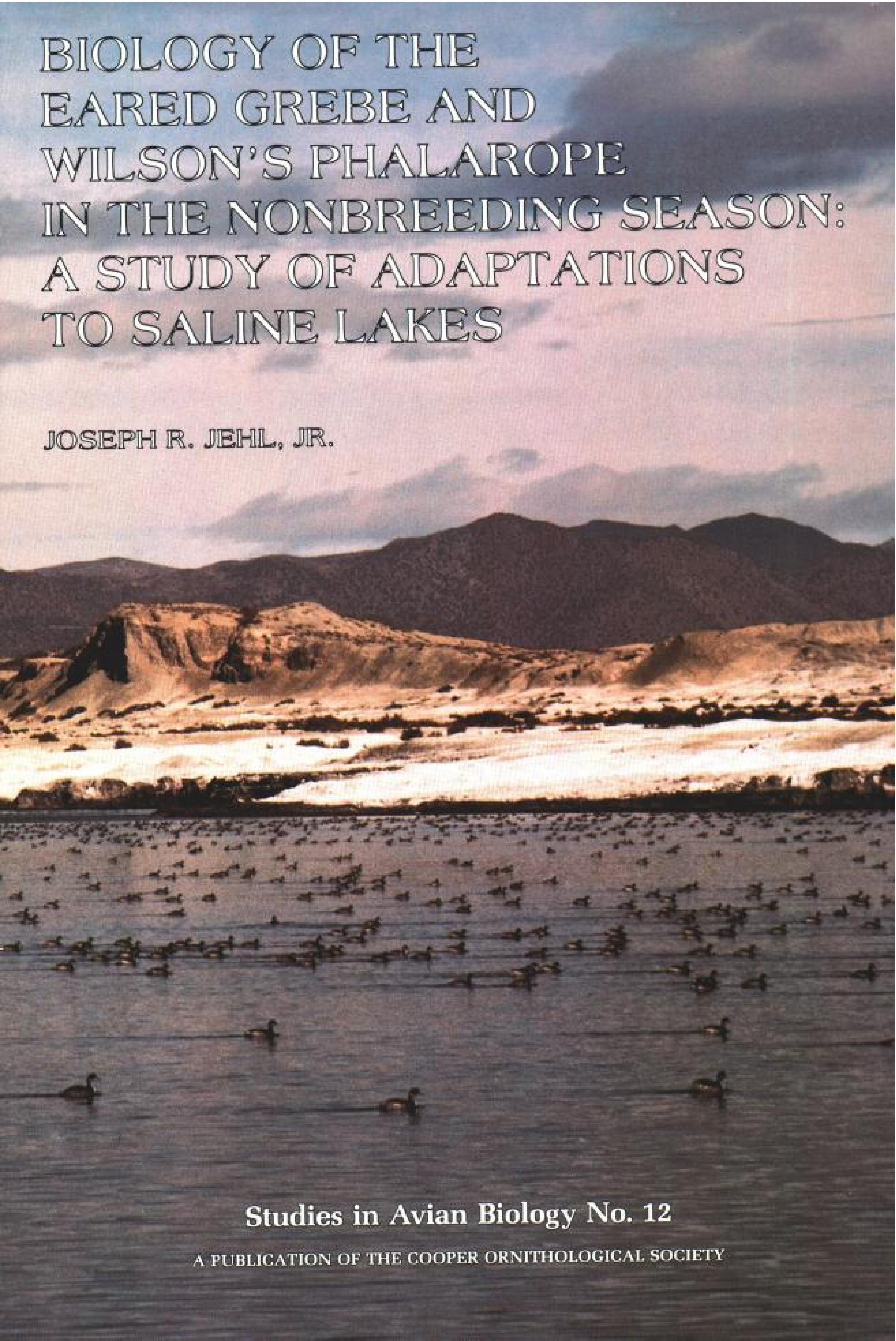

BIOLOGY OF THE EARED GREBE AND WILSON'S PHALAROPE IN THE NONBREEDING SEASON: A STUDY OF ADAPTATIONS TO SALINE LAKES

JOSEPH R. JEHL, JR.

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Joseph R. Jehl, Jr.

Sea World Research Institute
Hubbs Marine Research Center
1700 South Shores Road
San Diego, California
U.S.A. 92109

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Cover Photograph: Eared Grebes (*Podiceps nigricollis*) at Mono Lake, California, October, 1985. Photograph by J. R. Jehl, Jr.

Edited by

FRANK A. PITELKA

at the

Museum of Vertebrate Zoology
University of California
Berkeley, CA 94720

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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). Interannual 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.

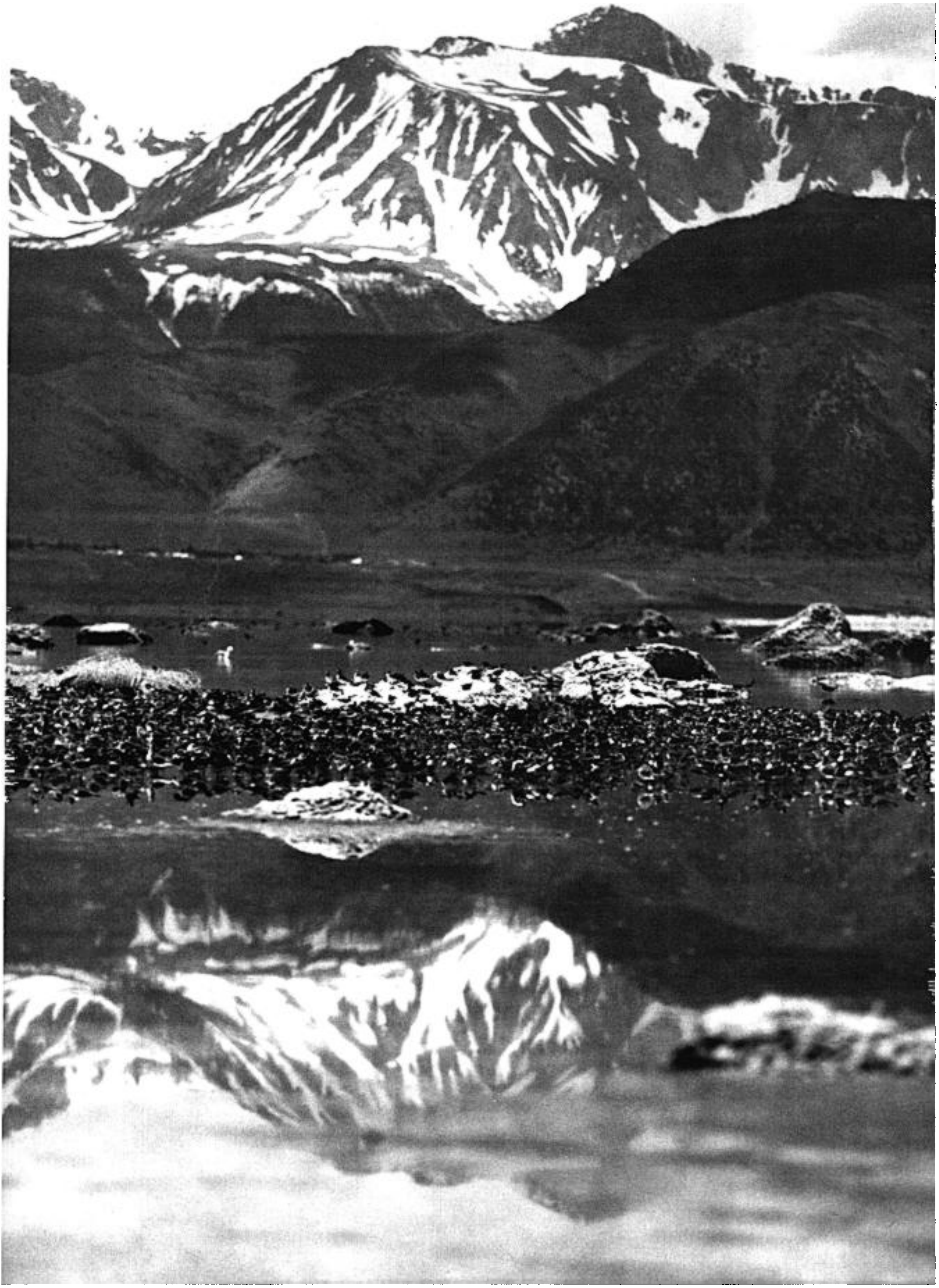
An estimated 80,000 Wilson's Phalaropes occur at Mono Lake in fall. This is approximately 5% of the total species population (~1,500,000), 10% of all adults, and 14% of all adult females.

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.

INTRODUCTION

Nothing in the whole system makes sense until the natural history of its component species becomes known.—E. O. Wilson (1984).

Studies of the life histories of North American birds are no longer the vogue. The completion of A. C Bent's compilations removed much of the impetus for continuing such work on a systematic basis, except for rare, imperiled, or taxonomically puzzling species; descriptive ornithology began to give way to the formulation of hypotheses. To be sure, the *breeding* biology of North American birds is well documented, but data for other phases of the annual cycle are often inadequate either for the development of theory or for practical application. Additional research will surely reveal aspects of the life histories of common species that are extraordinary or unpredictable.

Two such species are the Eared Grebe (*Podiceps nigricollis*) and Wilson's Phalarope (*Phalaropus tricolor*), the most halophilic members of the North American avifauna. Each spends a large part of its nonbreeding season at highly saline lakes. Throughout the world, these lakes with their simple ecosystems are commonly regarded as having little importance for wildlife. And even though they are preferred habitats for a few bird species, North American ornithologists have mostly ignored them, Behle (1958) being an important exception.

The studies reported in this paper are based largely on research at Mono Lake, California, where hundreds of thousands of Eared Grebes and tens of thousands of Wilson's Phalaropes occur in summer and fall. My major goals were to document the biology of these species in the nonbreeding season, clarify the degree to which they rely on Mono Lake and other highly saline lakes, and study how they are able to thrive in habitats that are shunned by most species.

Mono Lake is a massive and ancient salt lake at the western edge of the Great Basin in central California. Located at the eastern scarp of the Sierra Nevada, Mono Lake and its environs were designated as a National Scenic Area in 1985. A remnant of Pleistocene Lake Russell, Mono Lake is currently (1986) 178 km^2 in extent, with a mean depth of 17 m, maximum depth of 46 m, and a pH of 10. It may once have contained fish; if so, they were eliminated by increasing salinity or vulcanism and none has been present at least since the Tahoe stage of glaciation (~100,000 yr B.P.; Hubbs and Miller 1948). The absence of fish makes it possible for the halophilic invertebrates that inhabit the lake—brine shrimp (*Artemia monica*) and brine flies (*Ephydra hians*)—to attain great abundance. These comprise the major attraction for the grebes and phalaropes and the few other bird species that are able to cope with the lake's unique chemical environment and high salinity (see Mahoney and Jehl 1985b).

Some streams that feed Mono Lake are diverted into the Los Angeles Aqueduct; between 1941 and 1982 the surface elevation of the lake dropped by 13 m and salinity increased from 40‰ to 90‰. Runoff from heavy snowpack in the early 1980s interrupted these trends, so that by 1986 the lake stood 2.7 m higher than its 1982 low and surface salinity had declined to 72‰. These rapidly changing ecological conditions and the anticipated resumption of long-term declines in the lake's size stimulated much interest in the ecosystem (summarized by the National Research Council 1987) and provided the major impetus for this report.

In this report, as elsewhere (Jehl and Mahoney 1983, Jehl 1987a), I emphasize that biases in obtaining field data may be far greater than is often acknowledged (see also Balph and Balph 1983). Even such routine techniques as collecting and banding birds or salvaging carcasses can provide highly misleading results, owing to differences in the distribution, foraging behavior, or mortality of the various age groups, daily or seasonal movements, changes in prey populations, and other factors noted in the text. As my understanding increased I attempted to minimize sampling bias, but that was not always possible nor in accordance with my need to gather specific information. In hindsight, bias was especially obvious in data derived from banding phalaropes, which if applied naively to testing hypotheses of population composition would have provided statistically overwhelming but biologically nonsensical answers. Because many sources of error cannot be suspected until a species' biology is appreciated—the "Catch-22" of study design—informed judgment must always take precedence over interpretations based on statistical correlations.

EARED GREBE

The Eared Grebe breeds circumpolarly in the Northern Hemisphere and also maintains small populations in Africa and South America. In most of the Palearctic it is uncommon or rare, although it is evidently common in the drier regions of eastern Europe and southwest Asia (Cramp and Simmons 1977). In the Nearctic the center of its breeding range is in the northern

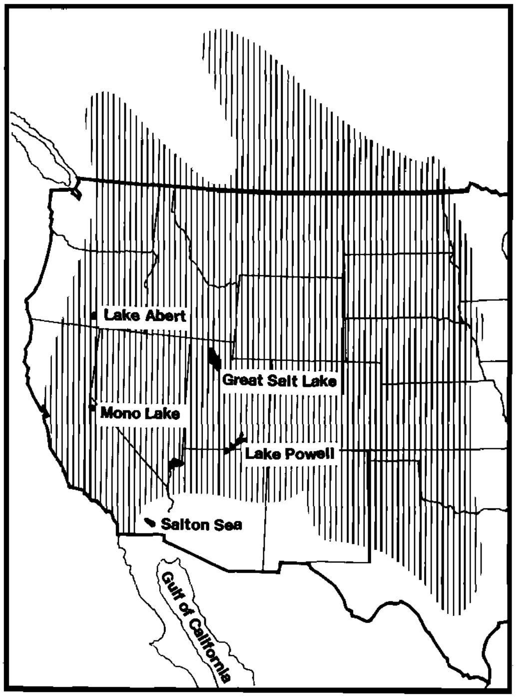


FIGURE 1. Breeding range (shaded) of the Eared Grebe in North America (after Palmer 1962). Major wintering areas are the Salton Sea and Gulf of California. Major staging areas are Mono Lake and Great Salt Lake.

Great Plains and Great Basin (AOU 1983; Fig. 1), where it breeds abundantly and colonially at open lakes of low alkalinity (Faaborg 1976). Its breeding biology has been studied in detail (McAllister 1958, Gauckler and Kraus 1968, Fjeldså 1973a, synopsis in Cramp and Simmons 1977:105–112), but its biology and ecological requirements during the major portion of the year have not been well documented. Lakes of high salinity as well as commercial salt works, however, are known to be seasonal concentration points (Schenk 1970, Cramp and Simmons 1977, Williams 1985, P. Kelly pers. comm.), with major concentrations occurring at Mono Lake, California, Salton Sea, California, Great Salt Lake, Utah, and the Caspian Sea, USSR.

Recent studies (e.g., Storer and Jehl 1985) have revealed that in early fall in North America, hundreds of thousands of Eared Grebes migrate to Mono Lake and other saline lakes in the Great Basin of the United States, where they replace their plumage and stage in preparation for migration to wintering areas. Such pre-molt movements, or molt migrations, are well known in nonbreeding or postbreeding waterfowl and other aquatic birds that undergo simultaneous loss of flight feathers. Typical destinations are large bodies of water, often not on a direct route toward wintering stations, that offer the birds abundant food and safety from predators. Molt migrations involving adults usually commence shortly after the breeding season. In waterfowl they are undertaken mainly by males, which have little or no role in parental care (Salomonsen 1968), and last for three to six weeks, or the duration of the flightless period, after which the birds resume migration. In Eared Grebes, by contrast, both males and females participate and remain after the wing molt and stage at the major molting sites to exploit the seasonally superabundant invertebrate prey.

The molt migration to Mono Lake is larger and more spectacular than that of any other grebe species—or even of any anatid reviewed by Salomonsen (1968)—and parallels a similar migration to Mono Lake by Wilson's Phalarope, as discussed below.

Actually, some Eared Grebes can be found at Mono lake at any season. Migrants pass through the region in spring and the summering flock may approach 40,000 birds. But it is not until autumn that they occur in spectacular abundance, and by mid-October upwards of 750,000 birds may be present. Indeed, from August through November or later this single species comprises over 99% of the lake's avian biomass.

Because individual grebes remain at molting and staging areas for several months in fall, knowledge of the events that occur there is essential for understanding this phase of the species' annual cycle.

METHODS

I studied the grebes year-round at Mono Lake from June 1980 to December 1987. Specimens were measured and examined for molt and external parasites. I used a dissecting microscope to examine gizzard contents and determine prey type and volume. Wet mass, including stomach contents, was determined to nearest gram, usually with a Pesola scale. Pelts of many specimens were retained for a study of molts and plumages (Storer and Jehl 1985), an essential prerequisite for clarifying the age and sex composition of the flock.

Determining the size of the grebe population was a major goal. Several census methods have been used at Mono Lake, but none is fully satisfactory. Cooper et al. (1984) and Winkler (1977) made estimates from shoreline observation posts or in an "index area"; those techniques may indicate the size of the nearshore population but cannot be extrapolated to account for offshore birds, whose distribution is neither uniform nor consistent. Cooper et al. (1984) and Lenz et al. (1986) used strip transects from a rapidly-moving boat; while this procedure reveals broad distributional patterns, its quantitative application depends on several assumptions that could not be met (e.g., random placement of transect routes, stable distribution of population during the cenusus; Burnham et al. 1980, Verner 1985). Most importantly, accurate counts of individual birds

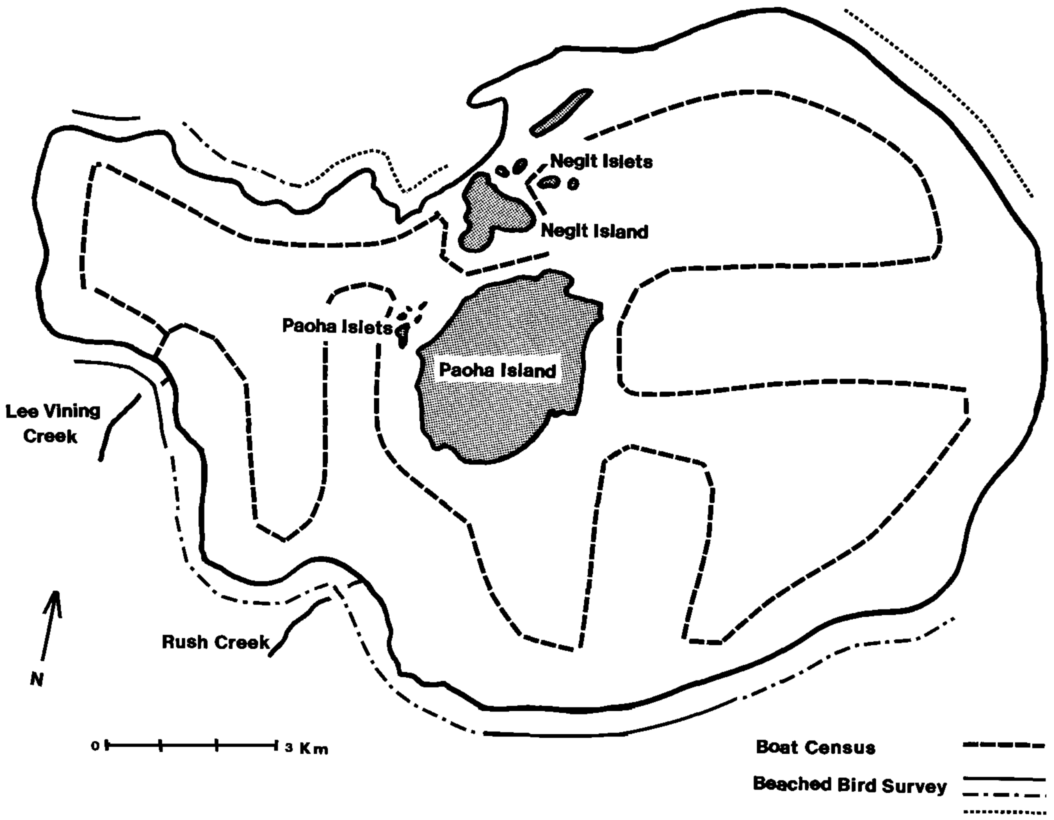


FIGURE 2. Outline map of Mono Lake in 1984 showing typical routes used in censusing grebes. Areas where beached bird surveys were conducted 1982–1984 are indicated on the periphery of the lake. Areas censused regularly in all years are shown by a solid line, those censused infrequently by a dashed line, and those censused only in 1983 and 1984 by a dotted line.

at the high densities that are attained in late fall are impossible, in part because the moving boat intensifies the grebes' diving behavior (Jehl and Yochem 1987), requiring guesswork in accounting for submerged birds.

I attempted to make a direct census of the entire flock from a small boat. Observations in San Diego, California, showed that under calm conditions grebes could be counted accurately from water level at ranges to 1.6 km. Accordingly, by cruising Mono Lake at 25 km/hr but stopping every four minutes to census, I was able to estimate and map numbers in non-overlapping areas; a typical transect route is shown in Figure 2. Depending on the size and distribution of the population, my procedure might involve counts of individual birds or estimates of groups numbering from 50 to 1000. Censuses were made only on days when surface conditions allowed the detection of individual birds within 1.6 km. I did not attempt to correct for the number of sumberged grebes, because the proportion is never constant; it varies by time of day, locality, season, and prey availability, and at times surface foraging is used exclusively. Moreover, grebes within ~0.5 km of a slowly moving or stopped boat typically stop diving and swim away at the surface, keeping careful watch on the observer. Thus, most birds within censusing range were detectable, and the use of "correction factors," even if available, would only have introduced a large but unknowable source of error.

The major drawbacks to a boat-based census were errors in estimating group size and in avoiding gaps or duplications in the counts because of the difficulty of fixing one's position on the lake. The first problem is inherent in any method; the second was minimized by using the navigational technique outlined above.

To check the accuracy of boat censuses, my assistants and I conducted simultaneous boat- and land-based surveys in three near-shore areas, each holding several thousand birds; results from the two techniques differed by 2%, 4% and 7%. From this, I judged that censusing errors usually did not exceed 20% when the population comprised fewer than 100,000 birds and was concentrated near shore; however, they may have reached 30% or more when numbers were immense in late fall and birds were widely dispersed. Despite its limitations, this technique provided consistent results, which are sufficiently accurate for the purposes of this study.

Beached-bird surveys were used to document mortality patterns. I made regular censuses along 5–15% of the lake shore (~96 km including islets) from January 1982 through November 1984 and supplemented these with data from other years. Censuses were usually

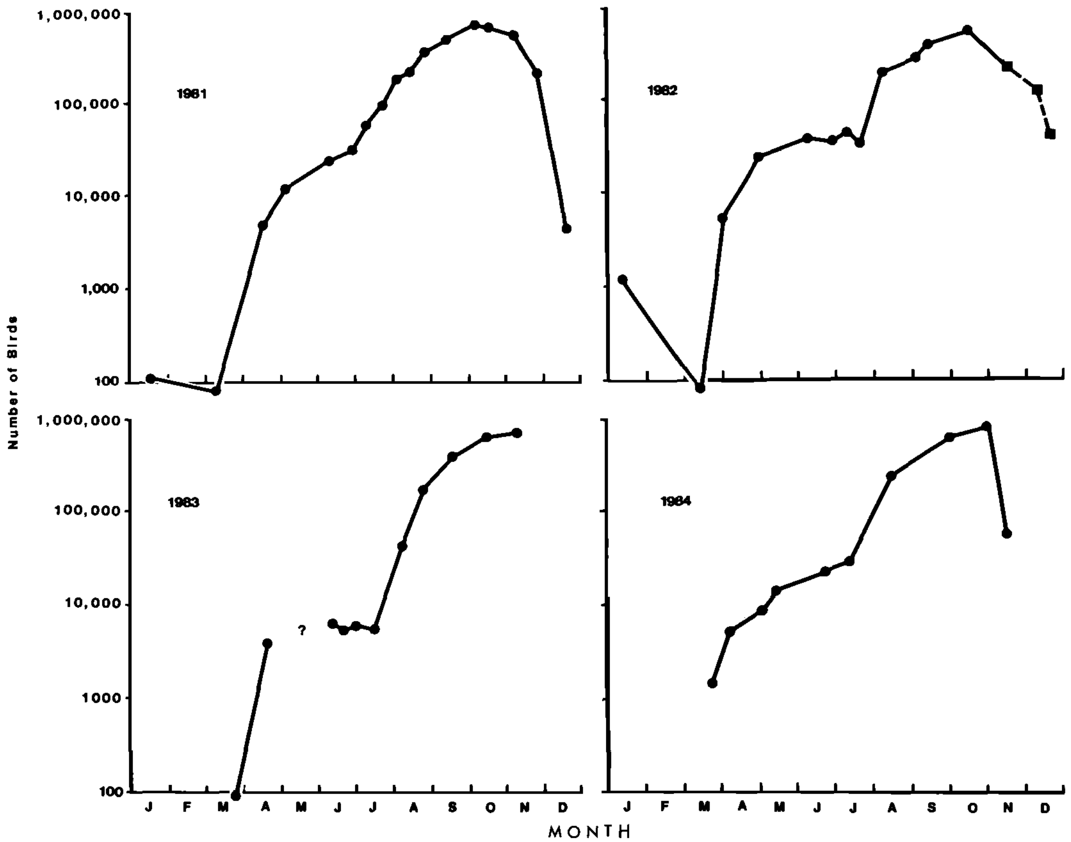


FIGURE 3. Numbers of grebes at Mono Lake, California, 1981–1984. Circles represent best estimates of the population; squares connected by a dashed line are estimates from incomplete censuses. Details in Appendix I.

made at one- or two-week intervals from late May through early September and at three- to six-week intervals in other months. For each carcass, I estimated the time of death as greater or less than two weeks and if possible determined age, sex, and body mass. Because scavengers (coyotes, *Canis latrans,* and rarely California Gulls, *Larus californicus*) move carcasses only a few feet—indeed, most carcasses were untouched—loss of specimens can be considered negligible. Shoreline access varied each year and census areas could not be held constant. In 1982 I surveyed parts of the south, west, and northwestern shores. In 1983 and 1984, effort was increased on north and northeastern shores, which had been largely inaccessible. Other areas on the perimeter and on some islets were checked opportunistically (Fig. 2). I also recorded dead grebes found on transects of the lake (at least 1200 km annually).

We took advantage of the evasive behavior of flightless grebes. By following their underwater movements with a small boat and catching them in a dip net as they surfaced to breathe, we were able to capture and band nearly 800 individuals from 1985 to 1987 (Jehl and Yochem 1987; and Jehl unpubl.). The resulting data greatly supplemented those obtained by collecting and were useful in determining changes in age composition, molt, and weight through much of the fall. We reviewed earlier banding data (Jehl and Yochem 1986) and conducted supplemental field work in the western United States (Jehl et al. 1987, Jehl and Chase unpubl.) to clarify the species' biology elsewhere and to help define the importance of Mono Lake as a staging area.

Further data on methods are presented in the text. Detailed information on some aspects of grebe biology at Mono Lake—molt (Storer and Jehl 1985), osmoregulation (Mahoney and Jehl 1985c), leucism (Jehl 1985), migration (Jehl and Bond 1983), energetics and feeding (Cooper et al. 1984, Winkler and Cooper 1986, Ellis et al. 1985) and banding recoveries and capture techniques (Jehl and Yochem 1986, 1987)—is presented elsewhere.

THE ANNUAL CYCLE AT MONO LAKE

CHRONOLOGY

Grebes that attempted to overwinter at Mono Lake were often in poor condition, and by late February fewer than 100 remained (Fig. 3; see Appendix I for census results). When migrants begin to leave wintering areas in southern Cali-

TABLE 1
MORPHOMETRICS OF EARED GREBES FROM MONO LAKE, CALIFORNIA

	Male			Female		
Measurement	N	Range	Mean ± SD	N	Range	Mean ± SD
			Adults			
Exposed culmen (mm)	48	22.5–29.2	25.6 ± 1.47	36	20.6–26.5	23.2 ± 1.60
Wing, arc (mm)	39	129–144	136.5 ± 3.67	32	127–140	132.5 ± 3.27
Tarsus (mm)	50	40.0–47.2	43.1 ± 1.53	37	38.0–44.4	41.4 ± 1.22
			Subadults			
Exposed culmen (mm)	46	22.0–28.3	25.8 ± 1.42	27	20.9–25.8	23.7 ± 1.51
Wing, arc (mm)	36	130–144	135.4 ± 3.61	20	121–140	130.0 ± 4.81
Tarsus (mm)	47	40.0–46.1	42.8 ± 1.36	27	38.0–44.8	41.4 ± 1.95
			Juveniles			
Exposed culmen (mm)	6	24.2–27.0	25.7 ± 1.19	12	20.8–24.2	22.7 ± 0.99
Wing, arc (mm)	7	128–140	135.3 ± 3.68	14	122–137	129.7 ± 3.93
Tarsus (mm)	6	41.1–45.0	43.3 ± 1.26	11	38.2–43.5	41.6 ± 1.96

fornia and Mexico in early March some evidently move northward along the Pacific coast, at least to central California, for by late March 30,000–50,000 occur on salt ponds at the southern end of San Francisco Bay (P. Kelly pers. comm.). Most probably pass northeastward toward Great Salt Lake, where large numbers have been reported at this season (Hayward et al. 1976, Ryser 1985). Spring recoveries at Mono Lake of a bird banded in Wyoming in fall, and at Walker Lake, Nevada, of one banded on breeding grounds in Alberta, indicate that some prairie-nesting grebes migrate as far northward as central California before turning eastward (Jehl and Yochem 1986).

Migrants can appear at Mono Lake in early March, but no significant influx occurs until late March or early April, by which time some birds have already arrived in breeding areas (Yocom et al. 1958), and after migration on the California coast has peaked. Spring numbers were relatively low, probably because food supplies at that season are unreliable. In mid-April 5000–10,000 were usually present, but in 1986 I estimated 12,000–14,000.

Numbers increased in late spring, owing to the arrival of nonbreeders that remained on wintering areas into early May. Nonbreeders are recognized by plumage and soft-part coloration (Storer and Jehl 1985). By late May the summering population was established, and it stayed relatively constant into late July.

Postbreeders began to return in late July, and from early August to mid-October, when peak numbers were attained, the lake population increased by an average of 10,000 birds per day. Grebes remained until food resources ultimately failed in late fall and then, over a span of about two weeks, moved to wintering areas. In this study major departures occurred as early as the last days of October and as late as the first days of February.

COMPOSITION OF THE POPULATION

In fall, grebes can be assigned to three age classes—juveniles, subadults, and adults—on the basis of molt and plumage characters, soft-part coloration, and the condition of the cloacal bursa (Storer and Jehl 1985; cf. Winkler and Cooper 1986). By late winter, plumage and soft-part distinctions between juveniles and older birds blur and bursal characters become unreliable, so that in spring and summer I recognized only two age groups, subadults (nonbreeders hatched in the two previous breeding seasons) and adults. Sex determination was based on examination of gonads. External size differences are too small to allow the sexing of any but the largest males and smallest females (Table 1).

Differences in the distribution, behavior, and survivorship of the several age classes and in the relative abundance of juveniles from year to year can bias samples. Nevertheless, major trends were clear (Table 2). The few specimens taken in January and February lacked bursas and were considered adults. Adults migrated through the Mono Basin from March to early May; there was no evidence of different periods for males and females. After 10 May I rarely saw birds in full breeding plumage, a further indication that potential breeders had left. Subadults also appeared in late March. Their representation increased gradually as a consequence of their later average arrival and the departure of adults for the nesting areas. Subadult males may have arrived earlier than females, which were not encountered until mid-April.

The summering flock, from mid-May through late July, consisted mostly of subadults and a few

TABLE 2

SEASONAL COMPOSITION OF THE EARED GREBE POPULATION AT MONO LAKE, CALIFORNIA

Month	1981–1984[a]					1985–1986[b]			
	Adults		Subadults[c]		Juveniles				
	Males N (%)	Females N (%)	Males N (%)	Females N (%)	Sexes combined N (%)	Adults N (%)	Subadults N (%)	Juveniles N (%)	Unknown N (%)
Jan	2 (40)	3 (60)							
Feb	1 (100)								
Mar	2 (18)	5 (45)	4 (36)						
Apr 1–15	4 (27)	5 (33)	6 (40)						
Apr 16–30	2 (10)	5 (25)	7 (35)	6 (30)					
May 1–15	15 (43)	10 (29)	6 (17)	4 (11)					
May 16–31									
Jun 1–15	1 (10)		7 (70)	2 (20)					
Jun 16–30	2 (17)	2 (17)	7 (58)	1 (8)					
Jul 1–15	2 (11)	1 (6)	7 (39)	8 (44)			12 (100)		
Jul 16–31	6 (24)	1 (4)	12 (48)	6 (24)			10 (100)		
Aug 1–15	6 (17)	8 (23)	7 (20)	9 (26)	5 (14)	139 (44)	139 (44)	17 (5)	19 (6)
Aug 16–31	8 (36)	3 (14)	1 (4)	3 (14)	7 (32)	4 (80)	1 (20)		
Sep 1–15	8 (27)	3 (10)	7 (23)	6 (20)	6 (20)	6 (46)	3 (23)	4 (31)	
Sep 16–30	4 (27)	5 (33)	2 (13)		4 (27)	11 (52)	3 (14)	6 (29)	1 (5)
Oct 1–15	4 (22)	5 (28)	4 (22)	2 (11)	3 (17)	6 (67)	1 (11)	2 (22)	
Oct 16–31	3 (18)	6 (35)			8 (47)	30 (64)		17 (36)	
Nov	3 (30)	2 (20)	1 (10)		4 (40)				
Dec									

[a] Combined data from 1981–1984, based mainly on collected and freshly dead birds.

