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HABITAT PREFERENCES OF WINTERING SHOREBIRDS IN A TEMPORALLY CHANGING ENVIRONMENT: WESTERN SANDPIPERS IN THE SAN FRANCISCO BAY ESTUARY

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ABSTRACT.—We examined habitat preferences of 106 radio-marked Western Sandpipers (*Calidris mauri*) in the San Francisco Bay estuary during winter and spring at two scales: comparing proportions of habitats in their home range with habitats available in the study area (second-order selection), and comparing proportions of radio locations in different habitats with their availability in the home range (third-order selection). Daily and seasonal habitat preferences differed significantly as habitat availability changed temporally. Under second-order selection, Western Sandpipers preferred tidal sloughs and mud flats on winter low tides, and salt-pond levees at high tides. They preferred salt-pond levees and mud flats at low tides, and salt-pond levees at high tides under third-order selection. During the spring, their preferred habitats were drained and tidal salt ponds, and seasonal wetlands at high tide. At low tide, their preferred habitats were tidal sloughs and tidal salt ponds. Salt-marsh plains were the least preferred habitats during both seasons. Adults were more selective than juveniles in use of low tide habitats, but salt-pond levees were the most preferred habitats for both. Habitat preferences varied considerably when different estimates of habitat availability and use were used. If mud-flat habitats were measured as linear foraging areas along the tide line, the preference for those habitats increased from second to first. When second-order selection was estimated from radio locations rather than home ranges, the resulting composition was similar to third-order selection. Our results suggest that regional conservation plans that restore salt marshes for the benefit of endangered species must consider the effects of losing artificial salt-pond habitats, which are locally important for sandpipers.
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SAN FRANCISCO BAY is one of the largest estuaries on the Pacific coast of North America (Conomos 1979), but beginning in 1850 most of the natural wetlands of the bay were diked and altered for agricultural, urban, and industrial purposes (Ver Planck 1958). Although much of the natural habitat has been lost over the past 150 years, the estuary still supports many species of wildlife, including the largest and most diverse community of wintering and migrating shorebirds on the western coast of the United States (J. Kjelmyr, G. W. Page, W. D. Shuford, and L. E. Stenzel, unpubl. 1991 report)

Despite the importance of the San Francisco Bay estuary for shorebirds, few studies have been conducted on their wintering ecology (Recher 1966, Kelly and Cogswell 1979, Holway 1990). Little is known about selection of habitats by shorebirds during the winter, or how their habitat preferences change temporally. Thus, the extent to which further modification of wetlands may change the distribution and abundance of shorebirds in the estuary is not known.

We describe habitat preferences of radio-marked Western Sandpipers (*Calidris mauri*) in South San Francisco Bay during winter and spring, 1991-1992. We examine preferences at two levels of selection (Johnson 1980): (1) use of habitats within home ranges of Western Sandpipers compared to available habitat in the overall study area (second-order selection); and (2) comparison of habitat use determined from radio locations to habitats available in home ranges (third-order selection). In addition, we address the inherent difficulties of measuring habitat availability in dynamic ecosystems, and

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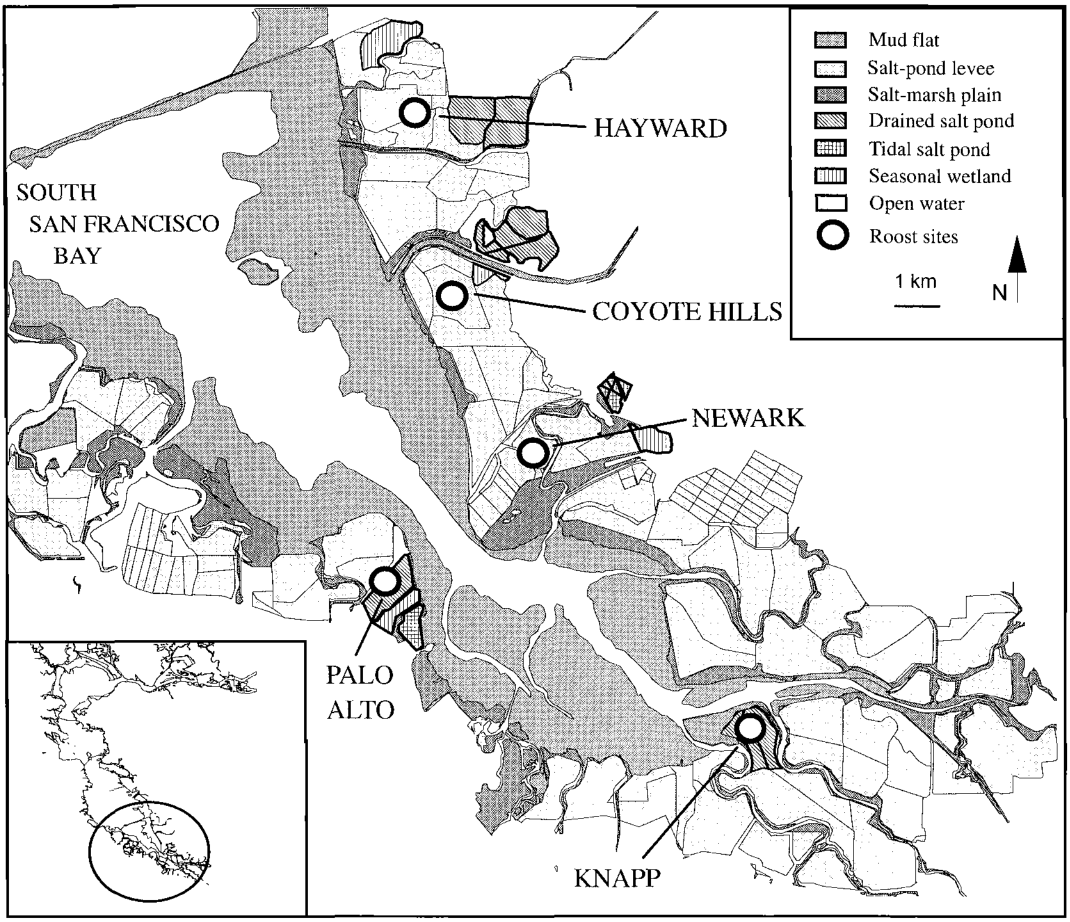

