



THE CONDOR

AN INTERNATIONAL JOURNAL OF AVIAN BIOLOGY

Volume 101

Number 3

August 1999

The Condor 101:461-471
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OVERVIEW OF SHOREBIRD ABUNDANCE AND DISTRIBUTION IN WETLANDS OF THE PACIFIC COAST OF THE CONTIGUOUS UNITED STATES¹

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Abstract. We coordinated censuses from April 1988 to April 1995 to obtain an overview of shorebird abundance and distribution in Pacific Coast wetlands of the contiguous United States. We attempted to acquire at least 3 years of data for all major wetlands from counts within a short time window each fall, winter, and spring. Fourteen abundant, 8 moderately abundant, and 21 rare-to-uncommon species were recorded. For temperate-zone breeders, peak periods of abundance were fall or winter and, when discernible for arctic breeders, mostly fall or spring. Arctic breeders were relatively more abundant than temperate-zone breeders in Oregon and Washington wetlands. All five of the most abundant temperate breeders were limited primarily to California wetlands in all seasons. Only for Western Sandpiper (*Calidris mauri*) and Dunlin (*C. alpina*) did the estimated total individuals present simultaneously in all wetlands exceed 100,000. Fifty-six of 66 sites surveyed had at least four counts and at least 100 shorebirds on one or more counts; 38 of the 56 sites held at least 1% of 1 of 13 key species during at least one season. San Francisco Bay accounted for 24-96% of the estimated totals for key species; Grays Harbor, Willapa Bay, Humboldt Bay, Tomales Bay, Point Reyes Esteros, Bolinas Lagoon, Elkhorn Slough, Morro Bay, Mugu Lagoon, Bolsa Chica, Mission Bay, and San Diego Bay held at least 1% of at least half the key species in at least one season. The usefulness of five criteria for selecting key wetlands for shorebird conservation are examined and potential threats are discussed.

Key words: censuses, Charadrii, distribution, Pacific Coast, relative abundance, shorebirds, wetlands.

INTRODUCTION

The Pacific Coast of the Americas is portrayed as a flyway along which shorebirds breeding in eastern Siberia and much of Alaska migrate to wintering areas from British Columbia to Tierra del Fuego (Morrison and Myers 1989). Although some of these shorebirds rely on sandy beaches or rocky shores for their primary foraging and resting habitat during migration and winter, most species concentrate in wetlands (Page and Gill 1994). Due to extensive human degradation of wetlands during the past two centuries (Dahl 1990), it has become important to identify those areas most critical to shorebirds (Senner and Howe 1984) and to protect and

manage them to avert shorebird population declines (Myers et al. 1987).

The primary conservation effort to emerge for migrating and wintering shorebirds in the Americas is the Western Hemisphere Shorebird Reserve Network (WHSRN), a network of key wetlands for shorebirds across the Western Hemisphere recognized by a consortium of government and private organizations (Myers et al. 1987, Bildstein et al. 1991). Criteria for inclusion in WHSRN are based primarily on the total number of shorebirds known to use a site annually, with a minimum of 20,000 for a site of "regional importance," the lowest ranking recognized, and 500,000 for a site of "hemispheric importance," the highest ranking (Bildstein et al. 1991). Although there are also provisions for inclusion based on the proportions of species'

¹ Received 16 June 1998. Accepted 29 March 1999.

total populations using potential sites, lack of information on population sizes of most species usually precludes use of such a criterion. Consequently, site selection is usually based on total numbers of shorebirds and, therefore, favors the most abundant species. This may or may not be a problem, depending on the degree of overlap in site use between more and less abundant species.

Isolated surveys of wetlands of the contiguous U.S. Pacific Coast during the past half century provide data on the abundance of migrating and wintering shorebirds at selected sites from Puget Sound, Washington near the U.S.–Canada border (Buchanan 1988) to San Diego Bay, California near the U.S.–Mexico border (Jehl and Craig 1971). Survey dates varied from the 1940s (Storer 1951) to the 1990s (Buchanan and Evenson 1997). Survey duration and frequency varied from daily during one 3-week period (Herman and Bulger 1981) to monthly for 10 years (King et al. 1987), and survey coverage varied from a small portion of a wetland (Storer 1951) to an entire wetland site (Colwell 1994). However, despite considerable variation in dates, duration, frequency, and coverage, these surveys provide useful information on seasonal abundance patterns of shorebirds. Some surveys also contribute information on annual variation in abundance (King et al. 1987, Shuford et al. 1989), spatial variation in abundance within wetlands (Page et al. 1979), or variation in abundance among wetlands (Jurek 1974, Shuford et al. 1989).

Based on these surveys and other information, 16 wetlands along the U.S. Pacific Coast are currently considered to meet at least the minimum threshold for inclusion in the WHSRN (Harrington and Perry 1995). To better identify and understand the most important wetlands for migrating and wintering shorebirds along the U.S. Pacific Coast, we arranged for volunteers to count shorebirds in wetlands during fall, winter, and spring. Due to the magnitude of this effort, we did not try to cover any wetland as frequently as in previous studies, but did coordinate surveys to occur within a short time window in each survey period, to cover all (or most) potential shorebird habitat in each wetland or wetland system on each survey, and to obtain at least 3 years of surveys at each site. These surveys enabled us to measure the relative abundance of different species within the Pacific

Coast wetland system, describe seasonal and geographical patterns in abundance, examine species' relative abundance among wetlands, and compare five methods of selecting key wetlands for the conservation of coastal shorebirds.

