer it remained there (*r_s* = 0.6, *P* < 0.001, *n* = 56).

We examined the relationship between date of arrival and the LOS for each site. There was no correlation between date of arrival on FR and LOS (*P* = 0.9, *n* = 5). At SR, birds arriving prior to peak numbers (3 May) were all males (*n* = 4) and stayed on average 3.8 days longer (\bar{x} = 6.8 days, SE = 1.4, *n* = 4) than birds (10 males and 4 females) arriving after the peak (\bar{x} = 3.0 days, SE = 0.8, *n* = 14; *Z* = 2.15, *P* = 0.03). Similarly, date of arrival on SR was negatively correlated with the LOS (*r_s* = -0.46, *P* = 0.05, *n* = 18). At CR, birds arriving before the peak migration (9 May) did not remain longer than birds arriving after the peak migration (before: \bar{x} = 3.2 days, SE = 0.4, *n* = 25; after: \bar{x} = 3.1 days, SE = 0.4, *n* = 23; *Z* = -0.28, *P* = 0.8). LOS on CR was not correlated with date of arrival on CR (*P* = 0.51, *n* = 48).

We also examined the relationship between migration time and previous LOS. There was no relationship between the number of days a bird remained in CA after capture and the number of days it took to reach the next stopover site (FR: *P* = 0.5, *n* = 4, SR: *P* = 0.06, *n* = 12, CR: *P* = 0.22, *n* = 26) or the number of days they stayed

TABLE 4. Migration times (days) for radio-marked Western Sandpipers between major stopover areas along the Pacific Coast of North America. N represents the total number of birds migrating between the Departure and Destination regardless of banding location and includes birds stopping at multiple sites. A value of <1 for minimum migration time indicates the bird was detected at both sites on consecutive days. Only males were banded or detected at Fraser River.

Departure location destination	Distance (km)	n	Mean	SE	Min.	Max.	Mean speed (km/day)
San Francisco/Bolinas Lagoon to:							
Grays Harbor	1,110	2	4.5	2.5	2	7	356
Fraser River	1,350	4	2.3	0.6	1	4	631
Stikine River	2,410	13	4.5	0.9	1	10	1,017
male		8	4.0	1.2	1	10	
female		4	5.0	1.8	1	9	
Copper River	3,250	26	7.7	0.8	1	16	677
male		14	7.5	1.0	2	13	
female		12	8.0	1.3	1	16	
Fraser River to:							
Stikine River	1,060	6	1.3	0.4	<1	3	935
Copper River	1,900	3	4.3	0.7	3	5	464
Stikine River to:							
Copper River	840	17	2.4	0.4	<1	6	513
male		9	3.0	0.7	<1	6	
female		7	1.6	0.5	<1	4	

at those sites (FR: $P = 0.7$, $n = 4$, SR: $P = 0.07$, $n = 12$, CR: $P = 0.9$, $n = 26$). Finally, the LOS of birds on CR was not significantly related to their previous LOS on SR ($P = 0.2$, $n = 12$). However, there was a negative relationship between the LOS of birds on CR and the number of days it took them to fly from SR ($r_s = -0.45$, $P = 0.06$, $n = 17$).

RATE OF MIGRATION

Western Sandpipers took an average of 12.1 days (SE = 0.8, range 2–24, $n = 37$) after departing SF to arrive and depart from CR. There was no significant difference in total migration days between the sexes ($Z = 0.13$, $P = 0.9$). Males spent an average of 11.8 days (SE = 1.1, $n = 19$) and females an average of 12.3 days (SE = 1.3, $n = 17$) to complete this segment of spring migration.

The mean flight speed between sites ranged from 356 km/day between SF and GH and 1,017 km/day between the SF and SR (Table 4). On average, the 3,250 km journey between departure at SF and arrival at CR required 7.7 days (422 km/day), but one bird flew the distance in less than 42 hours, or about 1,850 km/day (77 km/hr). Two birds detected at 16:00 on 6 May on SR were next detected 840 km to the north on CR at 12:00 on 7 May.