Fig. 1. Map of South San Francisco Bay, California showing distribution of habitat types and Western Sandpiper roost sites at Newark, Palo Alto, and Coyote Hills.

the effect different estimates of habitat use have on the outcome of selection tests.

METHODS

Study area.—We conducted fieldwork during the winter (November–March) and spring (April–May) of 1991–1992 in South San Francisco Bay (Fig. 1), which we define as the region in the estuary south of the San Mateo Bridge. The study area included a narrow (1 km), deep (12 m) navigation channel, surrounded by broad shallows (5,500 ha), which were exposed as mud flats during low tide. Near-shore areas consisted of extensive commercial salt-evaporation ponds and remnant salt marshes.

Capture and marking.—Five major shorebird roosts were located in South San Francisco Bay area salt ponds (Fig. 1). Each roost supported from 5,000 to 20,000 birds during high tide. Western Sandpipers from three of these roost sites (Palo Alto, Newark, and Coyote Hills) were radio-marked during the early winter (mid November), mid winter (late January), and spring (mid April). Birds were captured in mist nets erected at several locations within each roosting site on high tides during daylight. All captured birds were fitted with metal U.S. Fish and Wildlife Service leg bands and a location-specific combination of UV-resistant color bands. Birds were weighed, measured, and aged based on the presence (juvenile) or absence (adult) of chestnut-colored inner median wing coverts (Prater et al. 1977). Because this character was not reliable for age determination during the spring, only birds caught in the winter were aged. Sexes of the birds were determined from bill length (Page and Fearis 1971).

Western Sandpipers larger than 24 g were fitted with 1.0-g radio transmitters (Model BD-2, Holohil Systems Ltd., Ottawa, Canada) that were glued to their lower back with marine epoxy (Warnock and War-

TABLE 1. Total area (km²) and mean block size ($\bar{x}$ ± SE) of contiguous tracts of habitat in study area in South San Francisco Bay at low and high tide. Habitats listed in order of decreasing availability.

Habitat type	Low tide	High tide[a]	Block size
Mud flats	54.60	0	10.50 ± 3.91
Salt-marsh plains	12.06	9.04	1.96 ± 0.67
Salt-pond levees	4.26	4.26	4.90 ± 0.90
Drained salt ponds	1.90	1.90	5.33 ± 2.84
Tidal salt ponds	0.70	0.70	0.92 ± 0.40
Seasonal wetlands	0.63	0.63	0.43 ± 0.20
Tidal sloughs	0.39	0	0.44 ± 0.18
Total	74.54	16.53	

[a] Mud flats and tidal sloughs were excluded from high-tide analyses (see Methods).

nock 1993). In most cases (>80%), birds were caught, processed, and released within 15 min of capture. Transmitters had a lifespan of 30 days, and a range up to 4 km on level ground or up to 9 km from a 120-m hill.

Birds were given three days to adjust to transmitters. Locations were taken daily for each bird within 1 h of each low and high tide (4 locations per bird-day). No more than 33 birds were followed at one time. Tides were classified as low tides (≤0.76 m at Golden Gate Bridge) when mud flats were widely available, and high tides (≥1.30 m) when mud flats were not exposed. If weather changed the expected tide levels, we adjusted the observation period. Locations were taken during both day and night in the winter and only during the day in the spring.

Radio telemetry.—Ground surveys were conducted daily by two observers driving trucks with dual-Yagi null-peak antenna systems. Azimuth information was entered directly into a laptop computer, and a modified version of the XYLOG and UTMTEL triangulation programs (Dodge and Steiner 1986, Dodge et al. 1986) was used to estimate Universal Transverse Mercator (UTM) coordinates of each sandpiper. Locations that bordered on the edge (within 50 m) of two habitats were not used for analyses.