METHODS

Shorebird surveys of Pacific Coast wetlands commenced in April 1988 and concluded in April 1995. They began with San Francisco Bay (Stenzel and Page 1988) and expanded sequentially to the wetlands of northern California, southern California, Oregon, and Washington. Based on published accounts and first-hand knowledge, we attempted to survey all wetlands likely to hold 1,000 or more shorebirds at one time and to count all shorebirds in each wetland once annually in autumn (August–September), winter (November–January), and spring (mid April–early May) for 3 to 5 years. We tried to conduct all surveys during a period of 1 to 2 weeks in each autumn and 1 week in each spring.

We tried to identify wetlands or wetland system boundaries for coverage that were closed (or mostly closed) with respect to normal shorebird flock movements under census conditions. We did not know how predictable flock movement during the time of surveys would be within some moderately-sized to large wetland systems, and relied on survey coordinators with local knowledge of the wetlands to make necessary adjustments to discount for birds known to be counted by more than one census team.

We do not deal with shorebird distribution within larger wetland systems in this paper. For example, we report as single sites two very large wetland systems, the Puget Sound area and the San Francisco Bay estuary. Because shorebirds are known to move between the 68 embayments of Puget Sound (Brennan et al. 1985; J. Buchanan, pers. comm.), count organizers (J. Buchanan and J. Evenson from Cascadia Research Collective, Olympia, Washington) coordinated ground surveys with aerial flights and reported to us grand totals for Puget Sound; more detailed information on Puget Sound sites can be found in Evenson and Buchanan (1997). Drakes and Limantour esteros (hereafter Point Reyes esteros) in Marin County, California were considered to be a single site. Shorebirds move between Humboldt Bay and the Eel River mouth, Humboldt County (M. Colwell, pers. comm.); we did

TABLE 1. Number of years of shorebird surveys at 56 U.S. Pacific coast wetlands in fall (F), winter (W), and spring (S). Codes identify sites: 1 = having at least 1% of the cumulative wetland total of at least one of 13 selected species in at least one season based on medians conditioned on non-zero values as described in the Methods; 2 = considered of potential regional, international, or hemispheric importance by WHSRN (Harrington and Perry 1995); 3 = currently recognized as of hemispheric importance by WHSRN; 4 = among the top three for 1 or more of 13 selected species in at least one season; and 5 = selected by complementarity analysis as modified by Turpie (1995). CE is creek estuary, CM is creek mouth, FCC is flood control channel, NWR is national wildlife refuge, RE is river estuary, and RM is river mouth. Wetlands are listed north to south.

Wetland	Codes	F	W	S
WASHINGTON				
Puget Sound	1, 2, 4	3	4	3
Grays Harbor	1, 2, 3, 4	4	3	3
Willapa Bay	1, 2, 4	2	3	3
Columbia RE	1, 2, 4	4	3	5
OREGON				
Necanicum RE		4	1	3
Tillamook County				
Nehalem Bay		2	2	3
Tillamook Bay	1	2	3	3
Netarts Bay		3	1	3
Sand Lake		5	1	2
Nestucca Bay		4	2	4
Lincoln County				
Siletz Bay	1	6	4	5
Yaquina Bay		6	4	5
Alsea Bay		5	0	4
Siuslaw RE	1	5	4	5
Coos County				
Tenmile CE	1	1	0	3
Coos Bay	1, 2	6	4	5
Bandon/Coquille RE	1	6	4	5
New RE	1	3	4	5
CALIFORNIA				
Smith RE	1	4	3	4
Lake Talawa	1	4	3	4
Humboldt Bay	1, 2, 4	5	4	5
Garcia RE		5	5	5
Point Reyes/Bodega Area				
Bodega Harbor	1, 2	7	4	4
Estero Americano	1	1	2	2
Tomales Bay	1, 2, 4	7	6	6
Abbotts Lagoon		5	5	5
Point Reyes Esteros	1, 2	5	5	5
Bolinas Lagoon	1, 2	5	5	5
San Francisco Bay	1, 2, 3, 4, 5	3	3	6
Waddell CM		5	4	4
Monterey Bay Area				
Corcoran Lagoon		3	2	1
Pajaro RM	1	6	4	5
Elkhorn Slough	1, 2, 4	6	5	5
Salinas RM	1	6	4	5
Morro Bay	1, 2, 4	7	4	6

TABLE 1. Continued.

Wetland	Codes	F	W	S
Santa Maria RM	1, 4	2	1	2
Santa Barbara County				
Devereux Slough	1	6	5	5
Goleta Slough		6	5	6
Mugu Lagoon	1, 2, 4	4	3	5
Los Angeles County				
Malibu Lagoon		6	1	5
Los Angeles RM	1, 4	4	0	2
San Gabriel RM	1	3	0	3
Orange County				
Seal Beach NWR	1, 4	3	4	5
Bolsa Chica	1, 4	6	4	6
Upper Newport Bay	1, 2, 4	6	5	5
Northern San Diego County				
Santa Margarita RE	1	6	7	6
San Luis Rey RM		4	1	3
Buena Vista Lagoon		4	0	3
Agua Hedionda Lagoon		6	4	4
Batiquitos Lagoon	1	6	5	6
San Elijo Lagoon	1, 4	6	5	6
San Dieguito Lagoon		6	5	6
Penasquitos Lagoon		5	5	6
South San Diego County				
Mission Bay & FCC	1, 4	5	4	5
San Diego Bay	1, 2, 4	5	4	5
Tijuana RE	1	5	4	5

not obtain sufficient coverage of the latter site for its inclusion with Humboldt Bay. However, the maximum number of shorebirds counted on two surveys of the Eel River mouth was 1,911, which suggests that Humboldt Bay totals would not be greatly changed by the addition of Eel River mouth (Colwell 1994).

