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ABUNDANCE AND DISTRIBUTION OF MIGRATORY SHOREBIRDS AT MONO LAKE, CALIFORNIA

EMILIE A. STRAUSS, Stillwater Sciences, 2532 Durant Ave., Suite 201, Berkeley, California 94704

CHRISTINE A. RIBIC, U.S. Geological Survey, Wisconsin Cooperative Wildlife Research Unit, Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706

W. DAVID SHUFORD, PRBO Conservation Science, 4990 Shoreline Highway, Stinson Beach, California 94970

ABSTRACT: We counted migratory shorebirds and documented their patterns of shoreline distribution at Mono Lake in the Great Basin of California via annual spring and fall surveys from 1989 to 1995. We tallied a total of 30 species, 29 in fall, 25 in spring, and 24 in both seasons. Median counts of all shorebirds were 31,432 (13,901–50,916) in fall and 7792 (2683–25,616) in spring. Median counts exceeded 5000 each for the American Avocet and Wilson's and Red-necked phalaropes in fall and 1000 for the Western and Least sandpipers in spring. Of nine species with median counts of >50 individuals, medians were >50% higher in fall than spring for the American Avocet, Wilson's Phalarope, and Red-necked Phalarope, were >50% higher in spring than fall for the Semipalmated Plover, Western Sandpiper, Least Sandpiper, and Dunlin, and similar in both seasons for the Snowy Plover and Killdeer. The distribution around the lake of total shorebirds and of most individual taxa, except for the Spotted Sandpiper in fall, varied considerably from year to year. Shorebirds as a group as well as most species considered separately concentrated on the south, east, or north shores; except for the Killdeer and Spotted Sandpiper all taxa appeared to avoid the west shore at both seasons. Mono Lake is one of the most important sites for shorebirds in the Intermountain West, particularly for Wilson's and Red-necked phalaropes. Mono Lake's large size, varied habitats, and abundant food are very attractive to shorebirds; habitat availability and food supply are more reliable there than at many sites where they fluctuate widely with variations in climate. A water-rights decision that raises the lake's level likely will improve shorebird habitat, though effects will be mixed.

Widespread declines in shorebird populations in western North America (Page and Gill 1994) emphasize the need to identify and protect important migratory stopovers for this group of birds (Myers et al. 1987, Brown et al. 2000). Although recent studies give broad overviews of shorebird use of wetlands and agricultural habitats in western North America (Shuford et al. 1998, Page et al. 1999, Shuford et al. 2002), few data have been published on the patterns of shorebird use at individual sites, where most conservation and management efforts will focus.

Mono Lake is well recognized for its critical importance to breeding California Gulls (*Larus californicus*; Shuford and Ryan 2000), Snowy Plovers (*Charadrius alexandrinus*; Page and Stenzel 1981), migratory Eared Grebes (*Podiceps nigricollis*; Boyd and Jehl 1998), and Wilson's (*Phalaropus tricolor*) and Red-necked (*P. lobatus*) phalaropes (Jehl 1986, 1988), yet little is known about the abundance and distribution of most species of shorebirds at the lake. Prior data on shorebird migration at Mono Lake come primarily from five lakewide surveys of waterbirds from 8 July to 14 September 1976 (Winkler et al. 1977) and from localized counts of shorebirds at the Old Marina and South Tufa on 35 and 23 dates, respectively, from 1971 to 1973 (Jurek 1973, 1974). Similarly, prior data on the distribution of shorebirds around Mono Lake are restricted mainly to detailed descriptions for the Red-necked Phalarope (Jehl 1986) and anecdotal ones for other species (Gaines 1992). To add to this knowledge, we counted shorebirds at Mono Lake in spring and fall from 1989 to 1995 as part of PRBO's Pacific Flyway Project.

Here we report the abundance, species composition, and patterns of shoreline distribution of shorebirds at Mono Lake. We also discuss the importance to shorebirds of Mono Lake relative to other sites in the Intermountain West, the implications to shorebird populations of a 1994 water-board decision to raise the lake level substantially, and the need for additional shorebird research at the lake.

STUDY AREA AND METHODS

Mono Lake is a hypersaline terminal lake in eastern California located at the base of the Sierra Nevada at the western edge of the Great Basin. In 1941, the city of Los Angeles diverted streams flowing into Mono Lake. Consequently, the lake fell over 40 vertical feet and doubled in salinity, from 50 grams per liter in 1940 to 100 grams per liter by 1982 (Vorster 1985). Increasing salinity reduced the productivity of brine shrimp (*Artemia monica*) and alkali flies (*Ephydra hians*) (Herbst 1988, 1992; Herbst and Bradley 1993), the primary prey items of aquatic birds using the lake. During our study, the elevation of Mono Lake dropped from 6377.0 feet (1943.7 m) in April 1989 to 6374.1 feet (1942.8 m) in January 1992, then rose to 6377.6 feet (1943.9 m) by August 1995 (Los Angeles Aqueduct Daily Reports).

