# 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

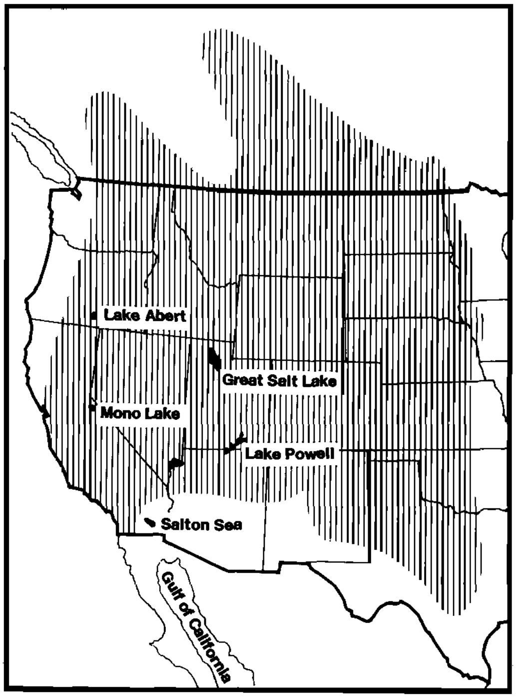

FIGURE 1. Breeding range (shaded) of the Eared Grebe in North America (after Palmer 1962). Major wintering areas are the Salton Sea and Gulf of California. Major staging areas are Mono Lake and Great Salt Lake.

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

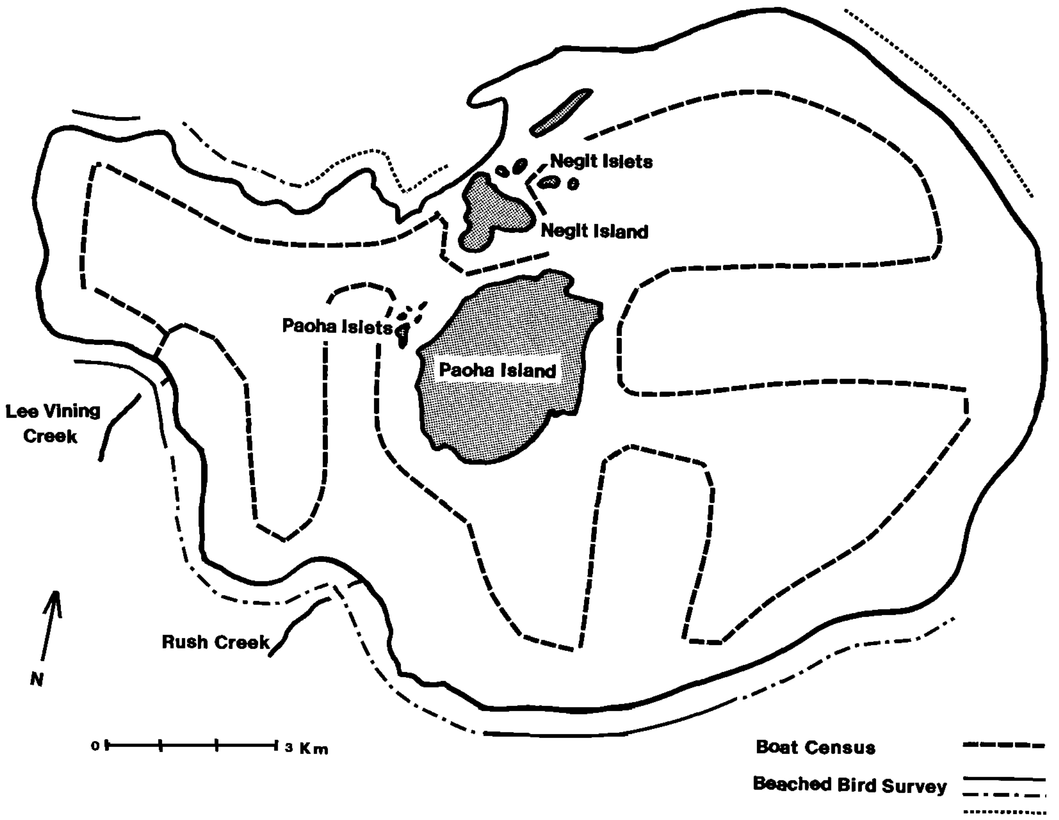

FIGURE 2. Outline map of Mono Lake in 1984 showing typical routes used in censusing grebes. Areas where beached bird surveys were conducted 1982–1984 are indicated on the periphery of the lake. Areas censused regularly in all years are shown by a solid line, those censused infrequently by a dashed line,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