Except for the somewhat inaccessible north shore of the San Francisco Bay system, where ground counts were sometimes supplemented by aerial counts, all areas south of the Columbia River Estuary in Oregon were surveyed from the ground or, in parts of Elkhorn Slough, Morro Bay, and Tomales Bay, California, from small boats. Because of their large size and the limited numbers of counters, combined aerial and ground surveys were usually taken at the Columbia River Estuary, Willapa Bay, Grays Harbor, and Puget Sound. Audubon Christmas bird counts, however, were used to estimate winter shorebird numbers on the Columbia River Estuary (combining Columbia River Estuary, Sauvie Island, and Portland counts 1992–1994) and for Grays Harbor (Grays Harbor counts for 1992–1994), due to the lack of aerial surveys in two of the three winters at both locations.

TABLE 2. Seasonal totals of 21 shorebird taxa on all surveys of 56 wetlands on the U.S. Pacific Coast.

Taxon	Range ^a	Fall	Winter	Spring
Black-bellied Plover (<i>Pluvialis squatarola</i>)	ab	69,958	74,800	51,552
Snowy Plover (<i>Charadrius alexandrinus</i>)	tn	3,067	2,489	1,425
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	ab	17,371	8,387	20,244
Killdeer (<i>Charadrius vociferus</i>)	tb	4,603	5,549	2,563
Black-necked Stilt (<i>Himantopus mexicanus</i>)	tb	26,008	17,845	9,966
American Avocet (<i>Recurvirostra americana</i>)	tn	57,596	81,543	29,372
Greater Yellowlegs (<i>Tringa melanoleuca</i>)	ab	4,298	2,972	6,450
Willet (<i>Catoptrophorus semipalmatus</i>)	tb	131,343	103,362	34,563
Whimbrel (<i>Numenius phaeopus</i>)	aab	2,726	706	5,768
Long-billed Curlew (<i>Numenius americanus</i>)	tn	12,007	11,110	3,759
Marbled Godwit (<i>Limosa fedoa</i>)	tn	161,031	129,150	181,346
Ruddy Turnstone (<i>Arenaria interpres</i>)	aab	1,652	901	1,567
Black Turnstone (<i>Arenaria melanocephala</i>)	an	3,267	4,943	3,424
Red Knot (<i>Calidris canutus</i>)	ab	7,981	4,813	9,035
Sanderling (<i>Calidris alba</i>)	aab	44,321	34,766	32,477
Western Sandpiper (<i>Calidris mauri</i>)	ab	1,140,397	625,577	5,004,640
Least Sandpiper (<i>Calidris minutilla</i>)	ab	276,110	147,903	193,347
Dunlin (<i>Calidris alpina</i>)	an	1,006	1,094,644	1,252,102
dowitchers (<i>Limnodromus griseus & scolopaceus</i>)	ab, an	118,202	98,851	443,777
Wilson's Phalarope (<i>Phalaropus tricolor</i>)	ts	3,204	2	427
Red-necked Phalarope (<i>Phalaropus lobatus</i>)	as	80,227	13	18,363

^a aab = arctic breeder, bicontinental/Oceania-Asia winterer; ab = arctic breeder, bicontinental winterer; an = arctic breeder, northern winterer; as = arctic breeder, southern winterer; tb = temperate breeder, bicontinental winterer; tn = temperate breeder, northern winterer, and ts = temperate breeder, southern winterer.

Shorebird counts were obtained from 66 sites but only 56, for which there were at least four surveys and at least 100 shorebirds on one or more surveys, were included in our analysis (Table 1). Professional and amateur ornithologists able to identify shorebirds were asked to participate in counts, with one or two experienced counters organizing and coordinating surveys in each wetland. We provided data recording forms, a protocol for counting and estimating shorebird numbers, and dates for each census. Training sessions on methods of identifying and counting shorebirds were offered to and attended by over 100 counters in the San Francisco Bay area and in Oregon. We advised organizers to divide wetlands into segments that could be covered by a team of observers in 1–2 hr and to count adjacent segments simultaneously to minimize chances of double counting birds. We also suggested conducting counts on a moderately high rising tide so birds would move toward observers and become easier to identify to species as surveys progressed.

We instructed census takers to identify all shorebirds to species, but when this was not feasible, to note which species were included in flocks of unidentified shorebirds. Groups of unidentified shorebirds mostly fell into four categories: small unidentified sandpipers of the ge-

nus *Calidris*, which were predominantly Least Sandpipers, Western Sandpipers, or Dunlins; unidentified yellowlegs (genus *Tringa*), which were either Greater Yellowlegs or Lesser Yellowlegs (*T. flavipes*); unidentified phalaropes (genus *Phalaropus*), which were either Red-necked Phalaropes or Wilson's Phalaropes; and dowitchers (genus *Limnodromus*), which were either Short-billed Dowitchers or Long-billed Dowitchers. For analytical purposes we grouped both the identified and unidentified dowitchers as dowitchers due to the difficulty of separating most individuals into species on surveys. Scientific names are given in Table 2.