The length of the Mono Lake shoreline, exclusive of islands, is about 38.0 miles (61.3 km) at a lake elevation of 6378 feet (1944 m). For analysis of distribution, described below, we grouped data from 25 subareas into four larger segments of shoreline: south (13.9 km), east (10.24 km), north (18.99 km), and west (18.17 km) (Figure 1). The south segment was characterized by alkali mudflats, with a relatively long (1–2 km) reach of freshwater marsh, springs, and tufa towers and shoals adjoining the beach at Simon's Springs. The east segment of Mono Lake was dominated by broad alkali mudflats with a few springs whose fresh water flows down to Mono Lake as shallow

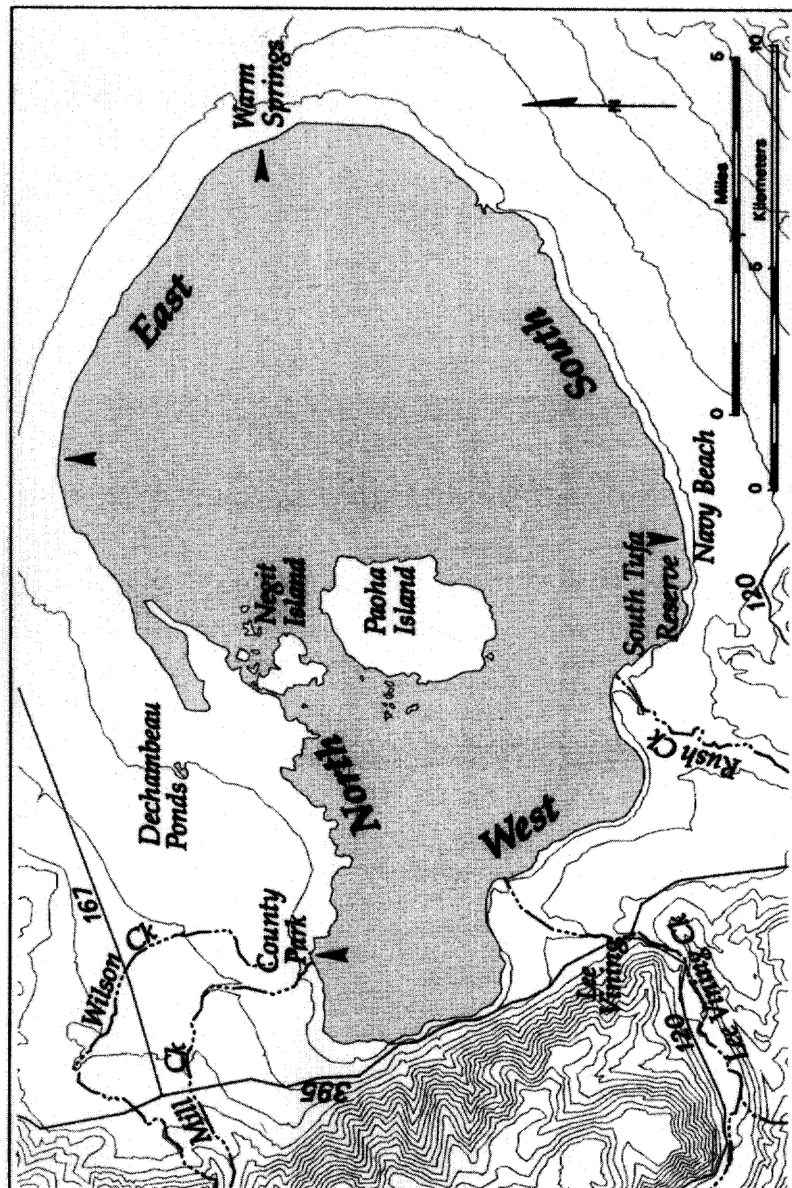

Figure 1. The Mono Lake study area, at a lake elevation of 6378 feet (1944 m), depicting four shoreline segments used for analyses.

laminar sheets and rills. During our study, some rills at Warm Springs ran for 0.4 to 0.8 km before reaching Mono Lake. The north segment consisted mostly of rocky shoals of tufa-encrusted pumice boulders interspersed with patches of mudflat, freshwater marshes, and creek mouths; springs were concentrated at Mono Lake County Park, Wilson Creek delta, and Bridgeport Creek delta (east of Dechambeau Ponds). Man-made Dechambeau Ponds contained fresh water. The west segment consisted primarily of a narrow beach dominated in many sections by sand, cobble, or tufa shoals rather than mud or alkali flats, especially between the Old Marina and Lee Vining Creek, where the steep drop-off provided relatively little shallow-water habitat. Shorebird habitat became more limited on the western shore from 1994 to 1995 when the lake rose and inundated most beaches, which had already narrowed from encroaching vegetation during years of dropping lake level. The lake's two largest freshwater sources, Lee Vining and Rush creeks, flowed into the west segment. A number of large springs also discharged on the western shoreline, but some of these were either surrounded by dense marsh vegetation or did not support shallow-water habitat. During some years, fresh water entering Mono Lake floats on the surface of saline lake water, providing hypopycnal habitat important to phalaropes. Most years, berms of sand created narrow lagoons adjacent to the shoreline; those in the northern portion of the east segment were hypersaline, whereas those along the south shore generally contained fresh or brackish water.

