Waterbirds around the world

A global overview of the conservation, management and research of the world's waterbird flyways

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Spring migration patterns in Western Sandpipers Calidris mauri

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ABSTRACT
One hundred and thirty-two Western Sandpipers Calidris mauri were radio-marked at two sites on the Pacific coast of North America (San Francisco Bay, California, and Grays Harbor, Washington) and at an interior wetland in the western Great Basin (Honey Lake, California). The northward migration of these birds was monitored at a network of 12 major stopover sites and four breeding areas. Eighty-eight percent of the birds were relocated at 10 stopover sites and two breeding areas between San Francisco Bay and the Yukon-Kuskokwim Delta, Alaska (c. 4 200 km). On average, birds were relocated at fewer than two sites, with the Copper River Delta in Alaska being the single most important stopover site. Migrant birds radio-marked at the interior site shifted to the coast between Oregon and Washington, and then continued their migration along the Pacific coast. Individual birds used a wide variety of migration strategies, from stopping at sites 200-300 km apart to flying as far as 2 100 km in under 48 hours. At the population level, we observed heterogeneity in phenology and site use, a strategy well adapted to the changing landscape that Western Sandpipers must navigate during migration, especially in interior regions.

INTRODUCTION
Large-scale marking studies have been successful in providing information on bird migration routes and stopover areas (Lincoln 1959, Butler et al. 1996). Determining how individual, small (<35 g) birds such as Calidrid sandpipers migrate over large distances has been challenging because of technological, logistical, and financial constraints. Systematic data on sites used or not used by individual shorebirds along major segments of their migration flyways did not exist until Iverson et al. (1996) first documented the coastal migration routes of individual Western Sandpipers Calidris mauri between San Francisco Bay, California, and Cook Inlet, Alaska, during spring 1992.

The Western Sandpiper, a mid- to long-distance migrant (Johnson & Herter 1990), is the most numerous shorebird along the Pacific Flyway. In some years, its population can number over four million individuals (Bishop et al. 2000). This Nearctic shorebird breeds principally in western Alaska, with smaller numbers in north-eastern Russia and northern and central Alaska (Kessel 1989, Wilson 1994, Bishop & Warnock 1998). The wintering areas extend from California to Peru, and from the southern Atlantic coast of the USA and the Gulf of Mexico to northern South America (Wilson 1994).

Along the Pacific Flyway, five coastal migratory stopover sites have been documented which support over 500 000 migrant Western Sandpipers in spring: San Francisco Bay (Stenzel & Page 1988), Grays Harbor, Washington (Wilson 1993), Fraser River Delta, British Columbia (Butler et al. 1987, Butler 1994), Stikine River Delta, Alaska (G. Iverson unpubl. data) and Copper River Delta, Alaska (Isleib 1979, Bishop et al. 2000). Areas in the Central Valley of California and the western Great Basin of the United States also host large numbers of migrating Western Sandpipers (Harrington & Perry 1997, Oiring & Reed 1997), but the use of these interior areas by Western Sandpipers and other shorebirds remains poorly understood.

Our previous work has shown that Western Sandpipers migrate northward from San Francisco Bay along the Pacific coast using a rapid, short-flight migration strategy (Iverson et al. 1996) which includes short (1-3 days) stays at large estuarine habitats (Warnock & Bishop 1998). Males precede females, and between the sexes there are differences in the likelihood of a stopover being used (Bishop et al. 2004). Our research also provided evidence that the Yukon-Kuskokwim Delta in Alaska is the final breeding destination for many of the birds migrating through San Francisco Bay and other areas on the Pacific coast (Bishop & Warnock 1998).

Here, we examine spring migration by individual Western Sandpipers radio-marked in 1995 and 1996 in North America at two sites on the Pacific coast and an interior site in the Great Basin. We describe and analyze the effects of year and banding location on phenology and use of stopovers during the northward migration to the breeding grounds, a distance of more than 4 000 km. We also describe a previously unknown migration route of Western Sandpipers through the western Great Basin.

