

# FACTORS INFLUENCING THE ABUNDANCE AND DISTRIBUTION OF THE SNOWY PLOVER AT MONO LAKE, CALIFORNIA

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**ABSTRACT:** The Snowy Plover is a species at risk, yet surveys of its numbers at most interior nesting sites in California have been infrequent. We surveyed the nesting population at one of the state's key sites at Mono Lake at the edge of the Great Basin near Yosemite National Park in 6 years from 1978 to 2014. Diversions of inflowing streams caused the lake level to decline steadily from 1941 to 1981, increasing the amount of exposed lakebed available for nesting and foraging plovers. Subsequently, the level has generally risen, despite periodic reversals, since diversions were curtailed in 1989. Numbers of adult plovers at Mono Lake declined from 384 in 1978 to 71 in 2007, over a relatively narrow range of rising lake levels. In all years, plovers were distributed around the lake unevenly, with most on the northern and eastern shoreline. We found a positive relationship between the amount of exposed lakebed and the number of plovers detected on surveys. Plover numbers at Mono Lake may be limited by the amount and quality of alkali playa for nesting and foraging, low population density as an adaptation to high rates of nest predation, and perhaps by birds shifting to improved habitat at nearby Owens Lake. In coming years, provided the lake rises to the target elevation of 6392 feet (1948.3 m), the extent of the plover's habitat will shrink, calling for more frequent monitoring.

The Snowy Plover (*Charadrius nivosus*) is one of the rarer shorebirds in North America, numbering about 26,000 birds (Thomas et al. 2012). Within this region the species has a broad but discontinuous distribution, occurring along the Pacific coasts of the United States and Mexico; along the coast of the Gulf of Mexico; and in the interior deserts, plains, and highlands of the western and central United States and central Mexico.

In California, the distinct population segment on the coast is listed as threatened by the U.S. Fish and Wildlife Service, whereas the interior population is designated a species of special concern by the California Department of Fish and Wildlife. The Snowy Plover continues to be at risk from habitat loss, water diversions, human disturbance, expanding populations of predators, and contaminants (Page et al. 1995, Shuford et al. 2008). Prior to the first statewide surveys in the late 1970s little was known about the size of the Snowy Plover population in the interior of California and the sites important to it. Henderson and Page (1981) estimated California's inland population at 1843 adults in 1978; Page et al. (1991) estimated it at 1745 in 1988. Mono Lake ranked second among sites in numbers breeding and accounted for about 20% of the inland total in both years.

Mono Lake has attracted much attention because of court battles over environmental degradation of the lake from decades of water diversions that lowered the lake level by 45 feet (13.7 m) and reduced its volume by half (Hart 1996). The fate of large numbers of nesting California Gulls (*Larus*

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*californicus*) and migratory Eared Grebes (*Podiceps nigricollis*), Wilson's Phalaropes (*Phalaropus tricolor*), and Red-necked Phalaropes (*P. lobatus*) figured prominently in the controversy. Although the Snowy Plover is considered at risk, the species received limited attention, apparently because it breeds on the barren alkali playa, which expanded greatly in extent with the falling lake level.

Here we report the Snowy Plover's abundance and patterns of distribution at Mono Lake from periodic surveys between 1978 and 2014 and evaluate the factors that might explain the observed trends. We also compare patterns at Mono Lake with those at Owens Lake, the species' other key nesting site in the vicinity, and discuss conservation, monitoring, and research needs to ensure a robust plover population is maintained at Mono Lake.

### STUDY AREA

Mono Lake is a hypersaline terminal lake located in east-central California on the western edge of the Great Basin just below the eastern escarpment of the Sierra Nevada near Yosemite National Park. At Mono Lake, Snowy Plovers nest in low densities on rolling ridges of sand and pebbles representing old shorelines and on broad alkali-encrusted sand flats more recently exposed by dropping lake levels (Page et al. 1983). Foraging plovers congregate at scattered pools of shallow water at seeps and springs (on barren alkali flats) and along the lake shore; some nests may be up to 0.9 mile (1.5 km) from these features.