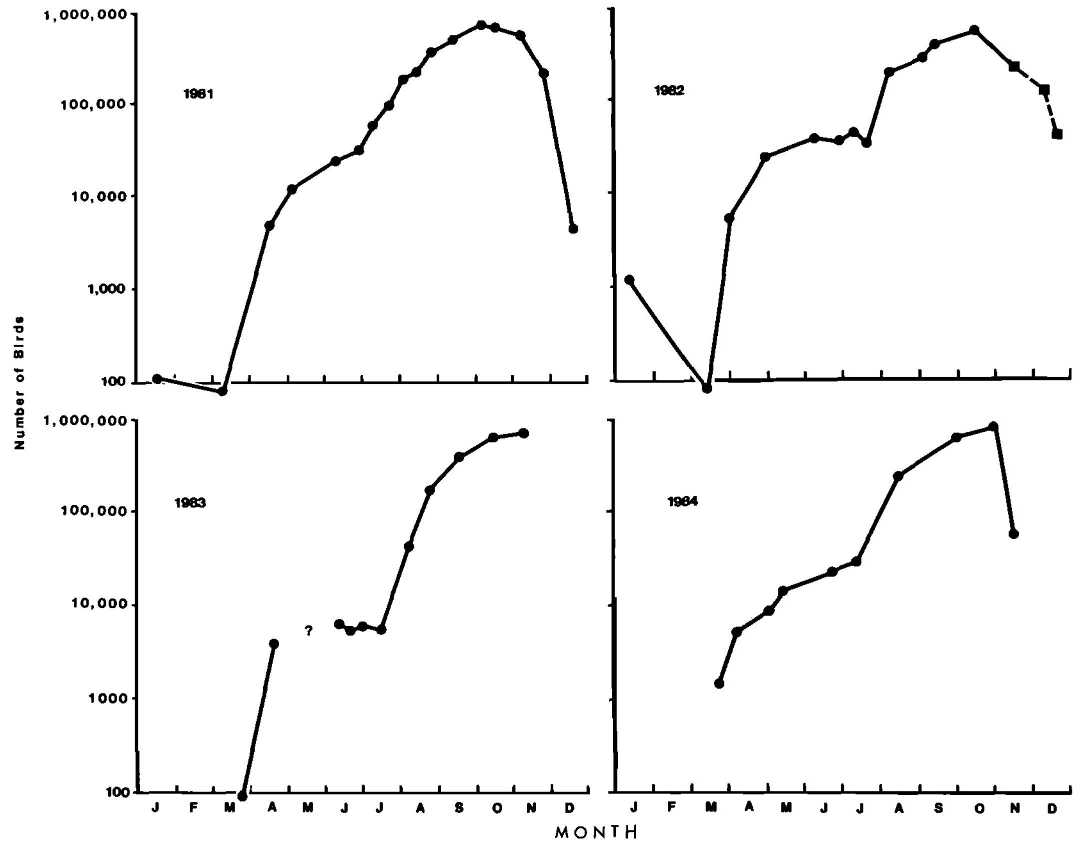

FIGURE 3. Numbers of grebes at Mono Lake, California, 1981–1984. Circles represent best estimates of the population; squares connected by a dashed line are estimates from incomplete censuses. Details in Appendix I.

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

| Measurement | Male |  |  | Female |  |  |
|---|---|---|---|---|---|---|
|  | 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

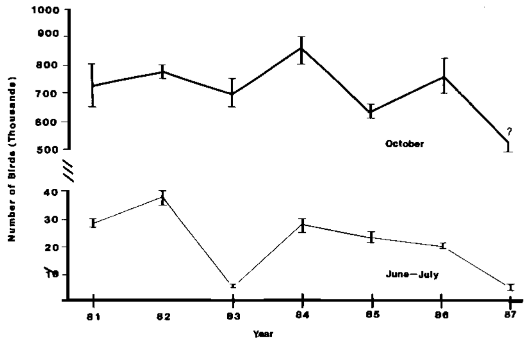

FIGURE 4. Summering and peak fall numbers of Eared Grebes at Mono Lake, California, 1981–1986. The error bars are my estimates of confidence intervals.