We tried to minimize location errors as birds moved by estimating their position from two bearings taken within 10 min and usually within 3 km of each other. At the beginning of the project, accuracy of the telemetry locations was determined by placing six test transmitters at randomly selected locations from 0.5 to 3.0 km apart within the study area. Three observers located test transmitters (n = 12 locations/observer) with the null-peak truck systems used in the project, and the linear differences between the actual and estimated locations were calculated.

Habitat categories.—The total study area was defined to include all habitat blocks (i.e. contiguous areas of a single habitat type; see Table 1) that contained at least one radio location of a Western Sandpiper, or which overlapped a home range (Aebischer et al. 1993). Seven habitat types (Table 1, Fig. 1) were identified as potentially available roosting or foraging areas for Western Sandpipers. Natural habitats included mud flats, salt-marsh plains, and tidal sloughs. Mud flats consisted of shallow benthic areas inundated during high tides and exposed during low tides. The salt-marsh plains included tidal wetlands thickly vegetated with pickleweed (*Salicornia virginica*) and cord grass (*Spartina foliosa*). This habitat occurred in strips along slough and levee edges and in a few large (>100 ha) habitat blocks. We classified drainage channels winding through a salt-marsh plain into a mud flat as tidal sloughs.

We divided the artificial salt-pond complex into four habitats: salt-pond levees, drained salt ponds, tidal salt ponds, and seasonal wetlands. Western Sandpipers primarily used levees because most ponds were flooded to levels that were too deep for wading. The salt-pond operator drained the ponds at irregular intervals, and when water levels became low enough (<5 cm) to permit the sandpipers to wade in the pond, we identified them as drained salt-pond habitats. We defined tidal salt-pond habitats as salt ponds that had been removed from production and were restored to tidal action. These ponds received diminished tidal flows, and their substrates remained exposed for several hours longer than those in the mud flats. We defined seasonal wetland habitats as those former salt ponds that had no tidal flow and received freshwater, primarily from rainfall.

Estimates of habitat proportions.—The amount of each habitat within the total study area and within each home range was estimated by entering radio locations and home-range ellipses into a geographic information system (GIS; ARCINFO) and by merging them with digitized versions of 1985 U.S. Fish and Wildlife Service National Wetland Inventory (NWI) maps. Each radio location was assigned a habitat type, and we calculated habitat composition of each individual's home range and of the total study area. The amount of mud flats, tidal sloughs, and salt-marsh plains was estimated at mean lower low water (MLLW). All seven habitats were available during low tides, but only five were present during high tides because mud flats and tidal sloughs were submerged.

Seasonal wetlands, drained salt ponds, and tidal salt ponds were identified and measured on the NWI maps. The extent of salt-pond levees was estimated by multiplying the perimeter of the ponds by the average inner width of the surrounding levee walls (10 m). We estimated the proportion (25%) of salt-marsh plain unavailable during high tide from the frequency of tides that flooded the salt-marsh plains during the winter and spring.

We also examined habitat preference with an alternate measure of mud flats. We conducted a separate analysis at low tide estimating availability of mud flats as a 25-m "linear" strip at the MLLW tide line based on studies that indicated Western Sandpipers foraged primarily along the falling tide edge (Recher 1966, Burger et al. 1977, Page et al. 1979), rather than on the exposed mud flat. We considered that the remaining area was unavailable for this analysis.

Home-range estimates.—Weighted (95%) bivariate elliptical home ranges (Samuel and Garton 1985) were computed for radio locations from the winter and spring. The HOME RANGE procedure from the program by Ackerman et al. (1990) reduced the effect of outliers that could result in excessively large estimates of home ranges (Samuel and Garton 1985). Home-range estimates were calculated for radio-marked Western Sandpipers located 20 or more times ($n = 77$) because home range size stabilized at or near that number of locations (Anderson 1982, Jaremovic and Croft 1987). In the spring, home ranges were calculated based on 15 or more locations at each tide level because many radio-marked birds departed from the study area during spring migration. Distribution of locations from each radio-marked bird were tested for goodness-of-fit to a bivariate normal distribution with the Cramer-von Mises test (Samuel and Garton 1985).

Compositional analysis.—Habitat preferences of Western Sandpipers were examined with compositional analysis (Aitchison 1986, Aebischer et al. 1993). We used compositional analysis because, unlike other preference analyses (Neu et al. 1974, Johnson 1980), it accounted for nonindependence of habitat proportions (i.e. habitat proportions sum to 1.0) and allowed statistical testing of differences among groups. Each bird was treated as an experimental unit. We divided the proportion of a bird's use of each habitat by availability of that habitat to estimate a preference ratio ($n = 7$ for low tide, $n = 5$ for high tide). The preference ratios were adjusted for nonindependence by dividing each of the $n - 1$ independent ratios by the most-used habitat ratio (mud flats at low tide, salt-pond levees at high tide). We transformed the resulting ratios to logarithms, making them linearly independent (Aitchison 1986).