Thirty days elapsed between the first departure

of a radio-equipped Western Sandpiper from SF (24 April) and the last departure from CR (22 May). Average travel time varied significantly (range 1.3–7.7 days, $\chi^2 = 29.49$, $df = 6$, $P < 0.01$) between stopover sites. Generally, travel time was greatest between farthest locations (Table 4). However, the migration rate was relatively evenly paced over those 30 days as the rate of the migration among sites (Table 4) was not different for all birds ($\chi^2 = 8.3$, $df = 6$, $P = 0.21$) or between males ($\chi^2 = 9.6$, $df = 6$, $P = 0.14$) or females ($\chi^2 = 3.1$, $df = 3$, $P = 0.37$).

DISCUSSION

USE OF SITES

We failed to find differences in LOS at different sites and in the proportion of each sex detected. These findings may suggest that for those individuals electing to stop and use a site that GH, FR, SR and CR serve similar ecological functions (e.g., energy reserve deposition) during spring migration. However, not all sites were used by all birds. The number of detections increased with latitude indicating that many CA birds bypassed intermediate sites and 12% of birds stopping at intermediate sites bypassed CR. This evidence supports the hypothesis by Gudmundsson et al. (1991) that some sites might be bypassed by individuals during migration.

However, we suspect that birds do not use the migration flyway in the same manner each year. Peak migratory single-day population estimates are of the magnitude of over 1 million birds at CR (Bishop and Green 1994), 500,000 for SF (Kjelmyr et al. 1991), GH (Herman and Bulger 1981) and FR (Butler 1994), and 350,000 for SR (Iverson and Walsh 1994), most sites reporting interannual variation in peak counts. Based upon these general peak magnitudes, we conclude among the sites we studied, most birds stop at CR relative to other sites and the specific combination of stopover sites used to the south in any given year may depend upon condition of the birds, weather, tides, and prey availability.

In addition to documenting that some shorebirds bypass major stopover areas such as CR in some years, we also established a linkage between Western Sandpiper stopover sites west of CR. Based upon aerial survey data, Senner et al. (1981) suggested that Western Sandpipers, unlike Dunlins, might need to stop in Cook Inlet after departing CR. We detected five birds in lower Cook Inlet that had previously stopped at CR thus establishing a migratory link between these stopover sites for migrant Western Sandpipers.

The variation in site use by our sample of banded shorebirds may be due to differing subpopulations of Western Sandpipers we studied. Western Sandpipers banded at SF in mid-April (13–19 Apr) remained at SF longer and were less likely to stop at CR than birds banded in late April (22–24 Apr). The earlier banded birds possibly represent a subpopulation that winters at SF, while later-banded birds represent migrants passing through SF. Similarly, the nine of ten BL birds detected at CR also suggest a degree of subpopulation structure and site fidelity. In addition, Western Sandpipers banded in FR during fall migration have been found in Kansas, Texas and Louisiana, as well as along the Pacific Coast of North America (Campbell et al. 1990). The return route in spring from wintering sites along the Atlantic and Gulf Coasts is unknown but population estimates might be boosted at FR and GH by an influx of potential subpopulations from Atlantic and Gulf Coast populations that may not stop in CA.

We are unable to explain the disproportionate representation of male Western Sandpipers among birds banded and recovered at FR and the relocation of all males prior to the peak migration at SR, but subpopulation differentiation

is a possibility. Butler et al. (1987) documented variation in timing of migration between sexes with males preceding females at FR but this fails to explain the underrepresentation of females there despite continuous monitoring throughout the migration period. Males with lower condition indices at banding at SF remained there significantly longer than females, thus smaller body size may predispose males to stop more frequently (e.g., at FR and SR) to replenish reserves. Importantly, in a one-year study, we were unable to address interannual variation in site use.