Since 1941, for municipal use and power generation, the city of Los Angeles has diverted water from the streams flowing into the lake. These diversions caused the lake level to drop from 6417 feet (1955.9 m) in 1941 to 6372.0 feet (1942.2 m) in 1982, for a total decline of 45 vertical feet (13.7 m; Figure 1). Since the California Water Resources Control Board modified the city's water-diversion licenses in 1994, the level of Mono Lake has been on an upward trajectory, despite periodic reversals, inundating some of the alkali playa on which plovers nested in the 1970s and 1980s. During any interval, however, rises or declines in lake level can be accelerated or reversed by wet or dry periods that affect the snowpack and runoff into the lake from the adjacent Sierra Nevada. Under the water board's decision 1631 (SWRCB 1994), the lake was projected to reach a target elevation of 6392 feet (1948.3 m) in about 30 years (i.e., 2024), assuming a continuation of the climate and hydrology from 1940 to 1989, but if the current 4-year drought continues it may take considerably longer.

### METHODS

#### Plover Surveys

Between 1978 and 2014, we surveyed almost all potential Snowy Plover nesting habitat at Mono Lake six times. Surveys spanned 9–17 May 1978, 27–29 May 1988, 31 May and (mostly) 1 June 2001, 31 May 2002, 29 May 2007, and 6 (mostly) and 7 June 2014. All surveys were in years of declining lake level (Figure 1). The number of observers participating in

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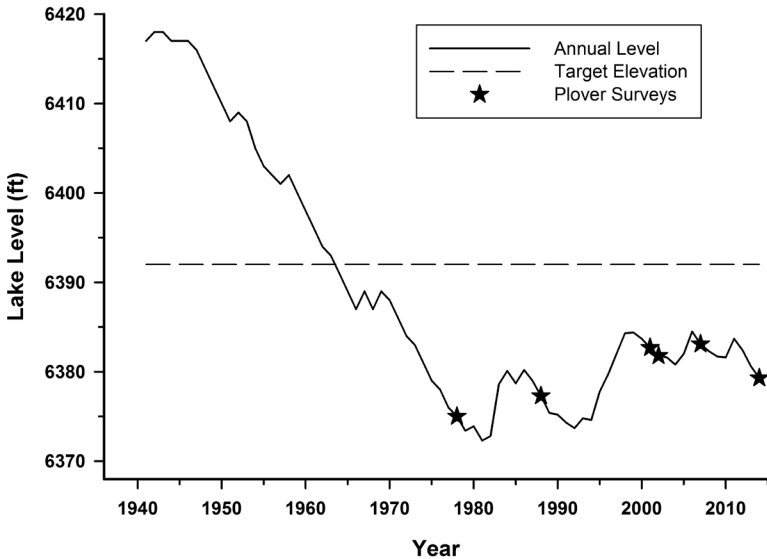


Figure 1. Level of Mono Lake on 1 October of each year from 1941, at the onset of water diversions, through 2014 (elevation above sea level; data from [www.monobasinresearch.org/data/levelyearly.php](http://www.monobasinresearch.org/data/levelyearly.php)). Dashed horizontal line is the target elevation of 6392 feet (1948.3 m), mandated by the State Water Resources Control Board, around which the lake's future level will fluctuate; this level is projected to be reached in 2024, provided that climate and hydrology remain the same as from 1940 to 1989. Stars indicate lake level in the six years with plover surveys.

surveys ranged from 4 to 12 per year. Still, in each year the coverage was roughly comparable, as in years with fewer participants the survey spanned up to four days and some observers counted on more than one day.

To facilitate comparisons of local patterns of distribution and abundance, we tallied plover numbers by seven segments of lakeshore demarcated by local landmarks (Figure 2). Teams of two observers covered most segments, but after the 1978 and 1988 surveys teams of at least three (rarely five) observers covered the widest and most complex segments on the northern shoreline. In no year did we survey about 10.6 miles (17 km) of shoreline from Navy Beach west and north to the shrimp plant adjacent to Mono County Park because the beaches along this stretch are narrow and plovers have never been known to nest on them.