METHODS
We captured Western Sandpipers from 17 to 30 April 1995 and 17 April to 3 May 1996 at two sites on the Pacific coast, San Francisco Bay (hereafter referred to as San Francisco; 37°46’N, 122°26’W) and Grays Harbor (46°57’N, 124°03’W), and at an interior wetland in the Great Basin, Honey Lake, California (40°14’N, 120°21’W; Fig. 1). Generally, capture dates corresponded with the peak migration at the trapping sites. Birds were trapped in mist-nets placed in salt ponds, mudflats, and
freshwater ponds during daylight hours. Each bird was weighed to the nearest 0.5 g, and the exposed culmen, flattened wing chord, and tarsus were measured (in mm). Sex was determined by length of exposed culmen (males <24.2 mm; females >24.8 mm; unknown 24.2-24.8 mm; Page & Fearis 1971); birds were not aged.

Radio-transmitters weighing 0.9 g (Model BD-2; Holohil Systems Ltd., Woodlawn, Ontario, Canada) were glued to the lower backs of 132 Western Sandpipers (1995, n = 61; 1996, n = 71), following methods described in Warnock & Warnock (1993). Retention time was previously found to be more than seven weeks in this species (Warnock & Takekawa 1996). The transmitter averaged about 3% of a bird’s body mass, and the expected battery life was more than four weeks. The battery life of test transmitters averaged 39.0 ± 2.5 days (n = 5).

We searched for radio-marked Western Sandpipers from the ground and fixed-wing aircraft at 15 sites in 1995 and 19 sites in 1996 (Fig. 1, Table 1; see Bishop & Warnock 1998 and Warnock & Bishop 1998 for dates and locations). Monitoring began north of the banding sites as soon as radio-marked birds were suspected of departing and continued until either all radio-marked birds had departed, or when minimal migratory activity was observed. The number and timing of flights varied by area and year. In 1996, daily flights occurred at Grays Harbor, in the Fraser River Delta, and in the Stikine River Delta, Yakutat Forelands, Copper River Delta and Kachemak Bay in Alaska (Fig. 1). During peak migration in 1996, two flights were flown per day at the Fraser River Delta (n = 2 days) and Copper River Delta (n = 6 days).

For our analyses, we combined monitoring sites into 11 sites (Fig. 1). Each site beyond the banding location where an individual bird’s radio signal was detected was counted as one relocation, with a maximum of one detection per monitoring site, regardless of how many times the bird was detected at that site. We assumed that all radio-marked birds present at a banding or monitoring site were detected regardless of the monitoring method. High winds prevented monitoring at the Copper River Delta on 6 May 1995; we assumed that birds detected on 7 May had arrived on 6 May (n = 7). Of the 71 radio-marked birds in 1996, four radio frequencies were identical to transmitters on Caribou Rangifer rangifer at Bristol Bay in western Alaska, and were only monitored at more southerly sites. Where appropriate, these four birds and one bird that died or lost its radio at Stikine River Delta were excluded in some analyses.

Statistical analyses were performed using STATA (Computing Resource Center, Santa Monica, California 1992). Data were examined for departures from normality and homogeneity by preliminary graphing and testing of data. For analyses, yearly dates were converted into Julian dates (JD). When reporting results, we adjusted all 1996 dates to 1995 (1996 date + 1 day), since 1996 was a leap year. For all tests, significance was determined if P ≤ 0.05. Means are reported ± one standard deviation (SD).

RESULTS
Relocations
In 1995, we relocated 51 of the 61 Western Sandpipers (84%) a total of 85 times at eight of the nine monitoring sites. In 1996, 64 of 69 Western Sandpipers (93%) were relocated a total of 140 times at 10 of the 11 monitoring sites (Table 2, Fig. 2). For all monitoring sites, the number of birds relocated between years was not significantly different (x^2 = 2.65, P = 0.10). We failed to relocate 15 birds after departure from their banding site (six males and nine females), both years combined. The number of birds not found was not significantly different among banding sites (x^2 = 9.1, P > 0.60).