We conducted 14 shorebird counts at Mono Lake, once each spring and fall from 1989 to 1995. Dates of spring counts ranged from 21 April to 6 May, those of fall counts from 13 to 26 August. We selected these dates because they represent peak migratory periods for most shorebird species in the western Great Basin (see Warnock et al. 1998). Our surveys were not timed to coincide with the breeding period of the six species, the Snowy Plover, Killdeer (*Charadrius vociferus*), American Avocet (*Recurvirostra americana*), Spotted Sandpiper (*Actitis macularia*), Wilson's Snipe (*Gallinago delicata*), and Wilson's Phalarope, that nest regularly at the lake in low to moderate numbers (Gaines 1992); the Black-necked Stilt (*Himantopus mexicanus*) is known to have nested only once (B. Miller pers. comm.). We did not conduct winter counts because no shorebirds regularly overwinter, with the exception of very low numbers of the Killdeer, Wilson's Snipe, and Least Sandpiper (*Calidris minutilla*; Gaines 1992).

To cover the long shoreline effectively, we allowed two days for each count. To minimize double counting, we divided observers (generally 10 to 15 per census) into groups of one to three and assigned them to contiguous stretches of lakeshore. Observers, walking parallel to the shore, tallied shorebirds within 25 discrete subareas from 0.8 to 6.8 km in length based on a lake level of 6378 feet (1944.0 m). In a few areas, observers occasionally counted using a telescope from a fixed point. We also usually surveyed Dechambeau Ponds but not the shoreline of any of the lake's islands. We used data from Dechambeau Ponds for tallies of shorebird abundance but not for analysis of distribution patterns around the lake. In most years, but not in fall 1989 and 1990 or spring 1992 and 1995, observers surveyed all or a portion of the land bridge connecting Negit Island to the mainland.

Our surveys provide minimal estimates of numbers of migrating shorebirds because of various limitations to our methods. Lacking adequate numbers of observers, we covered the entire lakeshore only in spring 1994. On other counts, we assigned available observers to areas that shorebirds typically use heavily. Coverage ranged from about 75% to 100% of the shoreline, with the exception of only 60% in spring 1989 and fall 1993. We estimate we probably counted 70% to 90% of all shorebirds present. Access to some areas was restricted by soft mud or quicksand or by massive alkali dust storms (spring 1995). In the falls of 1989 to 1991 and 1993, collaborators counted phalaropes by boat, which has proven the most reliable method for surveying these largely aquatic shorebirds. In these years we substituted the boat tallies of phalaropes for land-based counts; boat counts were on the same weekend as land-based counts in 1990 and 1992 and 8 and 13 days prior in 1989 and 1991, respectively. The protocol for boat counts was described by Jehl (1999).

Because the Flyway Project emphasized the geographic extent of surveys at the expense of their frequency, our twice-annual surveys underestimated the numbers of some early- or late-migrating species. In fall, we generally timed our surveys two to three weeks later than the peak occurrence of the Wilson's Phalarope (Jehl 1988) and about six weeks before the arrival of the Dunlin (*Calidris alpina*; Gaines 1992). In spring, most counts were too early to capture the peak in abundance of phalaropes, which occurs in early to mid-May (Jehl 1986, 1988), or of the Spotted Sandpiper, which is rare as a migrant or summer resident before early May (Gaines 1992). We also underestimated the abundance of some cryptic species that extensively use habitats away from the immediate shoreline of Mono Lake. These include the Snowy Plover and Wilson's Snipe, which use broad alkali flats and lake-fringing marshes, respectively. Similarly, once-per-season surveys may miss peak passage because of natural annual variation (Stenzel and Page 1988, Warnock et al. 1998), particularly in spring when species such as the Western Sandpiper (*C. mauri*), Least Sandpiper, and Long-billed Dowitcher (*Limnodromus scolopaceus*) have very short stopover periods (Warnock and Bishop 1998).

We instructed observers to identify all shorebirds to species when possible. Groups of unidentified shorebirds fell mostly into four categories: yellowlegs, either Greater (*Tringa melanoleuca*) or Lesser (*T. flavipes*); small sandpipers of the genus *Calidris*, primarily Western Sandpipers, Least Sandpipers, or Dunlin; dowitchers, either Short-billed (*Limnodromus griseus*) or Long-billed; and phalaropes, either Wilson's or Red-necked. We assigned unidentified shorebirds to species using methods described by Page et al. (1999), leaving some in unidentified categories when the ratio of unidentified to identified was high. For analyses, we grouped both identified and unidentified dowitchers as dowitcher spp. owing to the difficulty of identifying most individuals to species on surveys.

Data Analysis

To analyze distribution, we selected counts with adequate coverage of the lake's shoreline. For each survey, we tabulated effort per segment (south, west, east, and north) and calculated the proportion of each segment surveyed. We considered only segments that had at least 70% of their shoreline surveyed as representative of the segment and hence adequate for analysis. Coverage was adequate for all four segments in both spring and fall in 1991, 1992, and 1994, in spring only in 1990. Similarly, sample sizes were adequate for analysis for the Snowy Plover, Semipalmated Plover (*Charadrius semipalmatus*), Killdeer, American Avocet, Spotted Sandpiper, Least/Western sandpipers, Dunlin, and dowitcher spp.

We analyzed data for each species or species group by season. Because not all segments received equal coverage, we adjusted totals for individual species and all shorebirds combined by proportionately reducing counts to the smallest area surveyed in a segment in any year (7.38 km in spring, 8.41 km in fall). This adjusts coverage so it is equivalent across all segments and years in the season, as suggested by Haney (1986) and used by Ribic et al. (1997). *A priori*, we excluded phalaropes from analysis because of varying survey methods among counts and lack of breakdown by shoreline segment on boat surveys.