Observers used binoculars and spotting scopes to scan all suitable foraging and nesting habitats contiguous with the shoreline, including mainly alkali flats and beaches, old beach ridges above the alkali flats, freshwater seeps and springs bubbling up on the playa, and lagoons where saline or brackish water pooled behind berms created by waves along the lakeshore. Coverage of a long stretch of shoreline east of Black Point was difficult

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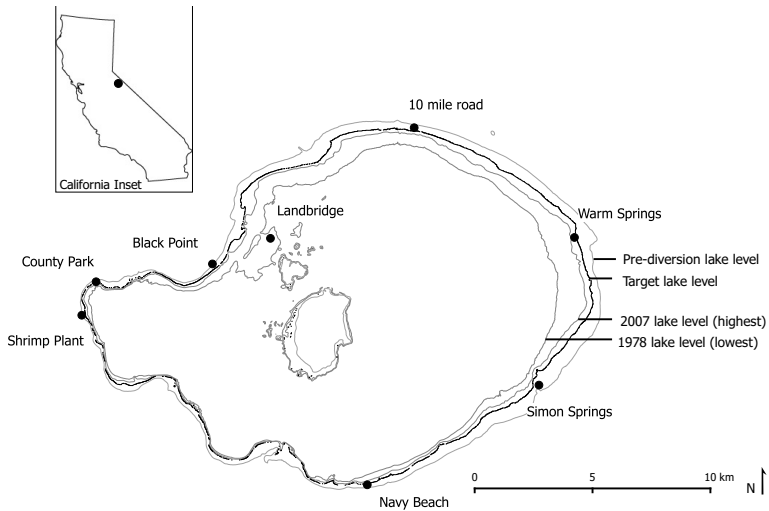


Figure 2. Location of landmarks demarcating seven lakeshore segments used for Snowy Plover surveys at Mono Lake, 1978–2014 (Table 1). The outermost gray line depicts the lake’s pre-diversion level of 6417 feet (1956 m), and the black line is the target level of 6392 feet (1948.3 m) for Mono Lake restoration. Interior gray lines show the lowest and highest levels (on 1 July) during the plover-survey period: 6375.8 feet (1943.3 m) in 1978 and 6384.2 feet (1945.9 m) in 2007, respectively.

because large blocks of pumice or tufa scattered across the playa reduced visibility, and during periods of falling lake level there were extensive areas of treacherous, deep mud that had to be given a wide berth. Coverage of the northeastern segment of the lake also was difficult because of the wide expanses of alkali flats and sandy ridges that stretched back 0.9 mi (1.5 km) or more from the shoreline. Observers in each team kept in close contact (sometimes by hand-held radios) as they scanned suitable habitat in front, behind, and between them as they moved slowly, parallel to each other, along each segment of shoreline, zigzagging frequently to enhance their chances of detecting plovers flushed from nests or brooding chicks. By scanning far ahead it sometimes was possible to detect a plover sitting on a nest at a great distance before the observer disturbed it; this strategy became less viable as the day wore on and heat distortion intensified.

Observers recorded the total number of adult plovers and identified individuals as male, female, or sex unknown; because surveys took place relatively early in the nesting cycle we did not record any adult-sized fledged juveniles that could have been confused with adults at a distance. Although our surveys did not specifically target nests, we also recorded all nests seen, the number of broods, the number of chicks in each brood, and the chicks’ size relative to the adults. All counts of total plovers reported in the text or tables include adults only.

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### Extent of Exposed Lakebed

To examine the relationship between the number of breeding plovers and the amount of exposed lakebed (particularly alkali playa), we first estimated the amount of lakebed that was exposed at the time of the six surveys relative to the benchmark of the lake's elevation of 6417 feet (1955.9 m) in 1941 when water diversions began and the lake level started to decline. Calculation of the amount of exposed lakebed for each of the 6 survey years first required obtaining data on the lake level on 1 July of that year ([www.monobasinresearch.org/data/levelmonthly.php](http://www.monobasinresearch.org/data/levelmonthly.php)) and the lake's estimated surface area at that elevation (Table A-1 in Appendix A of Jones & Stokes Associates 1993 [[www.monobasinresearch.org/images/mbeir/dappendix/tablea-1.pdf](http://www.monobasinresearch.org/images/mbeir/dappendix/tablea-1.pdf)], as calculated from the smoothed Pelagos bathymetry of the lake in Raumann et al. 2002). We then subtracted the surface area of the lake for each of the 6 years from that at the high stand of the lake at 6417 feet (1955.9 m) to estimate the amount of exposed lakebed available to plovers each year. It must be noted, however, that this is only a crude approximation of the extent of alkali playa (or comparable barren habitat) exposed as the lake's level changes. A falling level exposes other habitats including wetlands, wet and dry meadows, islands, and other substrates that may remain un- or sparsely vegetated. Nor is it clear how changing groundwater levels influence the spread or retraction of vegetation and hence the stability of the extent of exposed alkali over time. Still, from our field observations and from estimates of the extent of alkali flats and other lake-fringing wetlands at various lake levels (Jones & Stokes Associates 1993), it was evident that the collective extent of exposed alkali, sandy ridges, and pumice flats was strongly correlated with the extent of the lakebed exposed during our study.