The unidentified percent of total small *Calidris* sandpipers was 22.8% in fall, 19.8% in winter, and 13.9% spring; of total yellowlegs 14.8% in fall, 10.2% in winter, and 9.9% in spring; and of total phalaropes 10.4% in fall and 8.7% in spring. We assigned the unidentified shorebirds to species by allocating the unidentified ones in direct proportion to the identified shorebirds of the appropriate species, when the ratio of identified to unidentified shorebirds on the same survey was greater than one. If the ratio was less than one, unidentified shorebirds were apportioned in direct proportion to the total number of identified and allocated shorebirds on all surveys of the same site in the same season or, in

very few cases without data from the same site, from neighboring sites.

At the Columbia River Estuary and at Grays Harbor in fall and spring, the highest total from the aerial or ground survey for each species or species group (e.g., small sandpipers or unidentified yellowlegs) was used for each count. Shorebirds designated as small sandpipers on an aerial count were apportioned into Least Sandpipers, Western Sandpipers, and Dunlins in direct proportion to the number of each of these species on the corresponding ground counts where the combined number of identified Least Sandpipers, Western Sandpipers, and Dunlins was at least 25% of the unidentified small shorebirds on the aerial count. Unidentified yellowlegs were apportioned by the number of identified Greater and Lesser Yellowlegs on ground counts or in five cases as Greater Yellowlegs if no yellowlegs were identified to species. At Grays Harbor, 265 and 210 shorebirds reported as medium-sized sandpipers on the 1993 and 1994 fall aerial counts, respectively, were all classified as dowitchers based on the preponderance of dowitchers among the mid-sized sandpipers on the fall 1992 count; 28,690 medium-sized sandpipers on the 1993 spring aerial count were assigned to Red Knots and dowitchers in direct proportion to the 110 knots and 5,965 dowitchers identified on ground counts the days before and after the aerial count.

Species were categorized by their breeding and wintering ranges to examine relationships between their abundance and range. Arctic refers to an arctic or subarctic breeding range and temperate to a primarily temperate-zone breeding range. Northern winterer indicates a winter range primarily north of, and southern winterer a range primarily south of, the Tropic of Cancer in the New World. Bicontinental refers to a New World winter range broadly spanning the Tropic of Cancer. With a few exceptions, our designations are similar to those of Boland (1988). We compared the nonbreeding season latitudinal distribution of the moderately abundant to abundant (see Results for definitions) arctic vs. temperate-zone breeders (excluding the phalaropes in winter) as the proportion of each season's median totals in Oregon and Washington, vs. in California. These measures were compared using the Wilcoxon rank sum test with critical values for each of the three seasons adjusted to keep the overall testing level at $P = 0.05$.

We compared the relative abundance of each species within each season by summing all counts at the 56 sites across years. We also made four estimates of the number of individuals of each moderately-abundant to abundant species present simultaneously within the study region each season for inter-season comparisons of abundance within species. These estimates were the sum of the medians of each site, the medians conditional on each species' presence (non-zero counts), the maxima of each site, and the mean of the totals of all sites for the three years with the most complete data for each season; for the latter, we used the median for those year-site combinations with missing data. To determine regional seasonal abundance patterns for each species, we identified which seasons' means were higher or lower from nonoverlapping 80% confidence intervals.

We selected 13 moderately-abundant to abundant (key) taxa for a comparison of the relative abundance of species among wetlands each season. Included were most species that concentrate in estuaries or brackish wetlands and for which offshore waters, rocky shores, sandy beaches, uplands, or freshwater wetlands are not the primary habitat in the coastal zone. The abundance of each key taxon in each wetland each season was estimated as the median of all counts on which it was present during the season (median conditioned on non-zero values) unless only zero counts were available; in such cases the median value was zero. We used these medians to estimate the proportion of each taxon in each wetland each season. Although similar calculations also were made based on means, non-conditional medians, and maxima, we selected those based on conditional medians over the others because we felt this measure was the least likely to be biased by spurious low or zero counts.

Finally, we compared five methods of selecting key wetlands for shorebirds. From estimated proportions in each wetland, we determined the percent of each of the 13 key taxa encompassed by (1) all sites supporting at least 1% of the cumulative wetland total of at least one key taxon during at least one season (Cayford and Waters 1996), (2) all sites regarded by WHSRN to support at least 20,000 shorebirds annually (criterion for regional importance: Harrington and Perry 1995), (3) only WHSRN sites of hemispheric rank (supporting at least 500,000 shorebirds), (4) all sites within the top three sites of

TABLE 3. Sum of medians conditioned on non-zero values, mean of the 3 years with most complete data, and coefficient of variation (CV) of the mean for shorebirds in 56 U.S. Pacific coast wetlands for fall, winter, and spring.