The null hypothesis was that each species or species group had the same distribution around Mono Lake regardless of year. If there was no evidence that a species' distribution differed from year to year, then data from all years were combined and tested for a uniform distribution around Mono Lake. These hypotheses were tested with log-linear models and standardized residual analysis (Lloyd 1999). The null hypothesis was tested by means of the likelihood-ratio goodness-of-fit statistic (G). If the null hypothesis was rejected, standardized residuals showed where data were not fit well by the model. Large positive residuals indicate there are more birds in a segment than expected, whereas large negative residuals indicate fewer birds than expected. Standardized residuals are distributed as normal (0,1) variables, so "large" is a value of 2 or greater and would be considered significant at a probability of 0.05. Residuals less than 2 but greater than 1.6 would be significant at 0.10 and are considered as trends or tendencies. Analyses were done with STATISTICA (StatSoft 1995).

RESULTS

Species Richness and Abundance

We tallied 30 species of shorebirds on our surveys of Mono Lake (Table 1). Of these, we recorded 29 in fall, 25 in spring, and 24 in both seasons. We recorded 6 species every spring and fall and 11 others on every count in just one season (7 in fall, 4 in spring). Median counts of total shorebirds were 31,432 (range 13,901–50,916) in fall and 7792 (range 2683–25,616) in spring. For individual species, median counts were >5000 each for the American Avocet, Wilson's Phalarope, and Red-necked Phalarope in fall and >1000 for the Western and Least sandpipers in spring. Of nine species with median counts of >50 individuals, medians were >50% higher in fall than in spring for the American Avocet, Wilson's Phalarope, and Red-necked Phalarope, were >50% higher in spring than in fall for the Semipalmated Plover, Western Sandpiper, Least Sandpiper, and Dunlin, and similar in both seasons for the Snowy Plover and Killdeer.

Table 1 Numbers of Shorebirds at Mono Lake, California, 1989–1995[a]

	Fall[b]				
Species	19 Aug 1989	25 Aug 1990	24 Aug 1991	15 Aug 1992	22 Aug 1993
Black-bellied Plover *Pluvialis squatarola*	5	8	0	4	0
Snowy Plover *Charadrius alexandrinus*	18	49	31	7	81
Semipalmated Plover *C. semipalmatus*	25	30	8	0	4
Killdeer *C. vociferus*	147	202	32	66	30
Mountain Plover *C. montanus*	0	0	3	0	0
Black-necked Stilt *Himantopus mexicanus*	133	12	22	13	51
American Avocet *Recurvirostra americana*	8467	5398	7652	4520	8999
Greater Yellowlegs *Tringa melanoleuca*	4	9	16	7	4
Lesser Yellowlegs *T. flavipes*	9	11	15	1	3
Yellowlegs spp.	0	0	0	0	0
Solitary Sandpiper *T. solitaria*	1	2	0	0	0
Willet *Catoptrophorus semipalmatus*	31	11	9	4	11
Spotted Sandpiper *Actitis macularia*	43	53	24	15	0
Whimbrel *Numenius phaeopus*	0	0	0	0	0
Long-billed Curlew *N. americanus*	24	24	7	19	1
Marbled Godwit *Limosa fedoa*	3	124	16	2	1
Ruddy Turnstone *Arenaria interpres*	2	0	1	0	0
Red Knot *Calidris canutus*	3	0	0	0	4
Sanderling *C. alba*	0	6	1	0	0
Semipalmated Sandpiper *C. pusilla*	0	0	1	0	0
Western Sandpiper *C. mauri*	639	3573	3171	490	272
Least Sandpiper *C. minutilla*	204	1244	527	24	410
Western/Least Sandpiper	226	634	10	0	0
Baird's Sandpiper *C. bairdii*	19	31	19	2	7
Pectoral Sandpiper *C. melanotos*	0	0	0	0	2
Dunlin *C. alpina*	0	0	0	0	12
Western/Least/Dunlin	0	0	0	0	0
Dowitchers *Limnodromus* spp.[c]	28	46	27	4	20
Wilson's Snipe *Gallinago delicata*	2	7	2	2	0
Wilson's Phalarope *Phalaropus tricolor*	4500	478	10,000	1420	9000
Red-necked Phalarope *Phalaropus lobatus*	19,000	6320	18,000	5981	12,520
Red Phalarope *Phalaropus fulicarius*	0	0	0	0	0
Phalarope spp.	0	1050	0	510	0
Total shorebirds	33,533	19,322	39,594	13,091	31,432