In 1995, birds banded at San Francisco stopped at an average of 1.6 ± 0.6 sites (max. 3); birds banded at Honey Lake at 1.6 ± 0.8 sites (max. 3); and birds banded at Grays Harbor at 1.7 ± 0.5 sites (max. 2). In 1996, with more extensive aerial monitoring efforts at five sites (Humboldt Bay, Grays Harbor, Yakutat Forelands, Copper River Delta, and Bristol Bay), San Francisco radio-marked birds were relocated at an average of 2.6 ± 1.1 sites (max. 5), Honey Lake birds at 1.6 ± 0.7 sites

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**Table 1. Distance (km) between banding sites of radio-marked Western Sandpipers Calidris mauri and more northerly monitoring sites.**

<table>
<thead>
<tr>
<th>Banding site</th>
<th>San Francisco CA</th>
<th>Honey Lake CA</th>
<th>Grays Harbor WA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humboldt Bay CA</td>
<td>410</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grays Harbor WA</td>
<td>1 110</td>
<td>790</td>
<td></td>
</tr>
<tr>
<td>Fraser River Delta BC</td>
<td>1 350</td>
<td>1 030</td>
<td>240</td>
</tr>
<tr>
<td>Stikine River Delta AK</td>
<td>2 410</td>
<td>2 090</td>
<td>1 300</td>
</tr>
<tr>
<td>Yakutat Forelands AK</td>
<td>2 940</td>
<td>2 620</td>
<td>1 830</td>
</tr>
<tr>
<td>Copper River Delta AK</td>
<td>3 250</td>
<td>2 930</td>
<td>2 140</td>
</tr>
<tr>
<td>Cook Inlet AK</td>
<td>3 590</td>
<td>3 270</td>
<td>2 480</td>
</tr>
<tr>
<td>Mulchatna River AK</td>
<td>3 880</td>
<td>3 560</td>
<td>2 770</td>
</tr>
<tr>
<td>Bristol Bay AK</td>
<td>4 000</td>
<td>3 680</td>
<td>2 890</td>
</tr>
<tr>
<td>Yukon-Kuskokwim Delta AK</td>
<td>4 200</td>
<td>3 880</td>
<td>3 090</td>
</tr>
</tbody>
</table>

CA = California, USA; WA = Washington, USA; BC = British Columbia, Canada; AK = Alaska, USA.

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**Fig. 1.** Banding and monitoring sites for Western Sandpiper Calidris mauri telemetry study, spring 1995 and 1996. Combined monitoring sites include: Grays Harbor and Willapa Bay, Washington; Fraser River Delta and Tofino Beach, British Columbia; eastern and western Cook Inlet, and Bristol Bay, Alaska (combines two stopover and two breeding areas).
The Copper River Delta was the stopover site with the highest number of relocations, with 61% of marked birds stopping there in 1995 and 80% in 1996. Significantly more radio-marked birds were relocated at the Copper River Delta in 1996 than in 1995 ($\chi^2 = 4.97, P = 0.03$). San Francisco birds had the fewest relocations (55%, 1995), while Grays Harbor birds had the most relocations (93%, 1996; Fig. 2). In 1996, we conducted twice-daily flights on the Copper River Delta during six days and relocated 40 different radio-marked birds. Four birds (10%) were detected on one flight only, indicating that these birds migrated through the Copper River Delta in less than 12 hours.

We also relocated radio-marked Western Sandpipers at Humboldt Bay, Willapa Bay, Yakutat Forelands, Bristol Bay (a stopover and breeding area), and two other breeding areas in Alaska (Fig. 1). Although Willapa Bay is only 35-90 km (depending on location) south of Grays Harbor, no sandpipers relocated at Willapa Bay were detected within Grays Harbor. However, one Willapa bird was detected at the mouth of Grays Harbor on the outer beach. At the Yakutat Forelands, sandpipers were located along a 100 km stretch from Yakutat Bay southeast to the East Alsek River, with the majority of relocations occurring between Ocean Cape and the Seal Creek-Ahrnklin River estuary. On the breeding grounds, birds were relocated on Alaska’s Yukon-Kuskokwim Delta in both years and near the confluence of the Nushagak and Mulchatna Rivers in 1996, the only year that this site was monitored.

Despite extensive coverage in both years, no radio-marked birds were relocated north of Redoubt Bay (north-western Cook Inlet) or along the Alaska Peninsula between Naknek and Unimak Island. Nor were radio-marked birds relocated during our one year of monitoring efforts at Malheur Lake in eastern Oregon (Fig. 1) and at Cape Peirce, Alaska (west of Bristol Bay). In 1995, no birds were detected at Humboldt Bay in northern California, although they were detected in 1996 when we increased our effort.

