

BIOLOGY OF THE EARED GREBE AND WILSON'S PHALAROPE IN THE NONBREEDING SEASON: A STUDY OF ADAPTATIONS TO SALINE LAKES

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Abstract.—The Eared Grebe (*Podiceps nigricollis*) and Wilson's Phalarope (*Phalaropus tricolor*) are among the most halophilic species of birds in the world. Immediately after the breeding season thousands congregate at saline lakes in the western United States and Canada to prepare for their eventual migration to wintering grounds. For grebes, these are mainly the Salton Sea and Gulf of California; for phalaropes they are salt lakes in the central Andes.

From 1980 to 1987 I studied the postbreeding biology of both species at Mono Lake, California. This permanent saline and alkaline lake on the western edge of the Great Basin is one of the largest molting and staging areas in the world for each species. Abundant invertebrate prey in the form of brine flies (*Ephydra hians*) and brine shrimp (*Artemia monica*) provide the major attraction for these and a few other migratory bird species.

Eared Grebes may be found at Mono Lake at any season. The summering flock of nonbreeders often numbers 25,000 or more. Tens of thousands of postbreeding birds begin arriving in late July. Adults use the lake as the terminus for a molt migration. They continue to be joined through early fall by adults that have molted elsewhere as well as by juveniles, so that by early October ~750,000 grebes may be present. This is 30% of the North American fall population of ~2,500,000. They stage there until food supplies fail and then migrate to wintering areas. The Mono Lake flock seems to be derived from the western sector of the breeding range.

The grebes feed primarily on brine flies through early summer, then shift to brine shrimp for the remainder of the year. In fall, shrimp comprise >98% of the diet, and at peak numbers grebes probably consume 60 to 100 tons of shrimp daily.

Shortly after arriving, adults molt their remiges simultaneously. This process does not begin until after the birds have begun to gain weight, which event presumably signals that environmental conditions are acceptable for risking 35–40 days of flightlessness. After completing wing molt, the birds remain continuously at Mono Lake and do not fly for months. During molt their breast muscles atrophy. Nevertheless, they continue body molt and concurrently lay on vast fat stores, often more than doubling their arrival weights. To regain flying condition and to be able to resume migration, they metabolize fat reserves during a period of forced fasting but simultaneously rebuild breast muscles, in part by exercise. This takes approximately two weeks. Fat deposits laid down when food is superabundant probably ensure that the birds have sufficient energy to complete the molt and migrate should prey populations fail, but may have additional functions as well.

While at Mono Lake the grebes undergo pronounced daily and seasonal shifts in distribution, which in periods of food scarcity are controlled by the distribution of prey. Tufa shoals are a favorite feeding locality. Differences in distribution of age groups are evident, juveniles often being relatively more abundant nearer shore. Daily movements do not involve visits to fresh water; the birds satisfy their water requirements from the body fluids of their prey.

Beached-bird censuses revealed that mortality was highest in early spring and around the main southward departure period in late fall. Even so, over the entire year mortality at Mono Lake was trivial, probably involving no more than 0.5% of the fall population. Juveniles suffered higher losses than older birds, perhaps because of their later average arrival time and presumed inefficiency in foraging. Food shortages and downings due to bad weather during migration are likely the major causes of mortality. The risk of large die-offs in migration seems highest in years when invertebrate populations remain large into late fall, enticing the grebes to linger into periods of severe winter storms.

Small numbers of Wilson's Phalaropes pass through the Mono Basin in spring. Fall migrants occur between mid-June and late September. The earliest arrivals are adult females, which comprise ~70% of the population; these are followed by adult males (~30%) in early July, and finally by juveniles (<2%) in mid-July and early August. Peak numbers are reached in late July, when the southward exodus begins. Most adult females depart by 5 August, adult males by 15 August, and juveniles by 5 September.

Adults evidently remain at Mono Lake continuously from the time of their arrival until their eventual departure. For many, this is a duration of 30–40 days. During this time they are able to replace nearly all of their body plumage, the tail, and several primaries. Much of the molt is completed in about three weeks, at which time the birds become hyperphagic and begin to fatten in preparation for their long migration. During this period adults often double their arrival weights and may gain 2 g/d. The rapid molt, which is among the fastest known in birds, and the high rate of fattening are made possible by the superabundant prey. Juveniles, by contrast, gain little weight at Mono Lake and do not use it as a staging area.