[b] Combined data from 1985–1986 based mainly on birds captured for banding.

[c] Birds with cloacal bursas from 1 January–1 August assigned as subadults (see Storer and Jehl 1985).

TABLE 3
DIFFERENCES IN THE AGE DISTRIBUTION OF EARED GREBES AT MONO LAKE, CALIFORNIA

Date	Locality	Adults or subadults N (%)	Juveniles N (%)
23 Aug 1983	Negit Island, cove, <50 m from shore[a]	20 (33)	40 (67)
	Negit Island, entrance to cove[a]	19 (68)	9 (32)
	Channel between Negit and Paoha islets[a]	80 (87)	12 (13)
	>1 km off NE shore	144 (85)	26 (15)
	West side, 50–100 m from emergent tufa	1 (10)	9 (90)
14–15 Sep 1983	West side, <100 m off shore[b]	9 (9)	87 (91)
	West side, 100–200 m from shore[b]	19 (49)	20 (51)
	West side, >400 m from shore[b]	70 (78)	20 (22)

[a] These three points represent a transect from Negit Island toward Paoha Island.
[b] These three points represent a transect away from the west shore.

nonbreeding adults, with males outnumbering females by about 2:1. This suggests that males attain breeding age slightly later than females, on average, and that males tend to remain south of the breeding grounds through their first year.

Postbreeding adults began to return at about the time that the earliest young became independent. Whether males leave the nesting areas slightly earlier than females, as in the Horned Grebe (*Podiceps auritus,* Ferguson 1981), was undeterminable from my samples. Because the grebe's breeding season in western North America extends from April to September (pers. obs.), the arrival period for postbreeders was similarly protracted, extending from late July to late September, at least, as confirmed by molt and weight data. Occasional adults that appeared in early July (earliest arrivals: male, 5 July 1982; female, 12 July 1982) were probably failed nesters.

Juveniles were an important component of the flock. Some appeared in early August (earliest, 31 July 1986) coincident with adults; others arrived at least into mid-October. They were much less wary than older birds and tended to congregate near shore, especially late in the year, which made them more likely to be observed and captured. Some typical data are presented in Table 3. I estimated the representation of juveniles by visually determining age ratios in as many areas of the lake as possible. This procedure minimized locality bias but could not correct for the relative tameness of juveniles. I judged that the young ranged from 10% (1985) to 40% (1984) of the fall peak, and in 1987, they comprised 29.5% of grebes captured (N = 427). In my view, the high representation of juveniles in a large sample (62%, N = 73) obtained by Winkler and Cooper (1986) reflects unrecognized bias in sampling.

SIZE OF THE MONO LAKE FLOCK

How many Eared Grebes visit Mono Lake each year? Turnover among adult migrants in late March to mid-May is probably rapid, because some adults have already arrived on breeding areas and have clutches by late April (Bent 1919, Palmer 1962, Sadler and Myres 1976), and because both brine shrimp and brine fly numbers are meager at this season. Assuming an average population of 6000 adults and an average stay of five days, I estimated that approximately 48,000 breeding birds passed through. Other assumptions are possible, but the salient point is that the number of spring migrants is only a small fraction of the fall population. The summering flock averaged ~25,000 birds.

Through the fall, data on population size, body and breast muscle weight, molt, food availability, behavior, and migration (see below) all indicated that turnover was nil. Thus, postbreeders that appeared in July remained continuously for four months or so, and those that arrived in September for six to ten weeks or more. The sojourn of summering birds can be seven months or longer. Observations of individually recognizable leucinos confirmed continuous stays of at least 15 and 16 weeks (Jehl 1985). I conclude that the total number of birds using Mono Lake in fall was essentially identical to the peak count, or ~750,000 individuals.

In 1982 the fall population of Eared Grebes in North America numbered at least 2.5 million birds, most of which were concentrated at Great Salt Lake (1.5 million) and Mono Lake (0.75 million) (p. 32 and Appendix I). Similar estimates were realized in January 1988 (Salton Sea 1 to 1.75 million, Mono Lake ~500,000), and in March 1988, 3.5 million were reported at the Salton Sea alone (R. McKernan pers. comm.).

ANNUAL VARIATION

The summering flock varied from 5000 to 40,000 (Fig. 4). Estimates of the fall flock ranged from 625,000 to 875,000, although smaller but undetermined numbers were present in the fall

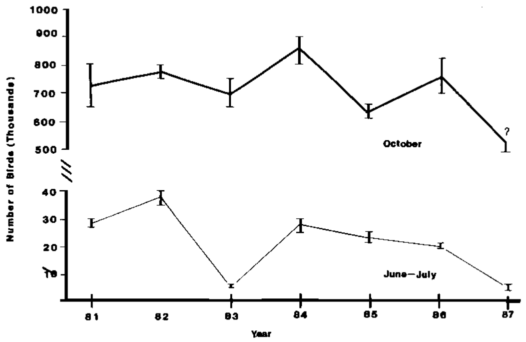


FIGURE 4. Summering and peak fall numbers of Eared Grebes at Mono Lake, California, 1981–1986. The error bars are my estimates of confidence intervals.

of 1987. In some years annual variations in population size and arrival dates seemed to be affected by differences in nesting success, winter survival, and the availability of alternative staging areas. For example, in 1982 and 1983, when nesting conditions were good in the Prairie Provinces, northern Great Plains, and western Great Basin (Faanes 1982; Gollop 1982, 1984; G. Krapu pers. comm., pers. obs.), numbers remained stable from May through July and postbreeders did not arrive until early August. By contrast, in 1981 (and probably 1980), when the mid-continent was experiencing a severe drought (Serr 1980, Faanes 1981), numbers grew through the summer, the influx of fall migrants was less pronounced, and juveniles seemed to be uncommon. In 1984 fall numbers were very large and juveniles were abundant, whereas in 1985 the fall peak was 15–20% lower than the 1981–1986 average and juveniles were scarce. Because waterfowl populations in 1985 were 22% lower than in 1984 (Fish & Wildlife Service estimates), the low grebe numbers can be similarly attributed to a poor nesting season.

In other years, facile correlations were not obvious. Both 1983 and 1987 were similar in that summering grebes were scarce and the fall peak was low, even though juveniles were numerous. Low summer numbers in 1983 might have reflected the large die-off of the previous winter (Jehl and Bond 1983); and low fall numbers, which were paralleled by decreases approximating 40% in Wilson's and Red-necked (*Phalaropus lobatus*) phalaropes, may have been associated with the strong El Niño, whose rains replenished wetlands throughout the western United States. In 1987, however, no similar causes could be associated with parallel findings. Thus, these "explanations" should be interpreted cautiously. Detailed monitoring over a very wide geographic area will be needed to provide verification.

Population data from earlier years are scanty. In late August 1973, the California Department of Fish and Game counted 246,470 grebes, a typical figure, but estimated a total of 345,000 by assuming that an additional 40% were submerged. That correction could only be justified if grebes forage nearly continuously, which is not the case (p. 23). Estimates of >700,000 in late August and mid-September 1976 cannot be evaluated, as they were derived from shore-based counts (Winkler 1977). I have not considered density figures from 1980 and 1981 because they are inconsistent (cf. Cooper et al. 1984, Fig. 3 and Lenz et al. 1986, Fig. 2), and because the 1980 data extrapolate to a peak of 1,500,000 birds. This is nearly double the population size accepted by those authors or that determined in this study.

BEHAVIOR

DISTRIBUTION

Distribution on Mono Lake, never random nor uniform, is influenced by population size, age and molt condition of individual birds, availability of prey, season and time of day. Association with near-shore habitats, a prominent behavior for much of the year, is promoted by several factors. Tufa shoals and other firm substrates (logs, vegetation, feathers) provide a place for brine flies to pupate, and brine shrimp are often far more concentrated there than farther offshore (F. Conte pers. comm.). The tufa's light color highlights the tiny prey (Fig. 5), which is a benefit when water transparency (Fig. 6) and prey numbers are low.

Seasonal patterns of distribution were similar from year to year; data for 1981 and 1982 (Figs. 7, 8) are representative. Overwintering birds congregated at tufa shoals along the north shore and fed on brine flies. Grebes continued to be concentrated there through spring and early summer, spreading laterally as their numbers increased. The greatest densities were often attained near Negit Island and along the northeastern shore.

By mid-July grebes began to move offshore. This shift was probably unrelated to increasing transparency, which would facilitate diving for shrimp in deeper areas, because shrimp were abundant throughout the lake. Rather, I suspect that the arrival of migrants, lowered abundance of brine flies near shore, and the onset of molt, which renders adult grebes flightless and exceptionally wary, were all involved. Nevertheless, densities through fall were usually greatest within 3 km of the north shore, indicating that shallow-water habitats continued to offer better foraging conditions or preferred prey, or both.

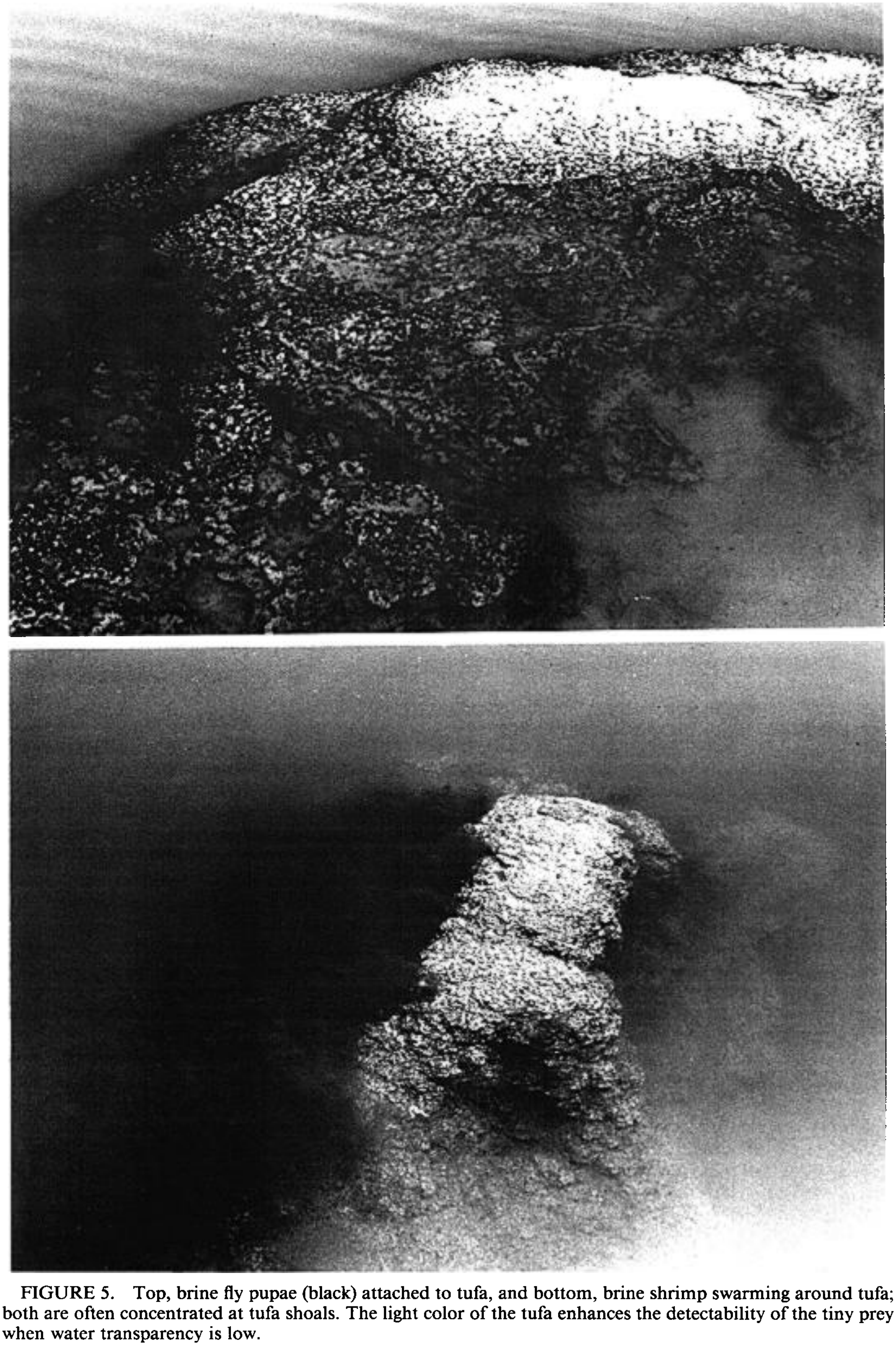


FIGURE 5. Top, brine fly pupae (black) attached to tufa, and bottom, brine shrimp swarming around tufa; both are often concentrated at tufa shoals. The light color of the tufa enhances the detectability of the tiny prey when water transparency is low.

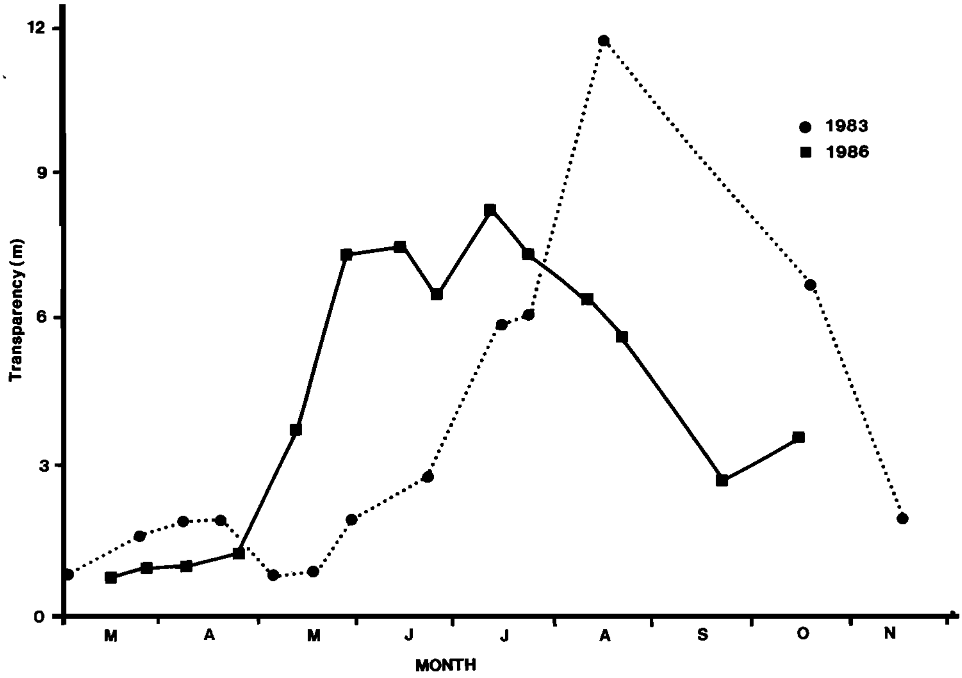


FIGURE 6. Seasonal variation in water transparency at Mono Lake in 1983 and 1986, based on Secchi disc readings. Data for 1983 provided by Los Angeles Department of Water and Power and for 1986 by J. Melack and G. Dana.

Typically 70% or more of the flock occurred on the eastern part of the lake and on 23 October 1981, 97% of the grebes were there (Fig. 7) along with virtually all of the shrimp (Lenz et al. 1986). Yet, there was much variation and distribution was unpredictable. In some years (e.g., 1983, Appendix I) the flock shifted back and forth across the lake, even when brine shrimp were common everywhere. After mid-October, grebes spent little time in shallow water, presumably because brine flies had been depleted. The majority remaining near shore (>90%) were juveniles, many of which were very thin and in poor condition.

Throughout the year, grebes remained rather regularly dispersed in loose flocks (Fig. 9). Sometimes in late fall I encountered clumps of several thousand (Fig. 10) diving persistently in a small area, presumably over concentrations of brine shrimp, which are patchily distributed at that season (Lenz et al. 1986).

DAILY MOVEMENTS

From nocturnal roosts far offshore, grebes swim several km to feeding areas. The timing and extent of these movements varied seasonally. In early spring birds arrived nearshore well after sunrise (~08:00) and returned to roosting sites by mid-afternoon (15:00–16:00). The few that stayed offshore seemed to have just arrived; their gizzards were usually empty, except for indigestible items obtained prior to their arrival at Mono Lake.

In summer daily movements were conspicuous and involved virtually the entire population. Some birds began to swim shoreward before sunrise, and by 05:30 the first had arrived. After feeding intermittently for several hours most withdrew 1–2 km and fed or rested offshore. The movement was reversed in mid-afternoon, when birds returned to the shallows and foraged until ~18:00, before swimming toward the roost.

As fall migrants appeared, an increasing fraction of the flock stayed offshore all day. Although shoreward movements were conspicuous into October, the birds tended to arrive well after sunrise (09:30) and depart long before dark (16:00) and by late October virtually the entire flock remained in mid-lake.

Several birds of known identity frequented specific nearshore areas for up to eight weeks in summer and two used the same areas, albeit intermittently, from early July through mid-October (Jehl 1985). This suggests that some birds maintain a home range on staging areas.

WATER USE

Mono Lake water is distasteful to birds (Mahoney and Jehl 1985a, b, c), which avoid drinking it; it also encrusts feathers. Nevertheless, the grebes, unlike other common water birds at Mono

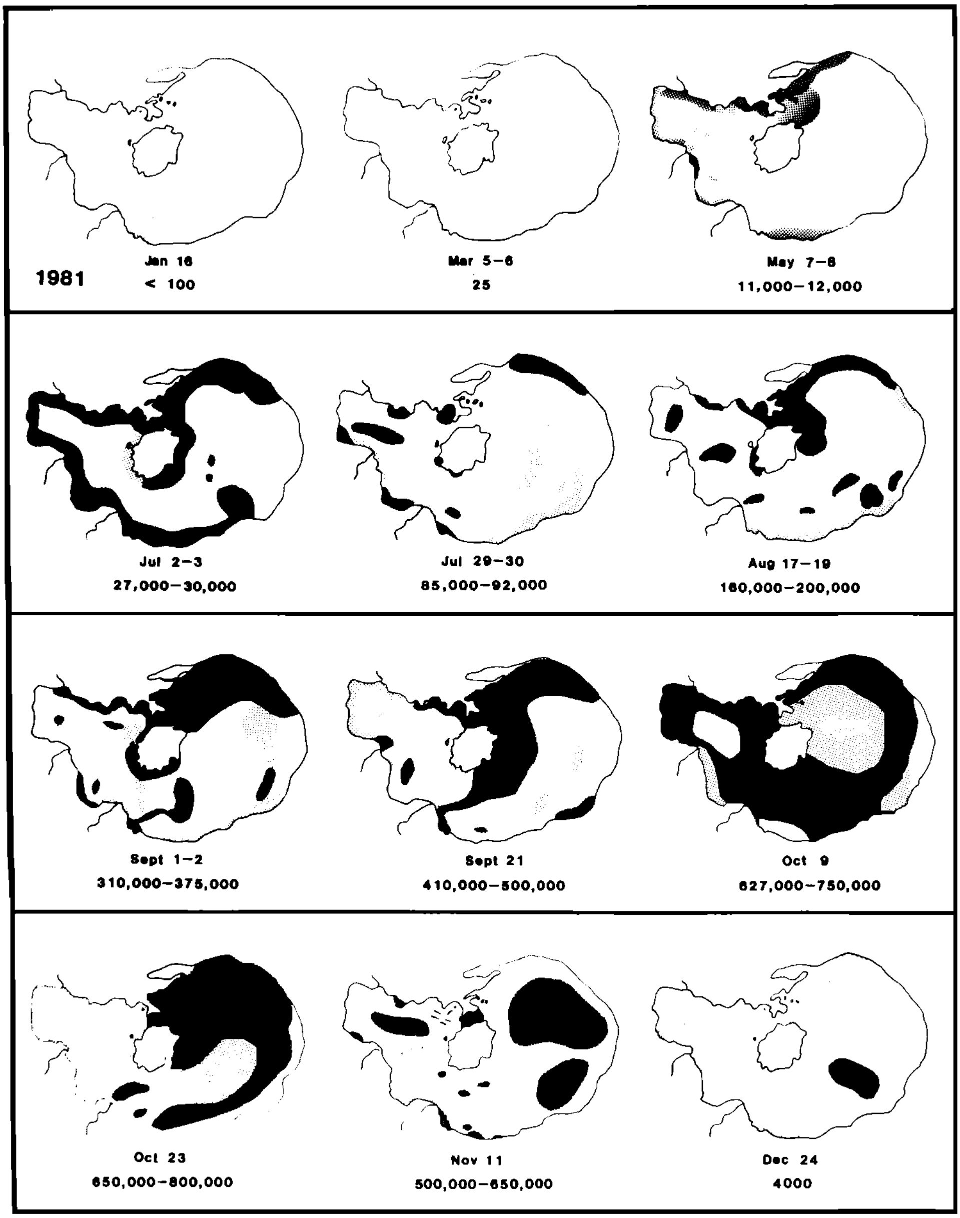


FIGURE 7. Distributional patterns and abundance of Eared Grebes at Mono Lake in 1981. The intensity of stippling reflects the relative density of birds in any one census period.

Lake, do not visit fresh water sources to drink or bathe. Despite the lake's high salinity, they go for months without drinking, relying instead on the high water content (80–90%) of their prey (Mahoney and Jehl 1985c). By diluting lake water by 90%, to ~8‰, Mahoney and Jehl determined that the taste rather than the salinity of Mono Lake was repugnant to grebes, which apparently use their large tongue to press most surficial water from their prey—even from that captured and ingested underwater. The small amount of lake water that is inevitably swallowed can easily be excreted by the salt glands, which are no larger than those of other marine birds. Indeed, salt glands of birds that have been present on Mono Lake for months rarely are fully hypertrophied, showing that highly saline environments pose only a weak challenge to this species (Mahoney and Jehl 1985c). This is further indicated by the grebes' abundance in other local-

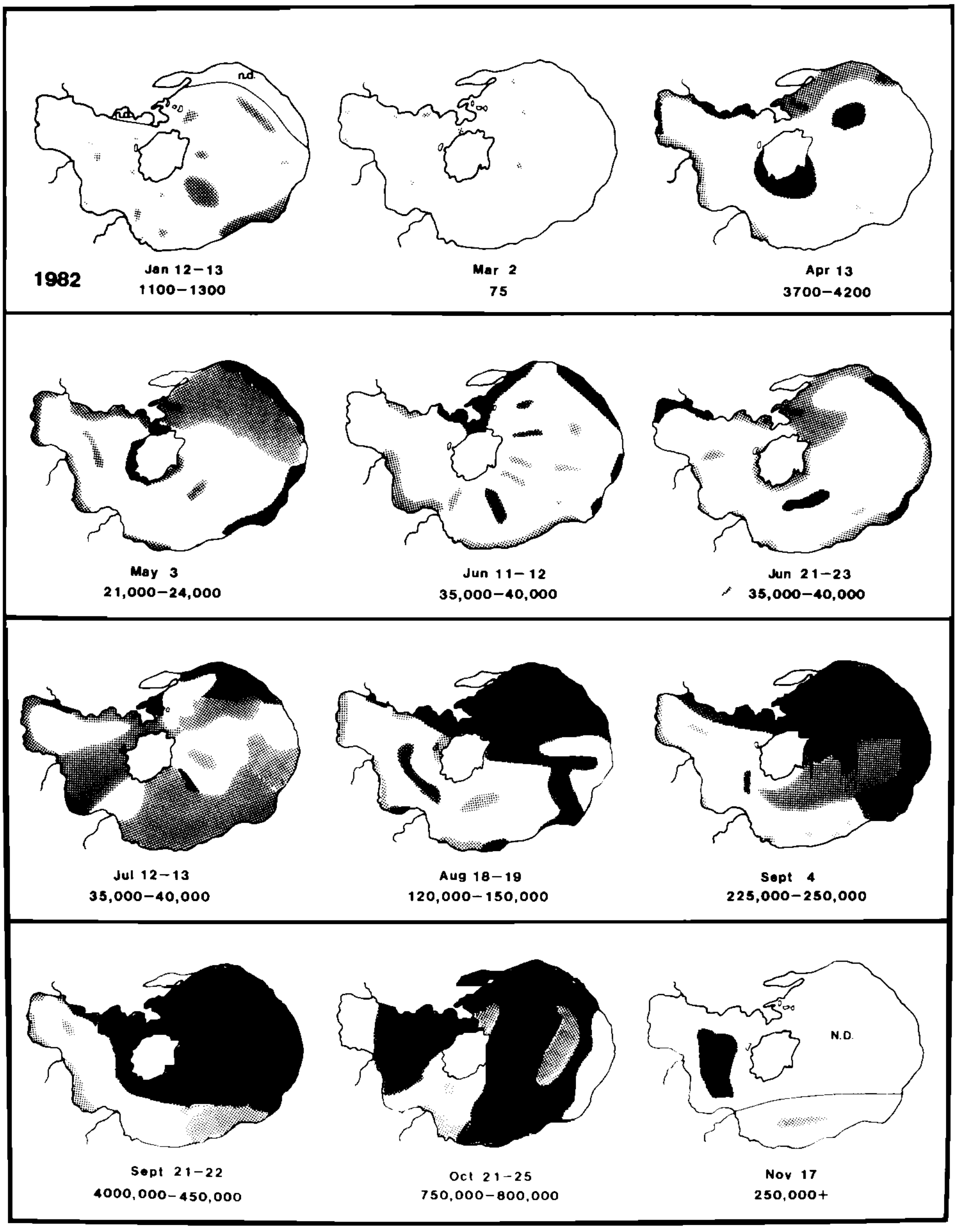


FIGURE 8. Distributional patterns and abundance of Eared Grebes at Mono Lake in 1982. ND = No data. The intensity of stippling reflects the relative density of birds in any one census period.

ities where osmotic concentrations far exceed those at Mono Lake, such as the north arm of Great Salt Lake in 1986 (160‰).

INTERACTIONS

Throughout their sojourn at Mono Lake, grebes do little but swim, preen, forage, and sleep. They remain aloof from each other and I saw no indications of intraspecific aggression. Penguin Dances, which are used in courtship but typically stop when pairs are formed (McAllister 1958), are occasionally performed by summering birds. Grebes are often vocal at night, which may enhance cohesion and communication in the roosts (D. Winkler pers. comm.).

Interspecific interactions were rare. I saw none involving other grebe species or the large numbers of Wilson's and Red-necked phalaropes that

FIGURE 9. A view of part of Mono Lake looking northeast toward Negit Island on 23 October 1985.

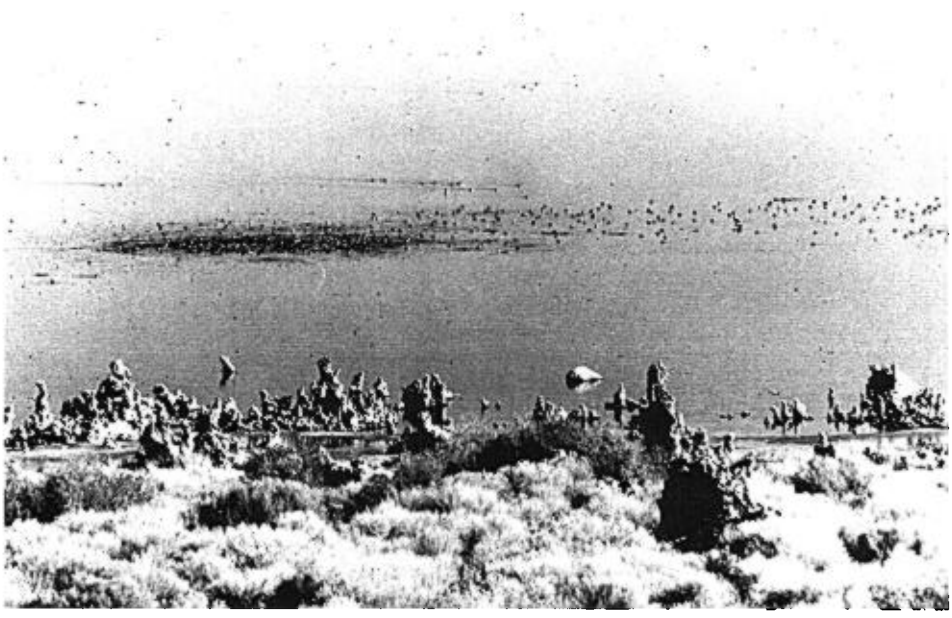


FIGURE 10. Locally high densities of grebes in late fall are presumably related to patchy distribution of the declining brine shrimp.

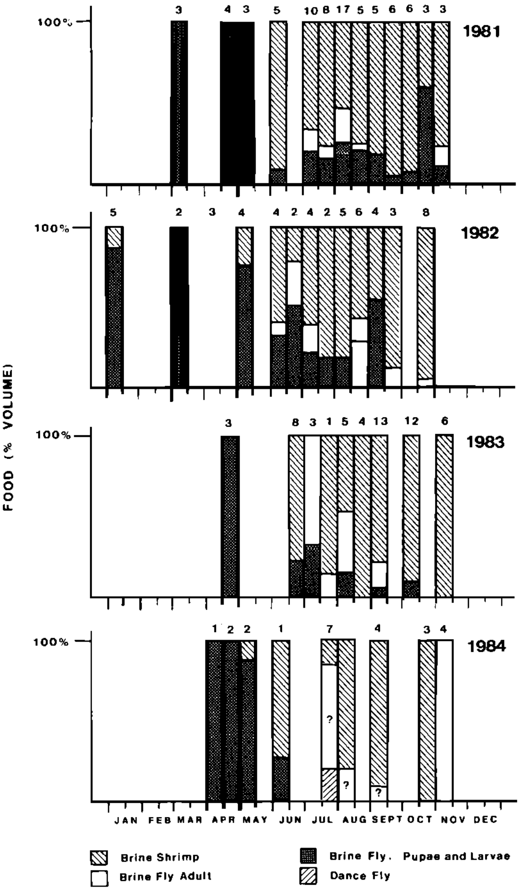


FIGURE 11. Food taken by Eared Grebes at Mono Lake, 1981–1984. Stages of brine flies were not separated in samples from July–September 1984; this is indicated by a question mark.

occur in summer. At Lake Abert, Oregon, in mid-September 1986, when food was very scarce, some grebes followed Northern Shovelers (*Anas clypeata*) and searched for food in mud stirred up by the ducks, even though they were repeatedly chased away. Grebes were wary of California Gulls and might dive if one flew low overhead, but they paid little attention to swimming gulls.

FOOD AND FORAGING

FOOD

Brine shrimp and brine flies are virtually the only food available to grebes and other waterbirds at Mono Lake. The shrimp, which hatch in spring, overwinter as eggs at the bottom of the lake. They occur in great abundance throughout the lake. Two generations are produced before the adults die off in fall (NRC 1987). Brine flies are common only near shore. Their larvae are aquatic and usually pupate on hard substrates in relatively shallow water, although some pupate on sandy bottoms at depths exceeding 10 m (C. Foley pers. comm.). Emerging adults form large mats along the shore from spring through fall, particularly where organic material accumulates on mud flats; they also form rafts on the lake surface in summer and early autumn.