### Data Analysis

We used nonparametric bootstrapping via the package "boot" (Canty and Ripley 2014) in program R version 3.1.0 (R Core Team 2014) to generate 720 bootstrapped ordinary least-squares estimates for intercept, slope, and  $r^2$ , and accompanying 95% confidence intervals, relating the number of plovers detected on surveys to the estimated amount of lakebed exposed at the time of surveys. The 720 replicates represent all possible combinations of the plover counts and the estimates of exposed lakebed for the six surveys.

## RESULTS

### Plover Abundance and Distribution

The total number of plovers recorded on surveys at Mono Lake declined from 384 adults in 1978 to 71 in 2007, during a period of generally rising lake levels, then increased to 143 adults in 2014, after a subsequent decline in lake level (Table 1, Figure 1). In all years, plovers were distributed around the lake unevenly with most occurring along the northern and eastern shores, specifically in the three survey segments from Black Point east and south to Simon Springs (Table 1, Figure 2). At lower lake levels in 1978 and 1988, 10–15% of the plovers occurred along the southeastern shore between Simon Springs and Navy Beach, where they were absent at higher lake levels

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**Table 1** Number of Adult Snowy Plovers Counted on Various Stretches of the Mono Lake Shoreline in late May to early June, 1978–2014<sup>a</sup>

Lake segment	1978 <sup>b</sup>	1988	2001	2002	2007	2014
Shrimp Plant to County Park	15	0	—	—	—	0
County Park to Black Point	—	1	—	0	—	3
Landbridge	?	46	5	5	2	10
Black Point to 10 Mile Road	?	60	31	13	9	53
10 Mile Road to Warm Springs	?	128	67	64	50	32
Warm Springs to Navy Beach	?	107	15	16	10	45
Warm Springs to Simon Springs	?	(59)	?	?	(10)	(45)
Simon Springs to Navy Beach	39	(48)	?	?	(0)	(0)
Total adults	384	342	118	98	71	143
Males	181	223	45	39	35	80
Females	139	101	42	32	21	40
Sex unknown	64	18	31	27	15	23

<sup>a</sup>The first surveys used slightly different shoreline segment boundaries, so it is not possible to directly compare numbers by segment for 1978 with those for other years. Numbers placed in parentheses when numbers available for subsegments but numbers for segments used in annual total. —, Segment not surveyed, usually because of knowledge of a lack of habitat there that year.

<sup>b</sup>See map and text in Henderson and Page (1979) for segments and their totals in 1978.

in 2007 and 2014. In 1978 only, 15 (4%) were along the northwestern shore around Mono County Park.

### Relationship to Extent of Exposed Lakebed

Bootstrapping results provided strong evidence for a positive correlation between the amount of exposed lakebed and the number of plovers detected on surveys (Figure 3). That is, the number of plovers was highest when the extent of exposed lakebed was greatest, lowest when it was smallest. The mean intercept and slope estimates and their 95% confidence intervals were  $-475.6$  ( $-713.5$ ,  $-90.3$ ) and  $0.15$  ( $0.05$ ,  $0.21$ ), respectively. The bootstrapped mean estimate of  $r^2$  was  $0.89$  ( $0.59$ ,  $1.00$ ). That the 95% confidence interval for the slope estimate does not overlap zero provides strong evidence for the positive relationship.