**Phenology**

The mean departure dates of radio-marked Western Sandpipers from the three banding sites ranged from 26 April to 3 May in 1995 and from 27 April to 8 May in 1996 (Table 3). The average arrival dates at sites monitored ranged from 29 April at Malheur Lake in eastern Oregon (Fig. 1) and at Cape Peirce, Alaska (west of Bristol Bay). In 1995, no birds were detected at Humboldt Bay in northern California, although they were detected in 1996 when we increased our effort.

**Fig. 2.** Relocations (%) of radio-marked Western Sandpipers *Calidris mauri* at areas north of banding sites in spring 1995 and 1996. Stopover areas, beginning at the southernmost monitoring site: HB = Humboldt Bay, California; GH = Grays Harbor and Willapa Bay, Washington; FR = Fraser River Delta and Tofino Beach, British Columbia; SR = Stikine River Delta, Alaska; YF = Yakutat Forelands, Alaska; CR = Copper River Delta, Alaska; CI = Cook Inlet, Alaska; BB = Bristol Bay, Alaska (a stopover and breeding area). Breeding areas: MR = Mulchatna River, Alaska; YK = Yukon-Kuskokwim Delta, Alaska. There were no relocations at Malheur Lake, Oregon.

(max. 3), and Grays Harbor birds at 1.6 ± 0.6 sites (max. 3). In 1996, we relocated three San Francisco birds (two males, one female) at five stopover sites.

### Table 2. Numbers of Western Sandpipers *Calidris mauri* radio-marked and percent relocated at least once to the north. Spring 1995 and 1996.

<table>
<thead>
<tr>
<th>Banding location</th>
<th>1995 Banded</th>
<th>% Relocated</th>
<th>1996 Banded</th>
<th>% Relocated</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Francisco, CA</td>
<td>Male 16</td>
<td>94</td>
<td>15</td>
<td>100$^1$</td>
</tr>
<tr>
<td></td>
<td>Female 13</td>
<td>69</td>
<td>15</td>
<td>87</td>
</tr>
<tr>
<td>Honey Lake, CA</td>
<td>Male 12</td>
<td>83</td>
<td>7</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td>Female 6</td>
<td>67</td>
<td>5</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Unknown 0</td>
<td>0</td>
<td>1</td>
<td>0$^2$</td>
</tr>
<tr>
<td>Grays Harbor, WA</td>
<td>Male 7</td>
<td>100</td>
<td>21</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>Female 7</td>
<td>86</td>
<td>6</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Unknown 0</td>
<td>0</td>
<td>1</td>
<td>100</td>
</tr>
</tbody>
</table>

$^1$ One bird not included due to overlap with Caribou frequency at northern site.

The Copper River Delta was the stopover site with the highest number of relocations, with 61% of marked birds stopping there in 1995 and 80% in 1996. Significantly more radio-marked birds were relocated at the Copper River Delta in 1996 than in 1995 ($\chi^2 = 4.97, P = 0.03$). San Francisco birds had the fewest relocations (55%, 1995), while Grays Harbor birds had the most relocations (93%, 1996; Fig. 2). In 1996, we conducted twice-daily flights on the Copper River Delta during six days and relocated 40 different radio-marked birds. Four birds (10%) were detected on one flight only, indicating that these birds migrated through the Copper River Delta in less than 12 hours.

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### Phenology

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On average, individual radio-marked Western Sandpipers were relocated at fewer than two of the 10 monitoring sites (including stopover and breeding sites). We may have missed some birds at our monitoring sites (i.e. birds passing through a site in less than 24 hours), but from our twice-daily flights at the Fraser and Copper River Deltas, the number of birds missed does not appear to be over 10%. It seems likely that birds were stopping at smaller, unmonitored sites, since travel times between known stopover areas were too long for uninterrupted flight (Bishop et al. 2004).