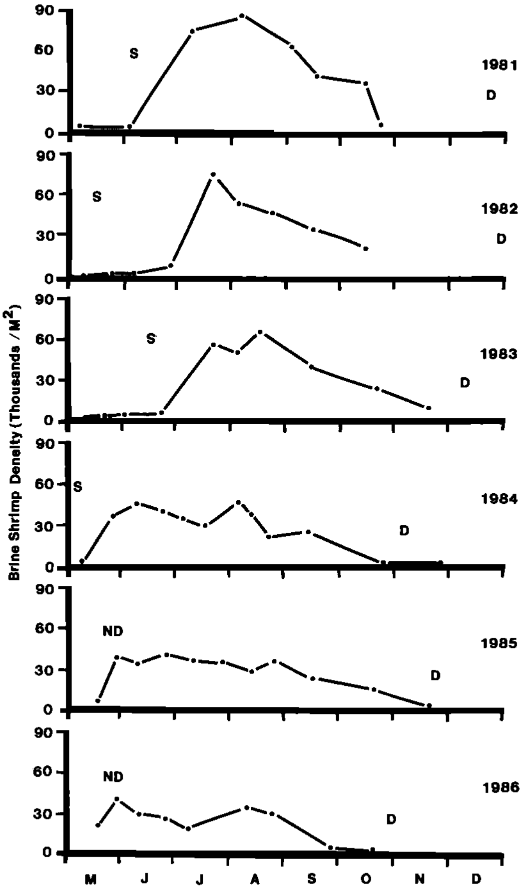


FIGURE 12. Densities of adult plus juvenile (stages 8–11) brine shrimp at Mono Lake. Data for 1981–1984 provided by C. Foley and B. White, Los Angeles Department of Water and Power, and for 1985–1986 by J. Melack and G. Dana. "S" indicates when shrimp were first found in gizzards, "D" periods of major departures, and "ND" no data.

To determine feeding habits, I collected birds in all months and estimated the percentage by volume of each prey species in their gizzards. (Food passes rapidly into the gizzard and is rarely found in either the esophagus or proventriculus.) Direct field observations of feeding behavior were unreliable because neither foraging techniques nor foraging localities were specific to prey type; for example, four birds diving over a single tufa shoal in August 1982 contained from 88% brine shrimp to 100% brine flies.

Samples obtained by collecting were potentially biased by locality, time of day, composition of the grebe population, or prey availability. Nevertheless, combined data for several years revealed obvious patterns (Fig. 11). Immature stages of brine flies comprised most or all of the diet from late winter through mid-May. Brine shrimp were first noted in the diet after densities of shrimp >5 mm in length (which includes late juvenile stages and adults) reached ca. 3000–4000/m^2 (Fig. 12). (Densities are calculated as the number of shrimp in a surface area of 1 m^2 obtained in a vertical tow through the upper 20 m of the lake, or from the bottom in shallow areas; see Lenz et al. 1986.) Although shrimp predominated in the diet by early June, brine flies, which are larger and have a higher caloric value (Herbst et al. 1983), were clearly preferred, and when flies became abundant during major emergences (e.g., early July 1983, Fig. 11) grebes thronged to tufa shoals and fed heavily on adults.

The percentage of shrimp increased in fall and by October–November comprised over 90% of the diet for the population (see also Winkler and Cooper 1986). The relatively high incidence of flies in late October–early November 1981 (Fig. 11) reflected biased sampling; all six specimens were juveniles obtained within 100 m of shore. In November 1984, by contrast, the prevalence of flies represented actual conditions as shrimp had virtually disappeared (Fig. 12).

I infer that differences in foraging distribution result in average differences in prey taken by adults and juveniles, but the question was not sufficiently important to justify collecting larger samples. In an extreme case, eight adults collected on 13 September 1986 had fed almost exclusively (98%) on brine shrimp, whereas four juveniles had fed mainly (68%) on brine flies. The general reliance of adults on brine shrimp in fall probably indicates the scarcity of flies at that season.

Seeds and other invertebrates (ants, beetles, one snail) were encountered occasionally, and Winkler and Cooper (1986) reported a small percentage of shore bugs (*Saldula*); their volume was inconsequential. For brief periods in July 1984 (Fig. 11) and also in 1985, grebes and California Gulls fed heavily on dance fly larvae (Empididae), which apparently were concentrated near seeps along the north shore.

Because grebes eat their own feathers, it is difficult to separate out the amount of food in the stomach contents. Innovative techniques allowed Cooper et al. (1984) to show that shrimp consumption increased through the fall, being more than twice as great in late October as in late August. My observations confirmed that food intake varied enormously through the year. In March and April gizzards of migrants were often empty, showing that birds had been unable to find invertebrate prey. Gizzard size increased in summer, the mass of contents (food and feathers) averaging ~16 g in July and August. Later in fall, when the birds were fattening rapidly, gizzards were typically crammed and greatly distended, with total contents weighing as much as 40 g, or 8% of total body mass.

In a few areas of Mono Lake upwelling springs pump aquatic invertebrates to the surface, creating natural feeding stations. These are often exploited by gulls and Red-necked Phalaropes (Jehl 1986), but grebes ignored them, even when gulls were absent. In early May 1982, when grebes were starving (p. 28), a few visited springs, but the shrimp were too sparse and tiny to exploit.

Other grebes cannot feed efficiently on the tiny Mono Lake invertebrates. Gizzards of three Western (*Aechmophorus occidentalis*) and two Horned grebes, which were diving and ostensibly foraging, were empty. Five other individuals of these species and one Pied-billed Grebe (*Podilymbus podiceps*) captured in banding operations were emaciated.

FORAGING BEHAVIOR

Throughout their range, Eared Grebes feed principally on bottom-dwelling invertebrates (Cramp and Simmons 1977). They are also accomplished surface-feeders and use that technique more prominently than other grebes (Fjeldså 1981), except perhaps *Tachybaptus dominicus* (Storer 1976). At Mono Lake foraging techniques varied seasonally. Grebes dived throughout the year to pluck larval and pupal flies from firm substrates and to capture free-swimming brine shrimp. However, surface-feeding predominated—and sometimes was used exclusively—in summer and early fall, when food in the upper layer of the lake was abundant, and in winter and spring, when food scarcity and the lake's low transparency made diving inefficient. Varieties of surface-feeding included: pecking or skimming prey from the surface, a behavior facilitated by the species' upturned bill (Fjeldså 1973a); lunging at adult brine flies as they rest on or fly from the surface; or gleaning adult flies from rock formations (Fig. 13).

When food was abundant dives were typically steep, and birds returned to the surface within several meters of their point of immersion. When food was scarce or patchy longer underwater transits were required, and grebes often peered beneath the surface before diving. Once when water transparency was high, I was able to watch

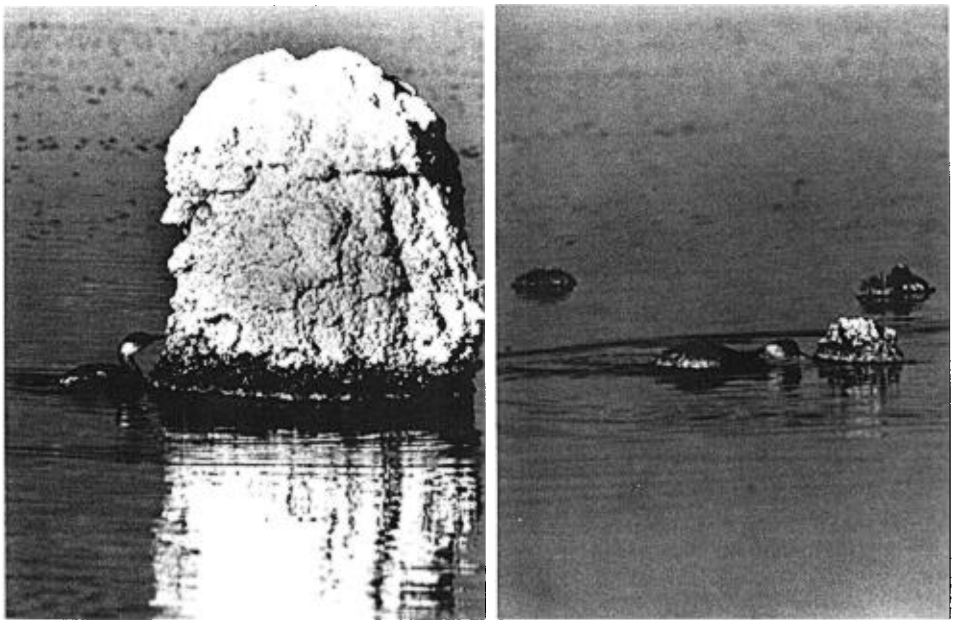


FIGURE 13. Two surface foraging techniques employed by a single grebe. Left, gleaning adult brine flies from emergent tufa; right, lunging at adult flies as they emerge from beneath the surface of the lake.

underwater foraging. Diving directly over a rock or clump of drowned vegetation, grebes attempted to hover underwater and pluck fly pupae from one small area. However, because of their buoyancy, they tended to bob toward the surface, and exploiting a spot required vigorous paddling and repeated approaches during the same dive. To find new food sources they searched back and forth through suitable habitat, but swam quickly and directly across barren sandy bottoms.

Diving episodes usually lasted about 15 minutes, with single dives averaging 24.0 s (range 8–44 s, N = 528). Those in shallow-water (<3 m) near shore were only slightly shorter ($\bar{X}$ = 23.2 s, range 5–43 s, N = 368) than those offshore ($\bar{X}$ = 26.5 s, range 7–44 s, N = 160), which is not surprising, because prey usually are concentrated in the upper 3 m of the water column (F. Conte pers. comm.). Intervals between dives averaged ~20 s, slightly shorter than dive duration, so that only 55% of each foraging bout was spent submerged.

The shortest average dives (9.0 s, N = 4), in March 1981, were exploratory and did not result in food being taken (Fig. 14); the longest (37.4 s, N = 33) occurred on 27–28 October 1984, when few shrimp remained. Dives averaging >30 s were sometimes recorded in April, May, October, and November, months when food may be scarce (Fig. 12).

To avoid capture (Jehl and Yochem 1986), grebes can dive repeatedly for 60–90 s (maximum ~180 s), which is far longer than the longest unforced dive (44 s). For dive durations in other localities see Sealy (1985).

The Ingestion of Feathers

All grebes pluck and ingest their own feathers, which form two discrete masses in the stomach. A small bolus (the pyloric plug) composed of well-fragmented feathers blocks the entrance to the small intestine; a larger mass, which includes fresher feathers, occupies the main chamber of the gizzard (Storer 1969). My observations in 1981 indicated that the size of the main ball varied seasonally, occupying from ca. 10–15% of the lumen from March through May, increasing to 80–90% in summer and fall, and then decreasing (see also Piersma and van Eerden MS). This pattern paralleled changes in body mass and food intake.

Explanations for feather-eating are varied. Some are plausible for individual species but few are widely applicable. Some are also highly imaginative, e.g., muffling the movements of living prey (Thompson 1890), or keeping the stomach "comfortably full" after food has passed into the intestine (Madsen 1957, Fjeldså 1973b). Wetmore's (1920) conjecture that feathers ward off hunger when food is unavailable is incompatible with my observations that feather mass was small when food was scarce. In late October 1984, for example, when brine shrimp were unavailable,

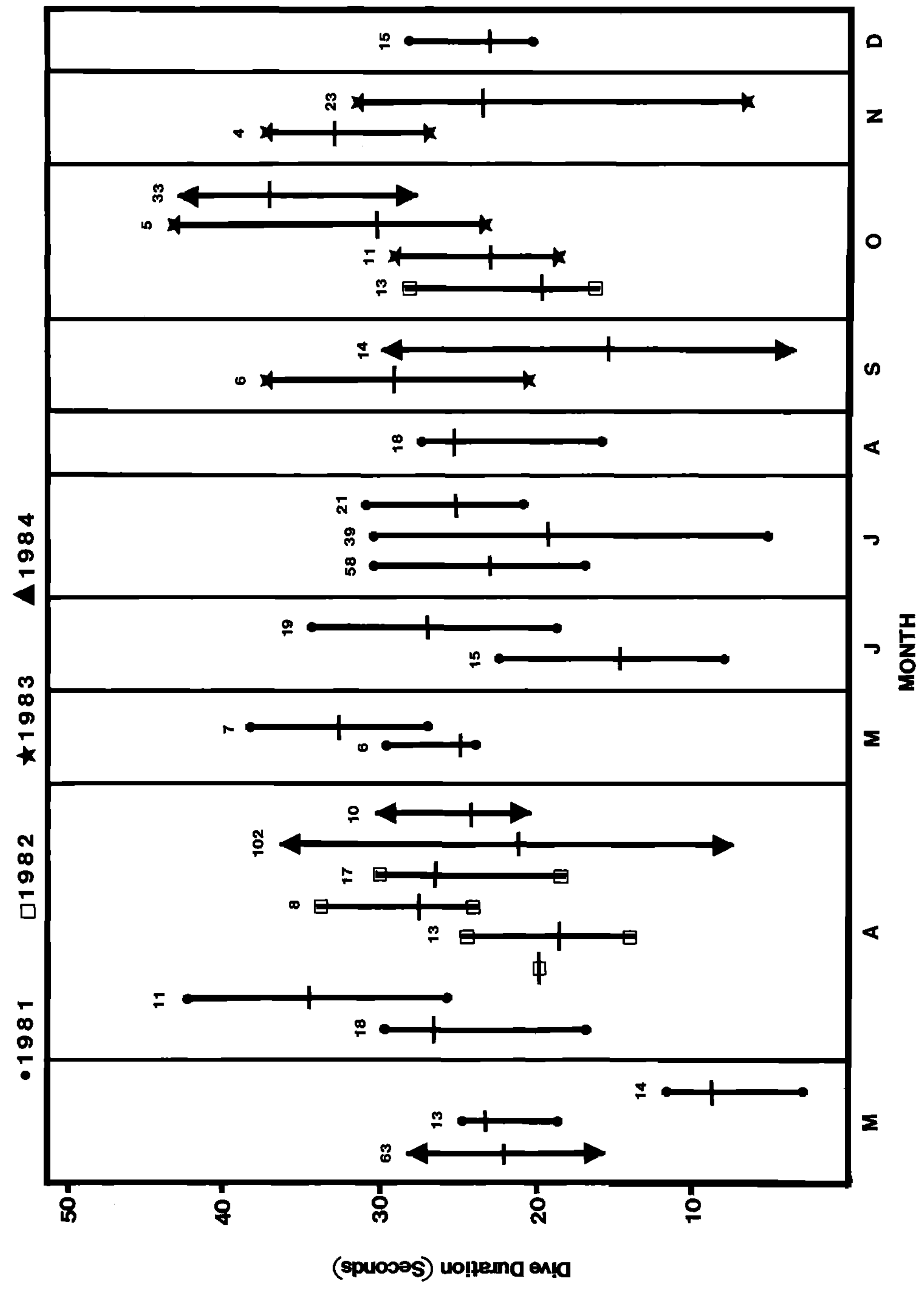


FIGURE 14. Seasonal differences in dive durations (range and mean) of Eared Grebes at Mono Lake, California, 1981–1984. Numbers above columns are sample sizes.

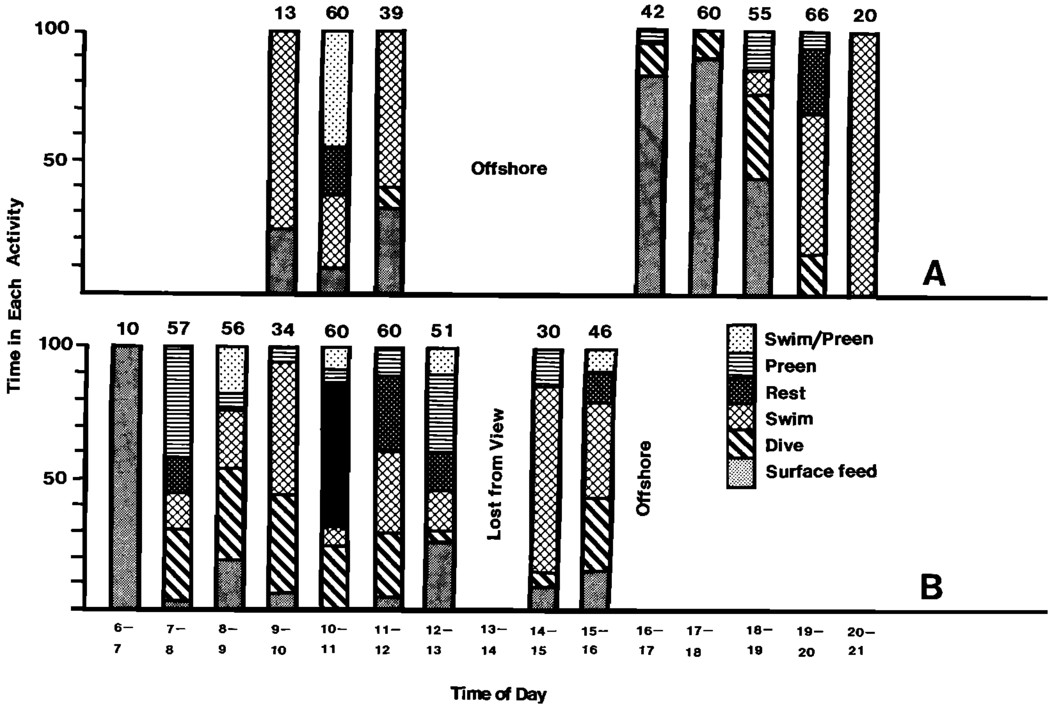


FIGURE 15. Activity patterns of two individual grebes (A, B) on 22 July 1981. Numbers above bars are minutes of observation. Also see Figure 16.

feathers filled only 15–20% of the gizzards of six specimens.

I doubt that the behavior functions mainly to help in regurgitating indigestible material (Storer 1961, cf. Simmons 1956) because, even though chitinous prey comprise all of the grebes' diet at Mono Lake, all the pellets that I have examined contained only finely ground feathers and minuscule bits of fly exoskeleton that could easily have been defecated and, once, a few shrimp eggs and a seed. Lawrence's (1950) view that the feathers promote rapid digestion by keeping prey in close contact with secretory surfaces is unlikely because the bolus occupies the gizzard, not the proventriculus, and because food is incorporated uniformly throughout the feather mass.

The idea that feather-eating is more pronounced in fish-eating grebes (Wetmore 1920, Fjeldså 1973b) led to suggestions that feathers prevented bones from passing into and puncturing the intestine (Wetmore 1920, 1924) or retained bones in the gizzard until they could be digested (Storer 1961, 1969). While further comparison of piscivorous vs. insectivorous grebes might be instructive, explanations based on piscivory are obviously inapplicable to Eared Grebes. Yet, a broader form of Storer's retention hypothesis seems tenable. The tiny eggs of brine shrimp, which can comprise 10–15% of the adult shrimp's mass, are durable and remain intact in the gizzard hours after adults have been digested (Winkler and Cooper 1986); any barrier that promoted their fuller utilization would be advantageous. Feathers might also increase the speed and effectiveness of digestion by keeping tiny prey items separated.

Piersma and van Eerden (MS) have postulated that feather-eating is advantageous because it promotes pellet *regurgitation,* which lessens the chance of parasites becoming established in the gut or gizzard.

I have not seen pellet casting in the wild, but several grebes kept captive for 24 hours have done so, and almost always at night. One cast three pellets measuring ca. 20 × 6 mm in 11 hours.

ENERGETICS

The energetic requirements of Eared Grebes have proved difficult to study. Ellis et al. (1985) determined basal metabolic rates, but efforts to measure energetics using doubly labelled water were unsuccessful, because the neck collars and radio-tags used to follow the movements of free-ranging birds affected their behavior, causing them to come ashore at night, where they were killed by Great Horned Owls (*Bubo virginianus*).

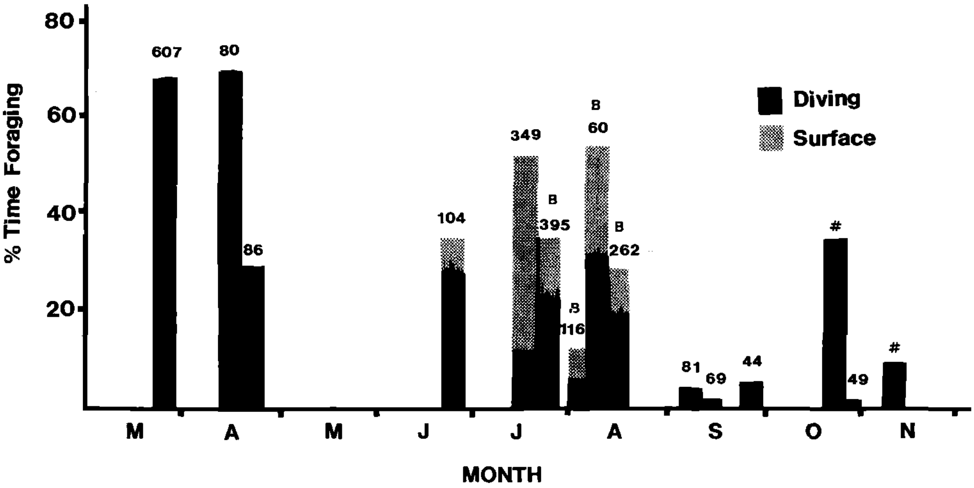


FIGURE 16. Seasonal variation in the percentage of time spent foraging. Numbers above columns are minutes of observation; # indicates estimate based on a minimum of 60 minutes of observation of flocks; B designates a leucistic grebe whose movements were studied on several days. Data from 1981–1984.

If grebes require a daily food intake of 20% of their body mass ($\bar{X}$ = 500 g) in fall (Herman 1973), the daily consumption of shrimp by the Mono Lake population at peak numbers (750,000) would average 82.6 tons; and this may be conservative because birds are fattening at this time. Even so, grebes seem to have relatively little effect on shrimp populations (Cooper et al. 1984). While this conclusion should be considered tentative until better estimates can be made on grebe numbers, shrimp numbers, and direct energetic requirements for various grebe behaviors, these preliminary estimates may help illustrate the immensity of the brine shrimp population.

Time budgets, widely used in energetic studies, were hard to obtain, given the grebes' extensive daily movements and wariness. Furthermore, their application is complicated by individual differences in age, sex and stage of molt or migration (factors that are usually undeterminable for wild birds) as well as by year, week, time of day, and weather conditions (Bailey 1985, Takekawa 1987, Mugaas and King 1981).

Variation in the behavior of individuals under similar regimes can be high. On 22 July 1981, my field team documented the daily activity of two summering nonbreeders (Fig. 15). One (A in Fig. 15) arrived near shore at 09:47 and concentrated its foraging near emergent tufa, where it fed mainly by surface feeding or gleaning. After moving offshore for several hours in midday, it returned near shore and continued to surface feed until 18:30, when it shifted to diving before swimming back to the roost; most of its foraging time (79%) was spent surface feeding. The second bird (B in Figs. 15, 16) was noted swimming toward shore at 06:05; it arrived at 06:47 and remained within view almost constantly until 15:46. It fed mostly by diving (67% of foraging time), except in the early morning, when it captured adult flies from the surface. Over the next month, however, its diving efforts were much lower (6–32% of foraging time, Fig. 16). Given these differences, I suspect that calculated energy budgets would remain crude even if reliable estimates of energy equivalents were available for the major types of activity (see also Weathers et al. 1984). Takekawa (1987:43) also showed that "energy budgets . . . based on average daily behavior may be an oversimplification."

Figure 16 depicts the seasonal foraging effort of grebes based on pooled data from several years. Because the data were collected opportunistically at different times of day (grebes do not feed at night; Cooper et al. 1984), they can only be used to show general patterns. Thus, foraging effort is high in early spring, when food is scarce, and diminishes gradually as food supplies increase later in the year. It follows that seasonal changes in energetic requirements owing to molt and fattening are met mainly by varying the time spent foraging and not by increasing the duration of individual dives (Fig. 14).

Many grebe species sunbathe (Storer et al. 1976). This behavior was conspicuous on chilly mornings at Mono Lake, where temperatures drop below freezing months before the birds depart. While warming, the grebes swam slowly, orienting the rump toward the sun; other activities were also reduced and in mid-October 1986 very few birds even began to dive before 09:30.

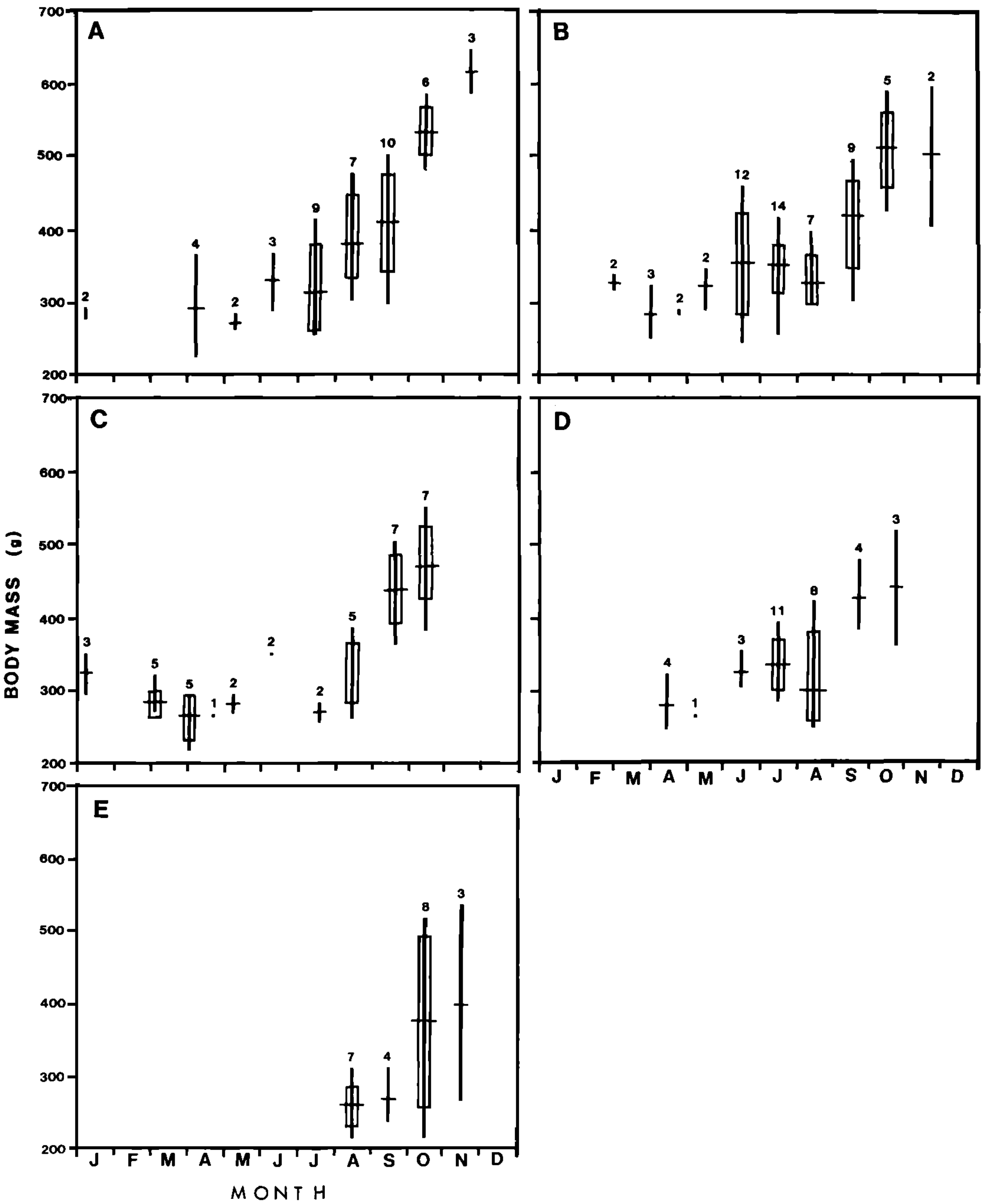


FIGURE 17. Body mass (range, mean ± 1 SD) of Eared Grebes at Mono Lake, 1981–1983. A, adult males; B, subadult males; C, adult females; D, subadult females; E, juveniles (sexes combined).

This slow start-up period suggests that grebes may sometimes undergo a shallow hypothermia to minimize energy requirements in cold seasons or when food supplies are reduced (see Paladino 1986).

MASS

Body mass of specimens taken in 1981–1984 is shown in Figure 17. In January grebes that have attempted to overwinter average ca. 300 g;

the few that endured into March were often lighter and in poor condition. Spring migrants averaged ~275–300 g, males being slightly heavier. Many birds were lighter, however, and those dropping below ~220 g are probably unable to recover, as indicated by observations of weak birds we have attempted to rehabilitate. The mass of subadults increased in late spring, concomitant with increased prey abundance, but remained relatively stable between 330–390 g from June through August (Figs. 17B, D).

Newly arrived adults in early autumn averaged 325 g (females) to 350 g (males). The birds began to fatten almost at once and continued to do so even though replacing wing and body feathers simultaneously. In 1985, two of 12 adults captured on 24–26 September weighed <300 g, had well-developed pectoral muscles (see p. 26) and were in unmolted breeding plumage, confirming that postbreeders continue to arrive through that month (see also data from Lake Abert, Oregon, p. 32). On a population basis, gains in September and October approximated 100 g/month (rates in individual birds were likely far greater), and by October weights exceeding 600 g were common. Maxima were: adult male 665 g, adult female 655 g, subadult male 660 g, subadult female 522 g.

Juveniles were very light on arrival (mean ~265 g; minimum 195 g, 11 August 1981). Although they grow rapidly, their weights were highly variable (Fig. 17E), which partly reflects their more protracted migration period and later average arrival. It may also indicate their relative inefficiency in capturing brine shrimp (also suggested by their inshore distribution), because in late fall few attained weights characteristic of older birds (maximum 550 g).

When shrimp die off the grebes are left with two options: migrate immediately, or linger and live off fat reserves. As shown below, the first option was precluded for most birds, making the second mandatory. Weight losses late in 1984 and 1986 are shown in Figure 18. They were not evident in 1981–1983 (Fig. 17), or in 1985 (Fig. 18), because sampling was not carried out sufficiently late in the season.

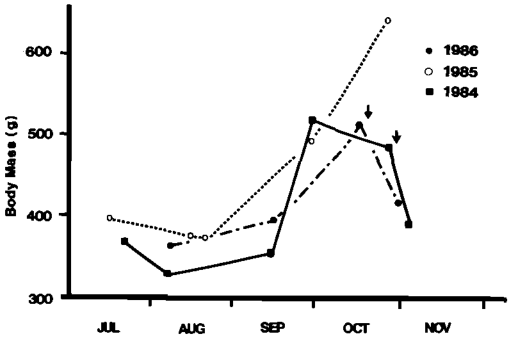


FIGURE 18. Mean body mass of adult and subadult Eared Grebes in the autumns of 1984–1986. Arrows indicate when brine shrimp were no longer detectable from the surface.

MOLT

Molts, plumages, and criteria for aging grebes have been documented by Storer and Jehl (1985). Briefly, adults and subadults undergo a complete prebasic molt in fall, whereas juveniles replace only the body plumage. In summering birds (mostly subadults) body molt may begin as early as May; in adults and juveniles it typically starts on the breeding grounds in late summer. Wing molt in adults begins shortly after they arrive at Mono Lake, but apparently not before they have accumulated ca. 40 g of fat (Fig. 19). All remiges and most coverts are dropped simultaneously. Studies of captive birds corroborated field estimates that full regrowth of the remiges takes 35 to 40 days, by which time body weight may exceed 500 g. Some nonbreeders may begin wing molt by early May. In all birds, but especially adults, molt is intensive and, except for persistent molt on the flanks, may be completed in about six weeks, the latest birds finishing by early November. Some late-arriving adults complete wing molt and much body molt elsewhere (p. 33) before appearing at the staging areas. The prealternate molt involves only the body plumage and a varying number of wing coverts. This molt is hard to interpret because it is less intensive and more protracted than the prebasic molt. In local non-breeding birds, these molts may overlap in late summer. In general, the prealternate molt seems to start in late February and to be mostly completed by late May.

FLIGHTLESSNESS

Grebes summering and staging at Mono Lake rarely flew; indeed, most were completely unable to do so. Adults and subadults were of course grounded while replacing remiges, but the flightless period can last six months or more in birds that have summered. This may be the longest flightless period regularly endured by any North American bird and it is associated with atrophy of the breast muscles. To study this condition I excised muscles from one side of the pectoral girdle, removed any superficial fat, and weighed them to the nearest 0.1 g.