A multivariate-analysis-of-variance (MANOVA) procedure (Johnson and Wichern 1988, SAS Institute 1989) was used to test whether a composition of use-to-availability log-ratios was significantly different than zero ($P < 0.05$), indicating that birds were using habitats preferentially. We reported Wilk's λ, F-value, degrees of freedom, and probability value for each MANOVA test. When analyses identified habitat preferences, ranks were assigned to each habitat type (see Aebischer et al. 1993). Means and standard errors for each of the log-ratios were calculated (Table 2), and t-tests were used to identify significant differences among habitat ranks (Aebischer et al. 1993) where the probability was 0.05 or less.

We also examined differences in habitat preferences among groups (i.e. scale, season, age) with a

TABLE 2. Example of log-ratio differences ($\bar{x} \pm$ SE) and ranking matrix used to determine third-order habitat preferences of Western Sandpipers in South San Francisco Bay during high tides. Habitat use for each radio-marked sandpiper based on proportion of locations in each habitat. Habitat availability determined from composition of home ranges. Habitats ranked from most (4) to least (0) preferred; ranks determined by adding number of positive log-ratio differences in each row.

Habitat type[a]	1	2	3	4	5	Rank
1 Salt-pond levees		1.05 ± 0.41*	1.30 ± 0.51*	2.04 ± 0.63**	0.53 ± 0.55	4
2 Salt-marsh plains	−1.05 ± 0.41*		0.25 ± 0.47	0.99 ± 0.49	−0.52 ± 0.43	2
3 Tidal salt ponds	−1.30 ± 0.51*	−0.25 ± 0.47		0.74 ± 0.69	−0.77 ± 0.51	1
4 Drained salt ponds	−2.04 ± 0.63**	−0.99 ± 0.49	−0.74 ± 0.69		−1.51 ± 0.43**	0
5 Seasonal wetlands	−0.53 ± 0.55	0.52 ± 0.43	0.77 ± 0.51	1.51 ± 0.43**		3

[a] Student's t-test indicating corresponding habitat types are used significantly different from each other (*, $P < 0.05$; **, $P < 0.01$).

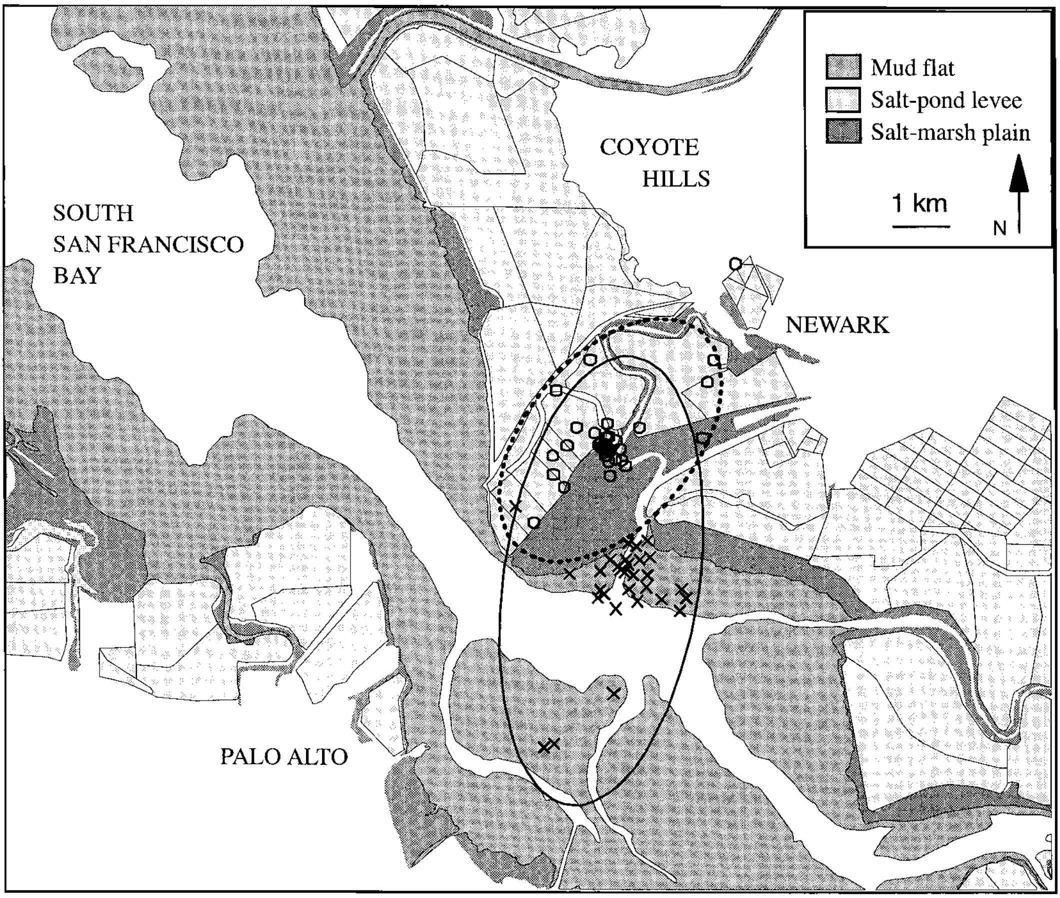

Fig. 2. Weighted bivariate 95% ellipses composing high (dashed line) and low tide (solid line) home ranges and associated high ("O") and low ("×") tide radio-locations for Western Sandpiper 5447.