Piersma (1987) hypothesized that shorebirds follow either a hop, skip, or jump migration strategy, the hopping strategy having comparatively lower ecological risks. Senner (1979) suggested that individual Western Sandpipers migrate independently of each other by making a series of short flights between intertidal habitats along the coast (hopping strategy), in contrast to a few long, sustained flights (jumping strategy) he suggested for the Dunlin *C. alpina*. Our findings support the short-hop hypothesis with some modifications. Sandpipers caught on the same day did not remain together during migration. While many of the sandpipers made several stops, some made long, sustained flights. One individual flew the 3,250 km between SF and CR in <42 hours without being detected at intermediate sites. Furthermore, the number of detections of birds increased with latitude.

Our findings suggest a pronounced variation in individual Western Sandpiper flight strategies that is likely the result of a combination of both intrinsic and extrinsic factors and an individual optimization of migration time, energy budget, and predation minimization (Alerstam and Lindstrom 1990). We detected relatively few differences related to sex or condition indices (intrinsic factors) and suspect that wind direction (Skagen and Knopf 1994), tidal fluctuation (Lank 1989), and time of day (Piersma et al. 1990), all extrinsic factors that have been shown to affect departure of migrating *Calidris* sandpipers, likely account for some variation in LOS of our Western Sandpipers. We were unable to examine the influence of other factors such as weather (Lank 1989) and food availability (Schneider and Harrington 1981, Piersma et al. 1994), age, or molting status (Holmgren et al. 1993).

Rates of migration vary between sites (Table 4), although calculation of these rates are confounded by a scale problem. Since we measure

LOS in 24-hour periods, migration rates of Western Sandpipers will be underestimated for sites less than a potential 24-hour flight away (a Western Sandpiper migrating at 85 km/hr would have a 2,022 km range). However, it does appear that even with a conservative estimate, birds flying between FR and SR (935 km/day) and SF to SR (1,017 km/day) moved rapidly. Both of these segments have in common a coastline between British Columbia and central Southeast Alaska characterized by coastal fjord topography with few intertidal wetlands and, thus, little opportunity for high-quality intermediate stops by migrant shorebirds. Relatively slower migration rates occurred within segments likely to provide intertidal habitats, such as those between SF and GH (356 km/day) and SR to CR (513 km/day). We also documented that birds traveling slower between SR and CR remained on CR for shorter periods suggesting that better intermediate opportunities exist for feeding and reserve replenishment with a resulting lesser reliance on CR (i.e., shorter LOS). This evidence collectively lends further support to a short-flight migration strategy, in which shorebirds take advantage of a series or complex of available intertidal wetlands.

Although it is difficult to make interannual comparisons because of differences in methods, previous LOS and turnover estimates (Isleib 1979, Butler et al. 1987, Senner et al. 1981) were similar to the average of 1–3 day LOS on our study sites using radio-telemetry techniques. This relatively short period of time spent at each wetland also suggests a gradual northward journey consisting of frequent short stops when considered in conjunction with an average of 12 days to make the entire journey from SF to CR.

Many migrating birds accumulate large energy reserves prior to and during migration (Alerstam 1990). It is believed that these energy reserves play a fundamental role in the rate of migration of birds (Alerstam and Lindstrom 1990, Gudmundsson et al. 1991). However, studies have also shown that body mass was a poor predictor of LOS of banded birds (Page and Middleton 1972, Lank 1983, Morrison 1984, Dunn et al. 1988, Holmgren et al. 1993, Skagen and Knopf, 1994).

Our study found that the distances flown by individuals, the LOS at banding site, and the LOS at the next stopover site appear not to be related to the body mass at the point of capture.

While our analyses are limited by an unknown accumulation of reserves between capture and departure, the failure to detect a relationship between body mass and LOS should not be unexpected assuming that Western Sandpipers follow the short-flight hopping migration strategy. This hopping approach entails a relatively low-risk reliance on a successive complex of wetlands and thus we would not expect to detect major fluctuations in condition indices due to depletion or deposition. This is in contrast to long-distance migrants that exhibit more variability through development of significant reserves prior to departure and arrive with reserves depleted (i.e., *C. alpina* at the Copper River Delta, Senner 1979). At the same time, the individualistic migratory strategy would make detection of fluctuations in condition indices difficult due to a heterogeneous mixture of birds that arrive lean and depart fat.