In adults and subadults the mass of the breast muscles varied in a complex fashion with body mass and, by inference, with the length of time an individual had been resident (Fig. 20). Mus-

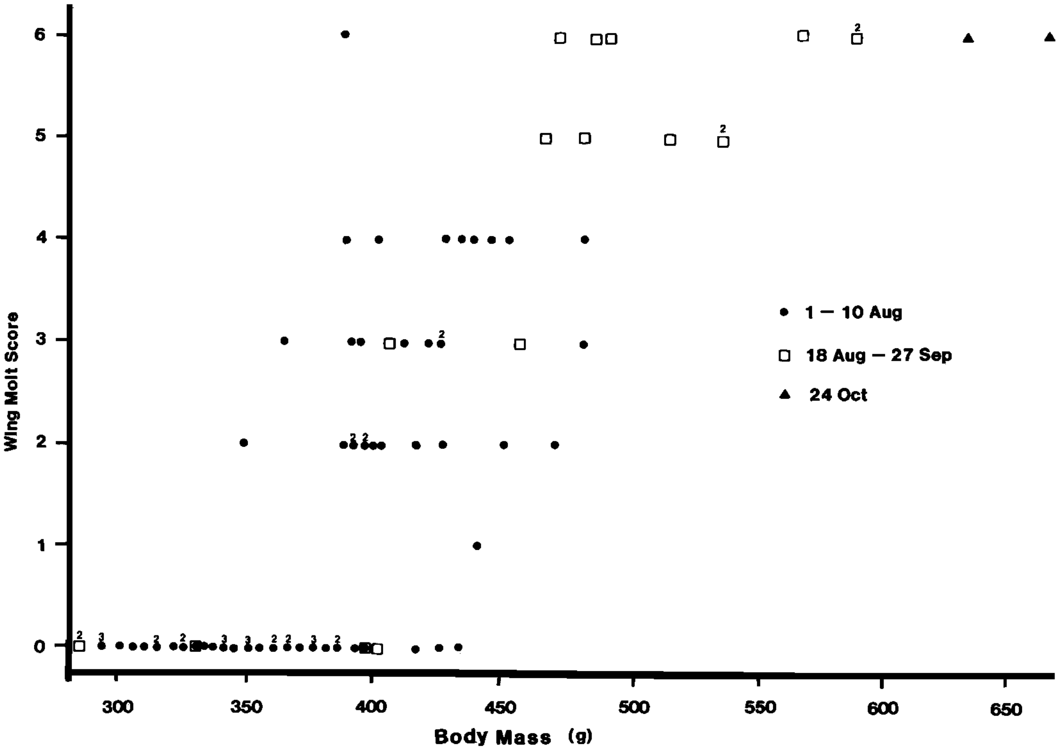


FIGURE 19. Relationship of wing molt to body mass in adult and subadult Eared Grebes. Molt scores range from 0 (no molt) to 6 (primaries fully replaced).

cles of newly arrived migrants were large and convex in cross section, averaging ca. 20 g. They shrank to 11–14 g and became concave within a week or two after arrival, then remained small through the remainder of the birds' residency. Very low masses (<12 g) occurred mostly during and shortly after the main period of wing molt (July–September), but were also noted in non-breeders by late April. They were also common among juveniles in late fall or in starving birds that had to catabolize muscle to survive. Just before the main exodus, however, the breast muscles hypertrophied rapidly, *even though the grebes were fasting and losing body mass at the same time.* I judge adults whose breast muscles were <16–18 g to be incapable of flight, and that even those whose muscles weighed >20 g were probably flightless when total body weight exceeded 450 g. The largest breast muscles (31 g) were recorded just before a major departure.

To emigrate the birds must lose body mass but rebuild muscle. Weight loss is a passive process, forced by the annual collapse of the shrimp population. I found that fasting captive grebes kept inactive in a darkened room lost an average of 1.5 g/h after an initial period (6–8 h) of more rapid loss, which resulted mainly from clearing the gut (Fig. 21). It follows that wild birds, which

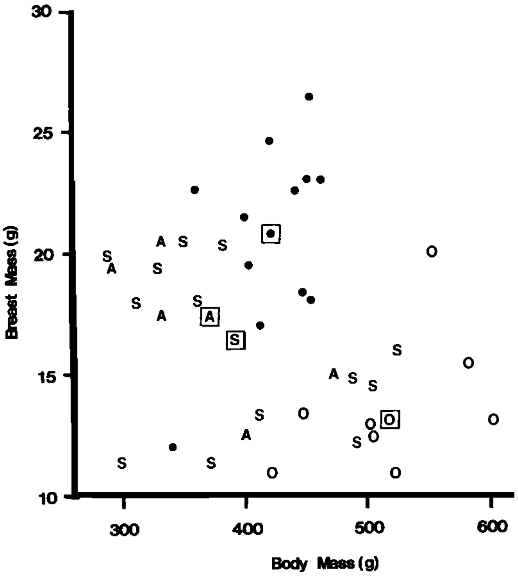


FIGURE 20. Seasonal changes in breast mass (from one side of pectoral girdle) and body mass in adult and subadult Eared Grebes at Mono Lake in autumn 1986. A = 3 August, S = 13 September, O = 14 October, and ● = 28 October. Squares indicate the means for each sampling period.

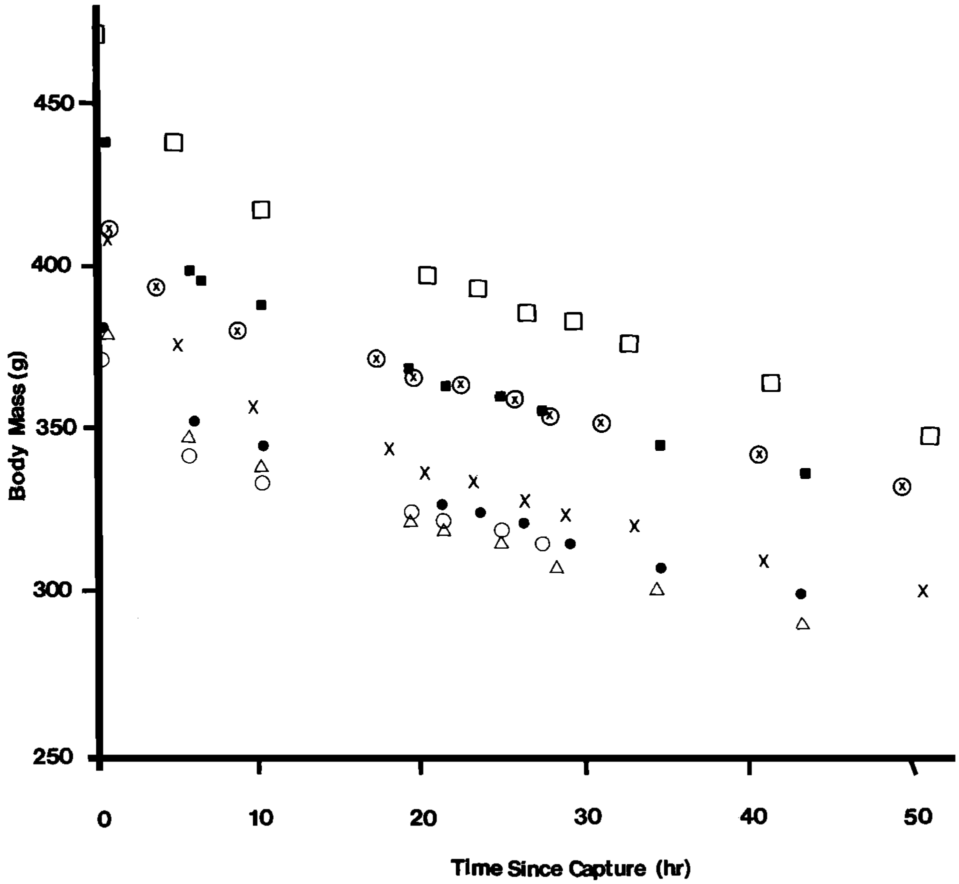


FIGURE 21. Weight loss in fasting, inactive Eared Grebes, in captivity.

never totally lack food but have much higher energy expenditures, could easily lose one third of their mass, say from a peak of 600 g to an estimated pre-departure weight of 400 g, in a week.

Rebuilding flight muscles is partly an active process involving exercise. The birds rear back and flap in place for 5–20 s (Fig. 22; see Piersma 1987b), and as departure time nears they may run and flap across the water for up to 100 m as they try to lift off. Exercise behavior is contagious and can involve dozens of birds. Although I have seen it in late September, it is not prominent until two weeks or so before the major exodus. On 14 October 1986, when it was conspicuous, few birds could fly or even rise a few inches off the water; the adults and subadults averaged 515 g with breast muscles 13.7 g (N = 11). Two weeks later, when 70% of the flock had departed, weights had dropped by 20% to 420 g and breast muscles had increased by 50% to 20.7 g (N = 13).

The causes of seasonal reduction in breast muscles have been debated (King and Murphy 1983). Some (Hanson 1962, Bailey 1985) have suggested that in ducks and geese, some of which are herbivorous, the muscles are a depot for sulfur-containing amino acids, which can be shunted as needed to growing remiges or other tissues. Others (e.g., Ankney 1979, 1984) have argued that disuse during the flightless period is a sufficient explanation. The central question is whether the birds actually lack protein during the molt (Bailey 1985). That is not the case for Eared Grebes, which fatten before and during the molt by feeding entirely on invertebrates. These facts support the "disuse" hypothesis. Piersma (1988) has come to similar conclusions for the Great Crested Grebe (*Podiceps cristatus*), in which the duration of flightlessness is shorter than in the Eared Grebe and the extent of breast muscle atrophy and the change in body mass is less pronounced.

The inverse condition, hypertrophy, has been studied in a few species (Fry et al. 1972). In the Cooper's Hawk (*Accipiter cooperii*), Marsh and Storer (1981) showed that it was accompanied

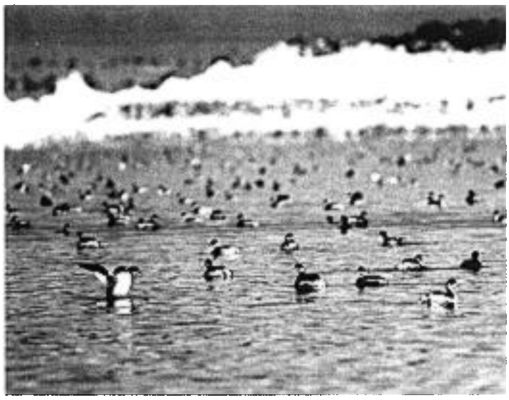


FIGURE 22. Exercise flapping, which aids in rebuilding pectoral muscles, becomes prominent shortly before the major departure period in late fall.

by an increase in body mass, which they interpreted as a compensatory response to increased wing loading. In grebes, however, hypertrophy begins long after the birds fatten but *before* they are challenged by increased wing loading and regain flying ability. Because the time spent in calisthenics is very short, and muscle regeneration is rapid, much of this change is evidently independent of exercise, indicating that an endogenous process is also involved (see Bailey 1985).

In 16 birds that were collected at various times of the year, including many that were probably flightless though otherwise in good health, the *M. pectoralis major* averaged 15.6 g (12.2–21.9 g) and the *M. supracoracoideus* 2.0 g (1.4–2.6 g), whereas in eight emaciated birds found dead in spring, the *M. pectoralis major* averaged 5.2 g (3.0–6.9 g) and the *M. supracoracoideus* 0.9 g (0.6–1.2 g). When birds are starving the *M. pectoralis major* undergoes the greater reduction.

MORTALITY

I used beached-bird censuses to determine the timing and extent of mortality throughout the year. Because of potential sampling errors these data could not be used to calculate precise mortality rates, even though the size of the source population was known for each month. Differences in wind direction and lake currents combined with the shifting location of the grebe flock resulted in impressive differences in the distribution of carcasses, which for practical reasons could not be accounted for by equal censusing efforts on all shores or by randomized searches. In late October 1984, for example, I found 58 grebes in 14 km; 54 (93%) were along 0.8 km of the western shore and two (3.5%) were along 6 km of the northeastern shore. Two weeks later, I found 432 grebes in 13.6 km; three (0.6%) were in the area previously checked on the western shore and 315 (73%) on the northeastern shore.

SEASONAL PATTERN

The pooled data from several years, however, illustrate seasonal patterns and provide an index to the risk of mortality at different seasons (Table 4).

January–February

The reduction of the wintering flock and the low weight and often poor condition of survivors suggested that death rates were very high at this season. The data are scanty because snow conditions impeded field work and because the chances of finding dead birds from so small a population are low.

March–May

Mortality among spring migrants [first noted by Denton (1949) in 1880] was inconspicuous in 1983 and 1984, but high in 1982. From 2–5 May 1982 I found 181 cadavers, all emaciated, and estimated that 500 to 1000 grebes died between 26 April and 10 May; males averaged 191 g (range 165–210 g, N = 11) and females 173 g (range 149–192 g, N = 10). Necropsies by the U.S. Fish and Wildlife Service failed to detect disease or toxins, and the mortality seemed attributable to local food shortage. Indeed, in this period food was so scarce that some grebes stumbled across mudflats seeking the few adult brine flies that had emerged. In 1983 some mortality was noted in late March and early April. Again, the birds were emaciated (males, $\bar{X} = 210$ g, range 188–230 g, N = 10; females, $\bar{X} = 186$ g, range 165–205 g, N = 10) and had evidently starved.

June–August

Mortality among summering birds was much lower than among spring migrants. The similar rates suggested in Table 4 are biased by the inclusion in June 1982 of birds that had succumbed in the May die-off noted above (Appendix II). Likewise, apparent high mortality in August 1983 resulted from the expansion of the survey areas and the finding of a large but undeterminable number of birds that had died much earlier.

September–December

Mortality was trivial through most of the fall; September and October rates were at least one order of magnitude lower than in spring. It increased after shrimp populations collapsed, owing to the demise of birds unable to emigrate. On 28 December 1981 I recorded densities of 53 dead birds/km (2.4 km surveyed) on the northeast shore; in the same area on 11 November 1984 I found 46 birds/km (8 km), and on 9 De-

TABLE 4

MORTALITY OF EARED GREBES AT MONO LAKE, CALIFORNIA, DECEMBER 1981–NOVEMBER 1984, BASED ON BEACHED-BIRD SURVEYS[a]

	Birds found dead[b]			Birds/km			
	<2 wks	Total	KM surveyed	<2 wks	Total	Approximate $\bar{X}$ size of population	Relative risk of mortality[c]
Jan	0	0	5.6	0	0	<100	High
Feb	0	1	1.6	0	0.62	<100	6×10^{-3}
Mar	0	1	15.7	0	0.06	1500	4×10^{-5}
Apr	7	44	36.8	0.19	1.20	65,000	2×10^{-5}
May	177	197	35.7	4.96	5.52	35,000	2×10^{-4}
Jun	44	97	89.4	0.49	1.08	25,000	4×10^{-5}[d]
Jul	28	56	153.0	0.18	0.37	25,000	1×10^{-5}
Aug	19	197	137.6	0.14	1.43	225,000	6×10^{-6}[d]
Sep	4	14	66.1	0.06	0.21	450,000	5×10^{-7}
Oct	55	60	32.0	1.72	1.88	750,000	2×10^{-6}
Nov	50	445	33.3	1.50	13.36	450,000	3×10^{-5}
Dec[e]	1	133	12.0	0.08	11.08	100,000	1×10^{-4}
Totals (means)	366	1245	618.8	(0.59)	(2.01)		

[a] Data from Appendix II.

[b] Separated by those judged to have been dead > or < 2 weeks.

[c] $\bar{X}$ birds/km ÷ $\bar{X}$ population size.

[d] Overestimated (see text, Appendix II).

[e] Includes one census in December 1981.

cember 1985 29 birds/ km (3.2 km). In each case, the mortality had occurred during the previous two weeks. While these dieoffs were conspicuous, they actually involved only a few hundred birds, which were concentrated by currents in a relatively short section of beach.

SOURCES AND EXTENT OF MORTALITY

Of 156 cadavers examined on 28–29 October and 11–12 November 1984, 137 (88%) were juveniles; most were emaciated ($\bar{X}$ = 191 g, range 165–245 g, N = 40) and had doubtless starved. The high mortality of juveniles may be caused in part by their later average arrival date, which gives them less time than adults to finish molt and prepare for migration—processes that must be accomplished when food is already dwindling—or by their evident lesser proficiency in capturing brine shrimp, or both. Starvation was not the major cause of death among adults, most of which died quickly and seemed to have been in excellent condition. Nine of 12 examined in late 1984 were fat ($\bar{X}$ = 410 g, range 360–425 g), and in late October 1986 adults found dead averaged as heavy ($\bar{X}$ = 442 g, range 390–510 g, N = 15) as those that were collected ($\bar{X}$ = 435 g, range 340–510 g, N = 7). All that I examined in both years had suffered massive internal bleeding, which presumably resulted from disease, because they had not been shot. At Great Salt Lake, Jensen and Cotter (1976) reported a die-off of 5000 in late November 1975. These were also in "excellent physical condition" but succumbed quickly from erysipelas, a bacterial infection caused by *Erysipelotrix rhusiopathiae.*

Other causes of mortality seemed insignificant. I saw no evidence of disease and on handling hundreds of specimens I rarely encountered external parasites, whose virtual absence was confirmed by parasitologists at the University of Michigan (R. W. Storer pers. comm.). Rausch (1983) reported that helminths were common internal parasites in grebes, including *P. nigricollis* collected in Europe. Although I did not study this directly, helminths were rare or absent in the many birds that I examined at Mono Lake. Avian predators capable of capturing healthy grebes (Peregrine Falcons, *Falco peregrinus,* Prairie Falcons, *Falco mexicanus,* and Bald Eagles, *Haliaeetus leucocephalus*) were rarely seen. Sickly grebes that remained ashore at night were dispatched by Great Horned Owls or coyotes, whichever came first.

Estimates of average monthly mortality for each of three years ranged from 1.19 to 3.02 birds/km (Appendix II); these extrapolate to an annual total of 1370 to 3628 birds, or only 0.18–0.48% of a fall peak of 750,000 birds. These estimates are probably high because I emphasized fall censuses in areas where cadavers were most likely to accumulate. If this low rate were typical of the situation throughout the year, it would correspond to an annual mortality of only 0.72 to 1.92%, which is unrealistically low.

It follows that most annual mortality occurs away from Mono Lake. There are no data from the breeding grounds, and large die-offs on win-

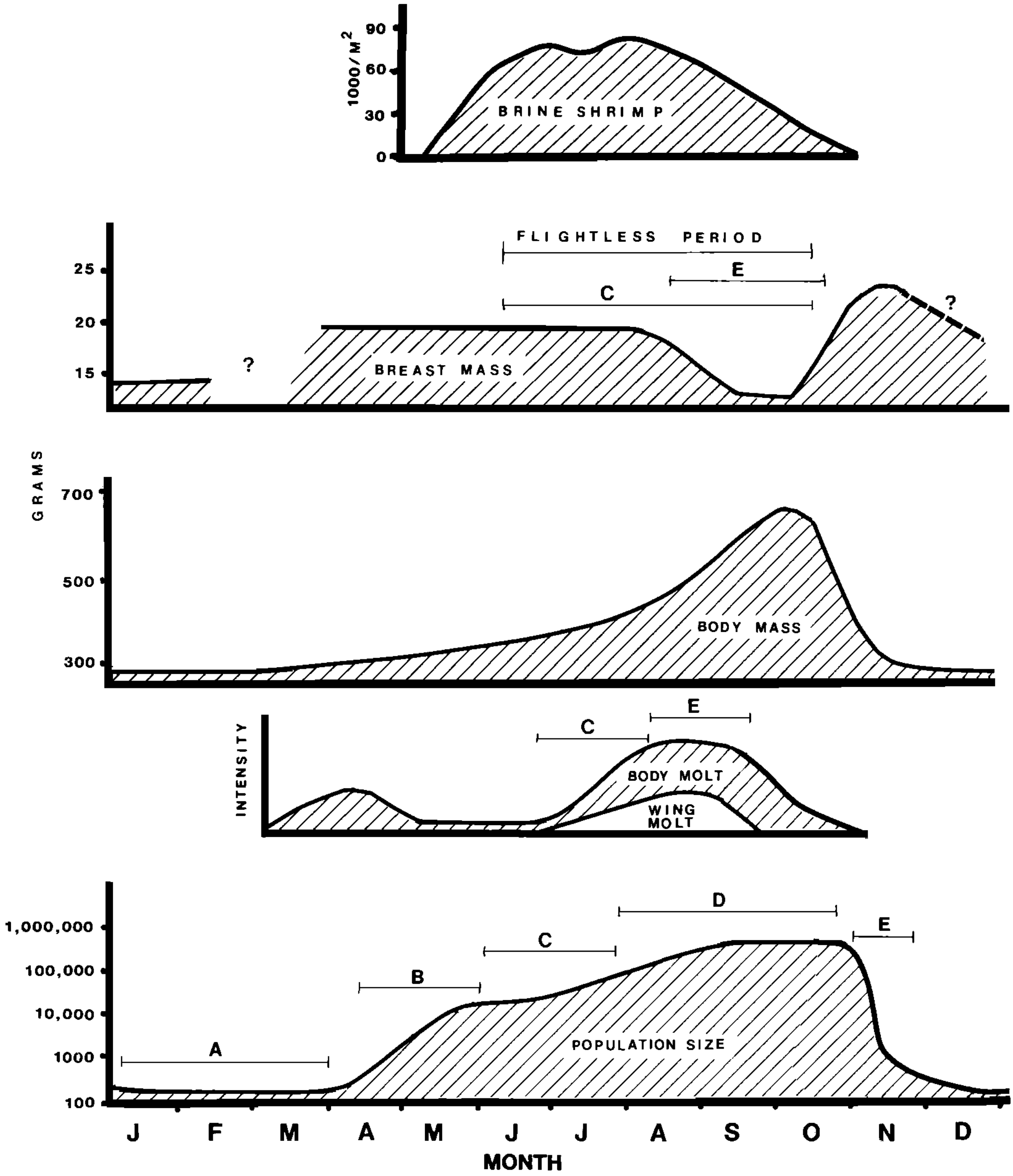


FIGURE 23. A synopsis of the major events in the annual cycle of Eared Grebes at Mono Lake, California. A, winter residents, B, spring migration, C, summering flock, D, staging period, E, departure.

tering grounds in southern California and the Gulf of California are not an annual event (D. Anderson, K. Nishikawa pers. comms.). Migration, however, is a regular risk for this species, and high mortality has been well documented among birds that have been downed by bad weather (e.g., Cottam 1929, Jehl and Bond 1983, Ryser 1985). Ironically, large-scale losses seem most likely in years like 1982 (see below) when food remains abundant late into the fall, as this entices grebes to linger into the period of winter storms. I suspect that catastrophic events are a major control on population size in this species (see also Fjeldså 1986).

MIGRATION

Departure from Mono Lake

Because Eared Grebes avoid flying and delay rebuilding their breast muscles until they have no alternative, they remain at Mono Lake until shrimp become too sparse to be exploited efficiently, i.e., at densities less than ca. 3000/m^2 (p. 00). In 1986, this occurred about 15 October and by the 28th 70% of the flock had emigrated. In the fall of 1987, an exceptionally late generation of brine shrimp allowed hundreds of thousands of grebes to remain at the lake as late as 31 January 1988.

Although some have contended that grebes leave Mono Lake "en masse" (e.g., Cooper et al. 1984, Lenz et al. 1986), the departure period actually extends over two or three weeks. Nightly departures of tens of thousands must occur, but have never been observed. Harsh weather had no obvious effect in stimulating departure. In mid-November 1983, for example, a storm with winds to 90 mph blasted the lake and dumped several feet of snow in the Sierra Nevada; yet, grebes remained in large numbers into early December.

Day length and gonadal hormones influence the timing of migration in birds. Other hormones probably affect "the metabolism of fat stores and responsiveness of the nervous system to environmental cues . . . [but] the possibility of direct neural simulation of migratory restlessness without endocrine metabolism should also be considered" (Meier and Fivizzani 1980). The Eared Grebe seems a good species in which to study endogenous and exogenous factors, because its departure from staging areas seems to be controlled entirely by the availability of food.

The timing of major aspects of the grebes' biology at Mono Lake is summarized in Figure 23.

OTHER STAGING AREAS

For a broader view of the grebes' postbreeding biology, my colleagues and I surveyed aquatic habitats in the Great Basin and Great Plains in late August and September 1985 and 1986, a time when many grebes would be expected to have arrived at staging areas. Despite extensive field work at saline lakes or other areas where grebes had been reported in the past, we encountered only 50,000 grebes in addition to the 500,000 estimated at Mono Lake in mid-September (Jehl and Chase unpubl.). They occurred at lakes of varied character, with large flocks (>1000) being mostly at saline lakes (Fig. 24). Major concentrations are summarized below.

Great Basin

Great Salt Lake has sometimes been the largest concentration point in North America; it is the only area other than Mono Lake where huge numbers of grebes may stage in fall migration. Grebe biology there is unstudied. Although thousands may be present in summer and early fall (e.g., 25,000–40,000 on 27 July 1987; D. Paul pers. comm.), the species' use of this lake as a major molting area remains inferential.

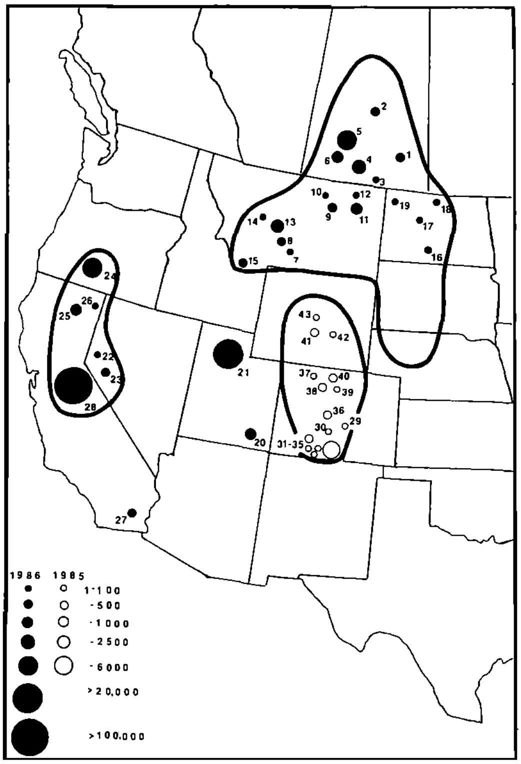


FIGURE 24. Localities at which Eared Grebes were encountered on surveys in August–October 1985 and 1986. Outlines show approximate limits of survey. Localities holding more than 1000 grebes are italicized. SASKATCHEWAN: (1) Southeastern Saskatchewan, (2) Southcentral Saskatchewan, (3) Coteau Lakes, (4) *Old Wives Lake,* (5) *Chaplin Lake,* (6) *Reed Lake.* MONTANA: (7) Halfbreed NWR, (8) Hailstone NWR, (9) Bowdoin NWR, (10) Nelson Lake, (11) Medicine Lake, (12) Westby Lake, (13) *Benton Lake,* (14) Freezeout Lake, (15) Red Rocks Lake NWR. NORTH DAKOTA: (16) Long Lake NWR, (17) Minot Sewage Lagoon, (18) Upper Souris NWR, (19) Lostwood NWR. UTAH: (20) Lake Powell, (21) *Great Salt Lake.* NEVADA: (22) Pyramid Lake, (23) Walker Lake. OREGON: (24) *Lake Abert;* CALIFORNIA: (25) *Eagle Lake,* (26) Middle Alkali Lake, (27) Salton Sea, (28) *Mono Lake.* COLORADO: (29) Lake Meredith, (30) Great Plains Res. System, (31) *San Luis Lake #1,* (32) *San Luis Lake #2,* (33) Monte Vista NWR, (34) Weatherall Prop., CO Div. Wildl., (35) San Luis Valley, (36) Antero Res., (37) Walden Lake, (38) Lake John Annex, (39) Delaney Buttes, (40) Arapaho NWR. WYOMING: (41) Pathfinder Res. and Bird Refuge, (42) Amoco Pond, Casper, (43) Bamforth Lake.

Access to Great Salt Lake is so limited that early Utah ornithologists (Behle 1958, Hayward et al. 1976), like their California counterparts at

TABLE 5
WINTER DISTRIBUTION OF EARED GREBES IN WESTERN NORTH AMERICA[a]

	1981–1982			1982–1983			1983–1984			1984–1985			1985–1986		
Area	Censuses	Total	%	Censuses	Total	%	Censuses	Total	%	Censuses	Total	%	Censuses	Total	%
British Columbia	31	47	0.1	32	15	0.0	33	10	0.0	38	30	0.1	33	21	0.0
Washington	26	185	0.6	28	133	0.3	27	91	0.5	30	179	0.8	32	171	0.4
Oregon	30	46	0.1	30	9	0.0	32	30	0.2	33	16	0.1	32	29	0.1
California	95	31,102	99.1	97	50,158[b]	99.7	100	16,841	99.2	98	22,762	9.0	100	39,905	99.4
(Salton Sea)[c]		(20,930)			(14,185)			(5622)			(3510)			(24,140)	
Total		31,380			50,315			16,972			22,978			40,126	

[a] Data from Christmas Bird Counts published in *American Birds,* Vols. 36–40; includes inland as well as coastal localities.

[b] Includes 30,000 at Mono Lake, where birds remained exceptionally late before migrating.

[c] South Salton Sea only.

Mono Lake, had little idea of grebe numbers. Aerial surveys on 20 September and 30 October 1982 revealed 1.7 and 1.4 million grebes on the south arm; the north arm was too salty to sustain invertebrates (Paul pers. comm.). In the next several years, the lake rose by 3 m, salinity in the south arm dropped from 120‰ to 35‰ and in the north arm from 270‰ to 160‰, which resulted in stunning changes in grebe abundance and distribution. On aerial surveys on 30 September 1985 and 6 October 1986, Paul and I encountered only 25,000 and 21,000 grebes, 97% on the *north* arm, which had recovered sufficiently to maintain a commercial brine shrimp fishery. Subsequent surveys later in the season, on 13 November 1986 and 7 October 1987, revealed over 100,000 and 130,000 grebes, respectively, again on the north arm (Paul pers. comm.).

From 1982 to 1986, 1500 to 2000 nonbreeding grebes summered at Lake Abert, in southeastern Oregon. Postbreeders arrived in early August, reached peak numbers of 5000 to 7000 by early September, and left by early October (K. Boula pers. comm., pers. obs.), when food disappears. On 15 September 1986 I counted 4960 grebes, whose departure had been delayed by several days of stormy weather. Although they were able to fly, they were also very hungry (see p. 18). Both adults and juveniles were present, but precise age ratios were indeterminable. Some adults were in worn breeding plumage; others had completed wing and much body molt.

The timing of fall migration at Lake Abert is similar to that at Malheur National Wildlife Refuge in east-central Oregon (Littlefield and Cornely 1985), where peak numbers for 31 autumns from 1944–1984 have varied from 300 to 10,000, with a mean of ca. 3100. In 1986, local saline lakes had freshened and the maximum count dropped to 20 (G. Ivey, C. D. Littlefield pers. comms.).

Great Plains

In 1985 and 1986, on surveys extending from Colorado and Nebraska to southern Saskatchewan, C. Chase III encountered large concentrations only at San Luis Lake #1, Alamosa Co., Colorado (4200), Chaplin Lake (5000), Old Wives Lake (3500), and Reed Lake, Saskatchewan (1000), and Benton Lake, Montana (2500). In the early 1980s, several thousand also occurred at Antero Reservoir, Colorado (Chase pers. comm.). At Colorado lakes some adults were in basic plumage and had completed wing molt.

WINTER RANGE

The species' main wintering areas are probably at the Salton Sea, where perhaps 1.5 million occur in mid-winter (R. McKernan pers. comm.), and the Gulf of California. The latter locality may hold several hundred thousand birds, mostly near islands in the central gulf where flocks of 5000 to 10,000 are often observed (D. Anderson, S. Wilbur, R. Schreiber pers. comms.). This leaves hundreds of thousands unaccounted for at that season. Very few winter in Sonora, either inland or on the coast of the Gulf of California or inland (S. Russell, G. Monson pers. comms.). Similarly, few are found on the Pacific coast of Baja California (Jehl pers. obs., Wilbur 1987) or of the U.S., with perhaps only several thousand occurring along the entire coast of California (Briggs et al. 1987). Monson (pers. comm.) estimated that 20,000–30,000 may winter in Arizona. In the Christmas Bird Counts of 1981–1982 through 1985–1986, the highest annual maximum was 50,315, recorded (inland as well as coastally) in British Columbia, Washington, Oregon, and California. In all years, over 99% were in California, with the majority often at the Salton Sea (Table 5), only a small part of which is censused.