There are marked differences in the distribution of the age and sex classes at Mono Lake: adult females forage mainly on the open lake; males feed on or closer to shore early in their stay but later shift to offshore localities; juveniles also prefer nearshore situations. These foraging patterns result in important differences in diet, with brine shrimp comprising ~80% of the diet of adult females and ~60% of that of adult males; in juveniles, brine flies make up nearly all of the diet.

During most of their sojourn phalaropes do not require access to fresh water. In the week or so preceding major departures, however, they begin to make regular, and often spectacular visits to creek mouths, especially in the evening. This behavioral change is evidently prompted by osmotic stress resulting from their unavoidably increased intake of lake water as food consumption increases.

Surveys for other staging areas in the western United States and southern Canada in July 1986 revealed a total of 21 localities holding concentrations of >1000 phalaropes; nine additional sites, most in North Dakota, were found in 1987. All were at salt lakes or commercial salt works. In 1986 over 741,000 birds, nearly all adults, were counted. Great Salt Lake, Utah, had the largest concentration (387,000); other major localities included salt lakes in southcentral Saskatchewan (>100,000), Mono Lake (56,320), Big Lake, Montana (40,000), South San Francisco Bay (40,000), and Stillwater National Wildlife Refuge near Fallon, Nevada (20,000). In 1987, in less extensive surveys, 417,000 were recorded in the last half of July. The largest concentrations were Great Salt Lake (193,700), Mono Lake (51,400), Stillwater NWR (42,000) and E. Coteau Lake, Saskatchewan (30,000). Inter-annual differences were pronounced in some localities due to drought.

All staging areas are not used equally by the several age or sex classes. At Mono Lake (and Great Salt Lake?) adult females predominate, whereas at lakes in Saskatchewan, Montana, North Dakota, and Oregon adult males are more numerous. Juveniles tend to avoid highly saline habitats, presumably because they are unable to handle the osmotic stress.