Species	Fall			Winter			Spring		
	Median	Mean	CV	Median	Mean	CV	Median	Mean	CV
Black-bellied Plover	19,667	18,930	6.5	22,315	21,438	4.3	8,021	7,755	19.7
Snowy Plover	705	586	17.1	824	701	11.9	286	236	15.2
Semipalmated Plover	4,558	4,216	11.4	2,302	2,343	23.7	3,378	4,542	16.8
Killdeer	1,163	1,175	11.7	1,383	1,271	17.2	497	392	21.0
Black-necked Stilt	7,136	7,693	14.7	5,542	5,616	40.9	1,529	1,162	39.9
American Avocet	18,068	18,646	39.6	26,177	26,187	8.8	4,548	4,170	19.9
Greater Yellowlegs	1,067	1,118	10.4	794	800	2.1	1,281	1,486	26.0
Willet	34,702	34,087	4.8	29,012	29,001	5.0	5,926	5,444	30.4
Whimbrel	685	614	22.5	213	200	15.2	1,013	1,066	12.5
Long-billed Curlew	2,987	2,987	23.2	3,034	3,240	20.1	622	856	50.5
Marbled Godwit	39,833	40,494	7.9	36,334	35,351	1.8	29,992	26,756	26.9
Ruddy Turnstone	353	380	30.6	248	272	9.3	314	242	20.9
Black Turnstone	720	573	23.9	1,265	1,191	16.5	912	596	20.9
Red Knot	2,398	2,262	20.8	1,172	1,466	59.3	1,944	1,453	27.1
Sanderling	15,303	10,801	15.8	10,352	10,085	12.3	11,138	7,348	33.2
Western Sandpiper	309,947	314,872	11.9	181,558	182,195	15.4	959,930	995,629	18.5
Least Sandpiper	72,182	78,442	9.6	37,066	36,962	14.1	32,572	35,053	30.4
Dunlin	489	271	101.8	320,613	309,818	6.1	259,554	300,348	19.8
dowitchers	32,987	33,421	4.8	27,992	29,090	7.7	88,917	88,638	1.4
Wilson's Phalarope	127	996	162.8	2	1	160.7	207	19	160.4
Red-necked Phalarope	24,291	23,478	38.2	6	4	68.9	2,073	2,688	48.7

any key taxon in any season, and (5) the minimum number of sites needed to support some representatives of each key taxon each season using complementarity analysis as modified by Turpie (1995). Complementarity analysis is designed to identify the minimum number of sites needed to maintain species diversity over a pre-defined area but is modified by Turpie (1995) to increase the likelihood of preserving viable populations of contributing species.

RESULTS

RELATIVE ABUNDANCE OF SPECIES

Forty-three species of shorebirds were reported on the surveys of 56 wetlands. The 14 most abundant species each totaled over 10,000 individuals in one or more seasons over all years and sites combined (Table 2); we believe both Long- and Short-billed Dowitchers fell into this category. Eight species, of moderate abundance, each totaled between 1,000 and 10,000 individuals in at least one season over all years and sites (Table 2). The remaining 21 species were rare to uncommon on our surveys, totaling fewer than 1,000 individuals per season over all years and sites combined. All but one of the species categorized as rare to uncommon in coastal wetlands either winter south of the Tropic of Cancer

or have northern or bicontinental winter ranges encompassing mostly habitats other than unvegetated coastal wetland; they are not included in any analyses in this paper.

Making up the abundant taxa were eight arctic-breeding species that are bicontinental or primarily northern winterers, the arctic-breeding Red-necked Phalarope, which spends the winter primarily offshore, south of the Tropic of Cancer, and five species that breed exclusively to primarily in the Temperate Zone and are bicontinental or northern winterers (Table 2). Included among the five temperate-zone breeders is the Marbled Godwit, whose breeding range extends into the subarctic. Estimated total individuals present simultaneously in all coastal wetlands exceeded 100,000 for only two species, Western Sandpiper in all seasons and Dunlin in winter and spring (Table 3). Western Sandpipers approached a million individuals in spring. Over 300,000 Dunlin were estimated to be present in winter and 250,000–300,000 in spring. Estimates ranging from 50,000–99,000 individuals were attained only for Least Sandpiper in fall and dowitchers in spring. Estimates of 10,000–49,900 individuals included six taxa (including Least Sandpiper and dowitchers) in at least two of three seasons, and the Red-necked Phalarope

in fall (Table 3). Approximately 10,000 Sanderlings were present in fall and winter.

The eight species of moderate abundance included five that breed in the arctic and three that nest primarily in the Temperate Zone; all except Wilson's Phalarope are bicontinental or northern winterers (Table 2). Our counts under-represented the abundance of the Wilson's Phalarope relative to other species in both spring and fall because its main spring passage is typically later than our April counts and main fall passage earlier than our August–September counts (Jehl 1988). Estimated total individuals of the moderately abundant species present simultaneously in all coastal wetlands was fewer than 1,000 individuals in all seasons for only Snowy Plover, Ruddy Turnstone, and Wilson's Phalarope (Table 3).

SEASONAL VARIATION IN ABUNDANCE

The seasons of peak abundance for temperate-zone breeders occurred in fall or winter, and peaks of arctic breeders, when discernible, were mostly in fall or spring (Table 3). Mean totals peaked in fall or winter for six of the eight temperate-zone breeders. Spring totals of the six species were 35% or less of winter totals, because many individuals had left for breeding areas by the time of the April surveys. Marbled Godwit also may share the above pattern but seasonal differences are obscured by high variability in spring count totals (Table 3). High variability in fall and spring totals for Wilson's Phalarope prevented us from identifying this species' obvious migratory peaks in those seasons using our criterion.

We identified seasonal variability for 7 of the 13 arctic breeders. Five were most abundant in fall or spring. Fall totals for Whimbrel, Western Sandpiper, and Least Sandpiper, and spring totals for Whimbrel, Western Sandpiper, and dowitchers were at least 1.7 times higher than winter totals (Table 3). For the Red-necked Phalarope, which is essentially absent in winter, both migratory peaks were clearly evident. Fall and winter Black-bellied Plover totals were over twice those of spring. Dunlin, which arrived in fall mostly after our census period, was clearly at peak numbers in winter and spring. We were unable to discern seasonal differences in wetland totals for Semipalmated Plover, Greater Yellowlegs, Ruddy Turnstone, Black Turnstone, Red Knot, and Sanderling, in part due to high within-season variability in totals (Table 3).