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.

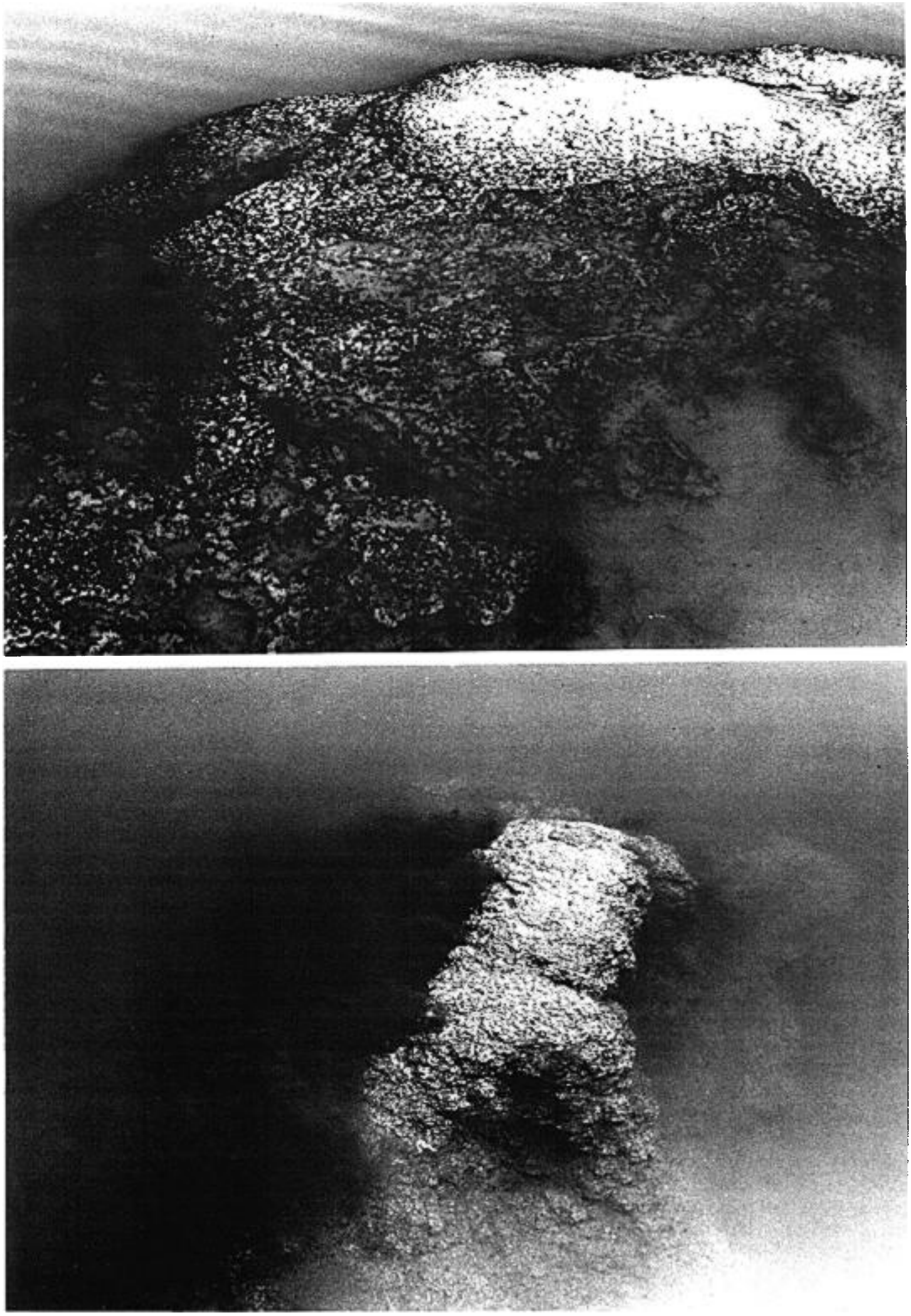

FIGURE 5. Top, brine fly pupae (black) attached to tufa, and bottom, brine shrimp swarming around tufa; both are often concentrated at tufa shoals. The light color of the tufa enhances the detectability of the tiny prey when water transparency is low.