Commercial salt works attract many grebes in migration, but few winter there: 8000 to 16,000 in south San Francisco Bay (Kelly pers. comm.); 500 to 1200 in San Diego Bay (E. Copper pers. comm.). The extensive salinas at Guerrero Negro, Baja California, are unstudied.

Prior to the early 1970s, 50,000 or more wintered on Lake Mead, Nevada, but the current flock is <10,000. Changing environmental conditions seem responsible, as Western Grebes (*Aechmophorus occidentalis*), formerly uncommon, now predominate. At nearby Lake Mohave, winter counts have remained at ~5000 (C. S. Lawson pers. comm.). Other major wintering areas inland are unknown. Lake Powell, Utah, has been suggested as being potentially important (Kingery 1984). Yet, aerial surveys by the Utah Dept. of Game and Fish on 24 November 1987 and 7–8 January 1988 revealed a total of three birds, and local game officials stated that significant numbers were never observed from 1984 to 1986 (Paul pers. comm.).

Banding recoveries suggest that many grebes winter in the interior of northern Mexico (Jehl and Yochem 1986). While no major concentration points are known (A. Phillips, R. Dickerman pers. comms.), there are numerous lakes in the states of Zacatecas, Mexico, Queretaro, Jalisco and coastal Colima that hold several hundred in winter (S. Howell pers. comm.).

MIGRATION ROUTES

Data from our field surveys, regional literature, banding recoveries (Jehl and Yochem 1986) and molt patterns (Storer and Jehl 1985) suggest that the autumnal migratory behavior of the grebes varies regionally. While general patterns seem evident, some important and perplexing details are unresolved.

In the northern Great Plains grebes disappear from breeding areas in mid-September (Chase pers. comm.). As in the Great Crested Grebe (Piersma 1987a), not all Eared Grebes undertake a molt migration to staging areas (Storer and Jehl 1985). Some, presumably from the eastern part of the range, evidently move early toward wintering areas in eastern Mexico and the Gulf Coast of the United States (Banks and Clapp 1987, Jehl and Yochem 1986), perhaps postponing wing molt until after they arrive. Others may molt on or near their breeding areas (e.g., Antero Reservoir, San Luis Lake, Colorado; see also Storer and Jehl 1985). The apparent lack of major staging areas east of the Rockies may be a consequence of the fresh water character of local lakes, which contain fish and therefore lack sufficient invertebrates to maintain large numbers of birds (cf. Hurlbert et al. 1986). They are also subject to early freezing, which would put flightless birds at risk.

Grebes from the western Great Plains, from as far east as Saskatchewan, evidently move southwestward toward Great Salt Lake. Mass downings in southern Utah and Nevada (p. 30) in early winter, as well as banding recoveries (Jehl and Yochem 1986), show that a large proportion then continues toward the Salton Sea and Gulf of California; some also winter in northern Mexico. Few move westward or stop at Mono Lake, because Eared Grebes winter in very small numbers on the Pacific coast, and because there is no evidence of a large influx at Mono Lake in late fall.

Mono Lake grebes are likely to be derived mainly from the western sector of the species' range. Nevertheless, the vast size of that flock suggests a broader origin, which is hinted at by a significant correlation ($P < .02$, Spearman test) between the peak numbers in fall from 1981–1987 and the number of ponds in the Prairie Provinces plus the north-central states (data from USFWS/CWS 1987). As grebes breed mostly on lakes, pond data can provide only a rough index to habitat availability in this large region. There was no correlation between grebe numbers and pond abundance when either the Canadian or U.S. conditions were examined singly. Thus, while these dates do not allow possible source areas for the migrants to be inferred more precisely, they may indicate that grebes are flexible in their use of breeding areas.

Source areas for the tens of thousands of migrants that arrive after mid-September are unknown. Because there is also a late influx at Great Salt Lake in some years (e.g., 1986), it follows that large numbers remain scattered through the interior until lakes and marshes freeze. Yocom et al. (1958) observed over 3000 at Lake Lenore, in eastern Washington, as late as 22 November.

I had long presumed that on leaving Mono Lake most grebes migrated directly to the Salton Sea or Gulf of California, with small numbers also moving to the Pacific coast (Jehl and Bond 1983, Jehl and Yochem 1986); these destinations are within the range of an overnight flight, and aquatic habitats in intervening deserts are too few and small to support more than a handful of birds. This "obvious" interpretation was challenged in 1986, when 745,000 grebes left Mono Lake by the first days of November and disappeared. By 11 November virtually none had appeared on the coast of southern California (pers. obs.) and no more than 60,000 were at the Salton Sea (R. McKernan aerial censuses). Not until 29 November—nearly a month after departure from Mono Lake—did large flocks, whose provenance is undeterminable, appear at the Sea (G. McCaskie pers. comm.). I cannot account for the grebes' disappearance. The most likely explanation is that they moved directly to the Gulf of California. If so, why did they by-pass the Salton Sea, a major wintering and spring staging area that lies along the same route?

WILSON'S PHALAROPE

Wilson's Phalarope is the largest and most terrestrial of the three species of phalaropes and the only one restricted to the New World. Its main breeding area is the prairie marshes of the northern United States and southwestern Canada (Fig. 25), where it prefers "larger bodies of alkaline water, which support a more abundant invertebrate fauna than small bodies of fresh water" (Howe 1975a:31). Recently, its range has expanded to include small and isolated breeding localities from the southern Yukon and Vancouver island to central Arizona in the west, and from James Bay, Quebec and Nova Scotia to Massachusetts in the east.

As with many other avian species, its breeding biology has been studied in impressive detail (e.g., Bent 1927; Höhn 1967; Johns 1969; Kagarise 1979; Howe 1975a, b; Murray 1983; Colwell 1986), but data from other seasons are largely lacking. Even such basic information as the location of the main wintering grounds has been a puzzle. Not until well into the 20th century did ornithologists in South America (e.g., Dabbene 1920, Wetmore 1927, Murphy 1936) realize that the species was locally common, and as late as the mid-1940s there was only one record for Chile (Johnson 1965). Blake (1977) reported its range from Peru south to Chubut Province, Argentina. Actually, only small flocks occur in coastal northern Argentina, once considered a major wintering area (Myers and Myers 1979), and no large concentrations have been reported farther south (Jehl pers. obs., Fjeldså in litt.), although it occurs through Patagonia to Tierra del Fuego (Humphrey et al. 1970, Jehl and Rumboll 1976, Devillers and Terschuren 1976).

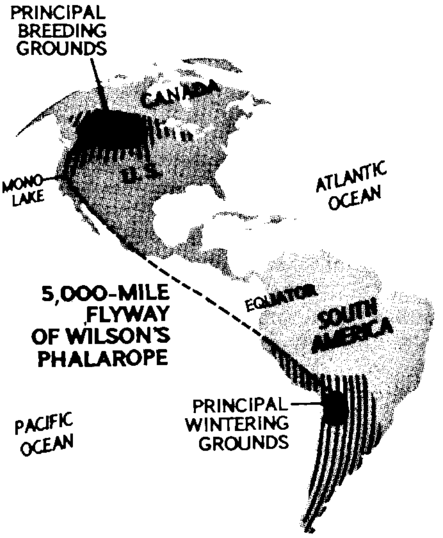


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FIGURE 25. Breeding (North America) and wintering (South America) ranges of Wilson's Phalaropes. Centers of abundance are solid-colored. Based on AOU (1957, 1983), Godfrey (1966), Blake (1977), Hurlbert et al. (1984), and Appendix IV.

It is now clear that Wilson's Phalarope inhabits highly saline lakes for much of the year, using those in western North America as staging areas in summer and those in South America as major wintering locales. The majority of the species winters along the Cordillera, from Cochabamba, Bolivia (17°30'S), to central Córdoba Province, Argentina (31°S). Hurlbert et al. (1984) found more than 500,000 in the puna of extreme southwestern Bolivia, at 4200–4500 m, and in adjacent regions of Chile and Argentina, usually in association with Chilean Flamingos (*Phoenicopterus chilensis*). The Argentine population also winters mostly at high elevations in the northwestern part of that country (J. P. Myers pers. comm.), including "quite sizeable numbers" at Lago de Pozuelos, Jujuy Province (J. Boswall pers. comm.), and in the Laguna Mar Chiquita and Rio Dulce regions of Córdoba Province, where up to 500,000 have been observed (Nores and Yzurieta 1980, Nores in litt. to S. Hurlbert). The northernmost wintering area of note may be Lago Alalay, near Cochabamba, Bolivia (3000–5000 birds; Dott 1985, J. V. Remsen pers. comm.).

This study of Wilson's Phalarope in the nonbreeding season is based largely on long-term

TABLE 6
Morphometrics of Wilson's Phalaropes from Mono Lake, California

	Male			Female		
Measurement	N	Range	Mean ± SD	N	Range	Mean ± SD
			Adults			
Exposed culmen (mm)	319	25.8–33.8	30.1 ± 1.2	100	30.2–36.1	33.1 ± 1.3
Wing (g)	318	115–132	121.2 ± 2.8	101	124–144	131.7 ± 3.3
Tarsus (mm)	317	27.3–37.0	31.6 ± 1.3	101	30.2–37.0	33.2 ± 1.2
Mass (g)	345	38–103	56.9 ± 10.0	138	52–122	75.6 ± 14.6
Fat free mass (g)	16	41.7–55.9	48.0 ± 4.1	14	51.2–63.8	59.2 ± 3.2
			Juveniles			
Exposed culmen (mm)	29	27.0–31.8	29.6 ± 1.2	21	30.0–34.9	32.8 ± 1.3
Wing (mm)	28	113–124	119.5 ± 3.0	21	125–134	129.4 ± 2.8
Tarsus (mm)	28	29.4–33.4	31.7 ± 1.0	21	30.0–36.0	33.6 ± 1.5
Mass (g)	33	41–66	49.6 ± 5.2	23	50–84	60.2 ± 7.6

research at Mono Lake, California, where tens of thousands congregate in early summer to prepare for their migration to South America a few weeks later (Jehl 1981). Only Great Salt Lake consistently maintains greater numbers at this phase of the annual cycle. These two lakes and a few other localities are destinations for a molt migration, a phenomenon well known in waterfowl but barely recognized in shorebirds (Jehl 1987b).

METHODS

Methods used in this study parallel those used in the grebe research. I conducted field work during the phalarope's entire fall migration period (mid-June to mid-September) from 1980 to 1987 and routinely made observations on behavior and ecology. In 1980 and 1981 I captured and banded several hundred migrants; these were weighed on a Pesola spring balance within one hour of capture and examined for molt and parasites. Some were color-marked to facilitate studies of their daily movements and length of stay. Unfortunately, the dyes used (picric acid, Rhodamine-B, "indelible" Magic Marker) were impermanent in lake water and usually washed out in 7–10 days, making it impossible to determine duration of residence directly.

Prior to completion of their body molt in late July, most adult phalaropes can be sexed by plumage characters and, in the hand, by size and weight, females being much larger than males (Table 6). Discriminant function analysis based on culmen, wing, and tarsus measurements allowed 95% of females and 98.5% of males to be sexed correctly, and by using a combination of size and plumage characters I was able to sex more than 99% of the captured adults. Juveniles could be differentiated from adults into late fall by retained feathers of the juvenal plumage and, sometimes, by coloration of soft parts (Jehl 1987b).

I determined the composition of the population at major phases of the migration by visually aging and sexing birds in all sectors of the lake. Supplementary data were obtained by photography. Data from diurnal roosts, which at times held the entire flock, were especially useful.

The most effective method of determining population size was to survey the entire lake from a small boat; indeed, this was essential in the latter half of the season, when birds spent much time offshore. Surveys required a half day or more. Because the lake is large and the birds are mobile, some omissions and duplications were unavoidable. From late June through mid-July, when molting heavily (Jehl 1987b), phalaropes roost in dense flocks along the shore, which facilitates censusing (frontispiece). In 1980, 1981, and 1982, these roosts were on the beach, so that numbers could be determined with good accuracy by pacing off the linear extent of the flock and counting the rows and ranks of birds in areas of different densities. Counts of birds flying to nocturnal roosts provided a further index to population size; simultaneous counts by several observers varied by less than 10%. These techniques produced replicable and consistent results, and I considered lakewide estimates to be accurate to within 25% of actual values. Detailed results of censuses are presented in Appendix III.

Throughout the study, but mainly in 1980 and 1981, I collected specimens in many parts of the lake for studies of feeding habits and energetics. I determined fat content on a few specimens using procedures modified from McNeil and Cadieux (1972) and Connell et al. (1960; see Ellis and Jehl MS).

To study daily and seasonal use of fresh water, I made direct observations at all sources of fresh water bordering the lake and used time-lapse motion picture photography (Super-8 mm) to document behavior at several major sites. Beached-bird censuses were made routinely in representative areas for mortality data (see p. 7).

To clarify migration routes my colleagues and I attempted to locate major concentration points in the western United States and Canada (Jehl et al. 1987), and I made brief comparative studies in several localities. Areas surveyed were chosen by consultation with local ornithologists and game managers, and by reference to regional reports in *American Birds*. At each area we estimated the size and composition of the population as precisely as possible. Information from other parts of the species' range was extracted from regional literature (Appendix IV) and museum collections (Appendix V).

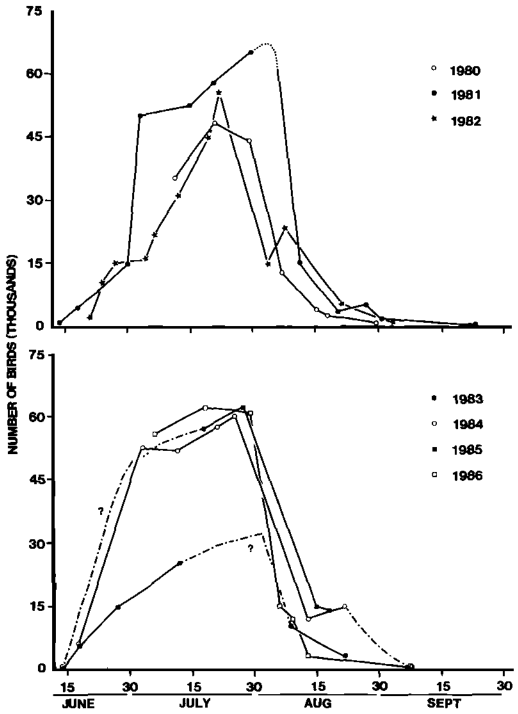

FIGURE 26. Numbers of Wilson's Phalaropes at Mono Lake, California, 1980–1986. Details in Appendix III.

THE ANNUAL CYCLE AT MONO LAKE

CHRONOLOGY

For most Wilson's Phalaropes the annual migration involves a round-trip flight of at least 11,000 miles, from the prairie marshes of the western Great Plains to the salt lakes of the central Andes. The southward movement starts earlier than that of other North American birds. As in other species of phalaropes, adult females begin to migrate shortly after laying. They may stay in the breeding areas for a few days—some produce a second clutch with a new male (Colwell 1986)—but by early June some are already en route toward staging areas and virtually all leave by late June. Adult males begin to leave nesting areas in early July, after the young have become independent, and disappear before the end of the month. Juveniles soon follow and are gone by the end of August (Höhn 1967; Johns 1969; Howe 1975a, b; Jehl et al. 1987).

During this study postbreeders began to arrive at Mono Lake in mid-June (earliest 12 June); nearly all were females, whose major influx occurred in the last week of June and first days of July. By 8 July, 50,000 migrants were often present (Fig. 26). Numbers increased through July with the appearance of adult males, most of which arrived between 7 and 25 July. Their numbers were supplemented by very small numbers of juveniles, which typically appeared about 20 July (earliest 12 July). Peak numbers for the year of 50,000–65,000 were realized in the last week of July, then dropped almost overnight to 15,000–20,000 when females departed, mostly between 31 July and 4 August. Usually numbers then declined slowly until the middle of the month, as adult males migrated. In some years (1982 and perhaps 1984) there seemed to be a second influx of males in early August, but data for that phase of the migration are too imprecise to confirm whether this was a regular event. By 1 September only a few hundred stragglers remained; nearly all were juveniles. Late dates were: adult female—14 August, adult male—4 September, juvenile—27 September.

COMPOSITION OF THE POPULATION

Because spatial and temporal differences in the distribution of adult females, adult males, and juveniles can be as pronounced as those associated with different species (see below), estimates throughout the season from all parts of the lake were needed to determine the composition of the population (Appendix III). Data from all years (1981 and 1982 are representative; Fig. 27) showed that adult females predominated, comprising 65–78% of the flock; adult males made up 27–34%, and juveniles less than 2%. These results contrasted with the relative abundance of birds caught for banding (N = 339, Fig. 28), which consisted primarily of adult males (69.8%) and juveniles (15.3%). The reason for this extreme bias is discussed below (p. 46).

SIZE OF THE MONO LAKE FLOCK

To estimate the total number of phalaropes that visit Mono Lake each year, one needs information on turnover rates. Several lines of evidence, including weight, molt, and distributional data from other localities showed that adult females remained continuously at Mono Lake from the time they arrived until they departed for South America in early August. Because very few lean (and therefore newly arrived) females were present after 1 August (p. 36), I infer that the total number of females probably did not exceed 10% more than their peak count. Similar reasoning applies to males, but because their arrival period was more protracted and might have involved a second influx in early August, I estimate their total at 30% greater than the maximum count. Juveniles gained little weight at Mono Lake (p. 44) and individuals probably passed through in a week or so (cf. Jehl 1963, 1979, 1986); I judge their total at 300% of their peak count. Given these assumptions, 77,950 Wilson's Phalaropes

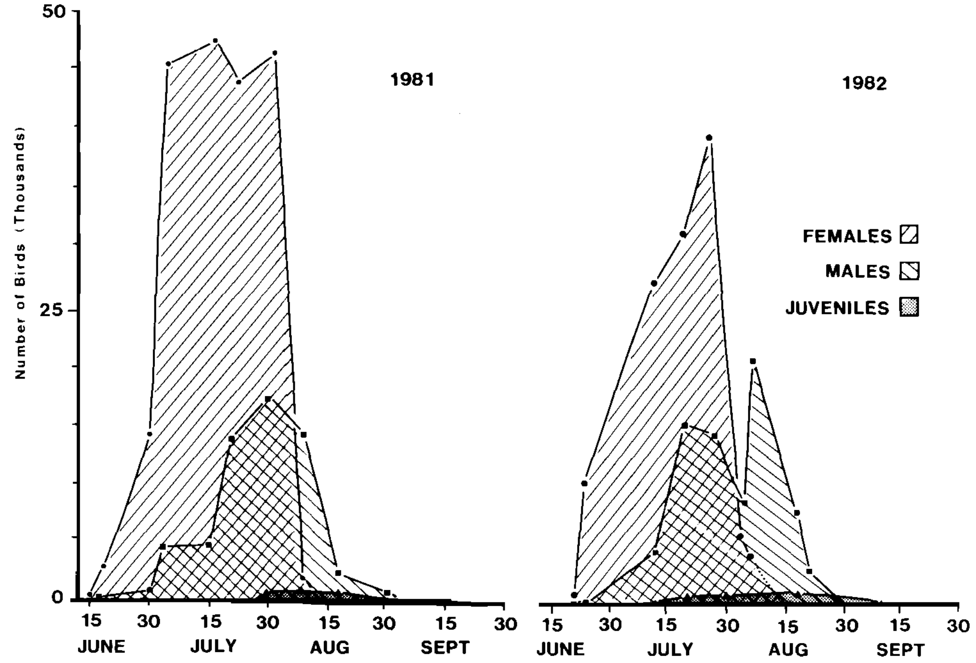

FIGURE 27. Composition of Wilson's Phalarope population at Mono Lake, California, 1981–1982. Details in Appendix III.

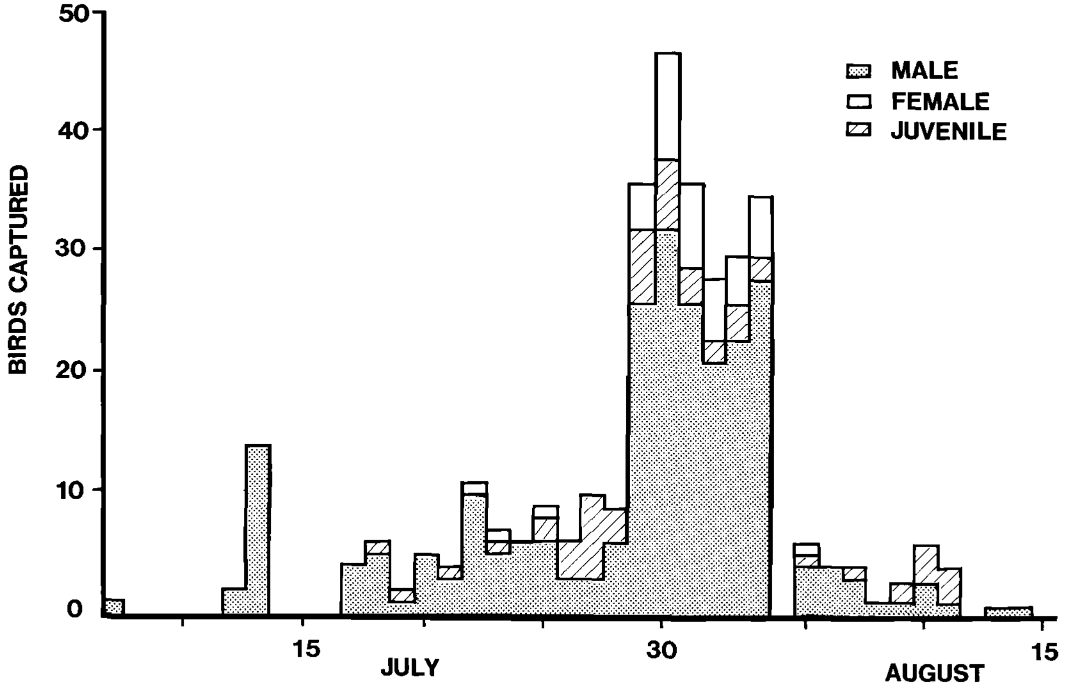

FIGURE 28. Composition of Wilson's Phalarope population at Mono Lake, California, in 1980–1981 as indicated by banding studies.

visited Mono Lake in 1981 (52,800 females, 22,750 males, 2400 juveniles) and 65,780 in 1982 (44,165 females, 19,965 males, 1650 juveniles); the totals are approximately 20% greater than the lakewide population in late July. These years were representative of conditions prevailing in 1980–1987 (Fig. 27).

ANNUAL VARIATION

Peak numbers approximated 50,000 to 65,000 except in 1983, when they probably did not exceed 30,000 to 35,000 individuals. Decreases were also noted in Red-necked Phalaropes and Eared Grebes in 1983 (p. 12), perhaps owing to the availability of other favorable sites.

Comparative data are meager. Estimates in 1976 (Winkler 1977) were mostly similar to those determined in this study, except for his somewhat higher count of 93,000 on 26 July. Whether this reflects differences in estimating procedures or the concentrating effect of a regional drought is unknown (cf. p. 12; Jehl 1986). Annual differences in the timing of migration (Fig. 26), and especially the late influx of males in some years, presumably reflect habitat conditions and the opportunity for polyandry on the breeding grounds.

BEHAVIOR

DISTRIBUTION AND DAILY MOVEMENTS

While at Mono Lake, adult phalaropes will replace much of their plumage and acquire large fat reserves. These two activities, which govern the birds' behavior, are mostly accomplished sequentially, although in slightly different ways by females and males.

For the first several weeks after arriving, females concentrated their activities on the eastern portion of the lake. In the morning they fed offshore for several hours, then began to move to diurnal roosts or, more precisely, molting stations on the beach (Fig. 29); in one typical roost I estimated 25,000 birds along 230 m of shoreline. By 12:00 most birds were ashore, and remained there until mid-afternoon, when they resumed feeding.

While roosting, phalaropes did little but preen, scratch, and wait for incoming feathers to grow; mostly they stood almost motionless, occasionally shifting a few feet to stretch. The flocks were eerily silent, the only sound being a soft gurgling that was almost imperceptible from a distance of 50 m.

By mid-July, when much body molt had been completed, the females' behavior changed. They began to disperse widely over the lake and spent much of the day offshore, and when they did come ashore it was in early morning and late afternoon to visit fresh water (p. 40). Roosting at night took place in large but diffuse flocks well offshore, from which the birds dispersed by 07:00 each morning.

Most females departed in the last days of July and the first days of August. A week or so before leaving, their behavior underwent further changes. On the lake they became hard to approach, and on shore were nervous when visiting water sources. In late afternoon and early evening, flocks of a few hundred might suddenly lift off and circle over the lake for several minutes, in premigratory behavior similar to that of other shorebirds. On many evenings the birds fed until nearly dark; on others they were still and appeared tense as night fell, perhaps signalling that departure was imminent.

When adult males arrived at Mono Lake in early July, they tended to remain somewhat segregated from females that were already present. Instead of joining flocks of females on the open lake, males centered their activities nearer shore, in shoal areas, or less often on mudflats, along the western and north-central shores, particularly near emergent tufa formations.

Differences in habitat use and distribution of adult males and females early in the season, though far from absolute, could be impressive, as several examples illustrate, each from a single locality in 1981:

1. On 2 July, 300 birds fed at the northwestern corner of the lake. Thirty-five were adult females, 32 of which were swimming or wading in shallow water and capturing food from the surface of the lake. Adult males (265) foraged exclusively on mudflats for adult brine flies.

2. On 23 July, the sex ratio of adults ashore was 42 females : 151 males; on the immediately-adjacent lake, and within 100 m of shore, it was 98 females:2 males.

3. Segregation is even evident on a finer scale: On 15 July, the composition of a flock on the upper beach adjacent to vegetation was 25 females : 89 males : 1 juvenile; at the waterline 9 females : 12 males; and on the lake 29 females : 11 males.

In late July, after males had replaced much of their plumage and begun to fatten they, too, moved well offshore and fed for much of the day. Even there sexual segregation could be pronounced. On 20 July 1981, males comprised 60–70% of a flock of 2000; 3 km away females comprised 90% of a similarly-sized flock. And on many occasions in late July, I saw flocks that seemed to be comprised entirely of females (maximum 8000).

Juveniles mostly frequented mudflat or nearshore habitats throughout their stay. Although

FIGURE 29. A shoreline roost of Wilson's Phalaropes, used for resting and molting at midday.

they occurred on the open lake, especially late in the season, they were not common there. Some additional data on the distribution of age and sex classes are presented in Appendix III.

Some color-marked males returned to the south Tufa site for several days (maximum 15), providing some evidence of regular daily movements. Others dispersed widely and were encountered on beaches 8–10 km away.

Hyperphagia

Several lines of evidence supported behavioral data that adults increased their foraging efforts and became hyperphagic after the molt was largely completed.

1. Weight increases (p. 43) were much greater in the post-molt period for each sex.

2. In a small sample, the average weight of stomach contents of adult females increased as the staging period progressed: 9 July—0.41 g; 28 July—0.77 g; 14 August—1.2 g (N = 2 in each case).

3. On 23 July 1981, feeding rates of two females that had largely completed molt and were taking brine shrimp from the surface of the lake were much faster than those of two partly molted males feeding alongside (0.73 vs. 0.44 pecks/sec).

Roosts

Sites of diurnal roosts remained fairly constant within each year, but varied considerably from year to year (Fig. 30). In 1980–1982 roosts formed along the eastern and northeastern shores, often in the proximity of very shallow lagoons bounded by an offshore bar. The beach in this area is broad and unvegetated, affording no concealment to predators. In 1983–1986 they were on shoals of emergent tufa in the north-central and western sectors.

The precise location of diurnal roosts was unpredictable from day to day, and seemed governed by the landing place of the first birds to come ashore, which flew back and forth until a likely spot was selected. New foci soon formed to either side, so that eventually the roost might be strung out over more than 2 km of shore.

The nocturnal roost in 1980 and 1981 was on the eastern half of the lake, probably near Simon's Spring; from 1982 through 1986 it was 2–3 km northeast of Rush Creek (Fig. 30). Birds arrived in late afternoon, typically in flocks of 10 to 500, and sometimes several thousand. In mid-July, the influx started about 17:45 and extended to 20:15, well after sunset. Later in the month, as the time of migratory departure neared,

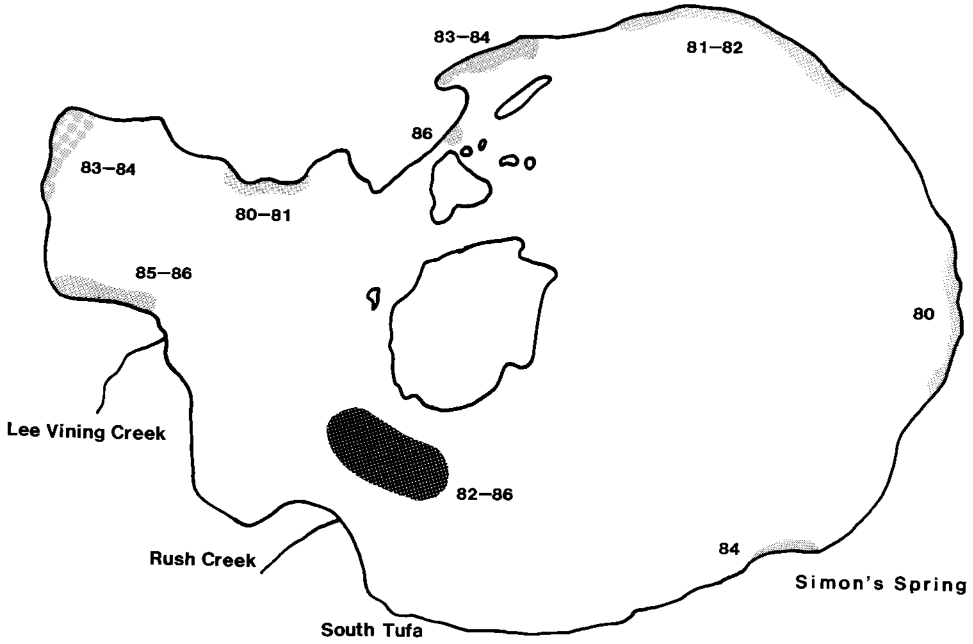

FIGURE 30. Location of diurnal roosts of Wilson's Phalaropes on the periphery of Mono Lake, California, 1980–1986, and of the nocturnal roost (cross-hatched) in mid-lake.

arrivals at the roost became progressively earlier (Fig. 31). In the morning dispersal began before sunrise and was mostly completed by 07:00.

I monitored movements to the roost from shoreline observation points. Although not all arriving birds were detectable, the counts provided a reasonable index to the total population. For example, on 22 July 1982, I counted 42,320 birds, 94% of the 45,000 indicated from an all-lake census. On 26 and 28 July 1983, I counted 16,500 and 18,000, respectively 66–72% of an estimated 25,000 lakewide. Once arrival patterns are understood, partial counts can also be instructive. On 24 July 1984, 22,700 birds arrived between 18:25 and 19:30; if 55% of the flock arrived in that interval (Fig. 31), the roost included 43,400 birds, or 75% of that estimated from boat censuses.

USE OF FRESH WATER

Through much of their sojourn, Wilson's Phalaropes made only sporadic visits to fresh water, and then only to sources immediately adjacent to the lake (cf. Red-necked Phalarope, Jehl 1986). Early in the season hundreds sometimes gathered at creek mouths or at mudflats near large seeps; the availability of sandbars for roosting rather than fresh water seemed to be the major attraction, however, because the number of birds visiting on any day was only a small fraction of the lakewide population.

Water use began to increase sharply in the last half of July, when phalaropes began to come ashore each morning and evening. At South Tufa in 1980–1981 birds arrived at 05:30–05:45, before sunrise. Landing 100–200 m off a small marshy area, they cautiously swam ashore and stood at the waterline for a few moments before rushing to drink and bathe, becoming uncharacteristically pushy and almost noisy in the process. After 15–30 sec, birds left the water and preened for several minutes, then resumed bathing, a sequence that might be repeated several times. The majority departed by 07:00. Visits resumed in late afternoon and sometimes continued until nearly dark.