GEOGRAPHIC VARIATION IN ABUNDANCE

Arctic breeders were relatively more abundant than temperate-zone breeders in Oregon and Washington wetlands in all seasons (Wilcoxon rank sum test, $W_s = 55$ in fall, $W_s = 45.5$ in winter, $W_s = 44$ in spring, all $P < 0.05$). In fall and spring, Washington and Oregon held fewer than 5% of the west coast totals of only 3 of the 13 arctic breeders, but fewer than 5% of 7 of the 8 temperate-zone breeders. In winter, Washington and Oregon held fewer than 5% of 6 of the 12 arctic-breeding taxa and 6 of 7 temperate-zone breeding taxa. Killdeer, with 11–38% of its west coast totals in Washington and Oregon wetlands, was relatively more abundant in the north than other temperate-zone breeders, with 0–4% in Washington and Oregon.

Although most arctic breeders were relatively more abundant in Washington and Oregon in fall or spring than in winter, the Least Sandpiper was always scarce (Table 4) and the region accounted for fewer than 0.1% of the Red-necked Phalarope in all seasons. In winter, the Dunlin was more abundant in wetlands north of than south of San Francisco Bay relative to its congeners, Red Knot, Western Sandpiper, and Least Sandpiper (Table 4). The relative abundance of Western Sandpiper, Red Knot, and dowitchers was much higher in Washington and Oregon wetlands in spring than in fall (Table 4) due mainly to their greater concentration in Grays Harbor and Willapa Bay.

Of the five temperate-breeding species selected for the inter-wetland comparisons, all were limited primarily to California wetlands in all seasons. Black-necked Stilt was essentially absent north of San Francisco Bay (Table 4). American Avocet, Willet, Long-billed Curlew, and Marbled Godwit were very scarce north of Humboldt Bay (Table 4).

RELATIVE ABUNDANCE AMONG WETLANDS

San Francisco Bay accounted for many more shorebirds than any other wetland in all seasons. It held 41.1–96.5% (mean = 66.7%) of the estimated totals for the key species in fall, 37.8–90.1% (mean = 55.7%) in winter, and 24.0–85.6% (mean = 52.3%) in spring (Table 4); no other site held more than 16.1% of these species in fall, 32.9% in winter, or 27.5% in spring, or a mean greater than 8.1% in any season. Twelve other wetlands held over 1% of at least half the key taxa in one or more seasons. They included

TABLE 4. Percent of 13 shorebirds attributed to four U.S. Pacific Coast regions in Fall (F), winter (W), and spring (S). North CA is north of and South CA is south of San Francisco Bay (S.F. Bay).

Species	WA and OR			North CA			S.F. Bay			South CA		
	F	W	S	F	W	S	F	W	S	F	W	S
Black-bellied Plover	13.8	8.4	18.6	8.9	12.6	11.3	61.9	59.4	55.5	15.4	19.7	14.6
Semipalmated Plover	16.0	3.4	13.9	12.2	23.0	12.7	52.0	40.1	46.7	19.9	33.4	26.6
Greater Yellowlegs	24.1	28.5	46.4	12.5	12.2	16.0	41.1	40.7	25.5	22.3	18.6	12.1
Red Knot	1.8	0.1	29.7	0.8	6.4	1.9	76.2	43.3	39.1	21.2	50.3	29.3
Western Sandpiper	17.9	2.3	38.6	13.6	9.5	2.3	58.6	67.7	53.8	9.9	20.4	5.3
Least Sandpiper	6.3	4.7	7.4	11.6	28.9	7.0	66.9	39.1	73.1	15.2	27.3	12.5
Dunlin	—	43.8	72.1	—	16.1	3.6	—	37.8	24.0	—	2.3	0.3
dowitchers	4.5	2.6	42.4	5.2	4.6	2.3	72.2	64.8	49.1	18.2	28.1	6.2
Black-necked Stilt	0.0	0.0	0.0	0.0	0.0	0.1	78.3	90.1	57.5	21.7	9.9	42.4
American Avocet	0.0	0.0	0.0	0.7	4.2	2.2	96.5	88.3	85.6	2.8	7.4	12.2
Willet	0.4	0.1	0.2	11.4	18.0	17.1	69.3	58.5	56.6	18.9	23.5	26.2
Long-billed Curlew	0.8	4.1	0.9	8.7	9.9	10.1	65.5	48.6	45.5	25.0	37.4	43.5
Marbled Godwit	0.3	1.3	0.7	20.8	31.9	21.0	61.9	46.3	67.7	17.0	20.5	10.6

Humboldt Bay and Elkhorn Slough for 12 of the 13 key taxa, San Diego Bay and Mugu Lagoon for 10 key taxa, Willapa Bay, Morro Bay, and Point Reyes Esteros for 9 key taxa, Mission Bay/San Diego Flood Control Channel and Tomales Bay for 8 key taxa, and Grays Harbor, Bolsa Chica, and Bolinas Lagoon for 7 key taxa.

Thirty-eight wetlands supported at least 1% of at least one key species during at least one season (Table 1); if means, medians, or maxima had been used instead of medians conditioned on non-zero values for the calculations, 32 of the same sites would have been selected (Table 1). Those wetlands not selected by all the above measures were Necanicum River Estuary (selected by maxima only), Agua Hedionda Lagoon (maxima and means only), Nestucca Bay (maxima and medians only), Siletz Bay, Pajaro River Mouth, and Devereux Slough (maxima and non-zero medians only), New River Estuary and Santa Margarita River Estuary (all measures except means), and Estero Americano (all measures except maxima).