We failed to detect 20 radio-equipped Western Sandpipers. There are several possible explanations. Battery failure is unlikely since the maximum time span from first banding to the last bird detected on CR was 39 days and all of our reference transmitters operated at least this length of time. Loss of transmitters is possible although retention times exceeding seven weeks have been achieved using this attachment method (Warnock and Warnock 1993). Although we could have missed some birds that were present we do not believe this to be a significant possibility due to detection distance capabilities from aerial monitoring and our daily monitoring schedule. Birds stopping for less than a 24-hour period however, could have been missed. This represents a reasonable likelihood since 11 (22%) and four (22%) birds remained at CR and SR, respectively for only one day. Some birds may have also been missed at GH since only ground monitoring was conducted there. It is also possible that some of these birds may have died during migration. The effect of carrying the radio-transmitter is largely unknown. Previous studies have shown that newly radio-marked *Calidris* shorebirds may experience higher predation rates within the first few days of banding, but this effect largely disappears after three to four days (Warnock and Warnock 1993, Warnock 1994). Of 61 Western Sandpipers radio-marked at SF/BL, three birds were known to have been depredated, all within a few days of banding. No other birds at these sites were found dead or behaving ab-

normally (i.e., roosting or foraging by themselves) and successfully departed. One radio-marked bird that had been recaptured had gained approximately 3 g in the two days since banding. Thus, while it is possible that some radio-equipped Western Sandpipers may have died during migration, we do not believe this to be a significant factor in explaining missing birds.

The most probable explanation for failure to relocate birds is that they stopped at wetlands intermediate between the principal sites we studied. Assuming that our banded sample is representative of the overall population, as much as 26% of the Western Sandpiper population bypassed our study areas which we considered to be the principal intertidal wetlands along the migration route. For example, Portage Bay and Duncan Canal in central Southeast Alaska supported an estimated 12,000 shorebirds during coordinated shorebird censuses at the same time peak populations of nearly 350,000 shorebirds were documented nearby on the SR (Iverson and Walsh 1994). There are likely other such sites along the migration corridor between SR and CR such as Dry Bay near Yakutat, Alaska (Peterson et al. 1981).

CONSERVATION IMPLICATIONS

While Western Sandpipers are capable of successfully launching long sustained flights of several thousand kilometers our data indicates this is the exception rather than a rule. Evidence suggests that Western Sandpipers use a short-flight migratory strategy. Successful migration up the coast therefore depends upon the availability of a series of intertidal wetlands along the migratory pathway similar to that suggested for interior continental migrating shorebirds that rely on resources in a highly ephemeral wetland environment (Skagen and Knopf 1993). Our study also provides supporting evidence of the importance of such sites as the Copper River Delta (Isleib 1979) and Fraser River Delta (Butler and Campbell 1987) to migrating shorebirds. We have identified a previously undescribed and significant migratory stopover site at the Stikine River Delta, and we have established migratory linkages of these stopover sites from San Francisco Bay to south central Alaska. Maintenance of the ecological integrity of these wetland habitats to support shorebird migration appears essential to shorebird conservation. Our study suggests that additional undocumented wetlands within this

region may be important components to Western Sandpiper migration. Further research is needed to identify and elucidate the relative importance of these sites.

The turnover rates we estimated provide an important variable for evaluating the relative contribution of a particular wetland complex to the ecology and conservation of shorebirds. Total bird use, calculated with turnover rates and periodic population estimates, may represent an equally important variable in evaluation of individual sites as single-day peak population estimates.

We suspect that the short-flight migration strategy and reliance upon a continuous supply of wetlands extends beyond our immediate study areas to points west of the Copper River Delta. Intertidal wetlands along the southcentral and southwestern coast of Alaska en route to western Alaska breeding areas may be equally important components of shorebird migratory habitat.

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