		Spring						
13 Aug 1994	12 Aug 1995	22 Apr 1989	21 Apr 1990	27 Apr 1991	25 Apr 1992	1 May 1993	5 May 1994	29 Apr 1995
40	50	4	49	11	14	0	0	1
87	216	35	81	88	56	135	101	23
6	16	286	178	244	70	128	159	133
153	48	67	97	64	23	25	65	30
0	0	0	0	0	0	0	0	0
55	0	21	11	1	17	8	82	0
10,999	2191	1564	650	353	805	317	425	15
4	1	9	6	2	2	0	3	6
10	1	0	0	0	0	1	0	0
1	0	1	0	0	0	0	0	0
4	0	0	1	0	0	0	0	0
35	9	0	0	4	50	3	6	9
49	7	4	4	5	1	10	209	3
0	0	1	0	0	2	0	4	0
43	7	2	0	0	0	1	0	2
16	5	0	0	19	0	36	0	0
0	0	0	0	0	0	0	0	0
1	0	0	0	0	3	0	0	0
0	3	0	0	0	0	0	14	0
0	0	0	0	0	0	0	0	0
725	1129	14,217	18,640	1178	4939	1482	8921	1952
196	305	1298	4693	3243	1178	329	188	148
1	0	1810	584	1989	0	108	0	0
27	18	0	0	3	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	183	430	313	263	88	725	325
0	0	540	0	0	0	0	0	
27	30	297	22	39	100	8	11	22
1	7	5	3	22	5	4	7	7
5478	46,542	126	61	33	51	852	764	7
1113	75	64	0	179	4	9	129	0
0	5	0	0	0	0	0	0	0
0	250	0	106	2	4	35	675	0
19,071	50,916	20,534	25,616	7792	7587	3579	12,488	2683

[a]Dates represent the first day of a two-day count period.

[b]Phalarope data from boat counts on 11 August 1989, 26 August 1990, 11 August 1991, and 22 August 1993 and from land-based counts on all other surveys. These counts tended to greatly underestimate numbers of Wilson's Phalaropes because they were two to three weeks later than the normal peak passage for that species.

[c]Long-billed (*L. scolopaceus*) and Short-billed (*L. griseus*) dowitchers were recorded in both fall and spring.

Table 2 Likelihood-Ratio Goodness-of-Fit Statistics Relative to the Null Hypothesis That Each Shorebird Taxon Had the Same Distribution around Mono Lake Regardless of Year

	Fall			Spring		
Species	G	df	*p*	G	df	*p*
Total shorebirds	1522	6	<0.001	4642	9	<0.001
Snowy Plover	17.3	6	0.008	45.9	9	0.02
Semipalmated Plover	—	—	—	107	9	<0.001
Killdeer	3.3	6	0.8	45	9	<0.001
American Avocet	1959	6	<0.001	353	9	<0.001
Spotted Sandpiper	0.5	6	0.9	—	—	—
Least/Western sandpipers	787	6	<0.001	4642	9	<0.001
Dunlin	—	—	—	15.4	6	0.02
Dowitcher spp.	—	—	—	58	9	<0.001

Lakewide Distribution Patterns

The distribution around the lake for total shorebirds, American Avocets, and Least/Western sandpipers varied considerably from year to year in both spring and fall, for the Snowy Plover, Semipalmated Plover, Dunlin, and dowitchers in spring, and for the Killdeer in spring but not fall (Table 2). The Spotted Sandpiper showed the most predictable pattern, as its distribution in fall did not vary from year to year.

Analyses by year showed that, in spring, shorebirds as a whole concentrated in numbers greater than expected in the south and east, as did the Semipalmated Plover, Least/Western sandpipers, and Dunlin (Table 3). In fall, shorebirds as a whole generally concentrated in numbers higher than expected in the east and north, as did the American Avocet and Least/Western sandpipers (Table 3). Shorebirds as a group occurred in numbers lower than expected in the west in both seasons (Table 3). Except for the Killdeer and Spotted Sandpiper, all species occurred in numbers lower than expected in the west in both seasons. The Killdeer occurred in numbers higher than expected in the west but generally in numbers lower than expected in the north and east. The exception was in spring 1991, when the Killdeer occurred in higher numbers in the east. In fall, the Spotted Sandpiper consistently occurred in numbers higher than expected in the west and in numbers lower than expected in the east and north.

Some individual species had additional distribution patterns of interest. In spring, the Snowy Plover consistently occurred in numbers greater than expected in the east and sometimes the south, the Semipalmated Plover mostly in the south and sometimes in the east, Least/Western sandpipers and Dunlin in the south and east, and dowitchers mostly in the east. Patterns for the American Avocet were among the most variable with numbers greater than expected mostly in the south in spring and the north and east in fall.

DISCUSSION

Despite their limitations, our surveys greatly expanded the knowledge of the species composition, abundance, and distribution of migrant shorebirds at Mono Lake. Our peak counts of American Avocets and Western Sandpipers, for example, are about three and nine times greater, respectively, than any prior counts (Jurek 1973, Winkler et al. 1977, Winter and Manolis 1978). We added little information, however, on phalaropes. Jehl (1999) reported counts of Wilson's Phalaropes at Mono Lake averaging about 55,000 (maximum 70,000) in the early to mid-1980s, declining to 2100 by 1992, and increasing again to about 38,000 in 1997. In fall our counts were too late in the season for peak numbers and hence are not comparable to Jehl's. In 1989, our land-based count on 12–13 August of 46,542 Wilson's Phalaropes was anomalous in that it exceeded Jehl's (1999) boat count of 34,800 taken that year during the typical period of peak numbers from 25 July to 3 August. Jehl's (1986) peak counts of Red-necked Phalaropes at Mono Lake from 1981 to 1984 ranged from 8000 to 14,000; on the basis of turnover he estimated 52,000 to 65,000 passed through each fall. Our comparable boat counts for the Red-necked on single dates in 1989, 1991, and 1993 ranged from 12,520 to 19,000. The highest estimate for this species at Mono Lake on a single date was >40,000 on 22 August 1958 (H. Cogswell in Jehl 1986).