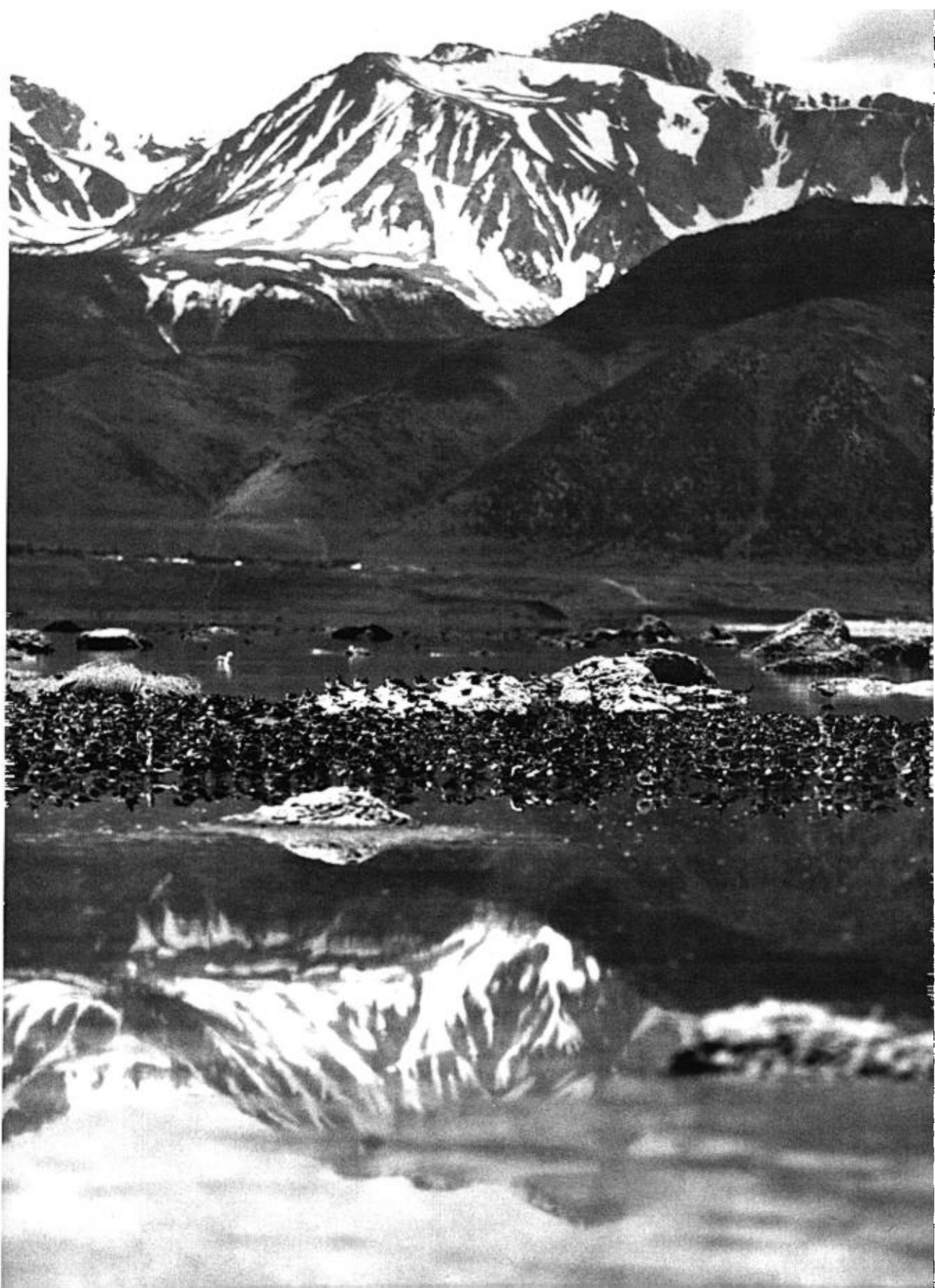
An estimated 80,000 Wilson's Phalaropes occur at Mono Lake in fall. This is approximately 5% of the total species population (~1,500,000), 10% of all adults, and 14% of all adult females.

Evidence synthesized from field studies, the regional literature, and museum collections supports the following picture of fall migration. After congregating briefly near the breeding areas in June, adult females undertake a molt migration to highly saline lakes in the Great Basin of the United States; appreciable numbers may also stage west of the Sierra Nevada. Most arrive by the first days of July. By early July, males also begin to flock at saline lakes; to date, the largest concentrations have been found in the western Great Plains, southern Prairie Provinces, and Lake Abert, Oregon. Adults tend to remain at their original staging areas until they have amassed sufficient fat reserves to migrate directly to South America. This is accomplished by a nonstop flight along a Great Circle Route over the Pacific Ocean, by-passing Middle America, to a presumed landfall in Ecuador or Peru. Flights of 4800 km (3000 mi) are within the capability of average migrants. Juveniles do not gather at staging areas but move slowly over a broad front to the southern United States or Mexico before flying directly to northern South America.

Highly saline lakes, which are often shallow and susceptible to rapid ecological changes, are important concentration points for Eared Grebes and Wilson's Phalaropes throughout their world ranges. Both species have evolved a series of attributes that allow them to thrive in these harsh habitats, which are avoided by most other waterbirds. In North America, Mono Lake and Great Salt Lake, probably because of their large size and relative stability, are or have recently been major molting and staging areas. Even these large lakes are not ecologically constant, however, which demands that species exploiting their rich invertebrate resources retain sufficient flexibility to thrive in other aquatic habitats as well.

Long-term, comparative studies of the saline lakes will more clearly resolve their importance to grebes, phalaropes, and other members of the North American avifauna.

KEYWORDS: Mono Lake CA, Eared Grebe, *Podiceps nigricollis*, Wilson's Phalarope, *Phalaropus tricolor*, saline lakes, distribution, migration, molt migration, staging areas, censusing, food, foraging behavior, feather eating, weights, muscle hypertrophy, flight range, flightlessness, mortality



Wilson's Phalaropes in molt stopover at Mono Lake, July 10, 1985. Photograph by Joseph R. Jehl, Jr.