## DISCUSSION

### Limiting Factors

The number of plovers detected at Mono Lake on six surveys between 1978 and 2014 varied by a factor of 5 during a period when lake level varied by 8.4 vertical feet (2.6 m; 6375.8–6384.2 feet [1943.3–1945.9 m]) and the estimated area of exposed lakebed varied by a factor of 1.6 (3651–5812 ha). These changes in plover numbers over a relatively narrow range of lake levels differ from projections by Jones & Stokes Associates (1993: chapter 3F) of the potential effects on the Snowy Plover of seven

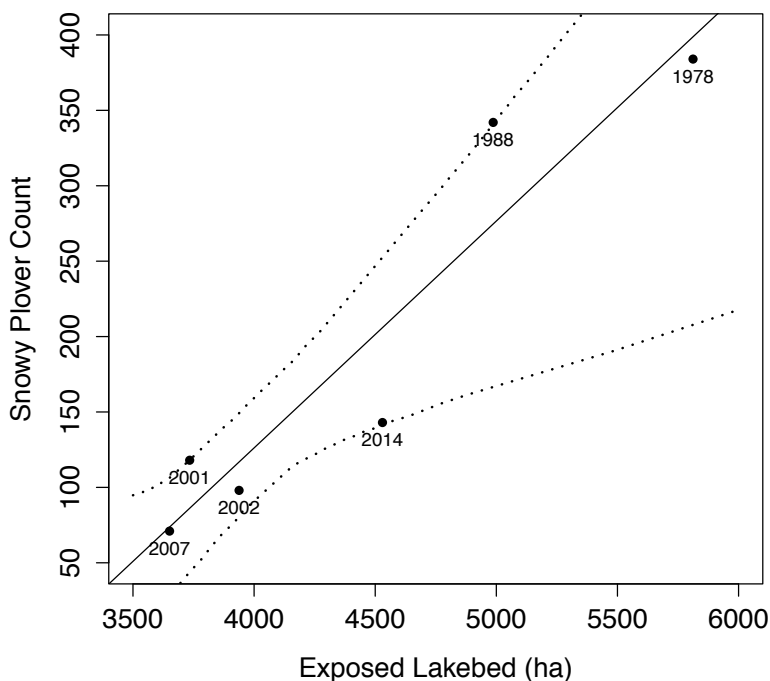


Figure 3. Scatter plot with solid line representing the mean of bootstrapped estimates by ordinary least squares depicting the positive correlation between numbers of Snowy Plovers detected and the extent of exposed lakebed at the time of six surveys at Mono Lake, 1978–2014. Intercept (95% confidence interval) =  $-475.6$  ( $-713.5$ ,  $-90.3$ ), slope coefficient =  $0.15$  ( $0.05$ ,  $0.21$ ),  $r^2 = 0.89$  ( $0.59$ ,  $1.00$ ). Dotted lines represent the 95% confidence interval of bootstrapped estimates. Plover counts labeled by year.

water-diversion scenarios over a wide range of lake levels. That analysis concluded that the range of lake elevations projected under five of the seven scenarios was unlikely to affect the species' abundance relative to that at a lake level of 6376.3 feet (1943.5 m) when the lake's plover population was roughly 340 adults. They projected no effect despite losses of alkali lakebed in the prime nesting areas ranging from 79 to 100% of that at the point of reference during subsequent rises to average lake levels ranging from 6375 to 6410 feet (1943.1–1953.8 m). These projections assumed that at the point of reference about 72% of the potential lakeshore habitat remained unoccupied and that even if all exposed alkali lakebed were flooded that a population of about 340 adult plovers could be maintained as long as about 1012 ha of barren sand, pumice berms, or other unvegetated nesting habitat remained. Adverse effects on plovers were projected to occur only at the extremes, i.e., at lake elevations below 6368 feet (1941.0 m) and above 6425 feet (1958.3 m).

Other factors besides habitat extent are likely to affect the size of the

lake's breeding population. Page et al. (1983) reported that at Mono Lake plovers nest in densities (maximum of 1 nest per 6 ha) lower than at some sites on the central California coast (maximum of 20 nests per 6 ha). They hypothesized that nest density at Mono Lake was most likely affected by food supply, nest-site availability, and predators. Their studies suggested, however, that foraging and nesting areas were not scarce but rather that predation on clutches and broods was the major factor limiting the Snowy Plover population at Mono Lake. Plovers nesting at the lake annually lose up to 40% of their clutches, mostly to predators including coyotes (*Canis latrans*), Common Ravens (*Corvus corax*), and, particularly, California Gulls (Page et al. 1983). In a series of experiments with artificial clutches placed at different densities in nesting plots, these authors demonstrated that predation rates were higher when the density of nests was higher, suggesting that a low density is an important antipredator adaptation.