Iverson et al. (1996) concluded that Western Sandpipers from San Francisco were more likely to be detected at stopover sites with increasing latitude. This study fails to support that contention. At Humboldt Bay, c. 400 km north of San Francisco, we relocated 30% of birds radio-marked at San Francisco in 1996 when we increased ground coverage and added aerial coverage. Relocations at Grays Harbor were slightly higher than the more northerly sites of Stikine River Delta and Yakutat Forelands during both years of this study, even though fewer aerial surveys were conducted at Grays Harbor. We suggest that the low stopover use at Grays Harbor (3.4% of San Francisco radio-marked birds stopping at the Fraser River Delta in 1992, we relocated 27-28% in both 1995 and 1996).

At the population level, all of the sites that were regularly monitored north of San Francisco up to and including the Copper River Delta were used by at least 20% of the radio-marked Western Sandpipers during one of the two years of this study. If we assume that the radio-marked birds are representative of the Western Sandpiper’s Pacific Flyway population, then each of these stopover sites qualifies, at a minimum, as an “international shorebird site” under the criteria used by the Western Hemisphere Shorebird Reserve Network (WHSRN), i.e. a site used by at least 10% of the flyway population of a species. As of January 2005, Humboldt Bay, Grays Harbor, the Fraser River Delta and the Copper River Delta are official WHSRN sites. However, Controller Bay, an area of high shorebird use (M.A. Bishop unpubl. data) located just east of the Copper River Delta, is not part of the Copper River Delta WHSRN hemispheric site designation. Alaska’s Stikine River Delta and Yakutat Forelands also lack WHSRN designation.

### DISCUSSION

#### Stopover use

Overall, individual radio-marked Western Sandpipers showed a wide variety of migration strategies, from stopping at sites 200-300 km apart to flying as far as 2 100 km in less than 48 hours.

![Fig. 3. Mean arrival dates (± SD; dates adjusted for leap year) for radio-marked Western Sandpipers *Calidris mauri* at stopover and breeding sites where four or more relocations were recorded; spring 1995 and 1996. Stopover areas: HB = Humboldt Bay, California; GH = Grays Harbor and Willapa Bay, Washington; FR = Fraser River Delta and Tofino Beach, British Columbia; SR = Stikine River Delta, Alaska; YF = Yakutat Forelands, Alaska; CR = Copper River Delta, Alaska; CI = Cook Inlet, Alaska. Breeding area: YK = Yukon-Kuskokwim Delta, Alaska.](image)

1. 1996 includes two birds dropped from other analyses (one from San Francisco and one from Honey Lake).

Table 3. Banding and mean departure dates from banding sites of radio-marked Western Sandpipers *Calidris mauri* captured at three locations. Dates adjusted so that the 1996 leap year dates equal 1995 (1996 date + one day).

<table>
<thead>
<tr>
<th>Banding location</th>
<th>Year</th>
<th>Banding dates</th>
<th>Mean departure date</th>
<th>Range</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Francisco CA</td>
<td>1995</td>
<td>17-19, 21-23 Apr</td>
<td>28 Apr</td>
<td>20 Apr - 5 May</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>18-23 Apr</td>
<td>28 Apr</td>
<td>22 Apr - 9 May</td>
<td>30</td>
</tr>
<tr>
<td>Honey Lake CA</td>
<td>1995</td>
<td>27, 28, 30 Apr</td>
<td>1 May</td>
<td>27 Apr - 8 May</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>26 Apr</td>
<td>27 Apr</td>
<td>27 Apr - 30 Apr</td>
<td>13</td>
</tr>
<tr>
<td>Grays Harbor WA</td>
<td>1995</td>
<td>24, 25, 28 Apr</td>
<td>3 May</td>
<td>24 Apr - 9 May</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>28-30 Apr, 1,3,4 May</td>
<td>8 May</td>
<td>3 May - 13 May</td>
<td>28</td>
</tr>
</tbody>
</table>
Similar to previous studies (Iverson et al. 1996, Bishop et al. 2000, Bishop et al. 2004), our relocations revealed the importance of the Copper River Delta in south-central Alaska for Western Sandpipers. It has been asserted that virtually all of the world’s population of Western Sandpipers stops at the Copper River Delta during their northward migration (Wilson 1994). Even accounting for birds that pass through too quickly to be relocated, it appears that in some years, some western Great Basin and San Francisco birds may not be stopping at the Copper River Delta. For birds radio-marked at Grays Harbor however, the high numbers of relocations recorded in both years (>71%) indicate that the Copper River Delta is of great importance for birds migrating through this site. In contrast, the Fraser River Delta (240 km to the north of Grays Harbor) in British Columbia had lower use (<15%) by Grays Harbor birds, and relocations at Stikine River Delta and Yakutat Forelands were only slightly higher.