Trips to fresh water became spectacular in the last days of July (Fig. 32), when 50,000 or more birds—mostly adult females—might assemble at a single source; in 1980–1982 this occurred at the South Tufa Park, and in 1983–1986 at the mouth of Rush Creek. Indeed, in 1980—1981 90% of the females that I captured at South Tufa were taken in the 6-day period coinciding with the major departure (29 July–3 August; Fig. 28). Mahoney and Jehl (1985a) interpreted the increased use of fresh water to temporary osmotic stress, resulting from the birds' unavoidable ingestion of lake water along with their prey during the hyperphagic phase. After females departed, mass visits to fresh water virtually ceased.

Although there are several sources of fresh water bordering Mono Lake, the largest and most

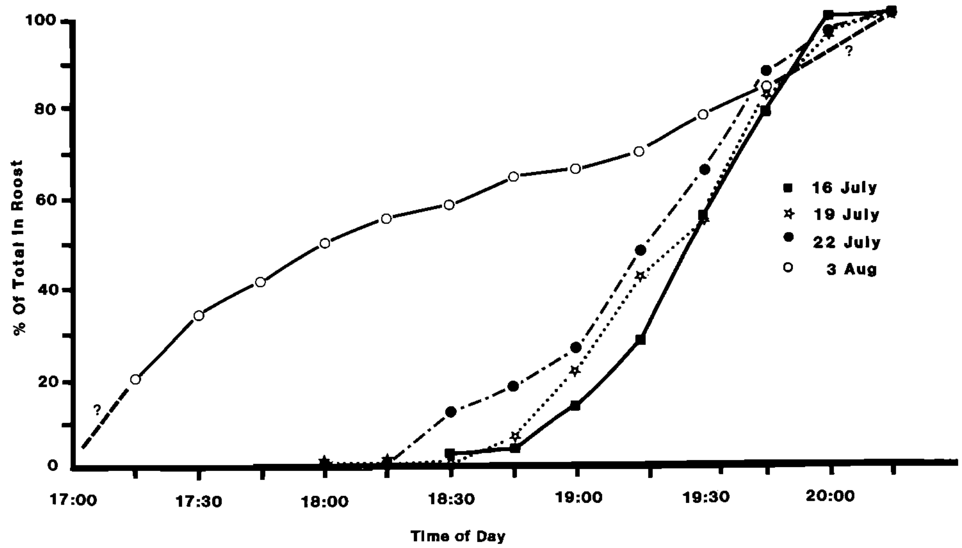

FIGURE 31. Schedule of Wilson's Phalaropes arriving at a nocturnal roost in 1982. Total counts were: 16 July, 33,755; 19 July, 31,985; 22 July, 42,320; 3 August, 10,847.

reliable are creek mouths, which are regularly occupied by loafing gulls. Phalaropes fear gulls, and on some evenings only a few dared to drink or bathe even momentarily. This was pronounced at Rush Creek, where phalaropes either had to land in a rapidly flowing stream, bathe 200–500 m offshore in the thin layer of fresh water that overlies the denser lake water, or go thirsty (Fig. 32). Their persistent attempts to gain access to water, despite danger, showed that the resource was highly desired, and that exclusion by gulls may be a problem.

INTERACTIONS

On the breeding grounds Wilson's Phalaropes sometimes feed on prey stirred up by Northern Shovelers and American Avocets (*Recurvirostra americana*) (Williams 1953, Siegfried and Batts 1972, Pinkowski 1981), and in wintering areas similar associations with Chilean Flamingos are common (Hurlbert et al. 1984). Commensal behavior was not observed at Mono Lake, although Red-necked Phalaropes occasionally robbed brine fly larvae spun to the surface by Wilson's (see Fig. 7 in Jehl 1986).

Intraspecific aggression was also unusual at Mono Lake. Sometimes when adult brine flies were scarce, males and juveniles defended short (35 m) stretches of beach—or even shorter spans (10 m) of the adjacent water—against conspecifics and sometimes Red-necked Phalaropes, though not Least Sandpipers (*Calidris minutilla*) or avocets. Rather surprisingly, in the few encounters that I saw between birds of different ages, juveniles always prevailed; this may be because the great bulk of fattening adults impaired their agility.

Territorial behavior is variable on the wintering grounds. Myers and Myers (1979) did not observe it in coastal Buenos Aires Province, Argentina, whereas I noted phalaropes defending shoreline territories against Magellanic Plovers (*Pluvianellus socialis*) in southern Patagonia (Jehl 1975).

FOOD AND FORAGING

FOOD

As noted above, brine shrimp are found throughout the lake and during the phalaropes' migration period occur in densities of 30,000 to 90,000/m^2 lakewide (Fig. 12). Brine flies are commonest near shore. Although both are consumed by phalaropes, differences in the distribution and behavior of male, female, and juvenile phalaropes resulted in important differences in the birds' diets. Throughout their stay adult females fed mainly on brine shrimp (Fig. 33), which occurred in 75% of the stomachs, whereas brine flies were found in 58%. In adult males the situation was reversed; brine flies occurred in 76% of samples, shrimp in 57%. Other food items occurred in trivial quantities. In a small sample juveniles fed only on brine flies. Gravel was present in most samples (Table 7).

Further analysis revealed seasonal changes in the adults' diet. For convenience I divided data into two groups, corresponding to the periods when adults were (1) molting heavily, and (2) gaining weight rapidly in preparation for migra-

FIGURE 32. Top, mass movements of phalaropes to fresh water. Bottom, flock of phalaropes unwilling to land at Rush Creek delta when California Gulls are present.

tion; for females the division point was 20 July, for males 31 July. In each sex the percentage of shrimp by volume increased in the latter part of the season, females from 60.3% to 78.6%, males from 35.4% to 43.1%. Although these shifts were not statistically significant (χ^2 test) because of the great variability among samples, they paralleled behavioral data showing the phalaropes' increasing use of offshore habitats, and I have no doubt of their biological reality. In each half of the season shrimp comprised a greater percentage of the diet of females than of males. Overall, shrimp comprised 66% by volume of prey taken by females vs 38% by males ($\chi^2 = 7.59$, $P < .01$).

While the sample sizes in these studies were large enough to show obvious trends, the data were unavoidably biased by sampling procedures and because brine flies are more resistant to digestion (Winkler and Cooper 1986). Thus, I suspect that the total contribution of brine shrimp

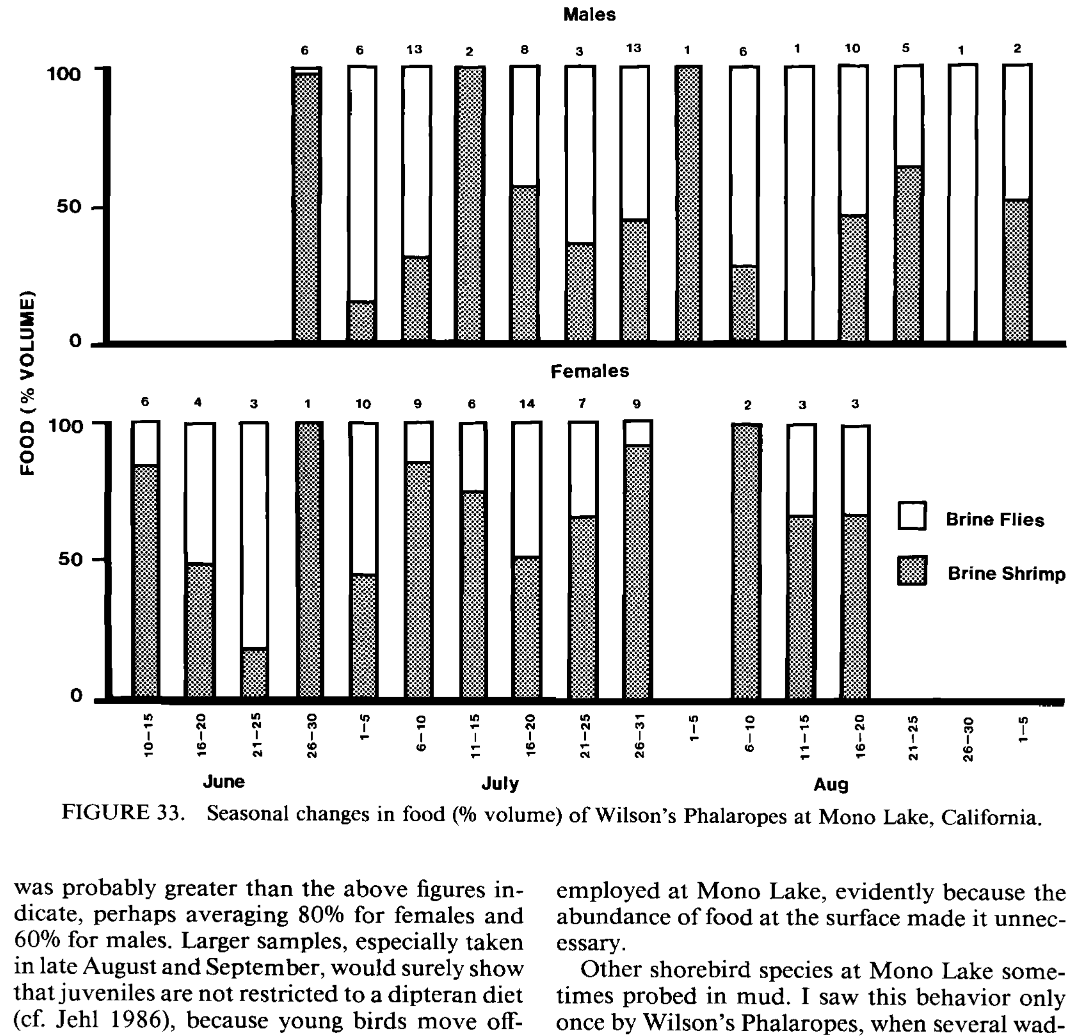

FIGURE 33. Seasonal changes in food (% volume) of Wilson's Phalaropes at Mono Lake, California.

was probably greater than the above figures indicate, perhaps averaging 80% for females and 60% for males. Larger samples, especially taken in late August and September, would surely show that juveniles are not restricted to a dipteran diet (cf. Jehl 1986), because young birds move offshore at that stage of the migration. Previous findings that brine flies comprised 93% of this species' diet at Mono Lake (Winkler 1977) were based on an inadequate and biased sample (probably all juveniles) taken in shoreline habitats and are not representative.

Foraging Behavior

Phalaropes employed several foraging methods, whose importance varied by age, sex, and phase of migration. All birds swam leisurely and pecked shrimp or larval flies from the upper few millimeters of the lake and speared adult flies resting on the lake; females used these techniques predominantly. By contrast, males and juveniles often ran along the shore to catch flies or, less commonly, stood in one spot and jumped vertically to catch those flying by (Fig. 34). Spinning to stir food to the surface, which is an important foraging technique in some localities, was rarely employed at Mono Lake, evidently because the abundance of food at the surface made it unnecessary.

Other shorebird species at Mono Lake sometimes probed in mud. I saw this behavior only once by Wilson's Phalaropes, when several waded in the shallows and swept their bills laterally through watery mud in the manner of avocets. Prey was not determined.

MASS

Adult females collected on breeding grounds in the United States in May and June average 61.2 g (range 49.8–70.7 g, N = 12; data from museum specimens); those from Alberta in May to mid-July average 68.1 g (range 55-85 g, N = 53; Höhn 1967). Adult males from those areas average 47.3 g (range 41.5–52.7 g, N = 14) and 50.2 g (range 30–64, N = 100), respectively. Evidently neither sex accumulates much fat before departing breeding areas.

Adults arriving at Mono Lake had few or no fat reserves: females averaged 62 g, or 2.8 g more than fat-free; arrival and fat-free masses of males averaged 48 g (Table 6). Over the next 35–40 days both sexes became incredibly fat (Fig. 35),

TABLE 7
STOMACH CONTENTS OF WILSON'S PHALAROPES FROM MONO LAKE, CALIFORNIA, 1980–1986

		Number and percentage of stomachs containing prey							
		Brine shrimp		Brine flies		Seed/plant[a]		Gravel[a]	
Age/sex	N	N	%	N	%	N	%	N	%
Adult females	77	58	75.3	45	58.4	6	12.5	44	91.6
Adult males	77	44	57.1	59	76.6	6	10.7	46	82.1
Juveniles	7			7	100			4	100

[a] Based on 1980–1981 data only.

more than doubling their bulk. Most of the increase occurred in the last half of the season (2.0 g/day on a population basis), when birds were hyperphagic, rather than in the first several weeks when they were molting and spending much time in roosts (~0.4 g/day) (Fig. 36). By early August, females weighing 100 g were common (maximum 123, 14 August), and by mid-August many males exceeded 90 g (maximum 103 g, 28 August).

FIGURE 34. Behavior of Wilson's Phalaropes foraging for adult brine flies. Top, spearing on the surface of the lake. Middle, chasing on mudflats. Bottom, plucking from air.

Juveniles were also thin on arrival and never attained the great weights characteristic of premigratory adults (Fig. 36; Table 6).

Weights of adults from the wintering grounds averaged less than fat-free weights at Mono Lake: eight females taken in South America between November and January averaged 56.3 g (range 46–62 g); 13 males, from September to January, averaged 45.0 g (range 35–56 g). As most of these birds probably could not have been newly arrived, emaciated migrants, it appears that phalaropes maintain lower protein reserves on wintering grounds than on breeding grounds (cf. Davidson et al. 1986, Dick et al. 1987), or increase muscle mass prior to migrating (Fry et al. 1972, Marsh and Storer 1981), or both.

Weights of juveniles (unsexed) from elsewhere in the United States are similar to those from Mono Lake ($\bar{X}$ = 59.4 g, range 43–87 g, N = 31), whereas those from Baja California in mid-August ($\bar{X}$ = 36.4, range 35.2–37.3 g, N = 4) and Peru and Paraguay in September ($\bar{X}$ = 43.8, range 31–54 g, N = 7) were lighter.

FIGURE 35. Obese adult females shortly before departure in late July.

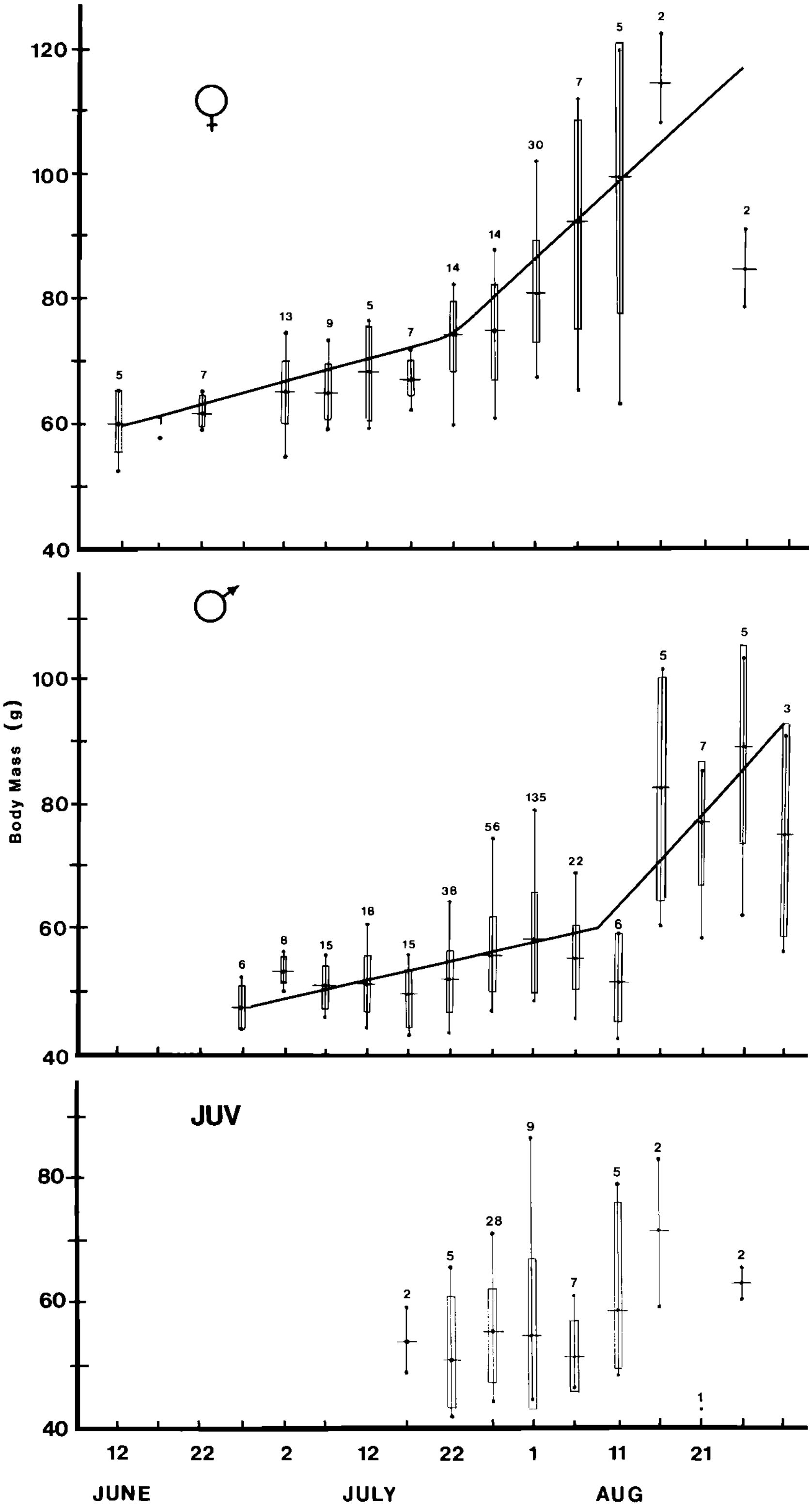

FIGURE 36. Body mass (range, mean ± 1 SD) of adult females, adult males, and juvenile Wilson's Phalaropes. Lines are fitted by eye.

SAMPLING

Weight data from Mono Lake were mostly derived from birds captured for banding. This resulted in skewed sex samples because of the males' preference for shoreline habitats, as well as in biased weight data. When phalaropes fatten they become less agile. Indeed, each year a few become so obese that they cannot fly and can be plucked from the lake with a dip net. Fat birds that came ashore could barely stagger across the mudflats and, consequently, did not wander into traps. As a result of these pre-departure weight changes, phalaropes became increasingly aquatic as the season progressed and shoreline samples, always biased in favor of males, became dominated by relatively light individuals of either sex and by juveniles. Banding became ineffective in early August, so that after 10 August most data were obtained from birds collected on the open lake. Wary at this phase of their stay, most flush well beyond shotgun range; yet, very heavy birds are clearly reluctant to fly and thus may be sampled disporportionately. For further discussion of potential bias in weight data see Pienkowski and Evans (1984:107).

MOLT

The prebasic molt, one of the two events that dominates the behavior of adult phalaropes at staging areas, is accomplished with extraordinary speed and may match the minimum duration of any bird species. Within 32–40 days adult females can replace the entire body plumage, the rectrices, and up to six primaries and their associated coverts. Feathers on the proximal part of the wing and the unmolted primaries are not replaced until after the birds arrive in wintering areas (for a detailed discussion see Jehl 1987b). This rapid molt is made possible by the superabundance of invertebrate prey; at its peak birds can be replacing 60–80% of the feathers in a given tract. Inevitably their insulation is impaired, which may account for their habit of spending long hours in roosts until much of the molt is accomplished.

Although males arrive later at staging areas, they are still able to replace nearly as much of the plumage as females, because they begin to molt before leaving breeding grounds. In juveniles molt is much less intensive, and flight feathers and much of the body plumage are not replaced until after birds reach winter quarters.

MORTALITY

Mortality at Mono Lake was barely detectable. Only two phalaropes were found in six seasons (1981–1986), despite intensive beached bird censuses (53, covering 516 km) from early June through early September 1981–1984. Losses to predators were trivial. Coyotes cannot capture healthy phalaropes, and avian predators (p. 29) were too rare to pose a threat, although Prairie Falcons, which are resident, and Northern Harriers (*Circus cyaneus*), which appear in the first week of August, probably captured a few each year. The only attack I witnessed, by a harrier on a swimming phalarope, was unsuccessful.

Phalaropes panicked if Great Horned Owls flushed nearby but ignored those sitting in the open. Indeed, hundreds fed daily at the base of a tufa tower where several owls roosted in plain sight only 10 m overhead. Several owl roosts and nests, and many pellets, that I investigated had no evidence of phalarope remains.

As with other birds at Mono Lake, the phalaropes were almost free from external parasites (Winkler 1977, Jehl 1986, see p. 29 above); evidently the alkaline water is inimical to their survival. In casual observations, I noted a single feather louse on only three of over 200 adults processed in 1981 (each of these birds was newly arrived), whereas in a sample of 41 juveniles I found a single louse on one, three on another, and dozens on a third. The greater frequency on juveniles reflects their shoreline feeding habits and general avoidance of highly saline (=open lake) habitats.

MIGRATION

DEPARTURE FROM MONO LAKE

Departures of 10,000 or more birds, mostly females, evidently occurred almost daily in the first several days of August, but none was witnessed, probably because they took place at night. Essentially all adults departed by 18 August. Winkler (1977) reported flocks of 200 to 750 flying SSE at dusk on several dates in August 1976; and on 5 August 1981 at Bridgeport Reservoir I watched 400 leave at 14:30 and disappear to the southeast.

Although southward flights of shorebirds are often associated with the passage of cold fronts and tail winds (Richardson 1979), phalarope departures seemed to occur in periods of stable weather, and after dark, when strong afternoon winds had abated. Such local conditions might be advantageous to very heavily wing-loaded birds embarking on a long journey. Major aspects of the phalaropes' activities at Mono Lake are summarized in Figure 37.

CONCENTRATION POINTS

To better understand fall migration in North America, I made observations at Lake Abert, Oregon, and Great Salt Lake, Utah, in several years. And in late June–early July 1986, late June–

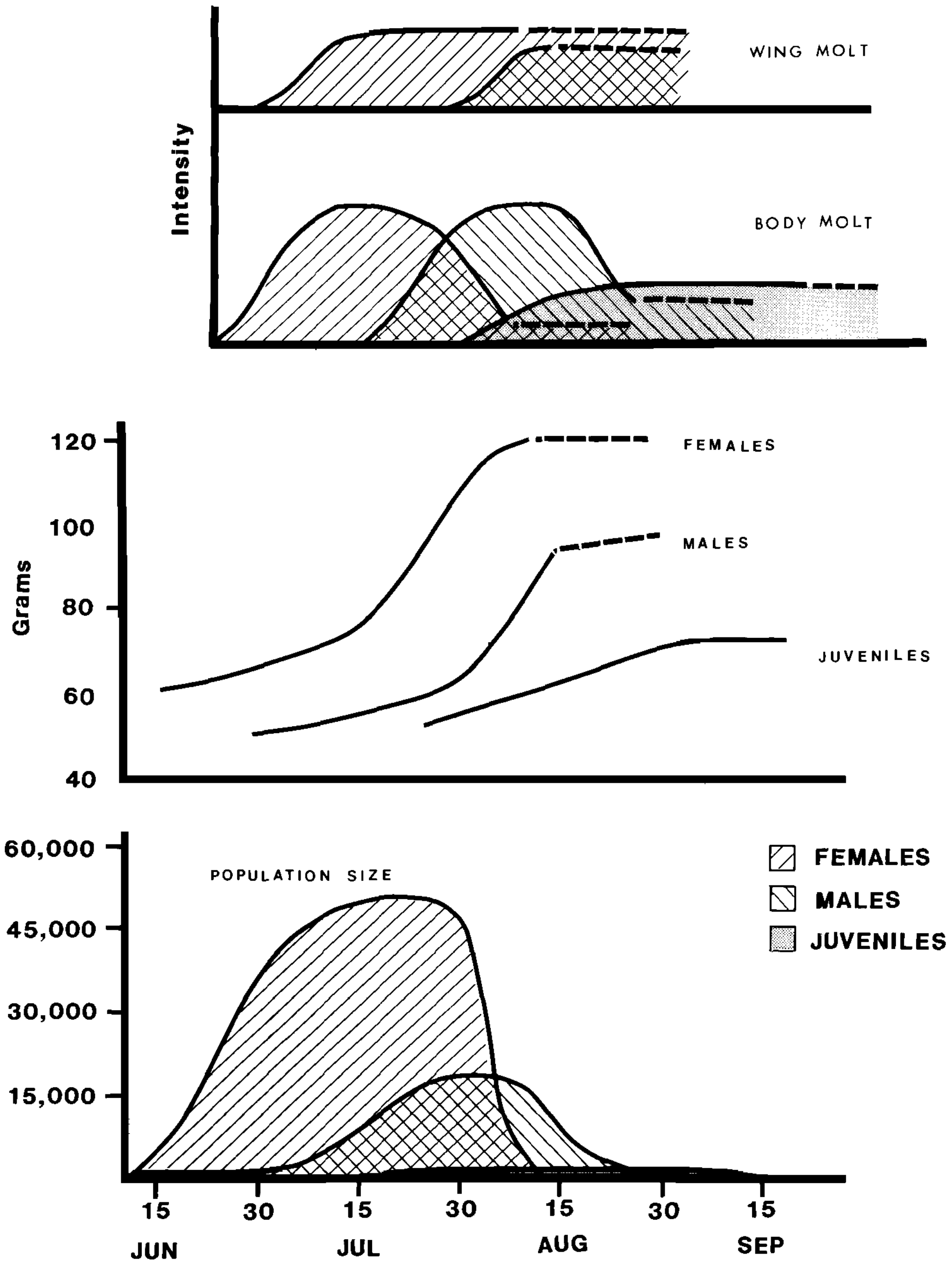

FIGURE 37. A synopsis of the major events in the annual cycle of Wilson's Phalaropes at Mono Lake, California.

early July 1987, and mid-July–early August 1987, my colleagues and I (Jehl et al. 1987, Jehl and Chase, unpubl.) sought other concentration points in the western United States and southern Canada. These surveys were done in as brief a period as possible to minimize the possibility of duplicate counts arising from movements between staging areas. Localities holding more than 1000 individuals (Table 8, Figs. 38, 39), along with information on areas that have sometimes held significant concentrations are discussed below. With one exception (American Falls Reservoir, Idaho), these were at saline or alkaline lakes that lacked fish.

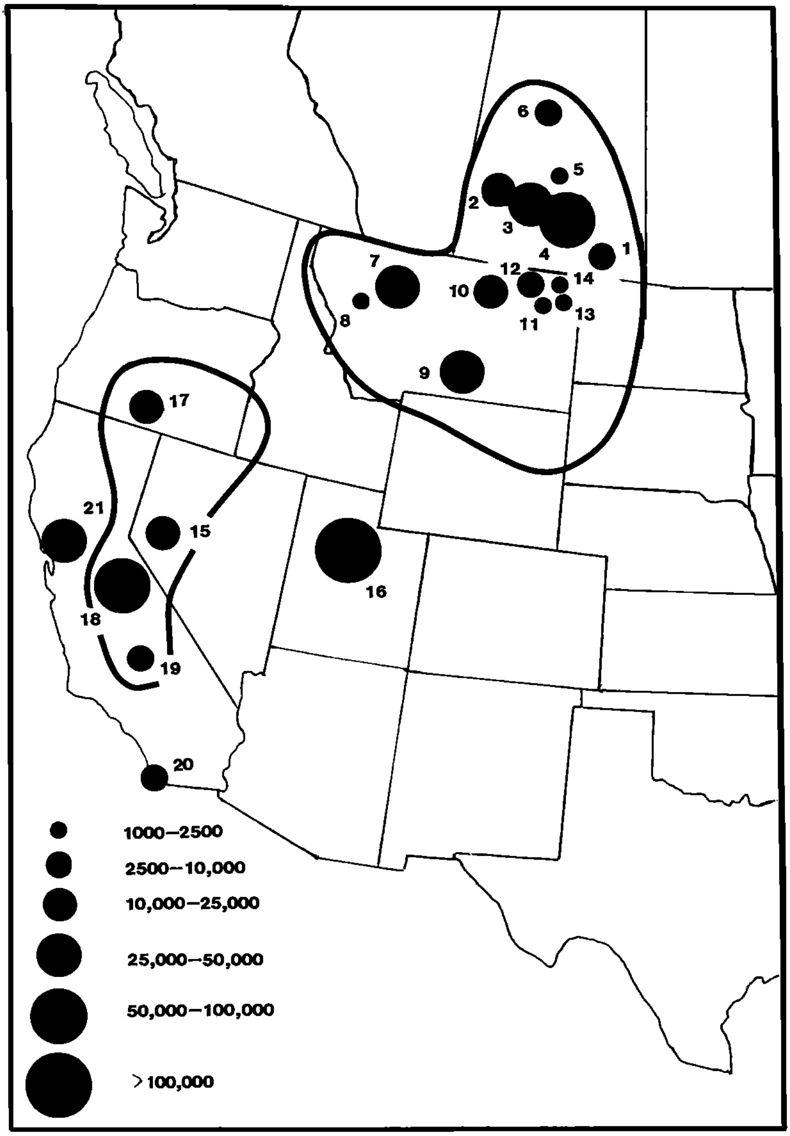

FIGURE 38. Localities at which >1000 Wilson's Phalaropes were encountered on surveys in July 1986. Outlines show approximate limits of major surveys. SASKATCHEWAN: (1) E. Coteau Lake, (2) Reed Lake, (3) Chaplin Lake, (4) Old Wives Lake, (5) Last Mountain Lake, (6) Big Quill Lake. MONTANA: (7) Benton Lake NWR, (8) Freezeout Lake State Wildl. Area, (9) Big Lake, (10) Bowdoin NWR/Medicine Lake NWR, (11) Katy's Lake, (12) Round Lake, (13) Brush Lake, (14) Salt Lake. NEVADA: (15) Stillwater NWR. UTAH: (16) Great Salt Lake. OREGON: (17) Lake Abert. CALIFORNIA: (18) Mono Lake, (19) Tulare Lake, (20) San Diego Bay, (21) San Francisco Bay.

California

Thousands of adult Wilson's Phalaropes occur and doubtless stage at commercial salt works in San Francisco Bay and San Diego Bay; peak numbers approximate 40,000 and 10,000, respectively (P. Kelly, G. McCaskie pers. comms.). On 20 July 1986 the San Diego flock seemed to be composed entirely of females.

Agricultural runoff ponds in the Tulare Lake area, Kern County, were constructed in 1981, and by 1984 had become important habitats for many species of birds. In mid-July 1985, 20,000–30,000 phalaropes were present (M. Heindel pers. comm.), and on 19 July 1986 I counted 6000, 95% of which were molting and fattening females. Sewage ponds near Lancaster also attract several thousand birds in some years (e.g., 4100

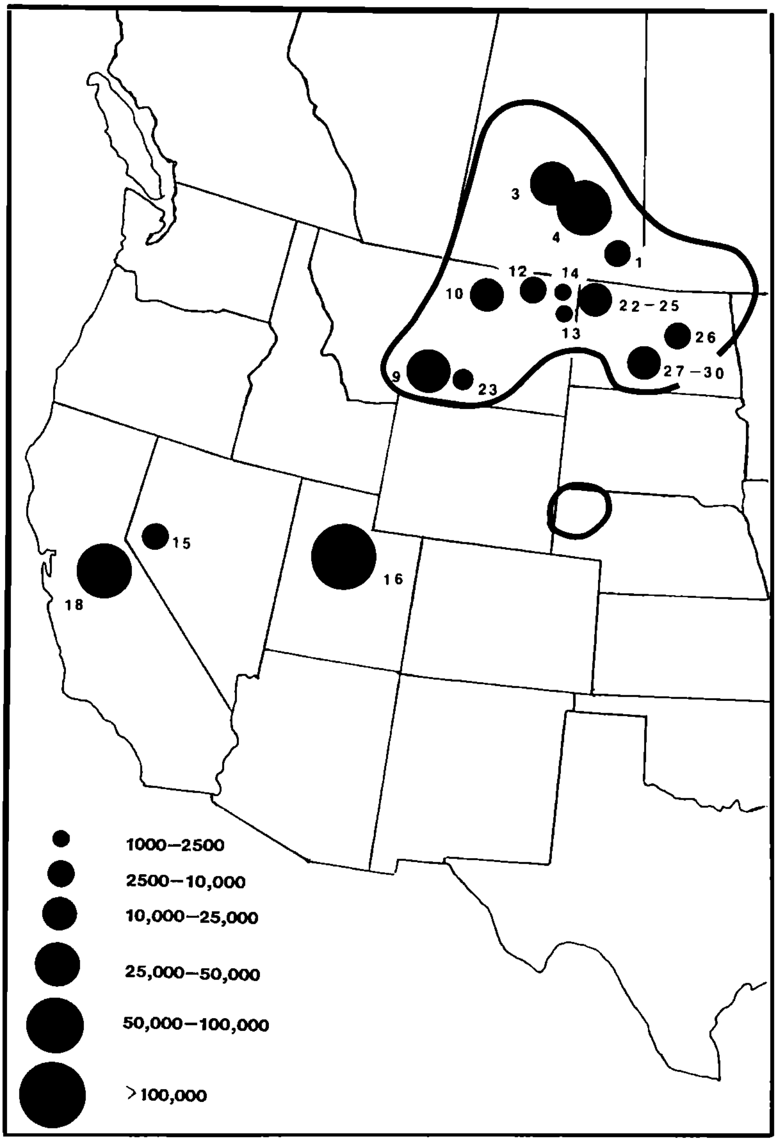

FIGURE 39. Localities at which >1000 Wilson's Phalaropes were encountered on surveys in July 1987. Outlines show approximate limits of major surveys. SASKATCHEWAN: (1) E. Coteau Lake, (3) Chaplin Lake, (4) Old Wives Lake. MONTANA: (9) Big Lake, (10) Bowdoin NWR/Medicine Lake NWR, (12) Round Lake, (13) Brush Lake, (14) Salt Lake, (22) Lake So. of Westby, (23) Half Breed NWR. NORTH DAKOTA: (24) Divide Co. lakes, (25) Miller Lake, (26) Stump Lake, (27) Cranberry Lake, (28) Horsehead Lake, (29) Peterson Lake, (30) Kidder Co. lakes. NEVADA: (15) Stillwater NWR. UTAH: (16) Great Salt Lake. CALIFORNIA: (18) Mono Lake.

adults on 17 July 1981; K. Garrett pers. comm.). The Salton Sea, surprisingly, is not a staging area, probably because zooplankters there are very small (<300 μm; S. Hurlbert pers. comm.).