Page et al. (1983) did not find any evidence that foraging or nesting habitat was limiting the plover population during their study period from 1978 to 1981, when the lake was at its lowest historical levels (Figure 1). Subsequently, rising lake levels have been inundating alkali flats exposed at that time. Our surveys from 1978 to 2014, under a broader range of precipitation cycles and water-management practices, showed a strong positive relationship between plover numbers and the spatial extent of exposed lakebed, suggesting that the amount of nesting and foraging habitat does influence the plover population. It is possible, however, that the size of the nesting population may still be mediated by predator pressure. That is, if the density remains the same in response to high predation rates while the amount of space available to plovers is shrinking, then the absolute population size should decline in proportion to the available space even though the reduced area theoretically supplies resources sufficient to support a larger population.

As the extent of plover habitat has declined with a rising lake it is also possible that the quality of remaining habitat has diminished. Swarth (1983) found that the abundance and distribution of plover prey (mainly flies and beetles) was strongly correlated with substrate moisture and proximity to water. Among various shoreline microhabitats at Mono Lake, ground-dwelling arthropods were most abundant within 25 m of the lakeshore and at freshwater seeps. The congregation of plovers at these places indicates their importance for foraging. Before water diversions the steeper slope above the lake's shoreline minimized the area exposed to springs and seeps (Jones & Stokes Associates 1993: chapter 3C). As the lake dropped, more springs and seeps were exposed on flatter beaches, but this pattern of exposure has generally been reversing itself as the lake level has risen since water diversions were curtailed in 1989. Relative to the low point of reference of 6376.3 feet (1943.5 m), the extent of alkali flats in key plover areas is reduced by about 28%, 79%, 97%, and 99% around average lake levels of 6375, 6379, 6386, and 6392 feet (1943.1, 1943.3, 1946.5, 1948.3 m), respectively (calculations from Table 3C-16 in Jones & Stokes Associates 1993). Although many local factors such as substrate, shoreline slope, groundwater inflow, and erosion affect the occurrence of seeps, in general the extent of seeps must be declining in tandem with the reduced extent of alkali flats as



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lake elevations rise from 6375 to 6392 feet (1943.1–1948.3 m). Thus a reduction of both habitat extent and quality may explain why plover numbers were much lower at lake elevations above 6382 feet (1945.2 m) than at elevations of about 6376–6378 feet (1943.4–1944.0 m). Habitat quality may be even lower at lake elevations above 6400 feet (1950.7 m), where the shores on the north side of the lake are steeply inclined, covered in pumice, perched well above the water table, and lack an alkali crust. Below that lake elevation the shores have a very low gradient, are fine-grained and alkali-encrusted, and the groundwater table is near the surface (Scott Stine in litt.).

Any changes in predator populations could affect plover numbers at the lake. Page et al. (1983) surmised that the high rate of gull predation on plover nests at Mono Lake was atypical, reflecting the proximity of a large gull colony on the lake's islands. Yet this situation has changed relatively little during a period of substantially declining plover numbers. During a period of annual standardized monitoring of the California Gull population at Mono Lake from 1983 to 2014, the number of nesting gulls has averaged 46,316 adults (range 33,548–64,976) (Point Blue unpubl. data). Although there has been a significant decline in the number of nesting gulls over this 32-year period ( $r^2 = 0.19$ ,  $P = 0.01$ ), the population has still averaged 40,983 (standard deviation  $\pm 4175$ ) adults over the last 10 years. Hence, the plovers' most important predator at the lake is still very numerous, and it is possible that predation pressure may even have increased as the reduced number of gulls has less habitat to patrol as the lake has risen. We know of no robust information on the trends of other plover predators, such as the raven and coyote, at Mono Lake. That the footprint of human activities near the lake is relatively small and mostly distant from plover nesting areas suggests, however, that these predators are not benefiting greatly from human subsidies, as they are elsewhere, and their predation pressure on the plovers may not have increased over the study period.