MANOVA. In this analysis, differences in the habitat log-ratios (dependent variables) were tested against the groups (independent variables). We did not compare habitat preferences between low and high tides statistically, because two of the habitats were unavailable at high tides.

We investigated how alternative use-and-availability measurements affected the results of compositional analyses. Second-order selection was examined with different estimates of use because White and Garrott (1990:201) suggested errors inherent in calculating home ranges could produce inaccurate results in habitat analyses. In this case, use was represented by bird observations (i.e. the radio locations), while availability was estimated as composition of the total study area rather than home ranges (Baines 1993). Finally, we compared two estimates of mud-flat availability (areal and linear) to examine how different measures of habitat availability affected preference results.

RESULTS

Accuracy of radio locations.—The mean azimuth error for the truck telemetry systems was 1.5° or less. Distances between calculated and true locations of test transmitters averaged 58 ± SE of 35 m. The error-polygon size (see White and Garrott 1990) was estimated to be 1.1 ha or 0.1 to 2.5% of the mean habitat block size (Table 1). A small number (<1%) of edge locations (see Methods) were deleted from analyses.

Habitat availability.—We measured habitat blocks in the study area to estimate availability for second-order selection tests. Habitat blocks varied from 0.4 to 10.5 km^2 in size (Table 1). During low tide, the largest habitat proportions were mud flats (0.72), salt-marsh plains (0.16), and salt-pond levees (0.06). During high tides,

TABLE 3. Mean proportions of habitat use and of habitat availability for radio-marked Western Sandpipers in South San Francisco Bay. Daily (low and high tide) and seasonal (winter and spring) proportions reported. Habitat use based on proportions of radio locations in each habitat and on proportions of habitat types within home ranges. Availability based on proportion of total study area in different habitat types.

Factor	Mud flats	Salt-marsh plains	Salt-pond levees	Drained salt ponds	Tidal salt ponds	Seasonal wetlands	Tidal sloughs
			Low tide				
Winter							
Radio locations	0.75	0.07	0.11	0.01	0.04	0.01	0.01
Home ranges	0.68	0.18	0.02	0.06	0.02	0.01	0.07
Availability	0.72	0.16	0.06	0.03	0.01	0.01	0.01
Spring							
Radio locations	0.65	0.01	0.03	0.06	0.07	0.01	0.17
Home ranges	0.70	0.19	0.06	0.02	0.01	0.01	0.01
Availability	0.72	0.16	0.06	0.03	0.01	0.01	0.01
			High tide				
Winter							
Radio locations	—	0.08	0.71	0.08	0.10	0.03	—
Home range	—	0.29	0.04	0.10	0.11	0.46	—
Availability	—	0.55	0.26	0.11	0.04	0.04	—
Spring							
Radio locations	—	0.01	0.11	0.42	0.03	0.43	—
Home range	—	0.31	0.14	0.26	0.01	0.28	—
Availability	—	0.55	0.26	0.11	0.04	0.04	—

when mud-flat and tidal-slough habitats were inundated, salt-marsh plains (0.54) and salt-pond levees (0.26) were the most abundant habitats.

Weighted bivariate home ranges.—We used home ranges to estimate habitat use in second-order selection tests and habitat availability in third-order selection tests. Results from Cramer-von Mises tests (Samuel and Garton 1985) showed that locations for most radio-marked Western Sandpipers fit a bivariate normal distribution ($P \geq 0.05$) during winter (74%) and spring (68%). Most Western Sandpipers used a relatively small area ($\bar{x}$ = 22 km^2; Warnock and Takekawa in press) of the South San Francisco Bay during the study (Fig. 2). The 95% weighted bivariate home ranges that encompassed low-tide (1,260 ± 300 ha) and high-tide (9,300 ± 2,500 ha) locations typically encompassed less then 5% of the total study area (Table 1, Fig. 2).

Second-order habitat selection in the winter.—At a regional scale, composition of habitats within winter home ranges of Western Sandpipers was significantly different from the total study area (low tide, $\lambda = 0.07$, $F = 23.67$, df = 6 and 10, $P = 0.001$; high tide, $\lambda = 0.38$, $F = 6.60$, df = 5 and 20, $P < 0.001$). During low tide, mean home ranges were composed mainly of mud flats (68%) and salt-marsh plains (18%, Table 3). Tidal sloughs and mud flats were identified as the most preferred habitats (Table 4), followed by salt-marsh plains and tidal salt ponds. Salt-pond levees, seasonal wetlands, and drained salt ponds were used significantly less than the other habitats.