Importance of Mono Lake

A combination of our data, for various shorebirds, and Jehl's (1986, 1988), for phalaropes, led to designation of Mono Lake as a site of international importance within the Western Hemisphere Shorebird Reserve Network (Harrington and Perry 1995). International sites annually support at least 100,000 shorebirds or 15% of a species' flyway population. Within the entire Intermountain West, Mono Lake is one of only 10 sites that hold >10,000 shorebirds in fall (Shuford et al. 2002) and, along with Great Salt Lake and Lake Abert, is one of the three most important sites for Wilson's and Red-necked phalaropes (Jehl 1986, 1988; Shuford et al. 2002). Mono Lake also is one of the most important sites in the interior of California for breeding Snowy Plovers (Page et al. 1991).

Mono Lake is very important to shorebirds because of its large size, long shoreline with varied habitats, and extremely abundant prey base of brine shrimp and alkali flies. Mono Lake is also a critical habitat because it is relatively deep yet its shallows provide mudflats and alkali flats in both wet and dry periods. By contrast, many wetlands in the arid Great Basin offer shorebirds habitat only in periods of above-average precipitation (Reed et al. 1997, Warnock et al. 1998, Plissner et al. 2000). Conversely, other important shorebird sites along the east side of the Sierra Nevada, such as Crowley Lake and Bridgeport Reservoir, are not attractive to most shorebirds during very wet years when high water levels inundate mudflats (E. Strauss pers. obs.).

Table 3 Standardized Residuals for Models of Distributions of Shorebirds around Mono Lake by Year[a]

Species		Segment			
		South	East	North	West
Total Shorebirds					
Spring	1990	**52**	−28.8	**35.6**	−58.7
	1991	**5.9**	**50**	−22.2	−33.6
	1992	**31.0**	**8.5**	−8.5	−30.9
	1994	**29.5**	**26.3**	−13.1	−42.8
Fall	1991	**10.6**	**36**	—	−45
	1992	—	**4.2**	**25**	−28
	1994	−17.1	**7.6**	**46**	−37
Snowy Plover					
Spring	1990	**3.3**	**2.3**	—	−4
	1991	−2.2	**11**	−4.2	−4.4
	1992	—	**4.5**	—	−3.5
	1994	**3.0**	**3.2**	−2	−4.2
Semipalmated Plover					
Spring	1990	**12**	−3.2	−3.1	−5.7
	1991	**5.1**	**6.4**	−5.4	−6.1
	1992	**6.5**	—	−3.8	−3.8
	1994	−2	**11.4**	−3.5	−5.9
Killdeer					
Spring	1990	—	−3.7	−3.2	**6.8**
	1991	—	**3.2**	−2.3	—
	1992	—	—	−2.0	**4**
	1994	—	−2.8	—	**4.4**
Fall	1991–94[b]	—	−5.5	—	**4.3**
American Avocet					
Spring	1990	**23**	−4.8	−6.9	−11
	1991	—	**2.9**	**3.8**	−6.2
	1992	**7.1**	−8.5	**11.3**	−9.9
	1994	**18.3**	−7.5	−2.6	−8.1

(continued)

Food Preference and Availability

Except for phalaropes and Snowy Plovers, very little is known about the food preferences of shorebirds at Mono Lake or elsewhere in the Great Basin (Warnock et al. 1997). Wilson's Phalaropes depend on both brine shrimp and alkali flies when staging at Mono Lake in fall, and their diet varies by sex and age (Jehl 1988). Snowy Plovers rely on alkali flies and a carabid beetle (*Bembidion ephippigerum*; Swarth 1983). Red-necked Phalaropes feed mostly on alkali flies (Jehl 1986) and cannot subsist on a diet of brine shrimp alone (Rubega and Inouye 1994). Mahoney and Jehl (1985) reported that samples of three stomachs of the American Avocet at Mono Lake contained only adult alkali flies, although Robinson et al. (1997) reported that at saline inland wetlands brine shrimp were also important. On the California coast, Ramer et al. (1991) found Western Sandpipers feeding

Table 3 *(Continued)*

Species		Segment			
		South	East	North	West
Fall	1991	**23.3**	**19.9**	-5.3	-38
	1992	—	**7.8**	**20**	-27
	1994	-17.7	—	**54**	-34.5
Least/Western sandpipers					
Spring	1990	**48**	-30	**38**	-57
	1991	**8.5**	**44**	-21	-31
	1992	**30**	**10**	-13	-28
	1994	**26**	**27**	-11	-42
Fall	1991	-14	**34**	**5.4**	-25
	1992	-4.2	-8.8	**20**	-7.2
	1994	-4.7	**29**	-11	-14
Spotted Sandpiper					
Fall	1991–94[b]	—	-2.9	-2.1	**6.5**
Dunlin[c]					
Spring	1990	**4.8**	**7.3**	-2.9	-9.2
	1992	**4.3**	3.6	—	-7.3
	1994	**11**	**7.1**	-6.3	-12
Dowitcher spp.[d]					
Spring	1990	—	**3.8**	—	—
	1991	-2.6	**3.4**	—	—
	1992	—	-4.0	**7.3**	-4.0

[a]Numbers in bold and Roman type are those for which counts were significantly greater and lower than expected, respectively, under the null hypothesis that, within a year, the distribution around the lake was uniform. Dashes indicate nonsignificant residuals. Significance was assessed at $p < 0.05$.