Oregon

Lake Abert, in south-central Oregon, is a major concentration point. On 15 July 1982, I saw 60,000–70,000, and in 1981 the flock may have been more than twice as large (K. Boula, S. Denny pers. comms.). From 1983–1986 peak numbers were much lower (6000–12,000, Appendix III, K. Boula pers. comm.), evidently because prey populations declined as the lake freshened. Numbers at Lake Abert have sometimes far surpassed those at Mono Lake. Quantitative com-

TABLE 8
SIZE AND COMPOSITION OF WILSON'S PHALAROPE FLOCKS OBSERVED ON SURVEYS IN THE WESTERN UNITED STATES AND SOUTHERN CANADA IN 1986 AND 1987[a]

Locality	Date	N counted	% female	% male	% juv.
Saskatchewan					
(1)[b] E. Coteau Lake	late June 1986	6000	100		
	10 July 1986	2000		100	
	19 June 1987	6600	80		
	21 July 1987	30,000		95	
(2) Reed Lake	11 July 1986	25,000	10	90	
(3) Chaplin Lake	11 July 1986	35,000		95	
	20 June 1987	4000	65		
	22 July 1987	7300		95	
(4) Old Wives Lake	13 July 1986	51,500			
	21 June 1987	14,000	75		
	23 July 1987	12,500		90	
(5) Last Mountain Lake	13 July 1986	1500		95	
(6) Big Quill Lake	17–19 July 1986	3000		90	
Montana					
(7) Benton Lake NWR	3 June 1986	20,000	100		
	15, 22 July 1986	2000		85	15
(8) Feezeout Lake State Wildl. Area	21 July 1986	1500	5	90	5
(9) Big Lake	4–5 July 1986	40,000	2	98	
	22 July 1986	40,000	92		8
	17 June 1987	3000	75		
	18 July 1987	17,000		98	
(10) Bowdoin NWR/Medicine Lake NWR	7 July 1986	11,250		95	
	late June 1987	"thousands"			
	2–7 Aug 1987	28–33,000		100	
(11) Katy's Lake	8–9 July 1986	1000	10	90	
(12) Round Lake	8–9 July 1986	2700			
	23 June 1987	2300	80		
(13) Brush Lake	8–9 July 1986	1000			
	23 June 1987	1000	85		
(14) Salt Lake	8–9 July 1986	2500	5	90	5
	23 June 1987	1500	80		
Nevada					
(15) Stillwater NWR	7 July 1986	20,000			
	9 July 1986	11,300	60	34	6
	2 July 1987	67,000			
	28 July 1987	42,000			
Utah					
(16) Great Salt Lake	25 July 1986	387,000			
	7 July 1987	159,000			
	27 July 1987	193,770			
Oregon					
(17) Lake Abert	10 July 1986	11,825	64	33	4
California					
(18) Mono Lake	5 July 1986	56,320			
	25–26 July 1987	51,400			
(19) Tulare Lake	19 July 1986	6000	95	4	1
(20) San Diego Bay	20 July 1986	5000–10,000	100		
(21) San Francisco Bay	July 1986[c]		40,000		
(22) Lake So. of Westby	2 July 1987	8000	85		
	20 July 1987	1100		100	
(23) Half Breed NWR	17 July 1987	4200		80	20
North Dakota					
(24) Divide Co. lakes	22 June 1987	2100	50		
	20 July 1987	2450		90	

TABLE 8
CONTINUED

Locality	Date	N counted	% female	% male	% juv.
(25) Miller Lake	22 June 1987	3600	85		
	1 July 1987	5800	90		
	20 July 1987	7560		95	
(26) Stump Lake	25 June 1987	3250	95		
(27) Cranberry Lake	26 June 1987	1215	95		
(28) Horsehead Lake	27 June 1987	10,300	95		
	28 July 1987	13,500		85	10
(29) Peterson Lake	28 July 1987	1000		90	
(30) Kidder Co. lakes	28 June 1987	3500	100		
	26–28 July 1987	3760		90	

[a] Data from Jehl et al. 1987 and Jehl and Chase unpubl. and restricted to localities holding >1000 individuals. Extent of areas surveyed shown in Figures 38 and 39.

[b] Numbered lakes are shown in Figures 38 and 39.

[c] Average annual peak (P. Kelly pers. comm.).

parisons provide an incomplete picture, however, because the composition of the population is different: males predominate (~65%) and juveniles are also more prevalent than at Mono Lake (Appendix III). These differences are reflected in migration schedules. Even though Lake Abert is 640 km north of Mono Lake, peak numbers are reached slightly later, in the first week of August (Boula 1986), as would be expected in a flock dominated by adult males.

In some years a few thousand phalaropes have congregated at Malheur National Wildlife Refuge; Littlefield and Paullin (1976) reported nearly 18,000 in mid-July 1976. No concentrations occurred in 1986, when saline lakes in that area had freshened.

Nevada

On 7–9 July 1986, aerial surveys revealed 12,000–20,000 phalaropes at Stillwater National Wildlife Refuge, near Fallon, Nevada (S. Thompson pers. comm.). Ground studies (Jehl pers. obs.) indicated that 60% were adult females (molting and already fattening), 34% adult males, and 6% juveniles. Much larger numbers occurred there in 1987 (62,000 in early July and 42,000 at the end of that month). Indeed, in early July numbers exceeded those at Mono Lake.

Utah

Great Salt Lake is the largest staging area for Wilson's Phalaropes in the world. Although some early estimates "have placed their numbers in the millions" (N. Nelson pers. comm. to D. Paul), aerial surveys in late July 1982, which were the first attempt to quantify numbers, indicated peak counts of 400,000–500,000. Ecological changes associated with the lake's subsequent rise in the 1980s resulted in major distributional changes. As with the grebes (p. 32), in 1982 virtually all phalaropes were on the south arm; the north arm was too salty to sustain invertebrates. By 1986 the south arm had freshened too greatly to be attractive, but the north arm was rejuvenated and held nearly all of the flock of 387,000. The same was true in 1987, when peak numbers in late July reached 194,000.

There is little information about composition. On 13 July 1982 Paul estimated that 95–98% of a group of 118,000 were females; nearby 80–90% of 5700 others were males. The phenology of the migration, particularly the massive departure of birds in early August, suggests that as at Mono Lake adult females predominate and juveniles comprise a small fraction of the total.

Idaho

The only reported concentration point in this state is American Falls Reservoir, a fresh-water reservoir, where "thousands" were noted on 28 June 1979 (Rogers 1979). The date suggests that these were post-breeding females.

Montana

In the first third of July 1986, C. Chase III encountered flocks exceeding 1000 individuals at eight localities. The largest was at Big Lake State Wildlife Management Area (40,000 on 4–5 July and 22 July). At all localities males comprised at least 85% (average > 90%) of the flocks, although a flock on 30 June 1983 at Benton Lake (Pearson pers. comm. to Chase) was probably mostly females. In late June and early July 1987, Chase encountered >1000 birds at each of five localities, and later in July at six localities. Both numbers and localities differed greatly from 1986, as a result of widespread drought (Chase pers. comm.).

Saskatchewan

Thousands of post-breeders typically congregate at alkali lakes in southern Saskatchewan, most notably Reed, Chaplin, and Old Wives. Flocks in late June are relatively small [e.g., 6000 at Coteau Lake (Chase), 7200 at (?) Old Wives Lake (Harris *in* Gollup 1984)] and consist of >99% adult females, whereas those in the first third of July can be very large (e.g., 50,000 at Old Wives Lake) and average 90–95% males. Chase reported a total of > 100,000 juveniles at Reed, Chaplin, and Old Wives lakes in mid-September 1986. In 1987, as in Montana, the size and distribution of large flocks differed from that recorded in 1986. Reed Lake, for example, which had attracted 25,000 birds in July 1986 was dry in 1987 and no phalaropes were recorded.

Kansas

Cheyenne Bottoms is a well-known stopping place for shorebirds in the Great Plains, but not for Wilson's Phalaropes. Concentrations of 500–1000, mostly juveniles, occur from mid-August to early September (E. Martinez, W. Hoffman pers. comms.).

North Dakota

Surveys in late June–early July 1987 revealed a half-dozen localities with concentrations exceeding 1000 birds at each (maximum count 10,300). Similar results were obtained later in July (four localities, maximum count 13,500).

THE NUMBER OF WILSON'S PHALAROPES

On surveys in July 1986 we accounted for 741,000 Wilson's Phalaropes, mostly adults. If we assume that counts were independent (i.e., that there was no movement between staging areas) and that the number of juveniles in fall is similar to that of adults, the total population approximates 1,500,000 birds. This seems consistent with data from the wintering areas (p. 34), indicating that we encountered most of the major staging areas for adults in North America *in 1986.* It follows that Mono Lake attracts approximately 5% of the total population of this species (80,000/1,500,000) and 10% of the adults (75,000/750,000). If we further assume that the sex ratio among adults is 1:1, Mono Lake holds approximately 14% of the total population of adult females (52,000/375,000). The last percentage may be conservative, because sex ratios favor males in polyandrous birds (Murray 1984).

In mid-July 1987, ~417,000 phalaropes were located, of which 51,400 (12.3%) were at Mono Lake. Allowing for the facts that (1) the area surveyed was much smaller than in 1986, (2) some major staging areas (e.g., San Francisco Bay, Lake Abert) were not checked, and (3) departure from the Prairie Provinces and Great Plains was relatively early owing to poor breeding conditions (Chase pers. comm.), the adult population and the proportion staging at Mono Lake probably did not differ much from that found in 1986.

MIGRATION ROUTES: A SYNTHESIS

Evidence from field surveys (above), Mono Lake, regional literature from Middle America and South America (Appendix IV), and museum collections (Appendix V) seems sufficiently complete and complementary to attempt a synthesis of the timing and routes of fall migration.

The southward movement of adults begins in early June, when females begin to flock near breeding areas; by early July very few remain in southern Canada or northern United States. They then undertake a molt migration, moving directly to a few saline lakes in the Great Basin. The relative importance of these varies from year to year in response to changing ecological conditions. Great Salt Lake and Mono Lake are probably the most consistent destinations because of their large size and relative stability. Females also stage successfully, and sometimes in large numbers, at man-made habitats in San Francisco Bay, San Diego Bay, and Tulare Lake, all of which are west of the Sierra Nevada.

By early July adult males also gather in large numbers at saline lakes in the western Great Plains and Great Basin, though not necessarily at those used by females. Thus far, the largest concentrations have been found in southern Saskatchewan and Lake Abert, Oregon. I infer that most males, like females, tend to stage at or near their first stopping point because (1) large numbers remain at staging areas in Sasketchewan and Lake Abert into early August (Chase pers. comm.; Boula 1986, pers. obs.), (2) the Mono Lake population remains fairly stable through July, and (3) influxes at Mono Lake and other localities in California in late July and early August are too small to account for the thousands of males that sometimes (e.g., 1981, 1982) congregate at Lake Abert, only 640 km to the north, earlier in July, and (4) there is no evidence of any significant concentration of males anywhere in the southernmost United States.

After molting and fattening adults disappear from North America, females mostly by the first week of August and males by the middle of the month. Elsewhere (Jehl 1981), I have inferred that adults undertake a direct, nonstop flight along a Great Circle route to landfalls in northern South America (Fig. 25). This idea is supported by several lines of evidence.

1. While at staging areas adults lay on immense fat deposits, as is typical of shorebirds that make long-distance migrations.

2. Although small numbers of adults occur south of Mono Lake and Great Salt Lake, their arrival and departure times coincide with those at the major staging areas; this does not allow for a leisurely southward movement.

3. Adults are essentially unrecorded in Middle America and northern South America in fall.

4. Some adults appear in South America in late July or early August, shortly after mass departures are noted at staging areas.

5. The southeastward heading of migrants leaving Mono Lake would take them along a Great Circle course toward Ecuador and Peru.

The migration of juveniles is also concentrated in the Great Basin and western Great Plains, but unlike that of adults extends across the entire continent. Movements start in the third week of July, peak in August, and in the United States are mostly finished by early September, with stragglers occurring away from the main route into early October. Although large numbers may flock in southern Saskatchewan at the same lakes used earlier by adults, that has not been detected at other staging areas (e.g., Mono Lake), where a few hundred to several thousand juveniles are the rule.

Juveniles do not amass the huge fat reserves characteristic of adults, and apparently migrate southward via a series of short hops to the southern United States or central Mexico before originating a major flight to northern South America. This idea conforms with evidence that arrival and peak migration dates average later at lower latitudes, and that juveniles are more widely distributed than adults in the southern United States and northern South America (Appendix IV) but are very rare south of Mexico. Similar differences in the migration routes of adults and juveniles have been noted in Baird's Sandpiper (*Calidris bairdii*; Jehl 1979).

Phalaropes arrive in the northwestern quadrant of South America, and almost always west of the Andes. I presume the first landfall is in Ecuador or northern Peru, perhaps at Lago Junín (J. Fjeldså in litt. to S. Hurlbert), where several thousand have been seen (mistranscribed as "hundreds of thousands" by Hurlbert et al. 1984). Little is known about subsequent migration routes in South America. Johnson (1972) thought that they followed the coast to southwestern Peru and then travelled "down the Chilean Andes" to Patagonia. Field data, however, show that the main wintering areas are along the Andean chain itself.

Flight Range

The flight range (FR) of a shorebird can be roughly estimated by the following formula:

$$\text{FR (in miles)} = F \times S \times 9.5 \text{ kcal/FM}$$

where F is the weight of fat in grams, and S is the flight speed in miles/hour. FM, flight metabolism in kcal/h, is determined from:

$$\log \text{FM} = \log 37.152 + 0.744 \log W + 0.074$$

where W is fresh weight in kilograms (McNeil and Cadieux 1972, Raveling and Lefebvre 1967). I estimate minimum departure weights of adult females at 105 g and of adult males at 85 g, of which 43% and 37% is fat. At a speed of 80 km/hr (50 mph) (McNeil and Cadieux 1972), flight ranges for females and males approximate 4814 and 4736 km (3009 and 2961 mi), respectively; for the heaviest birds (female 123 g, male 103 g) they are 6224 and 6104 km (3890 and 3815 mi). Davidson's (1984) simplified model gives similar results. Berger and Hart's (1974) equation predicts a flight duration of 52 hours for females and 43 hours for males, or ranges of 4160 and 3440 km, respectively (2600 and 2150 mi).

The Great Circle distance between Mono Lake and a landfall in northern Ecuador (Quito) is 5136 km (3210 mi), or slightly beyond the range of the average migrant, according to McNeil and Cadieux or to Davidson, and much farther than the range estimated by Berger and Hart. Thus, it appears that either the birds are (1) departing with larger reserves, or (2) maintaining higher speeds, or both, or that (3) the equations are crude when applied to shorebirds or other efficient long-distance migrants. (For further discussion of variability in estimating flight range see Pienkowski and Evans 1984.) At 60 mph, however, the South American mainland is within the range of the average female (5440 km; 3350 mi) and near that of an average male (4960 km; 3075 mi) and would require 53.5 hours of continuous flight. The fattest females have estimated ranges of 7136 km (4425 mi) and males 6864 km (4256 mi). The last distance approximates the Great Circle route between Great Salt Lake and Lake Titicaca and would require a nonstop flight of 71 h. Dott's (1985) description of what were evidently exhausted migrants in northern Bolivia on 29 July 1975 suggests that some adults can transit between staging and wintering areas in a single flight. If so, this phalarope's capabilities rival and perhaps exceed those of other long-distance migrants (cf. Johnston and McFarlane 1967, Thompson 1973, Morrison 1979, Jehl 1979, Dick et al. 1987).

THE USE OF SALINE LAKES

Highly saline lakes are used by Eared Grebes and Wilson's Phalaropes for much of the year. While such lakes are not uncommon in western North America, the majority are shallow and their environments can fluctuate rapidly from hypersaline to almost fresh. Few birds use their rich but unpredictable resources. Why are the grebe and phalarope such conspicuous exceptions? Several attributes seem important.

1. Both feed mainly on invertebrates and can capture tiny swimming prey, such as brine shrimp, that are unsuitable for or inaccessible to most other waterbirds.
2. Grebes can obtain all and phalaropes nearly all of their water requirements from their prey; both also avoid ingesting lake water when feeding. Thus, they finesse osmoregulatory challenges that preclude most species from occupying hypersaline environments.
3. In both species the body molt is intense and completed with great rapidity, evidently owing to their ability to exploit superabundant prey (Storer and Jehl 1985, Jehl 1987b).
4. While staging, both lay on enormous fat reserves in a very short time. For adult phalaropes, which can double their weight in several weeks, the fat is used to fuel a nonstop flight to South America. The fat deposits of grebes, however, are puzzling. Not only are they far greater than those needed for migration or insulation, they also impair the birds' ability to fly and even to dive, because they impart buoyancy. Why, then, do grebes get so fat? One possibility is that large reserves function to insure against unpredictable conditions, providing the birds with sufficient time to finish molting and rebuild breast muscles in years when food fails early. But that cannot be the whole answer because maximum weights are achieved and maintained long after the wing molt has been completed. Another possibility is that grebes do not regulate their body temperatures easily (p. 23) and may require large fat deposits for thermogenesis in cold periods (H. Ellis pers. comm.). The situation deserves further investigation.
5. Grebes do not become flightless immediately upon arriving at molting stations but postpone wing molt until they have begun to fatten. Weight gain may be the proximate factor that triggers this molt (A. S. Gaunt pers. comm.), signalling that environmental conditions are acceptable for risking 35–40 days of flightlessness. A delay in the start of wing molt relative to body molt also occurs, though less conspicuously, in the phalarope (Jehl 1987b).
6. The pattern of wing molt in Wilson's Phalarope is unusual in that the two inner primaries are typically lost simultaneously and regrown before other primaries are dropped; subsequent primaries (at least to no. 6) are lost and replaced singly. This pattern, which contrasts with that of most other waders, ensures that the wing surface will be essentially intact whenever the birds begin their nonstop migration to South America (Jehl 1987b).
7. The grebe's uropygial gland secretes large quantities of alkanes, which make up 35 to 40% of its total lipid production. Alkanes are rare or absent in other birds (including Wilson's Phalarope, Cheesbrough and Kolattukudy 1988) but are common in the leaves of desert plants, where they retard water loss. Such compounds would seem useful to Eared Grebes, to lessen cutaneous water loss in hypersaline habitats or to protect contour feathers against degradation in highly alkaline waters (Storer and Jehl 1985).
8. Both species are opportunistic. The grebe will shift nesting localities from year to year, forming colonies of up to several thousand pairs, and then breed for several months to take advantage of locally favorable conditions (Palmer 1962; Cramp and Simmons 1977, pers. obs.). Polyandry in the phalarope (Colwell 1986) is also a form of opportunism.

Because saline lakes are subject to rapid environmental change, birds that exploit them must be behaviorally flexible. As a result, relative abundance at staging areas would be expected to vary from year to year, as shown above. Flexibility is also shown by their ability to exploit new situations, such as the Salton Sea (by grebes), which formed in 1905–1907 and may now be the largest current wintering area, or Tulare Lake (by phalaropes), which formed in the 1980s. A consequence of flexibility is that major events in the annual cycle may vary regionally, as suggested by differences in molt schedule and use of staging areas by grebes in the eastern part of their North American range, and by an apparent difference in molt schedule between phalaropes in North Dakota and Mono Lake (Jehl 1987b).

The attractiveness of highly saline lakes to grebes and phalaropes can hardly be doubted by anyone who has witnessed the fall concentrations at Mono Lake and Great Salt Lake, which together at times have held more than 90% and 40%, respectively, of the North American populations. The birds' preference for such environments was demonstrated at Great Salt Lake, where both species virtually disappeared from the freshened south arm after 1982 and shifted to the rejuvenated but still hypersaline north arm.

Large and relatively stable salt lakes such as Mono and Great Salt probably take on added importance to grebes and phalaropes during droughts, when alternative habitats are unavailable. However, assessing whether they may be crucial (e.g., Winkler and Cooper 1986:490) or vital (Jehl 1981) requires information on how the birds might fare if food supplies at staging areas were depleted or if ecological changes precluded their occupancy. Some observations from "natural experiments" seem pertinent.

Regarding Eared Grebes, throughout this study fall mortality has been very low at Mono Lake, and late-arriving adults and juveniles do stage successfully even though they may not molt there and arrive after food supplies have begun to dwindle. In 1986, when shrimp became unexploitable by mid-October, grebes fattened as quickly as in other years but simply left earlier; even then, relatively low brine shrimp numbers exceeded the grebes' basic demands.

Especially interesting are data from Great Salt Lake, where peak numbers of 100,000–130,000 in 1986 and 1987 were less than one-tenth those recorded in 1982, even though there was no demonstrable change in the total North American population.

One could contend that grebes now mostly avoid Great Salt Lake because of changed environmental conditions. But that explanation is too facile, for it presumes that large numbers were typical in the past, a view for which there is no historical support. Perhaps the small numbers in 1986 and 1987 are more typical and their 1982 status was anomalous. All that is clear at present is that Great Salt Lake grebes did not shift to Mono Lake in 1986 and 1987, nor did they move early to the Salton Sea (R. McKernan pers. comm.) or Lake Powell (J. Hand, D. Paul pers. comms.). Evidently, they remained in freshwater areas, whose locations remain to be determined. This situation illustrates the problems in assuming that data collected in the first year of a study exemplify "normal" conditions.

For Wilson's Phalaropes, on surveys in 1986 and 1987, we encountered adults staging exclusively at saline habitats, including natural lakes, commercial salt works, and agricultural drainage ponds. Juveniles, however, avoided those habitats, as shown by their scarcity at Mono Lake but abundance at nearby freshwater lakes. In early August 1981, for example, 90–95% of 4000 phalaropes at Bridgeport Reservoir, 50 km to the north, were young, as were 65% of 858 at Crowley Lake, 50 km to the south; simultaneously at Mono Lake juveniles comprised 5% of the flock of 15,000. Behavioral differences were also evident; at Mono Lake juveniles frequented shoreline habitats, whereas at freshwater lakes they typically foraged while swimming on the open lake. This may reflect low salt tolerance among young birds (e.g., Swanson et al. 1984) whose salt glands are not yet fully developed.

In summary, highly saline habitats that lack fish predators are preferred habitats for Eared Grebes and adult Wilson's Phalaropes. Because some individuals, age groups, and evidently local breeding populations of each species are able to carry out their migrations without relying on these lakes to any great extent, it appears that the birds' use of them in fall has a large opportunistic component. For such flexible species, the prospect of developing "management plans" or defining what might constitute "critical habitat" will be more complex than observations at salt lakes alone might suggest.

In this context, it is interesting to review the historical record from Mono Lake (Table 9). The first direct reference to grebes is by Denton (1949), who had been told of "clouds" of "flying" grebes in 1873. He evidently surmised these were Westerns; but when he arrived in late May 1880 he found only "the smaller kind," mostly dead on shore. In September 1902, Fisher (1902) saw many grebes, but identified no Eareds and collected only Horned and Westerns, a feat that would be virtually impossible today.

Dawson (1923) established the prevalence of Eared Grebes, but little else. He guessed they bred abundantly, even though the lake then, as now, lacked emergent vegetation. This misconception was apparently widely shared, for a local newspaper had remarked at the "disappearance" of these "non-migratory" birds in the summer of 1907. Dawson's (1923) conception of abundance is hard to evaluate, as it is supported only by a photo, probably taken in June 1919, of about 60 birds scattered along the shore. And while Grinnell and Storer (1924) reported Eared Grebes among the commonest transients in summer and autumn, the numbers they considered noteworthy—"fully 150" in late May—are tiny by modern standards. In 1940, H. Cogswell (pers. comm.) saw thousands in early autumn. Yet, Grinnell and Miller (1944) provided no inkling that Mono Lake might be a major concentration point at that season. And Storer and Usinger (1963), ignoring Storer's earlier data (Grinnell and Storer 1924), only reported scattered flocks in spring. Small (1974) noted "many thousands" in winter and seems to allude to large numbers in spring and fall as well. Cogswell (1977) recognized the species' great abundance in fall, for which Winkler (1977) presented the first quantification.

Information on Wilson's Phalarope is even poorer. Sandpipers that "alight . . . only on the water" were common in mid-August 1870 (LeConte 1930), and into the early 20th century local residents hunted these "Mono Lake Pigeons." Ornithologists, perhaps naively, restricted that appellation to the Red-necked Phalarope and gave no indication that Wilson's might also occur. Since the 1960s the abundance of both species has been recognized, with Winkler (1977) providing the first numerical estimates (see also Jehl 1986). Reports of large numbers of Wilson's in spring (Storer and Usinger 1963, Small 1974) have not been duplicated in recent studies.

This sketchy record is hard to interpret. Most early visitors to Mono Lake had little ornithological knowledge, arrived at off-peak seasons, and made only land-based observations. As a result, impressions gained from their writings regarding the scarcity of grebes and phalaropes

TABLE 9
HISTORICAL DATA ON EARED GREBES AND WILSON'S PHALAROPES AT MONO LAKE, CALIFORNIA

Date	Comment	Source
	Eared Grebe	
1873	"Thousands of grebes (just clouds of them) flying over the lake and on the shore."	Reported to Denton 1949
1880, late May	"No large grebes, but hundreds of the smaller kind on the shore . . . here almost every step as we walk along can be seen the dead bodies of the small grebes. . . . There are literally hundreds of them and most full of worms. . . . We are disappointed for these are birds we intended to shoot for their skins."	Denton 1949
1902, 2–21 Sept	"Thousands of ducks, grebes, and gulls dotted the surface as far as eye could reach. . . . We secured both the western and horned grebes, and Mr. Vernon Bailey assures me he positively identified the American eared and pied-billed grebes the previous year. . . . It is wholly probable that the majority of the thousands of grebes that I saw everywhere along the south side of the lake belonged to these two later species."	Fisher 1902
1907, 2 June	"A strange thing has happened . . . every diver on the lake has disappeared. They are generally there by the thousands and as they are not a migratory bird their disappearance cannot be accounted for."	Bridgeport Chronicle-Union
1923	Said to breed "abundantly."	Dawson 1923
1924	"Common on Mono Lake during the summer and autumn months." "One of the commonest of these transient species is the American Eared Grebe. . . . In late May 1916, fully 150 Eared Grebes were to be seen."	Grinnell and Storer 1924
1938, 9–12 July	"Numerous around Paoha Island, but none was seen about Negit Island."	Nichols 1938
1940, early Sept	Many thousands. Observed from the western shore.	H. Cogswell pers. comm.
1944	Not mentioned at Mono Lake.	Grinnell and Miller 1944
1963	"Scattered flocks . . . in spring. . . ."	Storer and Usinger 1963
1972, 21 June	"Thousands along the shores of the islands and over the surface of the lake."	Jurek 1972
1974	"Many thousands . . . during the winter and at times of spring and fall migration these numbers are swelled by additional thousands of Wilson's Phalaropes. . . ."	Small 1974
1976	Hundreds of thousands in fall; first quantitative data.	Winkler 1977
1977	"Very abundant Aug.–Oct. at Mono Lake."	Cogwell 1977
	Wilson's Phalarope	
1870, 15 Aug	Phalaropes (probably Red-necked) very common near shore. "These birds seemed to collect in such numbers to feed upon the swarms of flies which frequented the shore."	LeConte 1930
1902, 2–21 Sept	Wilson's Phalarope not mentioned. Northern (=Red-necked) Phalaropes noted to "come in countless hundreds."	Fisher 1902
1918	Not mentioned. Red-necked Phalaropes identified as "Mono Lake Pigeons."	Grinnell, Bryant, and Storer 1918
1923	Not mentioned.	Dawson 1923
1924	"Summer visitant along east base of Sierra Nevada; dates of record at or near Mono Lake: May	Grinnell and Storer 1924

TABLE 9
CONTINUED

Date	Comment	Source
	6 and 20, and June 23, 1916." Also noted that Northern Phalaropes are "numerous . . . during seasons of migration."	
1944	Not mentioned.	Grinnell and Miller 1944
1963	"Many . . . in spring and autumn."	Storer and Usinger 1963
1974	"At times of spring and fall migration . . . thousands."	Small 1974
1976	Tens of thousands in fall; first quantitative data.	Winkler 1977
1977	"Very abundant."	Cogswell 1977

might be invalid. Indeed, that significant numbers of grebes, at least, were unrecognized among concentrations of unspecified waterfowl is suggested by R. K. Colcord's description of abundant, fat but inedible "ducks." Colcord, who settled in the region in 1859 and was later Governor of Nevada, noted (1928) that "thousands of ducks [almost certainly including many grebes] swam there every season and become hog-fat in a very short time. Those of us who had had the experience do not hunt this game."

I think it likely, nevertheless, that the abundance and composition of the Mono Lake avifauna prior to 1940, when salinity approximated 40‰, differed importantly from current conditions. Under a less saline regime the lake would have accommodated a greater diversity of birdlife (Jehl 1988), and the relative abundance of the salt lake specialists would have been reduced. This is illustrated by data from the south arm of Great Salt Lake, which has been largely avoided by grebes and phalaropes since it freshened in the early 1980s. Changes are further suggested by accounts that former waterfowl numbers at Mono Lake greatly exceeded those that are currently realized. Fisher (1902), for example, reported that in early autumn "thousands of ducks, grebes, and gulls dotted the surface as far as eye cold see," with "teal, shovellers, and redheads mingling together." That is no longer the case; indeed, Redheads (*Aythya americana*) are rare, although they remain common at nearby lakes. Other accounts (e.g., *Bridgeport Chronicle-Union* 23 Dec. 1905, 24 Dec. 1948) indicate that waterfowl were sometimes numerous in winter as well.

Because the record is poor, and often based on second-hand information (Jehl unpubl.), it is risky to draw conclusions. If grebes and phalaropes were scarcer in the past, the change is unlikely to have been solely the result of less saline conditions because such conditions are acceptable to the two species elsewhere (e.g., Lake Abert), and prey populations of brine shrimp and brine flies were abundant in the 1800s (Clemens 1891, Fisher 1902, Dawson 1923, Browne 1865), although probably not in the same relative or absolute abundance as now. Perhaps alternative staging areas such as Owens Lake, California (dry since the 1920s) and Lake Winnemucca, Nevada (lost to water diversions in the first third of this century) attracted migrants that might otherwise have staged at Mono Lake.

EPILOGUE

So right away I found out something about biology; it was very easy to find a question that was very interesting and nobody knew the answer to.—Richard Feynman (1986).

Much remains to be learned about the biology of migratory birds at saline lakes. Important questions about the Eared Grebe include the timing and extent of migration through Great Salt Lake and the extent to which it is used as a molting area, the size of populations wintering in mainland Mexico, the significance of fat deposits and the extent of breast muscle atrophy at localities other than Mono Lake, and the origin and destination of migrants throughout the species' range. The variability in the Great Salt Lake flock and my inability in 1986 to follow the fall movements of 745,000 grebes from Mono Lake across deserts of southern California to their wintering areas might be contemplated by those who consider field studies passé or that our knowledge of the natural history of common North American birds is adequate.