Winter home ranges at high tide were composed of seasonal wetlands (46%), salt-marsh plains (29%), tidal salt ponds (11%), and drained salt ponds (10%; Table 3). Salt-pond levees were the most preferred habitat, followed by drained salt ponds (Table 4), but no significant differences between drained salt ponds and other habitats were detected.

Third-order habitat selection in winter.—At a local scale, habitat use by Western Sandpipers was not in proportion to habitat availability in their home ranges ($\lambda = 0.32$, $F = 3.41$, df = 6 and 10, $P = 0.042$). The largest proportions of radio locations were in mud flats (75%) and salt-pond levees (11%; Table 3), but compositional analysis indicated that they preferred salt-pond levees most during winter low tide (Table 4). Mud flats ranked second and were used significantly more than the remaining habitats, while salt-marsh plains were used the least.

When only five habitats were available at high tide, Western Sandpipers displayed different preferences ($\lambda = 0.31$, $F = 8.70$, df = 5 and 29, $P < 0.001$). Most radio-marked birds were lo-

TABLE 4. Second- and third-order habitat preferences of Western Sandpipers during winter low and high tides, and spring low tides in South San Francisco Bay, California. Second-order habitat use determined from proportions of habitats within home range, and habitat availability estimated from size of habitat blocks in study area. Estimates of mud flat availability measured as both areal and linear habitats (see Methods). Third-order habitat use determined from radio locations, while availability is estimated from area of habitats in home ranges. Preferences of juveniles, adults and combined ages are reported. Habitats ranked in descending order of preference where "1" is most preferred habitat. Habitats with same superscript letter are not significantly different from each other ($P < 0.05$).

Comparison	Mud flats	Salt-marsh plains	Salt-pond levees	Drained salt ponds	Tidal salt ponds	Seasonal wetlands	Tidal sloughs
Second-order preference							
Tide							
Low	2^{A}	3^{AC}	5^{BC}	7^{C}	4^{AB}	6^{B}	1^{A}
High	—	5^{BC}	1^{A}	2^{ABC}	3^{B}	4^{B}	—
Availability							
Area	2^{A}	3^{AC}	5^{BC}	7^{C}	4^{AB}	6^{B}	1^{A}
Linear	1^{A}	3^{B}	4^{B}	7^{B}	5^{B}	6^{B}	2^{A}
Third-order preference							
Low tide							
Juveniles	2^{B}	7^{B}	1^{A}	6^{B}	4^{B}	5^{B}	3^{B}
Adults	2^{AB}	7^{D}	1^{A}	4^{B}	5^{BC}	3^{B}	6^{BC}
Combined							
Winter	2^{B}	7^{E}	1^{A}	5^{CD}	3^{C}	4^{D}	6^{D}
Spring	4^{BC}	7^{D}	5^{C}	3^{BC}	2^{B}	6^{C}	1^{A}
High tide							
Juveniles	—	5^{C}	1^{A}	2^{ABC}	3^{AC}	4^{BC}	—
Adults	—	5^{B}	1^{A}	2^{ABC}	3^{A}	4^{BC}	—
Combined							
Winter	—	5^{D}	1^{A}	2^{ABC}	3^{AC}	4^{BC}	—
Spring	—	5^{D}	4^{C}	1^{A}	3^{B}	2^{A}	—
Availability							
Areal	2^{A}	7^{C}	1^{A}	5^{B}	3^{B}	4^{B}	6^{B}
Linear	1^{A}	7^{C}	2^{A}	5^{B}	3^{B}	4^{B}	6^{B}

cated on salt-pond levees (71%), tidal salt ponds (10%), and drained salt ponds (8%; Tables 2 and 3). Salt-pond levees were ranked as the most preferred habitat, followed by drained salt ponds, tidal salt ponds, and seasonal wetlands (Table 4). All other habitats were preferred significantly more than salt-marsh plains.

Third-order habitat selection in spring.—Western Sandpipers preferred certain habitats on spring low tide ($\lambda = 0.29$, $F = 7.80$, df = 6 and 29, $P < 0.001$), and those preferences were significantly different from those in the winter ($\lambda = 0.29$, $F = 7.84$, df = 6 and 19, $P < 0.001$). At low tide, their home ranges were composed mainly of mud flats (70%) and salt-marsh plains (19%; Table 3). They were located in mud flats (65%), tidal sloughs (17%), tidal salt ponds (7%), and drained salt ponds (6%). Birds preferred tidal sloughs over tidal salt ponds, drained salt ponds, and mud flats; the least preferred habitat was salt-marsh plains (Table 4).

Habitat preferences of Western Sandpipers also differed seasonally at high tide ($\lambda = 0.54$, $F = 4.96$, df = 5 and 20, $P = 0.002$). Their home ranges (Table 3) consisted mostly of salt-marsh plains (31%), seasonal wetlands (28%), and drained salt ponds (26%), but they were located in seasonal wetlands (43%), drained salt ponds (42%), and salt-pond levees (11%). They preferred drained salt-pond and seasonal-wetland habitats during the spring ($\lambda = 0.40$, $F = 8.50$, df = 5 and 29, $P < 0.001$). Again, salt-marsh plains were the least preferred habitat (Table 4).