Our study has also revealed the importance of Yakutat Forelands for the Pacific Flyway population of Western Sandpipers. Radio-marked birds from all three banding sites used Yakutat Forelands in both years, in particular the area between the town of Yakutat and the Ahmknik River. Subsequent ground surveys at the Seal Creek-Ahmknik River estuary confirmed that Western Sandpipers are the most abundant shorebird in spring in this area (Andres & Browne 1998).

### Migration routes

The western Great Basin is one of the least studied areas in North America for shorebirds (Neel & Henry 1997). For the first time, we established a northward migration route for Western Sandpipers passing through the western Great Basin. Western Great Basin birds, represented by birds marked at Honey Lake, were relocated at coastal sites from Grays Harbor to the Copper River Delta. However, no Honey Lake birds were detected at Humboldt Bay in either year, nor were Honey Lake birds detected inland at Malheur National Wildlife Refuge, Oregon, in spring 1996 during four monitoring days that included one aerial survey. Many sites used by Western Sandpipers in the western Great Basin are dry in some years (Robinson & Warnock 1997). The springs of 1995 and 1996 were wet (N. Warnock unpubl. data) and habitat was abundant. In wet years, these birds may be moving more slowly through the Great Basin than in dry years, before shifting to the coast.

Western Sandpipers can be abundant in the Willamette Valley of Oregon during spring (Paulson 1993). A possible migration route for these interior migrating birds is to travel up the western side of the Great Basin through the Klamath Basin in northern California, into the Willamette Valley of Oregon to the Columbia River, and then shift westward onto the Washington coast. Greater White-fronted Geese Anser albifrons migrating through the Central Valley of California, just west and parallel to the western Great Basin, follow a similar route to their breeding grounds (Ely & Takekawa 1996) which overlap with those of the Western Sandpiper

### Effects of radio-marking on phenology

Several studies have shown that shorebirds lose body mass during and immediately after capture (Pienkowski et al. 1979, Davidson 1984, Lindström 1995, Warnock et al. 1997). Our previous work suggests that radio-marked birds may require additional days to regain weight and adjust to the radio (Warnock & Bishop 1998, Warnock et al. 2004). In this study, we radio-marked birds just prior to and during peak migration at San Francisco (about 20-25 April; Storer 1951, Stenzel & Page 1988) and at Grays Harbor (late April to early May, N. Warnock unpubl. data). Nevertheless, the average departure from both sites occurred a few days later than peak migration in both years. This pattern was repeated at other stopover sites. We cannot rule out an effect of capture or the radio-transmitter on the migration timing of the marked birds; however, it appears to be a short-term effect, as evidenced by our very high relocation rate at sites to the north, including the breeding grounds. For some birds, there was no apparent capture effect. For instance, two Grays Harbor birds left the day they were captured and were seen at Fraser River one day later.

### CONCLUSIONS

At the individual level, data on inter-annual differences and flight strategies used by shorebirds during migration are still lacking. This would involve trapping and tracking the same individual in consecutive years, an improbable event in the case of Western Sandpipers, or use of a long-lived transmitter and attachment. At the population level, however, this study suggests that the migration strategies of Western Sandpipers vary, as they do in other shorebirds (Myers et al. 1990, Davidson & Wilson 1992, Skagen & Knopf 1994, Warnock et al. 2004). There appears to be heterogeneity in phenology and site use during migration, a strategy that is well adapted to the changing landscape that Western Sandpipers must navigate during migration, especially in interior regions.

In future studies, it would be valuable to examine the migration strategies of Western Sandpipers during early and late spring migration and during autumn migration, periods not covered by this study. Our study reveals the importance of maintaining a network of stopover sites along the coast and interior of the Pacific Flyway. At the same time, our study demonstrates the singular importance of the Copper River Delta for migrant Western Sandpipers in spring. The conservation of Western Sandpipers clearly hinges on this network of stopover areas.

### ACKNOWLEDGMENTS

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