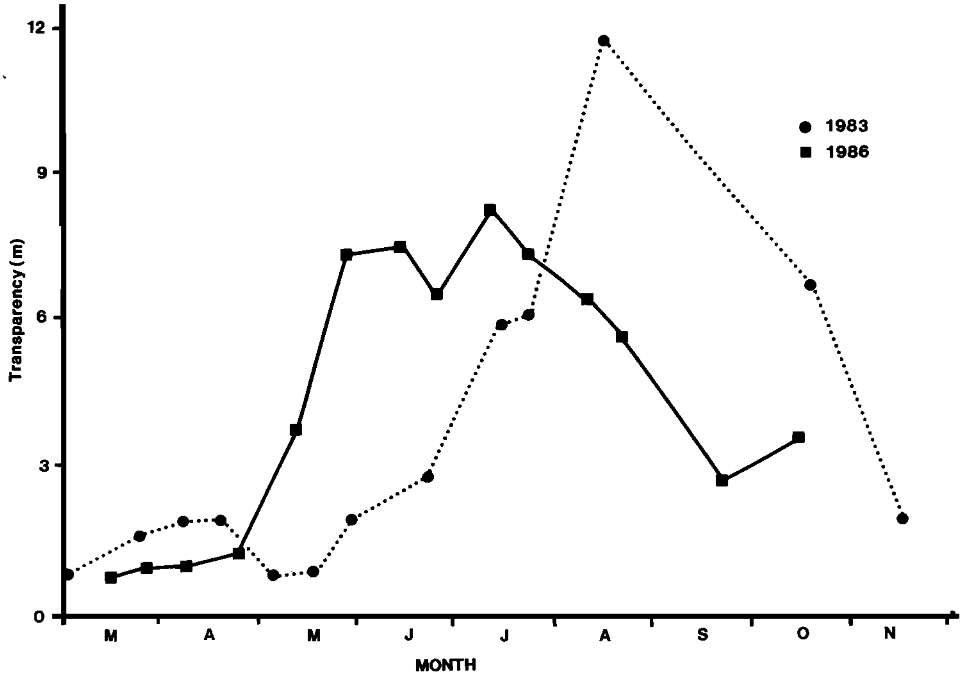

FIGURE 6. Seasonal variation in water transparency at Mono Lake in 1983 and 1986, based on Secchi disc readings. Data for 1983 provided by Los Angeles Department of Water and Power and for 1986 by J. Melack and G. Dana.