[b]No evidence was found that the pattern of distribution differed by years, hence data for all years were pooled and tested for a uniform distribution around the lake.

[c]No Dunlins were recorded in spring 1991.

[d]The number of dowitchers recorded in spring 1994 was too low to analyze.

predominantly on ephydrid fly larvae and pupae, suggesting that at Mono Lake ephydrids, such as alkali flies, may provide an important food source.

Variation in Shorebird Abundance and Species Richness

Shorebird numbers at Mono Lake varied substantially from year to year. This may reflect annual differences in habitat availability elsewhere in the western Great Basin, north-to-south variation in climatic conditions, annual variation in the period of peak migration, or annual fluctuations in sizes of shorebird populations. Warnock et al. (1998) and Shuford et al. (2002) also found large annual fluctuations in shorebird totals at other western Great Basin sites.

In all years except 1991, shorebird totals at Mono Lake were greater in fall than spring. This difference most likely reflects great seasonal fluctuations in the availability of brine shrimp and alkali flies, which attract large numbers of American Avocets and phalaropes to the lake. Although little is known about other shorebirds' food preferences at Mono Lake, prey are probably limited at Mono Lake during April but abundant during most years in August. During April, brine shrimp are immature and not large enough for shorebirds to eat (R. Jellison pers. comm.), and densities of alkali fly larvae, pupae, and adults are low (Lenz 1984, Herbst 1988). During most years, brine shrimp have grown to a size appropriate for shorebirds by late May or June (Lenz 1984, Jehl 1988).

In California, species richness of shorebirds is often slightly higher in fall than in spring because of the presence in fall of juveniles of some species that are rare to absent in spring (Page et al. 1979, Shuford et al. 1989). At Mono Lake, we observed six species—the Mountain Plover (*Charadrius montanus*), Ruddy Turnstone (*Arenaria interpres*), Sanderling (*Calidris alba*), Semipalmated (*C. pusilla*), and Pectoral (*C. melanotos*) sandpipers, and Red Phalarope (*Phalaropus fulicarius*)—during fall surveys only.

Distribution Relative to Habitat Use

During our studies, shorebirds were distributed around Mono Lake nonuniformly, reflecting in part the arrangement of various habitats. Most species, except the Killdeer and Spotted Sandpiper, occurred more than expected on either the south, east, or north shores. A large proportion of shorebirds appeared to be attracted to the juxtaposition of alkali mudflats and freshwater springs found in all but the west segment.

Although substantial numbers of shorebirds used dry alkali mudflats near the edge of Mono Lake, the majority, especially *Calidris* sandpipers, concentrated near rills, especially those at Warm and Simon's springs. Another habitat feature that attracted shorebirds was a set of shallow freshwater pools that formed most years at the mouth of Wilson Creek and along the south segment. Most shorebirds on the north segment also concentrated at freshwater sites. In 1994 and 1995, Mono Lake's level rose and inundated much of the shoreline between Navy Beach and Simon's Springs. The remaining narrow beach tended to support fewer shorebirds, though some shorebird use here shifted to narrow lagoons created by flooding from the rising lake.

The west segment typically had less shorebird habitat than the others, and what was there did not attract large concentrations. The Killdeer and Spotted Sandpiper, the only species occurring at a frequency higher than expected in the west segment, use primarily gravel bars and other hard substrates, a predominant habitat in this area. The Spotted Sandpiper, in particular, typically associates with deltas of freshwater streams (Gaines 1992) and gravelly or cobbly beaches. The Killdeer is often found on gravel bars (Jackson and Jackson 2000), especially those adjacent to fresh water (D. Shuford pers. obs.). The creek deltas, as well as mudflats below the Old Marina and southern portion of Mono County Park, attracted most of the other shorebird species in the west segment.

Most of the species commonly associated with muddy margins of lakes, such as the Semipalmated Plover, Western and Least sandpipers, and

Dunlin (Gaines 1992), used primarily the south, east, and north segments, rarely the west segment. Page et al. (1983) observed Snowy Plovers feeding either along the shore of Mono Lake or at seeps, which is consistent with our observations. Like most migrant shorebirds at the lake, dowitchers were attracted to muddy lake margins (Gaines 1992) on the south, east, and north shores, but they also use narrow mudflats adjacent to marshes and freshwater pools on the west shore. American Avocets, which feed on flies and shrimp obtained by wading in shallow water (Robinson et al. 1997), were often observed in areas away from sources of fresh water, such as the Negit Island land bridge.

Our anecdotal observations showed that phalaropes concentrated offshore except in fall 1995, when large numbers roosted and preened on alkali flats at the lake's edge. Wilson's Snipe used primarily freshwater marshes on the lake's western shore.