Differences in third-order selection by age.—Adults and juveniles had different preferences at low tide ($\lambda = 0.156$, $F = 23.35$, df = 6 and 10, $P = 0.001$). Under third-order selection, low-tide home ranges for both ages were composed mainly of mud flats (68%). Salt-marsh plains composed 12% of juvenile and 27% of adult home ranges. Drained salt ponds made up 11% of juvenile and 1% of adult home ranges. Salt-pond

TABLE 5. Differences in second-order selection of Western Sandpipers wintering in South San Francisco Bay comparing tests incorporating habitat use estimates from home ranges or radio locations. Habitat availability estimated from proportions of habitats within total study area. Habitats ranked in descending order of preference where "1" is most preferred habitat. Habitats with shared letters are not significantly different from each other ($P < 0.05$).

Comparison	Mud flats	Salt-marsh plains	Salt-pond levees	Drained salt ponds	Tidal salt ponds	Seasonal wetlands	Tidal sloughs
			Low tide				
Home ranges	2^{A}	3^{AC}	5^{BC}	7^{C}	4^{AB}	6^{B}	1^{A}
Radio locations	2^{A}	7^{C}	1^{A}	6^{BC}	5^{B}	4^{B}	3^{AB}
			High tide				
Home ranges	—	5^{BC}	1^{A}	2^{ABC}	3^{B}	4^{B}	—
Radio locations	—	4^{B}	1^{A}	5^{B}	2^{A}	3^{B}	—

levees and mud flats were the most important habitats for both ages (Table 4). However, juveniles used mud flats significantly less than salt-pond levees, while no significant preference between the two habitats was detected for adults. Juveniles had no preference among the remaining habitats, while adults showed a significantly lower preference for salt-marsh plains compared to other habitats (Table 4).

Juveniles and adults also had significantly different habitat preferences at high tide ($\lambda = 0.43$, $F = 5.19$, df $= 5$ and 28, $P = 0.003$), although the habitat ranks were the same (Table 5). Salt-pond levees ranked as the most preferred habitat for both adults and juveniles. Drained salt ponds ranked second, but preference for drained salt ponds was not significantly different than for the other habitats (Table 5).

Linear vs. areal mud-flat availability under second- and third-order selection.—We found significant differences ($\lambda = 0.36$, $F = 115.01$, df $= 6$ and 26, $P < 0.001$) in second-order selection when we defined available mud-flat habitats at low tide as a linear strip. The relative availability of mud flats was reduced from 72% of the study area to 22%, and all other habitat proportions increased. Mud flats and tidal sloughs were significantly preferred over other habitats (Table 4). When an areal estimate of mud flats was used, ranks for salt-pond levees and tidal sloughs were reversed, but these habitats remained significantly preferred over other habitats, and salt-marsh plains were least preferred.

Habitat ranking under third-order selection was similar for linear and areal mud-flat availability, but there were significant differences ($\lambda = 0.16$, $F = 23.36$, df $= 6$ and 26, $P < 0.001$) separating those ranks. Salt-pond levees and mud flats were the first and second ranks for both cases. However, when the areal estimate was used, the ranks for mud flats and salt-pond levees were reversed (Table 4).

Habitat use based on home ranges vs. radio locations.—The effect of using different estimates of habitat use was examined under second-order selection (Table 5). Western Sandpipers preferred tidal-slough and mud-flat habitats most when habitat use was estimated from home ranges at low tide. Preferences differed ($\lambda = 0.26$, $F = 4.87$, df $= 6$ and 10, $P = 0.014$) when habitat use was determined from radio locations. Salt-pond levees and mud flats were the most preferred habitats (Table 5), whereas salt-marsh plains were least preferred. Habitat preferences at high tide also differed ($\lambda = 0.22$, $F = 20.92$, df $= 5$ and 29, $P < 0.001$); drained salt ponds were more highly preferred when home ranges, rather than radio locations, were used to estimate habitat use (Table 5).

DISCUSSION

Determining the habitat preferences of Western Sandpipers in a dynamic environment such as the San Francisco Bay estuary requires consideration of the temporal variation in their habitats. Daily, their mud-flat and tidal-slough foraging habitats become submerged and, thus, unavailable at high tide. Seasonally characteristics (e.g. rainfall, benthic invertebrate densities) of their environment change, which results in differences in their habitat preferences. Selection also must be examined at different scales to understand their overall habitat requirements. Third-order selection reveals preferences at a local level, while second-order selection identifies preferred habitats at a regional level, a perspective often of interest for habitat conservation planning.