### Regional Perspective

Sites where Snowy Plovers nest near the base of the Sierra Nevada in Mono and Inyo counties are few (Henderson and Page 1981, Page et al. 1991, Shuford et al. 2008). Plovers breed either irregularly or in small numbers (<15 adults) at Bridgeport Reservoir, Crowley Lake, Little Alkali Lake, and Adobe Valley in Mono County, and at Deep Springs Lake, Salt Lake, and Tinemaha Reservoir in Inyo County. Other than Mono Lake, the only other site that supports large numbers of breeding plovers is Owens Lake, Inyo County, about 190 km south of Mono Lake, where plovers have been surveyed over many years (Ruhlen et al. 2006, LADWP 2014). After a steep decline from 499 adults in 1978 to 195 in 1988, numbers at Owens Lake ranged from 101 to 203 on nine counts from 1990 to 2001. After the initiation of shallow flooding to control fugitive (air-suspended) dust on the Owens Lake playa in 2001, numbers steadily increased to 658 adults in 2004, representing the highest total at any inland or coastal site in California. Subsequently, plover numbers have remained elevated, ranging from 361 to 736 (mean 534, standard deviation  $\pm 101$ ) from 2005 to 2014 (LADWP 2014). It is possible that habitat quality at Owens Lake might influ-

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ence the numbers of plovers breeding at Mono Lake if birds migrating north along the east side of the Sierra in spring were to stop when they find good conditions at Owens Lake and not continue north to Mono Lake. Owens Lake may be particularly attractive now that it has extensive shallow water and alkali playa as a result of the dust-control project. Adult flies (*Ephydra hians* and *E. auripes*) are more numerous in May at Owens than at Mono Lake because the shallow water and many of the dust-control ponds are moderately saline and are much warmer and more productive at that time than at Mono Lake (Dave Herbst pers. comm.).

### Future Research and Conservation

Although the overall health of Mono Lake and most of its wildlife are expected to benefit from an increasing lake level (Jones & Stokes Associates 1993), it is clear that plover numbers at the lake have declined since 1978. Fortunately, to date this decline has been offset by a recent dramatic increase in plover numbers at Owens Lake in response to extensive shallow flooding of the playa for dust control (Ruhlen et al. 2006, LADWP unpublished data). Although the overall effect so far has been positive, the long-term effect of dust-control measures at Owens Lake is uncertain given the potential for flooding to be substantially curtailed if other more efficient or cost-effective control measures are implemented (Ruhlen et al. 2006).

Given the decline in the plover population at Mono Lake and the uncertainty that offsetting numbers at Owens Lake will be maintained in the future, it would be valuable to monitor the Mono Lake population more frequently, as the lake rises toward its target elevation of 6392 feet (1948.3 m). This would complement the surveys at Owens Lake, conducted annually through 2014 and scheduled again in 2016, 2018, and 2023 (Debbie House in litt.). Such surveys would provide important information on trends in plover abundance and distribution at Mono Lake and would serve as an early warning system to allow timely conservation actions as needed.

Research is also needed to evaluate changes in both the quantity and quality of plover habitats at Mono Lake. It would be valuable over time to monitor and map in detail the distribution and extent of the various vegetation communities and types of barren habitat, as well as the extent and outflow of seeps, within the zones at Mono Lake where plovers nest and forage. These will, of course, vary with lake level, but changes with respect to climate or plant succession may take place over periods from a few years to centuries (Jones & Stokes Associates 1993: chapter 3C). The extent of various vegetation types and unvegetated areas around lake-fringing wetlands has been mapped during 4 years from 1999 to 2014 in relation to waterfowl use (Debbie House in litt.), but it is unclear if this effort is adequate to monitor changes most relevant to plovers.

Insight could also be gained by research on factors operating away from Mono Lake that may influence plover numbers, including overwinter survival and the level of dispersal between Mono and Owens lakes.

Conservation of the current population of nesting plovers at Mono Lake will take diligence. Because of the remoteness of the plover nesting areas, there is little human disturbance or nearby development, conditions likely to

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remain constant in the future. On the other hand, the lack of easy access to the regions of the lake where plovers nest, as well as a scarcity of funding, makes it hard to monitor plover numbers and the condition of their nesting habitat. Periodic vegetation monitoring now instituted (Dave Marquart pers. comm.) should be continued to detect the spread of any invasive species, such as tamarisk (*Tamarix* spp.), that might degrade plover nesting habitat. A public-awareness campaign could educate the public about this inconspicuous species that lives in remote areas of the lake and better inform them about the variety of conservation issues at Mono Lake.

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