

# THE BEACHED-BIRD ASSEMBLAGE OF A HIGHLY SALINE LAKE AND ITS RELEVANCE FOR RECONSTRUCTING PALEOENVIRONMENTS

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**ABSTRACT.**—The beached-bird deposits of saline (80–90‰) Mono Lake, California, are dominated by Eared Grebes (*Podiceps nigricollis*) and California Gulls (*Larus californicus*), which together comprise 95% of the specimens. Nevertheless, the diversity of waterbirds in these deposits is high (31 species), because mortality is high among migratory species that are poorly adapted to saline environments. The composition of the Mono Lake assemblage differs markedly from local Pleistocene faunas that accumulated in fresh or slightly saline habitats. Received 4 August 1987, accepted 3 October 1987.

STUDIES of paleofaunas are commonly used to reconstruct paleoenvironments. While the ecological preferences of paleospecies and their descendants are likely to be similar, the abundance and diversity in fossil faunas is not necessarily proportional to their abundance in life. Testing the degree to which the actual and preserved faunas vary is usually impossible. Here I suggest that studies of beached-bird deposits at lakes where the abundance and diversity of the extant fauna is known can provide clues to detecting differential mortality and preservation, and may therefore help in interpreting the fossil record.

This paper is based on research at Mono Lake, California, a large (178 km<sup>2</sup>), highly saline (80–90‰ between 1980 and 1986), and alkaline (pH = 10) lake at the western edge of the Great Basin in central California. As at other highly saline lakes, the extant avifauna is dominated by very few species. Indeed, three migrants (Eared Grebe, Wilson's Phalarope, Red-necked Phalarope; scientific names are given in Table 1) and one breeding species (California Gull) account for more than 98% of the biomass in the extant avifauna (Jehl unpubl. data). All occur by the tens or hundreds of thousands, and all but the Red-necked Phalarope remain continuously for weeks or months as part of their annual cycle (Jehl 1986, unpubl. data; see also Winkler 1977).

## METHODS

As part of a long-term study of the avifauna, my research team conducted regular beached-bird censuses along 5–15% of the shoreline. During 1981–1984 these were made at 1–2 week intervals from late May

through early September and at 3–6 week intervals in other months. Supplementary data were obtained in 1985 and 1986, mostly from April through October. From 1981 through 1986, we censused on 213 days, concentrating our efforts in four areas on the south, southwest, north, and northeast shores. In addition, we traversed a minimum of 750 km of lake surface in a small boat each year to determine population sizes of the dominant species and obtain estimates for the others; all cadavers were recorded.

## RESULTS

We encountered 2,494 carcasses representing at least 46 species (Table 1). These included 31 species of waterbirds, of which Eared Grebe (1,690), California Gull (687), Western Grebe (15), American Avocet (15), and Common Loon (8) occurred most frequently; no other waterbird was found on more than four occasions. We also recorded 15 species of land birds, which bred along the lake shore, were washed in by streams, or died flying across the lake. The commonest were blackbird spp. (8), Northern Flicker (7), Great Horned Owl (4), and American Kestrel (4).

For waterbirds I estimated vulnerability (total number of each species found dead in 1981–1986/annual population) and plotted this against the annual population. Although the data for most species were approximate, the vulnerability varied inversely with abundance (Fig. 1). For the four dominant species, whose populations exceeded 50,000, the risk of dying at Mono Lake was trivial, although the chance of being sampled as a fossil was great for two species. For rare species, on the other hand, a

TABLE 1. Mortality data from beached-bird censuses at Mono Lake, California, 1981-1986.