Second- and third-order selection differences during the winter.—At low tide, tidal sloughs and mud flats were ranked highest while salt-pond levees were ranked fifth under second-order selection (Table 4). In contrast, tidal sloughs were ranked sixth, while salt-pond levees were first under third-order selection. Western Sandpipers showed a preference for tidal sloughs at the regional level because little of that habitat remains in the South San Francisco Bay. Locally, their home ranges included a relatively large proportion of tidal sloughs, which were seldom used. Salt-pond levees were not preferred because that habitat was more widely available in the study area than in home ranges. Salt-pond levees composed less than 6% of the available habitats (Table 1) but 11% of the radio locations.

Salt-marsh plains were ranked third under second-order selection. Salt-marsh plains only composed 16% of the study area but a large proportion of home ranges. However, few radio locations were found in that habitat, and it was ranked last under third-order selection.

During high tides, salt-pond levees were the most preferred habitat at both scales of selection (Table 4). Salt-marsh plains were the least preferred habitat under third-order selection. Apparently, Western Sandpipers found few suitable roosting or foraging areas in this habitat. Organic material originating in the salt-marsh plains has been correlated with high productivity of benthic invertebrates in mud flats upon which sandpipers depend (Warwick and Price 1975). Thus, salt-marsh plains contribute indirectly to their food resources in mud flats and tidal sloughs.

Third-order selection differences between the winter and spring.—In the spring, 82% of the Western Sandpipers were located in mud flats and tidal sloughs during low tides, and 17% were found within the salt-pond systems (Table 3). In comparison to winter, they preferred tidal sloughs, drained and tidal salt ponds rather than salt-pond levees, and seasonal wetlands (Table 4). During high tides, they preferred drained salt ponds and seasonal wetlands more in spring, but salt-pond levees less than in winter.

Salt-evaporation ponds of lower salinity (≤ 60 ppt) supported an abundance of benthic invertebrates (Anderson 1970; C. W. Swarth, C. Akagi, and P. Metropulos, unpubl. 1982 report). Artificial impoundments like these salt-evaporation ponds were reported to provide valuable foraging areas for small sandpipers in South Africa (Martin and Randall 1987, Velasquez and Hockey 1992), India (Sampath and Krishnamurthy 1988), and England (Davidson and Evans 1986). However, foraging by sandpipers in the South San Francisco Bay salt-evaporation ponds has only been mentioned incidentally in the literature (Murie 1935, Carpelan 1957, Anderson 1970; C. W. Swarth, C. Akagi, and P. Metropulos, unpubl. 1982 report).

The numbers of Western Sandpipers in San Francisco Bay increased by more than 200% in the spring, with the influx of as many as 350,000 migrants (J. Kjelmyr, G. W. Page, W. D. Shuford, and L. E. Stenzel, unpubl. 1991 report). Shorebirds have been reported to deposit large amounts of fat (Goeda et al. 1990) and increase total time spent feeding (Zwarts et al. 1990) prior to spring migration. Western Sandpipers likely were taking advantage by foraging in these salt-pond habitats during the spring. Competition for food resources might have affected habitat preferences if some birds were displaced into less preferred habitats (Goss-Custard 1984).

Third-order selection differences of adults vs juveniles in winter.—Adults were more selective in their use of winter habitats than juveniles during low tides (Table 4). Both preferred salt-pond levees, but juveniles used each of the remaining habitats similarly. Adults preferred salt-pond levees and mud flats, and had a significantly lower preference for salt-marsh plains. Adults may have excluded juveniles from the most profitable, but limited foraging areas as was demonstrated in studies of Eurasian Oystercatchers (*Haematopus ostralegus*; Goss-Custard 1984).

Preference under different availability and use definitions.—Western Sandpiper preferences were different (Table 4) when availability of mud flats was defined as a linear strip along the falling tide line (Recher 1966, Burger et al. 1977). Under second-order selection, a Western Sandpiper's preference for mud flats and tidal sloughs was greater, while their preference for salt-marsh plains, salt-pond levees, and drained salt ponds was less when comparing linear and areal estimates. Under third-order selection, their preferences were not significantly different using linear estimates, but there were differences in rank order. Our results showed that recognizing microhabitats within the mud flats changes the interpretation of habitat preferences.

Preference ranks also are altered when individual radio locations, instead of proportions within the home range, are used to estimate habitat use (Table 5). If the mosaic of habitats in the regional and local areas is similar, we found that determining second-order selection with locations rather than with home ranges (Baines 1993) produces a hybrid preference measure. Preferences are more similar to third-order (Table 4) instead of second-order selection, although the same habitat estimates are used for evaluating habitat availability.

Conserving habitats preferred by Western Sandpipers.—Western Sandpipers use artificial salt-pond habitats during the winter and spring, and the sizeable populations of shorebirds in South San Francisco Bay suggest that suitable resources are available to them. However, regional conservation efforts directed at restoring salt ponds to tidal salt marshes for the benefit of endangered species may result in reducing preferred habitats and use of the South San Francisco Bay area by Western Sandpipers. On a local scale, salt-pond levees provide Western Sandpipers with valuable high-tide roosting sites, but additional behavior and energetic studies are needed to determine the extent to which small sandpipers rely on habitats within the salt-pond systems as supplemental foraging sites.

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