Fresh water is extremely important to shorebirds in a hypersaline environment such as Mono Lake. Although shorebirds have developed adaptations to avoid stress, such as excreting excess salt through salt glands and kidneys, avoiding ingestion of saltwater, choosing prey low in salt, manipulating or straining prey to minimize salt ingestion, and visiting fresh water to drink and bathe (Rubega and Robinson 1997), these behaviors consume energy and can reduce fitness. At Mono Lake fresh water is clearly important to Wilson's and Red-necked phalaropes, Least and Western sandpipers, and California Gulls for drinking and bathing (Mahoney and Jehl 1985; Jehl 1986, 1988; Rubega and Robinson 1997). Mahoney and Jehl (1985) indicated that Wilson's Phalaropes and American Avocets probably require limited fresh water when at Mono Lake because they avoid some salt loading by using the tongue and bill to squeeze lake water from prey items before ingestion. During the last several weeks of their fall visit, Wilson's Phalaropes escalate feeding rates to put on fat for a nonstop flight to South America; during this hyperphagic period they may inadvertently swallow additional lake water and thus require fresh water as often as twice a day (Mahoney and Jehl 1985, Jehl 1997). During the 1980s when Mono Lake's salinity was especially high, Jehl (1988) observed up to 50,000 Wilson's Phalaropes bathing and drinking at Mono Lake in the deltas of streams and springs. Red-necked Phalaropes also visit fresh water (Winkler et al. 1977).

Future Prospects

Concern over ecosystem collapse from increasing salinity was largely alleviated by a water-rights decision that mandated allowing Mono Lake to rise over 20 years to a dynamic equilibrium centered around a lake level of 6391 feet (1943 m; SWRCB 1994a). If water diversions had continued, hypersalinity would have greatly reduced the abundance of alkali flies and brine shrimp and increased the energetic cost of salt excretion and prey manipulation by shorebirds.

Changing habitat conditions as the lake rises to reach dynamic equilibrium should affect patterns of shorebird use. Most shorebird species likely will benefit from an increase in food. Herbst and Bradley (1993) predicted that alkali fly abundance will increase because of a reduction in salinity and an increase in submerged hard substrate used as attachment sites by fly pupae. Brine shrimp abundance also is expected to increase (Dana and Lenz 1986). Immediately after the decision to restrict water diversions and raise the lake level these long-term benefits of less saline conditions were partially offset when a large influx of fresh water in 1995 initiated an episode of meromixis or persistent salinity stratification (Jellison et al. 1998). The absence of a winter period of holomixis (complete mixing) and stronger density stratification in summer reduces internal recycling of nutrients and algal and zooplankton productivity (Jellison and Melack 1993a). A similar episode of meromixis was initiated by exceptionally high runoff in 1983 (Jellison and Melack 1993b). As during the earlier (1983–1988) episode, however, three years (2000–2002) of modest declines in lake level have resulted in weakening of meromixis and a return to average levels of productivity even prior to its breakdown (R. Jellison pers. comm.). The lake is currently well mixed above a depth of 28 m. While meromixis is expected to break down in 2003, productivity is predicted to remain near or above average even if it persists (R. Jellison pers. comm.).

Most types of shorebird habitat will likely increase in abundance and quality, except that mudflats may contract somewhat. Inundation of protected coves by the rising lake will allow fresh water to form a hypopycnal layer over denser, more saline lake water (Stine 1995), benefiting phalaropes by providing additional sources for drinking and bathing. Ephemeral brackish lagoons are expected to expand, but some of them will be surrounded by dense marsh vegetation; freshwater pond acreage will remain about the same (Stine 1995). Wilson's Snipe will likely lose breeding habitat as freshwater marshes and seasonal wet meadows are inundated by the rising lake; still, marshes will remain more extensive than at prediversion levels. The total length of shoreline will increase (SWRCB 1994b), but not all of it will be available to shorebirds. During our study the width of alkali mudflats decreased on the south and west shores as the lake rose, but on the north and east shores habitat was still abundant. The extent of mudflat will vary as the lake reaches and fluctuates around the dynamic equilibrium, reducing habitat during wet periods over that available to shorebirds during our study. There will also be seasonal variation in the lake level. In April, the lake is generally relatively low, and substantial mudflats should be available (S. Stine pers. comm.). During most years, by August snowpack runoff will have raised the lake level, and mudflats may be less available than in April, especially along the western shore. It is unclear if the suitability of alkali flats and mudflats will be altered, as some springs will migrate upslope of the existing lake level, whereas others will become sublacustrine. Shallow water should remain abundant (S. Stine pers. comm.). Although the acreage of alkali flats will decline, it will stabilize at a level high enough to provide ample habitat for maintaining Snowy Plover populations (SWRCB 1994b:4-99).

If shoreline access and human disturbance increase, shorebirds feeding at the lake edge and roosting phalaropes could be affected negatively (e.g., Pfister et al. 1992, Burger et al. 1995). Foraging phalaropes may be disturbed if recreational boating increases.

Research and Monitoring Needs

Long-term monitoring is critical to assessing shorebirds' response to changes in lake levels and the potential effects of human disturbance. Understanding population changes at the lake will be possible, though, only within the context of information from broader efforts to assess continental populations, which likewise will be aided by monitoring at Mono Lake. Knowledge of shorebirds at Mono Lake could be enhanced by studies that better document seasonal use patterns via more frequent surveys, determine the migratory pathways of shorebirds passing to and from Mono Lake, investigate the diet of poorly known species, and assess the relation of prey availability to shorebird concentrations. Research, monitoring, and management at Mono Lake should be coordinated with similar efforts throughout the Intermountain West (Oring et al. 2000).

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