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

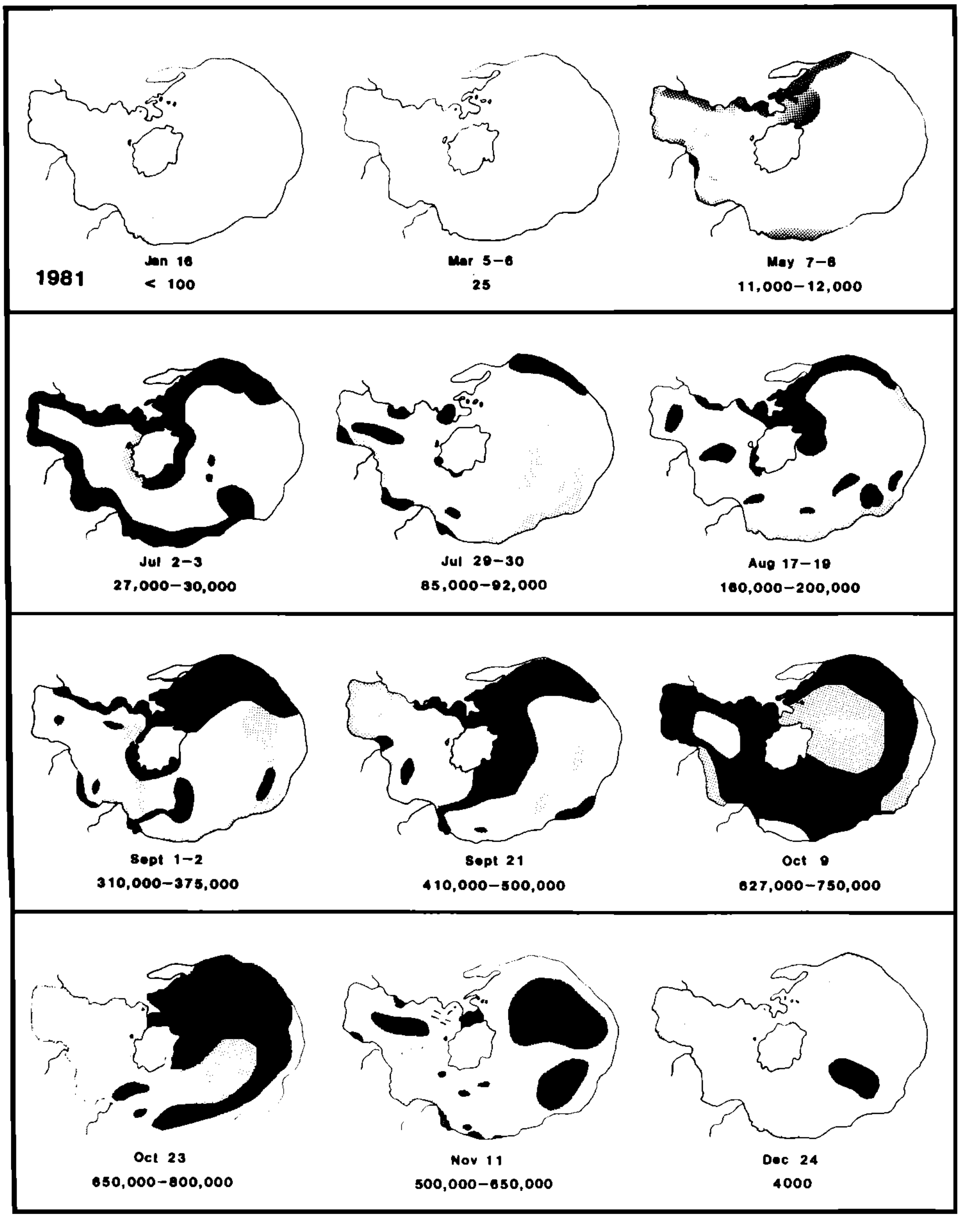

FIGURE 7. Distributional patterns and abundance of Eared Grebes at Mono Lake in 1981. The intensity of stippling reflects the relative density of birds in any one census period.