Species	Number of individuals						Total dead	Estimated annual population <sup>a</sup>
	1981 (35 days)	1982 (54 days)	1983 (62 days)	1984 (42 days)	1985 (9 days)	1986 (11 days)		
1. Arctic Loon ( <i>Gavia arctica</i> )		1					1	10
2. Common Loon ( <i>G. immer</i> )		2		4	2		8	50
3. Pied-billed Grebe ( <i>Podilymbus podiceps</i> )		2					2	50
4. Horned Grebe ( <i>Podiceps auritus</i> )			1				1	20
5. Eared Grebe ( <i>P. nigricollis</i> )	32	313	665	530	106	44	1,690	800,000
6. Western Grebe ( <i>Aechmophorus occidentalis</i> )		2	6	6	1		15	200
7. Cormorant?			1				1	200
8. Magnificent Frigatebird ( <i>Fregata magnificens</i> )				1			1	<1
9. Ross' Goose ( <i>Chen rossii</i> )					1		1	1
10. Canada Goose ( <i>Branta canadensis</i> ) <sup>b</sup>				2			2	500
11. Mallard ( <i>Anas platyrhynchos</i> )				1			1	2,000
12. Northern Pintail ( <i>A. acuta</i> )				1			1	2,000
13. Northern Shoveler ( <i>A. clypeata</i> )	1						1	5,000
14. Oldsquaw ( <i>Clangula hyemalis</i> )				1			1	<1
15. Ruddy Duck ( <i>Oxyura jamaicensis</i> )		1	2				3	1,000
16. Osprey ( <i>Pandion haliaetus</i> ) <sup>b</sup>						1	1	5
17. Northern Harrier ( <i>Circus cyaneus</i> )				1	1		2	
18. Swainson's Hawk ( <i>Buteo swainsoni</i> )				1			1	
19. Red-tailed Hawk ( <i>B. jamaicensis</i> )			3				3	
20. American Kestrel ( <i>Falco sparverius</i> )	1		2			1	4	
21. Sora ( <i>Porzana carolina</i> )		1	1				2	200?
22. American Coot ( <i>Fulica americana</i> )		1	1			1	3	500
23. Killdeer ( <i>Charadrius vociferus</i> ) <sup>b</sup>		1		1			2	500
24. Black-necked Stilt ( <i>Himantopus mexicanus</i> )				1			1	200
25. American Avocet ( <i>Recurvirostra americana</i> ) <sup>b</sup>			2	12		1	15	1,000
26. Willet ( <i>Catoptrophorus semipalmatus</i> )			1				1	200
27. Spotted Sandpiper ( <i>Actitis macularia</i> ) <sup>b</sup>		1					1	150
28. Marbled Godwit ( <i>Limosa fedoa</i> )			1				1	200
29. Sandpiper sp.				1			1	
30. Wilson's Phalarope ( <i>Phalaropus tricolor</i> ) <sup>b</sup>	1			1			2	80,000
31. Red-necked Phalarope ( <i>P. lobatus</i> )	1						1	50,000
Phalarope sp.				1			1	
32. Ring-billed Gull ( <i>Larus delawarensis</i> )	1				1	1	3	600
33. California Gull ( <i>L. californicus</i> )								
(Adult) <sup>c</sup>	13	24	44	78	2	2	163	70,000
(Juvenile)	173	68	163	105	6	9	524	
34. Marbled Murrelet ( <i>Brachyramphus marmoratus</i> )	1		3				4	<1
35. Ancient Murrelet ( <i>Synthliboramphus antiquus</i> )					1		1	<1
36. Rock Dove ( <i>Columba livia</i> )			1				1	
37. Great Horned Owl ( <i>Bubo virginianus</i> ) <sup>b</sup>			3	1			4	
38. Small owl				1			1	
39. Hairy Woodpecker ( <i>Picoides villosus</i> )						1	1	
40. Northern Flicker ( <i>Colaptes auratus</i> )	1	1	5				7	
41. Clark's Nutcracker ( <i>Nucifraga columbiana</i> )		1					1	
42. Common Raven ( <i>Corvus corax</i> )	1						1	

TABLE 1. Continued.

Species	Number of individuals						Total dead	Estimated annual population <sup>a</sup>
	1981 (35 days)	1982 (54 days)	1983 (62 days)	1984 (42 days)	1985 (9 days)	1986 (11 days)		
43. Townsend's Solitaire ( <i>Myadestes townsendi</i> )		1					1	
44. Savannah Sparrow ( <i>Passerculus sandwichensis</i> )				1			1	
45. Icterid spp.	2		6				8	
46. Small passerine		1		1			2	

<sup>a</sup> Waterbirds only.  
<sup>b</sup> Breeds in small numbers.  
<sup>c</sup> Breeding population ≈ 50,000.

stop at this terminal lake had a strong likelihood of being a terminal event.

DISCUSSION

Eared Grebes and California Gulls comprised 95% of the specimens in the beached-bird deposits. The prevalence of grebes reflects their great abundance, long continuous residence in fall (4-7 months), and relatively high mortality among juveniles (Jehl unpubl. data); the large representation of gulls is attributable to mortality during the 4-5 month breeding season, especially among young (Table 1). By contrast, mortality among the two other dominant species was almost undetected, perhaps because juvenile Wilson's Phalaropes, presumed to be the more susceptible age class, comprise less than 2% of the migratory population at this locality (Jehl unpubl. data) and Red-necked Phalaropes of all ages pass through in a few days (Jehl 1986).

Despite the predominance of Eared Grebes and California Gulls, the diversity of the beached-bird fauna is relatively high, comprising 31 (31.6%) of the 98 waterbird species recorded locally. This diversity results mainly from high mortality among the rare and out-of-range species, which are attracted by open-water habitats but are unaware of the lakes' high salinity. Such species typically land for a few hours and then leave because they are unable to deal with the osmotic challenges or to feed efficiently on brine shrimp and brine flies, the only available prey. Individuals that arrive exhausted, however, and are unable to replenish their energy stores will not be able to depart.

The composition of the beached-bird deposits at Mono Lake differs importantly from the faunas of two Pleistocene lakes within 600 km of Mono Lake. At Fossil Lake, in south-central Oregon, Howard (1946) reported 53 species of waterbirds, dominated by Western Grebe, American Coot, and Canada Goose; the Eared Grebe comprised only 3.5% of the remains, and gulls were rare. Diversity was greater than at Mono Lake, and 12 species accounted for 79% of the fauna (Table 2). The depositional environment was evidently a large freshwater lake whose avifauna was very similar to that found today at Klamath Lake, Oregon, or Tule Lake, California, which are major concentration points for waterfowl (Howard 1946).