COMPARISON OF METHODS FOR IDENTIFYING SITES AS CONSERVATION PRIORITIES

Of the five methods examined for identifying wetlands critical for conservation of west coast shorebird populations, selecting those wetlands supporting at least 1% of one or more key species in at least one season encompassed 38 sites (Table 1) averaged 99%, and never fell below 95%, of the individuals of the 13 key taxa (Table 5). Those sites identified by WHSRN as holding 20,000 or more shorebirds (Harrington and Perry 1995) included 16 sites (Table 1) and averaged 90–92%, but fell as low as 72%, of the individuals of the key taxa depending on season; however, if only the two sites of hemispheric importance are used, averages dropped to 57–68%, and could be as low as 33%, for key species (Table 5). Selection of the top three sites for any key species any season resulted in the inclusion of 18 sites (Table 1) and averaged 91–92%, but fell as low as 68%, of the individuals of the 13 key taxa depending on season (Table

TABLE 5. Percent of 13 shorebird taxa encompassed by five methods of selection of U.S. Pacific Coast wetlands.

Method	Fall		Winter		Spring	
	Range	Mean \pm SE	Range	Mean \pm SE	Range	Mean \pm SE
1% or more of wetland population	95.8–99.9	98.8 \pm 0.4	97.6–100.0	99.2 \pm 0.2	96.3–99.6	98.8 \pm 0.3
All potential WHSRN sites	81.1–98.2	91.3 \pm 1.7	81.8–98.4	92.2 \pm 1.4	72.3–99.0	89.8 \pm 2.8
Only WHSRN hemispheric sites	41.9–96.5	67.9 \pm 3.9	39.2–90.1	57.3 \pm 4.7	33.3–85.6	60.3 \pm 3.8
Among top 3 sites for any species	80.6–99.0	91.9 \pm 1.7	82.1–98.5	92.1 \pm 1.5	68.0–98.8	91.1 \pm 2.3
Modified complementarity analysis	41.1–96.5	66.7 \pm 4.0	37.8–90.1	55.7 \pm 5.0	24.0–85.6	52.3 \pm 4.8

5). Modified complementarity analysis (Turpie 1995), selected only San Francisco Bay as necessary for conserving representative populations of all species, averaged only 52–67%, and could be as low as 24%, of the estimated totals of the 13 key taxa (Table 5).

DISCUSSION

Although it would have been preferable to conduct more surveys at each site, both within and between seasons, the large area covered and the considerable effort required to organize the hundreds of volunteers for each survey prevented us from making these improvements. Despite its limitations, our study provides the first overview of the relative abundance of shorebird species and their distribution among wetlands of the Pacific Coast of the United States. Our study categorized 22 shorebird species as moderately abundant to abundant in the wetlands. Of the 14 of these species that breed in arctic regions, all except the Red-necked Phalarope, which winters offshore mainly south of the Tropic of Cancer, winter primarily in North America or widely in both North and South America (Table 2). No arctic-breeding species that winters on the continent south of the Tropic of Cancer was even moderately abundant on our surveys. For the other eight species from temperate-zone breeding latitudes, the coastal wetlands of California also were an important migration corridor and winter destination. Thus the Pacific Coast of the contiguous United States is best characterized as a migratory corridor and a winter destination for arctic-breeding shorebirds that winter in North America or in North and South America, and for shorebirds with temperate-zone breeding ranges.

In contrast, the U.S. Atlantic Coast is more important as a migratory corridor for arctic breeders that winter primarily south of the Tropic of Cancer (Morrison 1984), and the interior wetlands of the Great Plains is a migratory corridor for small to medium-sized, arctic-breeding species that winter primarily from the tropics south (Skagen and Knopf 1993). The interior wetlands of the inter-mountain region of the western United States comprise an important migratory corridor for temperate-zone breeders wintering primarily in North America (except Wilson's Phalarope) and arctic breeders wintering widely in both North and South America (Skagen and Knopf 1993, Warnock et al. 1998).

San Francisco Bay was identified as a criti-

cally important wetland for shorebird conservation because of the occurrence of relatively high numbers of shorebirds in all seasons. Twelve other wetlands also held over 1% of at least half of the 13 key taxa in one or more seasons. WHSRN criterion defines any site accounting for 20,000 shorebirds annually to be regionally important for shorebird conservation. Data from our study suggest this criterion would include a high proportion of the shorebirds concentrating in the wetlands along the Pacific Coast of the United States. However, the proportion of birds covered would be much lower if only WHSRN sites of hemispheric importance were considered (Table 5). Of 56 wetlands surveyed, we consider the 38 holding at least 1% of at least one species' regional total during at least one season (Table 1) to be the minimum key sites for conservation of shorebird populations along the Pacific west coast.

Although government programs and legislation serve to protect wetlands of the United States for shorebirds and other wildlife (Bildstein et al. 1991), factors not covered by legislation will alter the value of Pacific Coast wetlands for shorebirds in the future. State and federal agencies' habitat enhancement projects, which occurred since our study or are being planned for the future, may have positive or negative effects for shorebirds. Since our study, Batiquitos Lagoon, San Diego County, California has been opened to continuous tidal action through a large dredging project, and thus we would expect to see a changed pattern of shorebird use. Plans also are underway to reconfigure the wetland types within San Francisco Bay if and when certain key areas become available for restoration. One proposed reclamation is the conversion of large portions of the South Bay salt evaporation system to salt marsh. Such a conversion could have a detrimental effect on shorebirds such as Snowy Plover, Wilson's and Red-necked Phalaropes, and Black-necked Stilt, which are salt pond specialists in the Bay, if provisions are not made to preserve salt pond habitat for them.