Data from other phases of the post-breeding season are also needed. For example, there seem to be no dietary studies in winter. Circumstantial evidence from the Salton Sea, which lacks brine shrimp, indicates that grebes feed on larger prey (Mahoney and Jehl 1985c), including a tube-dwelling amphipod (*Corophium latreilli*) that is common in the Gulf of California but which was not known to occur in the Sea as late as 1961

(Linsley and Carpelan 1961). The Salton Sea (salinity 41‰), whose ecology is changing rapidly (Skrove 1986), may soon become too salty or polluted to maintain fish populations. If, as at other hypersaline lakes, this results in the establishment of brine fly and brine shrimp populations, the Sea might develop into a molting area in addition to its use as a wintering area. Given the grebes' reluctance to fly, the availability of year-round food there, in a saline lake adjacent to freshwater nesting areas, could set the stage for the evolution of a population or even a new species of flightless grebe.

Gaps in our knowledge of Wilson's Phalarope biology include the distribution, importance, and stability of staging areas, especially in the eastern part of the range, and the relative abundance of age and sex classes at different staging areas. Why do adult males and juveniles predominate at Lake Abert when adult females prevail at Mono Lake? How do juveniles, which by-pass saline lakes on their first migration, find these areas in subsequent years? Does the rate of salt-gland maturation affect the distribution of age classes on the wintering grounds? There are no data to test whether flocks at highly saline lakes on the altiplano are dominated by adults, although specimens taken elsewhere in South America show a preponderance of young (Appendix V).

Finally, I hope to have shown that many interesting questions remain for those interested in the biology of salt lakes and their avifaunas. While studies of individual lakes will be valuable, it should be obvious that from a bird's viewpoint these lakes represent an interconnected series of salty oases. Thus, our understanding is likely to be advanced most rapidly through broad, long-term, and comparative studies of these dynamic and evolving habitats.

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APPENDIX I
EARED GREBE POPULATIONS AT MONO LAKE, CALIFORNIA, 1981–1987

	Western half				Eastern half					
Date	Count	% coverage	Error[a] (±%)	Method[b]	Count	% coverage	Error (±%)	Method	Total count	Estimated population
1981										
16 Jan	29	95	10	F	4	25	—	F	33	<100
5–6 Mar	12	95	5	F/B	0	30	—	F	12	25
20–21 Apr	2538	95	10	F/B	1828	50	—	F/B	4466	4800–5200
7–8 May	3593	80	10	F/B	5692	50	—	F/B	9285	11,000–12,000
13–15 Jun	7111	75	20	F/B	1500	20	—	F	8611	18,000–25,000
2–3 Jul	14,479	100	5	B	10,000	100	5	B	24,479	27,000–30,000
14–15 Jul	32,086	100	5	B	14,138	100	10	B	46,224	50,000–56,000
24 Jul	30,000	—	—	B	—	—	—	—	—	—
29–30 Jul	68,735	100	10	F/B	15,399	90	15	B	84,134	85,000–92,000
10–11 Aug	56,823	100	10	B	88,590	90	15	B	145,413	145,000–180,000
17–19 Aug	37,953	70	10	B	120,000	80	25	B	157,953	160,000–200,000
21 Aug	40,945	100	10	B	—	—	—	—	—	—
26 Aug	—	—	—	—	160,510	95	20	B	—	—
31 Aug	28,630	100	10	B	—	—	—	—	—	—
1–2 Sep	48,576	100	10	B	257,200	90	20	B	305,776	310,000–375,000
21 Sep	46,440	100	10	B	333,100	90	35	B	379,500	410,000–500,000
9 Oct	202,700	100	20	B	424,600	90	30	B	627,300	627,000–750,000
23 Oct	17,972	95	<5	F	700,000	65	30	F/M	717,972	650,000–800,000
11 Nov	59,330	100	5	F	499,000	50	30	F/M	558,330	500,000–650,000
28 Nov	200,000	—	—	F	—	—	—	—	—	>200,000[c]
24 Dec	183	90	5	F	3640	60	20	F/M	3827	4000
1982										
12–13 Jan	33	90	5	F/B	893	80	15	B	926	1000–1300
2–3 Mar	43	95	5	F/B	12	85	15	F/B	55	75
9 Mar	—	—	—	B	—	—	—	B	—	100[d]
11 Mar	—	—	—	F	—	—	—	F	—	75[c]
13 Apr	1104	95	10	B	2659	90	15	B	3763	3700–4200
3 May	1512	95	5	F/B	19,291	90	10	F/B/M	20,703	21,000–24,000
11–12 Jun	7274	95	10	F/B	28,030	90	20	B	35,304	35,000–40,000
19–21 Jun	9322	95	15	B	27,195	85	30	B	36,517	35,000–40,000
3–5 Jul	8450	65	30	B	8455	50	?	B	—	—
12–13 Jul	14,315	95	10	B	24,656	80	30	B	38,971	35,000–40,000
25–26 Jul	18,192	90	20	B	11,470	80	30	B	29,662	28,000–35,000
18–19 Aug	29,080	85	20	B	95,300	70	30	B	124,380	120,000–150,000
4 Sep	21,715	90	20	B	182,100	80	30	B	203,815	225,000–250,000
21–22 Sep	59,890	90	25	B	367,200	80	35	B	427,090	400,000–450,000

APPENDIX I
CONTINUED

Date	Western half				Eastern half				Total count	Estimated population
	Count	% coverage	Error[a] (±%)	Method[b]	Count	% coverage	Error (±%)	Method		
21–25 Oct	290,300	80	30	B	395,000	90	35	B	685,300	750,000–800,000
17–18 Nov	250,060	80	25	F	100+	20	?	F/M	—	>250,000
mid Dec	—	—	—	—	—	—	—	—	—	200,000[c]
27 Dec	200	60	—	F	—	—	—	—	—	>30,000[c]
					1983					
5–8 Mar	0	70	—	B	6	70	—	B	—	<50
21 Apr	2226	95	15	B	2061	80	15	B	4287	4500–5000
14 May	660	75	—	B	—	—	—	—	—	—
13–14 Jun	818	90	10	B	5135	80	15	B	5953	6000
21 Jun	1617	80	10	B	3671	80	15	B	5288	5400
27–28 Jun	1626	75	10	B	2404	50	—	B	4030	5500–6000
12–13 Jul	2913	100	10	B	2411	95	5	B	5324	5500
6–7 Aug	1900	100	10	B	28,750	85	—	B	38,650	40,000
21–22 Aug	10,422	100	10	B	134,500	80	—	B	144,922	150,000–165,000
5 Sep	209,700	100	30	B	175,300	85	30	B	385,000	375,000–415,000
12–14 Oct	72,840	100	10	B	484,000	80	30	B	556,840	575,000–650,000
14 Nov	425,000	100	30	B	170,000	75	30	B	595,000	650,000–750,000
					1984					
26–27 Mar	1130	50	20	B/F	—	—	—	—	1130	1500–2000
13 Apr	2809	75	15	B/F	200	5	5	B	3109	5000–8000
29 Apr	1735	80	10	B/F	6490	50	15	B	8225	8500–10,000
13 May	7225	100	15	B	8275	75	15	B	15,000	15,000–17,500
12 Jun	8092	95	10	B	—	—	—	—	—	—
23 Jun	8500	90	10	B	13,600	60	15	B	22,100	23,000–25,000
3–4 Jul	14,030	90	10	B	12,655	90	15	B	26,685	25,000–30,000
14 Jul	10,343	100	10	B	16,770	85	15	B	27,113	25,000–30,000
13–14 Aug	51,300	100	20	B	186,000	75	25	B	237,300	225,000–240,000
6–7 Sep	65,000	90	20	B	310,000	40	25	B	375,000	375,000–425,000
27–28 Sep	114,500	90	20	B	554,000	75	30	B	668,500	700,000–800,000
27–29 Oct	430,000	85	30	B	429,000	70	30	B	859,000	800,000–900,000
11–12 Nov	6500	50	—	F	25,000	15	—	F	31,500	60,000

APPENDIX I
CONTINUED

Date	Western half				Eastern half				Total count	Estimated population
	Count	% coverage	Error[a] (±%)	Method[b]	Count	% coverage	Error (±%)	Method		
					1985					
6 Jan	1	50	—	F	15	10	—	F	16	<50
17–20 Feb	5	70	—	F	17	30	—	F	22	<50
11–12 Apr	100	60	—	B	—	—	—	—	100	<1000
14 Jun	4240	100	10	B	18,700	80	10	B	22,940	25,000
1 Aug	—	—	—	—	—	—	—	—	—	50,000–75,000
6 Aug	17,000	80	15	B	121,500	80	20	B	138,500	135,000–150,000
18 Aug	61,490	90	15	B	104,010	80	20	B	265,500	275,000–300,000
24 Sep	113,000	100	15	B	414,000	90	25	B	527,000	500,000–550,000
23 Oct	299,000	100	30	B	251,000	90	30	B	550,000	600,000–650,000
9 Dec	40	10	—	F	100	10	—	F	140	<1000
					1986					
23 Mar	1165	50	—	F	300	10	—	F	1465	1500–2000
16 Apr	3500	70	—	B	6510	30	—	F	10,010	12,000–14,000
30 Apr	15,800	90	10	B	—	—	—	—	—	16,000–20,000
4 Jul	3135	100	10	B	16,325	90	—	B	19,460	18,500–21,500
14 Oct	431,000	100	30	B	314,000	90	30	B	745,000	700,000–800,000
28 Oct	27,700	100	20	B	187,500	90	30	B	207,200	200,000–225,000
29 Nov	50	10	—	F	27	10	—	F	77	<1000
					1987					
16 Jun	2500	70	20	B	<200	70	20	B	2700	5000
26–27 Jul	375	100	10	B	4350	85	10	B	—	6000–8000
30 Sep–1 Oct	68,560	100	30	B	353,000	100	30	B	421,560	400,000–450,000
31 Dec	—	—	—	F	—	—	—	F	—	500,000[c]

[a] Estimated by Jehl.

[b] F = foot, B = boat, M = motorcycle.

[c] Estimate by D. Gaines.

[d] Estimate by M. Thun.

[e] From Annual Christmas Bird Count.

APPENDIX II

Mortality Patterns of Eared Grebes at Mono Lake, California, 1982–1984, Based on Beached-bird Surveys

	1982					1983					1984				
	Birds found dead[a]		Km surveyed	Birds/km		Birds found dead		Km surveyed	Birds/km		Birds found dead		Km surveyed	Birds/km	
	<2 wk	Total		<2 wk	Total	<2 wk	Total		<2 wk	Total	<2 wk	Total		<2 wk	Total
Jan	0	0	5.6	0	0	—	—	—	—	—	—	—	—	—	—
Feb	—	—	—	—	—	—	1	1.6	—	0.62	—	—	—	—	—
Mar	0	0	8.0	0	0	—	—	—	—	—	0	1	7.7	0	0.13
Apr	4	4	9.6	0.42	0.42	1	37	16.3	0.06	2.23	2	3	10.9	0.18	27
May	176	191	13.3	12.09	13.90	0	4	10.9	0	0.62	1	2	11.5	0.09	7
Jun	23	73	35.5	0.70	2.03	1	5	23.2	0.04	0.22	1	19	30.7	0.0	0.61
Jul	20	45	62.4	0.32	0.71	4	5	45.1	0.09	0.10	4	6	45.4	0.09	0.13
Aug	2	2	48.0	0.04	0.04	17	195	81.6	0.20	2.36	0	0	8.0	0	0
Sep	2	5	19.2	0.10	0.25	0	2	21.6	0	0.09	2	7	25.3	0.08	0.27
Oct	0	2	8.0	0	0.25	0	0	9.6	0	0	55	58	14.4	3.79	3.99
Nov	1	1	10.4	0.12	0.12	3	12	9.3	0.32	1.30	46	432	13.6	3.35	31.51
Dec	1	1	1.6	0.62	0.62	—	—	—	—	—	—	—	—	—	—
Total (mean)	229	324	221.6	(1.03)	(1.46)	26	261	219.2	(0.12)	(1.19)	111	528	167.5	(0.66)	(3.15)

[a] Separated by those judged to have been dead > or < 2 weeks.

APPENDIX III

Size and Composition of Wilson's Phalarope Populations at Mono Lake, California, Lake Abert, Oregon, and Great Salt Lake, Utah, 1980–1987[a]

Date	Census	Composition of population				
		Area[b]	Sample size	% female	% male	% juvenile
Mono Lake, California						
1980						
6 July	30,000?	R	100s	90	10	
9–11 July	35,000 ± 5000*	R	100s	95	5	
21–22 July	48,000 ± 10,000*	A	100s	70	30	†[c]
26 July	34,000	A	100	83	15	2
28–29 July	45,100 ± 1000	L	8000	83	16	1
		NS	100s	60	39	1
6–7 Aug	12,000 ± 1500*	A	200	1	94	5
14 Aug	4300 ± 500*	L	3000	100		
		M	41	7		93
		A	>3000	88		12
16 Aug	3250 ± 200	NS	150	88		12
27–30 Aug	150 ± 50*	A	50	5		95
1981						
14–16 June	300*	R	100	100		
18 June	3000*	R	100s	98	2	
30 June	15,000*	R	100s	95	5	
		M	450	10	90	
2–3 July	50,026 ± 3000*	A	100s	91	9	
7 July	52,000	A	100s	81	19	
14–15 July	52,600 ± 5000*	R	376	91	9	
		M	101	32	67	1
20–21 July	58,120 ± 8000*	A	100s	76	24	†
		L	123	88	12	
23 July		R	521	92	8	
25 July	57,500 ± 2500	L	113	75	25	
		R	367	81	19	
29–30 July	64,980 ± 5000*	M	400	29	70	1
		A	100s	72	27	1
3 Aug	70,000 ± 10,000	M	1000	5	95	†
10–11 Aug	15,000 ± 1500*	A	1000s	95		5
17–19 Aug	3200 ± 700*	L	100s	73		27
21 Aug		A	100	75		25
27 Aug	4250*					
31 Aug	2000	L	100s	85		15
1–2 Sept	1000*	A	200	90		10
21 Sept	2*	A	2	50		50
1982						
21 June	1000*	R	201	96.1	3.9	
23 June	10,400 ± 600	R	214	99.5	0.5	
27 June	15,000 (min)	R	549	95.6	4.4	
1 July		T	16	44	56	
		NS/R	151	89.4	10.6	
3 July	20,000 (min)	R	100s	95	5	
6 July		T	141	14.1	84.4	†
7 July	23,000 ± 1000 (min)	R	403	79.8	20.2	
9 July		T	39	10	90	
		L	69	90	10	
11 July		M	190	16.9	83.1	0.5
12 July	31,700*	R	128	86	14	
		M	2000	50	50	

APPENDIX III
CONTINUED

Date	Census	Composition of population				
		Area[b]	Sample size	% female	% male	% juvenile
13 July		L	53	74	24.5	0.5
		T/R	300	82	18	
16 July	34,000 (min)	T/R	194	68.5	31.5	
17 July		L	341	89	11	
19 July	47,400 ± 4000*	L	312	67	32.4	0.6
23 July		M	30		93	7
24 July		R	178	93.4	6.4	0.6
25 July		L	216	88.9	11.1	
26 July		R	169	89	11	
25–26 July	55,000 ± 5000*	A		73	26	1
27 July		L	80	80	19	1
2 Aug		M	35	7	48	45
		L	42	62	38	
3–4 Aug	14,300	A	60	38	62	
4 Aug		M	66		20	80
		L	75	1.3	88.6	12.0
6 Aug	26,000 ± 2000*	L	1000s	95		5
7 Aug		M	24	12.5		87.5
17 Aug		M	48	27		73
18–19 Aug	7500–10,000*	A	100s	95		5
20 Aug	4500 ± 500*					
4 Sept	235*	M	40			100
21 Sept	0*					
		1983				
13 June	<100*	L	6	100		
19 June		L	72	97.2	2.8	
28 June	14,410*	R	260	96.5	3.5	
4 July	20,000 (min)	R	129	87	13	
12 July	25,000 ± 1000*	R	167	75	25	
19 July		T	334	67.7	31.4	0.9
23 July	18,025 (min)	T	100s	87	13	†
26 July	16,500 (min)					
27 July	18,500 (min)					
29 July		T	128	78.1	20.3	1.6
30 July		L	1000s	100		
		M	23	4.3	60.9	34.8
6–7 Aug	10,500 ± 500*					
20 Aug		M	21			95.5
21–22 Aug	2500 ± 500*	L	100s			20
		M	200			100
		1984				
12 June	2*	L	2	100		
18 June	1800*	L	100s	100		
25 June		L	100s	100		
3 July	53,272 ± 2000*	L	100s	98	2	
14 July	52,250 ± 4000*					
16 July	52,000 ± 4000*					
20 July	57,500 ± 2500*					
25 July	60,000 ± 10,000*					
13 Aug	11,500 ± 1500*					
18 Aug	14,000 ± 1000					
7 Sept	1*					
27 Sept	1*					

APPENDIX III
CONTINUED

		Composition of population				
Date	Census	Area[b]	Sample size	% female	% male	% juvenile
1985						
2 June	5*	L	5	100		
12 June	6*	L	6	100		
27 June	3000	T	600	40	60	
8 July	20,000 (min)					
17–18 July	56,500 ± 10,000*					
1 Aug	63,000 (min)					
8–9 Aug	15,000 ± 200*					
18 Aug	13,850*					
25 Sept	1*					
1986						
5 July	56,320 ± 8400*					
15 July		L	23	83	8	8
17 July	60,000–65,000*	R	1000s	85	14	1
29 July		NS	12,000–15,000	95		5
		L/NS	30,000	90	8	†
1 Aug	60,000 ± 5000*	R	8000	99	1	†
6 Aug	15,000*					
9 Aug	10,000–12,000*					
11 Aug	3000–5000*					
7 Sept	300*					
13 Sept	0					
1987						
25–26 July	51,400*					
Lake Abert, Oregon						
1981						
11 July	150,000+[d]					
22 Aug	none					
1982						
15 July	60,000–70,000*	R	146	24	67	9
1983						
30 June	5500–6000*	R	100s	80	20	
		NS	141	72.3	26.7	
20 July	4000–5000*	NS	91	18	41	41
		L		50	50	†
		M	17	6	88	6
1984						
30 June		NS	101	5	95	
1 July	6395*	R	100s	90	10	
		NS	200	6.5	93.5	
		NS	100s	30	70	
		A	1000s	81	19	
1985						
15 July	4500+	N	155	10	82	8
1986						
10 July	11,825*	A	1000	64	33	4
Great Salt Lake, Utah						
1982						
13 July		P	118,000	90	10	
13 July		NS	5700	10	90	

APPENDIX III
CONTINUED

		Composition of population				
Date	Census	Area[b]	Sample size	% female	% male	% juvenile
27 July	533,000*[e]					
12 Aug	12,000*					
		1984				
10 July	4200	P	116	92	8	
11 July	100s	M	100s	†	95	†
12 July	54,000*[e,f]					
		1986				
25 July	387,000*[e]					
		1987				
7 July	159,000*[e]					
27 July	193,770*[e]					

[a] Censuses sufficiently complete for use in population estimates are indicated by an asterisk.

[b] Areas in which the age and habitat composition were determined are coded: A = All areas; L = Surface of open lake; M = Mudflat, NS = Near shore, on water; P = Ponds; R = Shoreline roost; T = Resting on emergent tufa formations.

[c] Symbol † = present.

[d] K. Boula and S. Denny pers. comm.

[e] Aerial survey.

[f] South arm only.

APPENDIX IV

STATUS OF WILSON'S PHALAROPE IN FALL AND WINTER MIGRATION IN MIDDLE AND SOUTH AMERICA

MEXICO. Status poorly known. Most of the regional literature (e.g., Griscom 1934, Loetscher 1955, Lowery and Dalquest 1951, Blake and Hanson 1942, Urban 1959) provides no information for autumn, when the species is very uncommon or rare in the northwestern part of the country (Galluci 1981, Wilbur 1987). S. Howell (pers. comm.) considers it a "common transient" in the Districto Federal from mid-August to mid-October. Friedmann et al. (1950) state that it is "little known south of United States on migration, except in Mexico and Argentina."

EL SALVADOR. Rare fall migrant. Three immatures were collected on 6–9 September (Dickey and van Rossem 1938). Two recent records for 2 and 11 October probably pertain to young birds (Thurber et al. 1987).

HONDURAS. Rare but regular in fall, with specific fall dates from 4–12 October; maximum 25 individuals (Monroe 1968). The dates are within the expected period of the migration of juveniles.

BRITISH HONDURAS. No records (Russell 1964).

GUATEMALA. One record (Land 1970).

NICARAGUA. No data.

COSTA RICA. Not recorded by Slud (1964). First noted in 1974 (Stiles and Smith 1977), who found small numbers in mid-October. A few winter (Smith and Stiles 1979).

PANAMA. "Rare and apparently irregular fall transient (late August–late September), thus far reported only from Canal Zone and vicinity, mostly on Caribbean side" (Ridgely 1976). The dates suggest that most records pertain to immatures.

OCEANIC ISLANDS. There are records for several of the Pacific islands, including Clipperton (specimen LACMNH). Gifford (1913) reported three immatures from the Galapagos in early November, and Butler (1979) considered it an 'uncommon visitor' there.

WEST INDIES. Vagrant. Report from Little Exuma, Jamaica, Guadeloupe, Martinique, and Barbados (Bond 1971).

COLOMBIA. Rare fall migrant. Recorded in September on the Pacific coast and in October from the upper Cuaca Valley (de Schauensee 1964).

VENEZUELA. One recorded at Refugio de Fauna Silvestre de Cuare on 5 and 7 November 1977 (Altman and Parrish 1978).

ECUADOR. Apparently a common fall migrant in the southwestern part of the country (Marchant 1958), from August through late October. Butler (1979) notes that it occurs and that its distribution is coastal.

PERU. Common migrant in coastal areas of SW Peru (Hughes 1970, 1979; Johnson 1972), with some wintering. Also occurs at high elevations inland (Morrison 1939). Small numbers occur in winter in SE Peru; thousands may occur at Lago Junín in fall migration but not in winter (Fjeldså in litt.). Until the last several decades, the species was almost unrecorded (see also Argentina). Johnson (1972) believed it traveled down the coast as far as SW Peru. He (1965) gives several midwinter records for lakes at high altitude (to 12,000 ft), but no data on wintering populations. Evidently winters in highland areas in the northern half of the country.

BOLIVIA. Migrates through Cochambamba area and winters at Laguna Alalay with many records from mid-August to late April, and "occasional birds in June and July" (Dott 1985; and pers. comm.). Hundreds of thousands winter on saline lakes in the southwestern part of the country (Hurlbert et al. 1984).

BRAZIL. Accidental in the interior of the country (Blake 1977).

URUGUAY. Gerzenstein (1965) considered it rare along the coasts, being commoner in spring than in fall. This suggests that the main flight is to the west.

PARAGUAY. Status unrecorded. Myers and Myers (1979) reported that birds arrived by 4 September.

CHILE. Regular migrant in Andean regions, wintering abundantly at high altitude saline lakes near the border with Bolivia and Argentina (Hurlbert et al. 1984), and locally in desert regions (Howell 1975). Almost unknown until the last several decades.

ARGENTINA. Early in this century Wilson's Phalarope was almost unknown in Argentina (Dabbene 1920, 1929), its widespread distribution being noted first by Wetmore (1926, 1927). It winters commonly in wetlands in the northern half of the country (Myers and Myers 1979) and as far south as Chubut (Olrog 1963), but the major concentrations are at Laguna Mar Chiquita (500,000) and Rio Dulce (8000–10,000) areas of Cordoba Province (Nores and Ysurieta 1980, Scott and Carbonell in press), Lago de Pozuelos, Jujuy Province (J. Boswall pers. comm.), and high altitude saline lakes in the extreme northwestern corner of the country (Hurlbert et al. 1984).

FALKLAND ISLANDS. Rare vagrant (Wace 1921).

APPENDIX V

THE FALL MIGRATION OF WILSON'S PHALAROPES: EVIDENCE FROM MUSEUM COLLECTIONS

Because analysis of museum specimens helped clarify the fall migration of Baird's Sandpiper (*Calidris bairdii*), I attempted a similar study for Wilson's Phalarope (for methods see Jehl 1979). It was based on 347 specimens taken south of obvious breeding grounds, from 1 July through 31 December (Table 10).

RESULTS

NORTH AMERICA (267 SPECIMENS)

Specimens confirm that *adult females* are migrating by early July, but the sample (N = 13, 4.9%) is too small to reveal anything about timing or peaks. Females were collected exclusively in the Central, Rocky Mountain, and West regions, all but two in inland localities. Four of ten specimens from the southern tier of states (California, Arizona, Texas) were taken between 20 August and 4 September.

Adult males comprise a larger but still inadequate sample (59, 22.0%). All but four specimens are from the Central-Rocky Mountain-West area, and only three are from coastal locations. Dates extend from early July to 17 September, the great majority occurring from mid-July to 5 August; six specimens, including one each from Midwest and East regions, were taken from 15 August. Dates from the southern U.S. are no later than from farther north.

Juveniles comprise the vast majority (195, 73.0%) of the U.S. sample. Their migration begins in the second third of July, peaks in August, and is essentially terminated by the first week of September, although stragglers occur away from the main route into early October. Most specimens (93.3%) are from the Central-Rocky Mountain-West axis, but migration is not confined to the interior; there are records from coast to coast, and 55% of the California specimens are coastal. The migration period is longer than in adults and arrival dates in the south, as well as away from the major routes, are slightly later than to the north.

MIDDLE AMERICA, WEST INDIES, OCEANIC ISLANDS (13 SPECIMENS)

Phalaropes are rare in Middle America, occurring regularly but in very small numbers south only to northern Mexico (Appendix IV). The only adult is a female from Campeche on 2 July. The remainder are juveniles: six from Baja California taken between 28 July and 19 August; three from oceanic islands (Bermuda, Clipperton, Johnston Atoll) from 11–16 August; and apparent stragglers from Honduras, Martinique, and Barbados from 18 September–4 October.

SOUTH AMERICA (67 SPECIMENS)

Specimens from South America are few and dominated by juveniles (45, 67%). The earliest records (adult female 15 August, Bolivia, 20 August, Ecuador; adult male 9 August, Colombia; juvenile 28 August, Ecuador) are from coastal as well as interior localities in the north-western quadrant of the continent. The earliest records for southern or eastern countries (Paraguay, Argentina, Brazil) are a month or so later.

DISCUSSION

Specimen data suggest that adults move relatively rapidly through the interior of the western United States. The high incidence of females in the southern United States in late August and early September could be interpreted as evidence of a protracted movement, but field data show that these are stragglers, not part of the main migration; also there is no evidence of a protracted movement in adult males. That adults then continue directly to South America is indicated by arrival dates there in early August and the lack of specimens from Middle America.

Juveniles move slowly and over a broad front through the United States, but mostly through the interior West, apparently making several stops before originating a major flight to South America from the southern U.S. or northern Mexico. The presence of large numbers in central Mexico is not evident from collections.

Most birds arrive in northwestern South America, to the west of the Andes, probably remaining there for several weeks before moving to wintering stations.

Because adults were so poorly represented specimen data alone cannot provide a good picture of fall migration. This inadequacy is best illustrated by the scarcity of females from North America. Assuming unbiased sampling, one could posit that these polyandrous birds were exhausted after breeding and quickly succumbed (if this seems far-fetched, see Jehl 1987c). From field studies described above, however, we understand that the samples are highly biased because of the adults' tendency to congregate at staging areas that were unknown to early collectors. Even had these locations been known, sampling bias would have been inevitable because post-breeding adults are either in incredibly heavy molt or are obese. These are rarely converted into satisfactory skins and are more likely to have wound up in soup pots than collections. There was no economic motive for collectors to work in these areas. This is yet another example of the need for caution in using preserved material (cf. Jehl 1987a), and the need for larger and more representative museum collections.

ACKNOWLEDGMENTS

For this study I examined specimens in the following institutions: Los Angeles County Museum of Natural History; University of California Los Angeles; U.S. National Museum of Natural History; American Mu-

TABLE 10
DATES OF WILSON'S PHALAROPE MIGRATION IN AUTUMN BASED ON MUSEUM COLLECTIONS[a]

	N	Adult female	N	Adult male	N	Juvenile
North America West						
British Columbia			1	16 July	5	28 July–2 Oct *13 Aug*
Oregon	1	16 July	3	7 July–17 Sept	1	13 July
Nevada			2	5–6 July	4	27 July–25 Aug *10 Aug*
California	5	7 July–5 Aug. *27 July*[a]	5	4 July–10 Aug *27 July*	30	12 July–15 Sept *8 Aug*
Total	6		11		40	
Rocky Mountains						
Saskatchewan	1	19 July	6	2 July–22 July *11 July*	2	17–22 July
Idaho			13	1 July–4 Aug *10 July*	6	26 July–19 Aug *7 Aug*
Montana			1	15 Aug	5	25 July–8 Aug *28 July*
Wyoming			1	21 July	3	23 July–2 Aug
Colorado			2	25 July–28 July	21	28 July–11 Sept *1 Aug*
Utah			7	3 July–14 July *5 July*	7	18 July–8 Sept *29 July*
Arizona	3	27 July–2 Sept *20 Aug*	2	24 Aug–2 Sept	31	31 July–29 Aug *16 Aug*
New Mexico			1	28 Aug	1	6 Aug
Total	4		33		76	
Central						
Manitoba					1	18 July
No. Dakota			5	8 July *16 July*	20	25 July–30 Aug *1 Aug*
Kansas	1	28 July	7	28 July–6 Sept *11 Aug*	37	16 July–6 Sept *23 Aug*
Nebraska					1	20 July
Oklahoma					5	17 July–6 Sept *6 Aug*
Texas	2	28 Aug–4 Sept			2	24 Aug–28 Aug
Total	3		12		66	
Midwest						
Wisconsin					1	14 Aug
Michigan			1	19 Aug	2	5 Aug–19 Sept
Mississippi					1	1 Sept
Alabama					1	5 Sept
Total			1		5	

TABLE 10
CONTINUED

	N	Adult female	N	Adult male	N	Juvenile
East						
Maryland					1	3 Aug
New York			1	12 Aug	4	20 Aug–3 Oct
						14 Sept
Virginia					1	9 Oct
No. Carolina					2	17 Aug–13 Sept
Total			1		8	
Total North America		13 (4.9%)		59 (22.0%)		195 (73.0%)
Middle America, West Indies, Oceanic Islands						
Mexico	1	2 July			6	28 July–19 Aug
						11 Aug
Honduras					1	4 Oct
Bermuda					1	11 Aug
Pacific Islands					2	16 Aug
Barbados					1	18 Sept
Martinique					1	25 Sept
Total Mid. Am., etc.		1 (7.7%)				12 (92.3%)
South America						
Colombia			1	9 Aug		
Ecuador	4	21 Aug–7 Sept	1	10 Sept		28 Aug–21 Oct
		25 Aug			3	*28 Aug*
Brazil						5 Oct
Peru	3	27 Aug–12 Sept	5	31 Aug–18 Oct	1	31 Aug–8 Dec
		3 Sept		*27 Sept*	21	*30 Sept*
Bolivia	5	15 Aug–6 Sept				26 Sept–6 Nov
		17 Aug			2	
Paraguay	1	15 Oct			5	1 Sept–15 Oct
						2 Oct
Argentina	2	16 Nov			13	29 Sept–23 Nov
						7 Oct
Total S. Am.		15 (22.4%)		7 (10.4%)		45 (67.2%)
Total—All areas		29 (8.4%)		66 (19.0%)		252 (72.7%)

[a] Mean dates are given in italics.

seum of Natural History; The University of Michigan Museum of Zoology; University of Wisconsin; California Academy of Sciences; Texas A&M University; Philadelphia Academy of Natural Science; Museum of Vertebrate Zoology, University of California; British Columbia Provincial Museum; Louisiana State University; Denver Museum of Natural History; San Diego Museum of Natural History; Stovall Museum, University of Oklahoma; Carnegie Museum of Natural History; Field Museum of Natural History; Museum of Natural History, University of Kansas; University of New Mexico Museum of Southwestern Biology; Museo de Historia Natural "Javier Prado," Lima, Peru.