At Manix Lake, in the Mojave Desert of California, the waterbird fauna was also diverse.

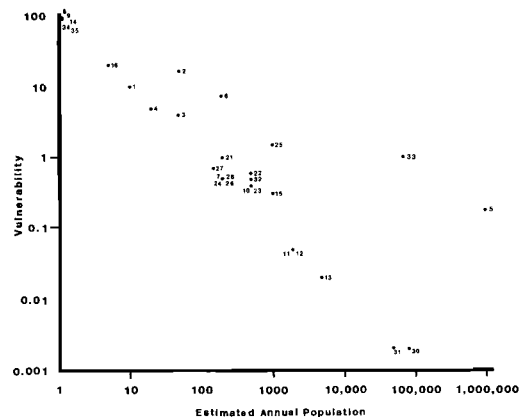


Fig. 1. Estimated mortality rates (see text) of waterbirds at Mono Lake, California, as a function of the annual population. Numbers refer to species listed in Table 1.

TABLE 2. Comparison of the dominant waterbird species represented in beached-bird deposits at Mono Lake, California, and fossil deposits from Fossil Lake, Oregon, and Manix Lake, California.

Mono Lake		Fossil Lake		Manix Lake	
Species	%	Species	%	Species	%
<i>Podiceps nigricollis</i>	68.0	<i>Aechmophorus occidentalis</i>	43.7	<i>Aechmophorus occidentalis</i>	29.5
<i>Larus californicus</i>	27.3	<i>Fulica americana</i>	8.5	<i>Phalacrocorax auritus</i>	10.8
<i>Aechmophorus occidentalis</i>	0.6	<i>Branta canadensis</i>	5.9	<i>Phoenicopterus minutus</i>	10.1
<i>Recurvirostra americana</i>	0.6	<i>Cygnus paloregonus</i>	3.7	<i>Pelecanus erythrorhynchos</i>	8.6
<i>Gavia immer</i>	0.3	<i>Podiceps nigricollis</i>	3.5	<i>Branta canadensis</i>	7.9
<i>Brachyramphus marmoratus</i>	0.2	<i>Oxyura jamaicensis</i>	3.0	<i>Ciconia maltha</i>	4.3
<i>Larus delawarensis</i>	0.1	<i>Phalacrocorax macropus</i>	3.0	<i>Phoenicopterus copei</i>	2.8
<i>Fulica americana</i>	0.1	<i>Anas americana</i>	1.8	<i>Podiceps nigricollis</i>	2.8
<i>Oxyura jamaicensis</i>	0.1	<i>Anabernicula</i> sp.	1.7	<i>Aythya</i> sp.	2.8
Others	0.1	<i>Cygnus buccinator</i>	1.6	<i>Larus cf. oregonus</i>	2.1
		<i>Chen hyperborea</i>	1.5	<i>Fulica americana</i>	2.1
		<i>Anas carolinensis</i>	1.0	<i>Oxyura jamaicensis</i>	2.1

To date, 25 species have been reported (Jefferson 1985), dominated by Western Grebe, Double-crested Cormorant (*Phalacrocorax auritus*), and an extinct flamingo (*Phoenicopterus minutus*). As at Fossil Lake, Eared Grebes and gulls were poorly represented, and 12 species comprised 86% of the remains (Table 2). Jefferson (1985: 11) interpreted the depositional environment as "a complex of fresh-water lake and lake margin habitats," where "open water, sandy beach flats, and extensive reedy marshlands must have been persistent lacustrine features." He based this on the abundance of ostracode and fish remains associated with the avian deposits and the habits of the bird species. Actually, all of the common birds tolerate or prefer slightly saline conditions, the assemblage being very similar to those occurring today at Pyramid or Walker lakes, Nevada (salinity 5–10‰). Although salinity at Manix Lake was probably variable, exhibiting annual or seasonal changes as at many Great Basin lakes, it is unlikely that it greatly exceeded 20‰ (Jefferson pers. comm.). If so, the abundance of flamingos (two species), which typically occur mainly in highly saline and fish-free waters (Hurlbert et al. 1984), poses a paradox. Flamingos require frequent access to fresh water (Brown 1973), however, so perhaps they represented visitors from a nearby colony rather than local residents.

I conclude that the fossil avifaunas of highly saline lakes, such as Mono Lake, are likely to be dominated by the few salt-tolerant species that breed or stage there in huge numbers. High diversity may also be realized, as in freshwater habitats, because many species attracted to such

lakes are unable to tolerate highly saline environments and soon succumb. These clues may help paleontologists interpret seemingly incongruous assemblages like those now accumulating at Mono Lake, where a Magnificent Frigatebird from Mexico may be found with Marbled Murrelets from Siberia (all specimens from Mono Lake are referable to *B. m. perdis*), the latter species being represented twice as frequently as Horned Grebes from North America.

Surveys of beached birds at other basin lakes of less saline character can be used to test these ideas.

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