Introduced species, both plant and animal, continually alter shorebird wetland habitat. The introduction of the salt marsh cordgrass, *Spartina alterniflora*, to Puget Sound, Willapa Bay, Siuslaw River Estuary, and San Francisco Bay (Frenkel 1987, Daehler and Strong 1996) may make tidal flats less suitable for foraging shorebirds than tidal flats with native vegetation. This

introduced exotic out-competes and grows at lower elevations in the tidal zone than the native cordgrass (Callaway and Josselyn 1992), and shorebirds are not as likely to forage in cordgrass marsh as on unvegetated tidal flats (Goss-Custard and Moser 1988). Frequent introductions of invertebrates into the larger coastal wetlands, due especially to bilge pumping by ocean going vessels, are creating continuously changing benthic communities in large wetlands such as San Francisco Bay (Cohen 1998, Cohen and Carlton 1998). Benthic invertebrates are the primary food of shorebirds in west coast wetlands and the effect of the changing invertebrate communities on shorebirds is unknown.

Rising sea levels, resulting from global warming, are another human-related factor with the potential to reduce the extent of tidal flat foraging areas for shorebirds in many wetlands in the future (Nicholls and Leatherman 1996). Also, rapid filling with sediment of some wetlands such as Bolinas Lagoon and Upper Newport Bay, California, because of human alterations to watersheds during the past century, threatens to increase the extent of tidal marsh at the expense of tidal flats, another detrimental change for shorebirds. Lastly, there is growing recreational use of shallow water areas of west coast wetlands by people using personal watercraft, sea kayaks, and wind surf boards. For at least personal watercraft, Burger (1998) recorded detrimental effects on breeding marine birds, but the effects of these recreational activities on migrating and wintering shorebird populations are unknown and should be investigated.

Based on the most comprehensive shorebird survey data to date, we have identified the most important U.S. Pacific Coast wetlands for migrating and wintering shorebirds from temperate-zone and arctic breeding ranges. Ever changing conditions of coastal wetlands, due to the interaction of human activities and natural successional processes, will alter their value for shorebirds in the future. Understanding the effects of these changes, avoiding or mitigating for those likely to be detrimental, and promoting those likely to be beneficial are necessary actions for conserving shorebird populations in the coastal ecosystem.

ACKNOWLEDGMENTS

Funding for the project was contributed by the Bay Foundation of Morro Bay, Bradford Foundation, Chev-

ron USA Incorporated, Dakin Foundation, David and Lucile Packard Foundation, Dean Witter Foundation, Genentech, Walter and Elise Haas Foundation, Marin, Morro Coast and Stockton chapters of the National Audubon Society, National Fish and Wildlife Foundation, San Francisco Foundation, True North Foundation, and members of Point Reyes Bird Observatory. Dave Shuford provided valuable assistance in the design and implementation of the project. We are very grateful to the following people for organizing counts of key areas: Patrice Ashfield, Alan Barron, John Bradley, Joseph Buchanan, Ester Burkett, Robert Chaney, Deborah Parker-Chapman, Al Clark, James Collins, Mark Colwell, Peter Connors, Alice DeBolt, Jack Dougherty, Richard Erickson, Joseph Evenson, Leora Feeney, Kimball Garrett, Rebecca Goggans, CC Gorman, Freeman Hall, Marlin Harms, Loren Hays, Kathy Hobson, Jan Hodder, Dave Jensen, Max Johnson, Tom Keeney, John Kelly, John Konecny, Barbara Kus, Dick Kust, Steve Langenstein, Robin Leong, Jayne Lesley, Roy Lowe, Neal Main, John Maron, Vern Marr, Helen Matelson, Kathy Merrifield, Tom Mickel, Eric Nelson, Jeff Newman, Robert Patton, Bill Perry, Phil Persons, Joe Pesek, Lina Prairie, Bernadette Ramer, Susan Reimer, Bob Richmond, Craig Roberts, Keith Smeltzer, Donald Starks, Nancy States, Terri Stewart, Larry Thornburgh, Louise Vicencio, Nils Warnock, Sarah Warnock, Herb Williams, Cora Wilson, Peg Woodin, and Dick Zembal. They, as well as Mary Anne Bishop, Robert Butler, Robert Gill, Brian Harrington, and Guy Morrison shared with us their insights about regions and species with which they had a special familiarity. We thank the hundreds of talented volunteers who counted shorebirds in the wetlands and made this project possible. The cooperation of Jean Takekawa and Rick Coleman of San Francisco Bay National Wildlife Refuge (NWR), Tim Burr of Southwest Division Naval Engineering Command, and Robert Douglass of Cargill Incorporated was critical to the project. Personnel at Cargill Incorporated, Mare Island Naval Air Station (NAS), North Island NAS, Oliver Brothers, Pacific Gas & Electric, Pendelton Marine Corps Base, San Diego Gas & Electric, San Diego Port District, San Francisco and San Pablo Bay NWR, Mugu NAS, Seal Beach Naval Weapons Reserve, Tijuana River Estuary NWR, and Venture Corporation, and many private landowners granted access to their shoreline, which allowed us complete coverage of wetlands. Jane Church, Mark Colwell, Brian Harrington, and an anonymous reviewer greatly improved the presentation of this paper. Anne Hoblitzelle and Laurie Wayburn helped to secure funding for this project. Without the help of all these people, this project would have been impossible. This is Contribution No. 819 of Point Reyes Bird Observatory.

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