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-

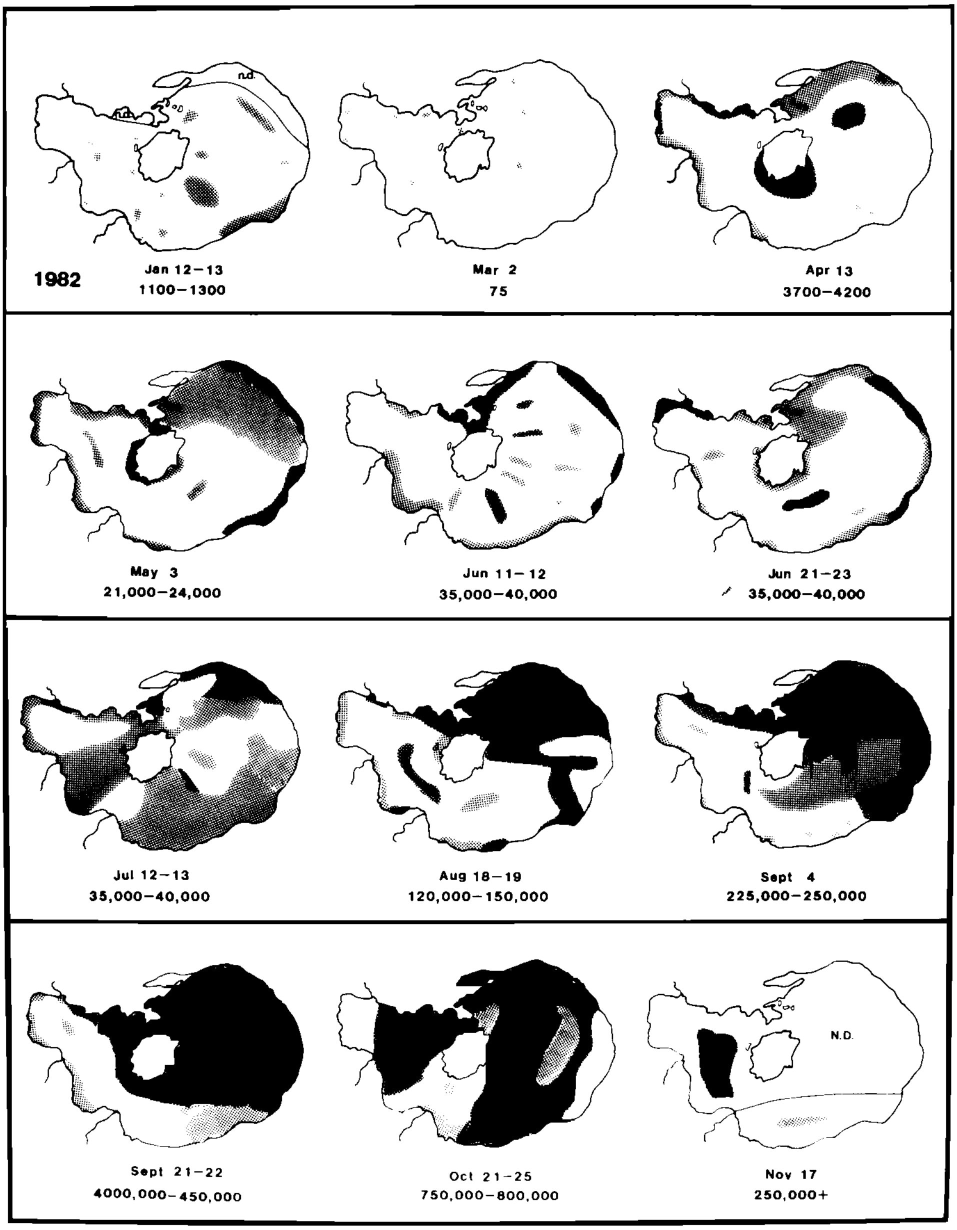

FIGURE 8. Distributional patterns and abundance of Eared Grebes at Mono Lake in 1982. ND = No data. The intensity of stippling reflects the relative density of birds in any one census period.

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.

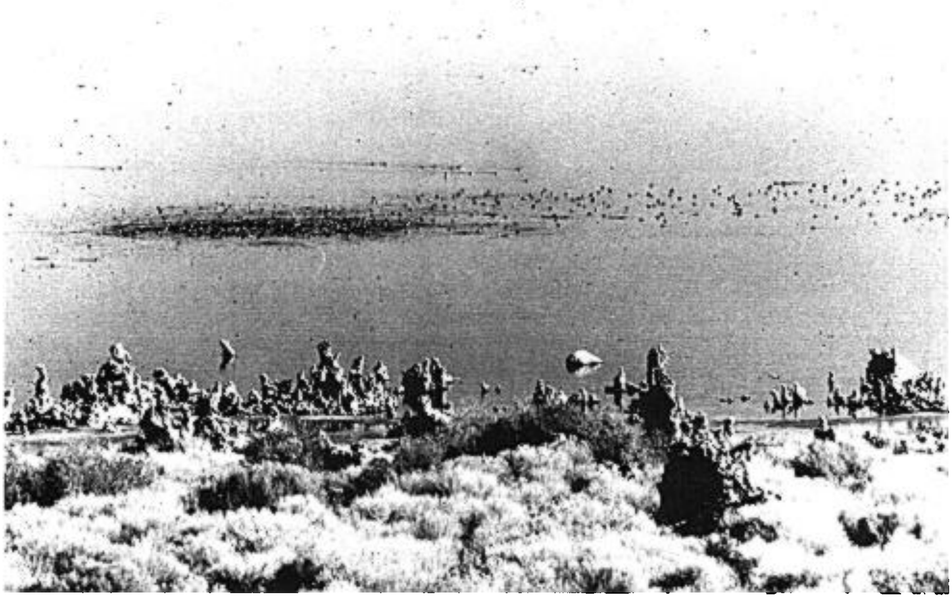

FIGURE 10. Locally high densities of grebes in late fall are presumably related to patchy distribution of the declining brine shrimp.

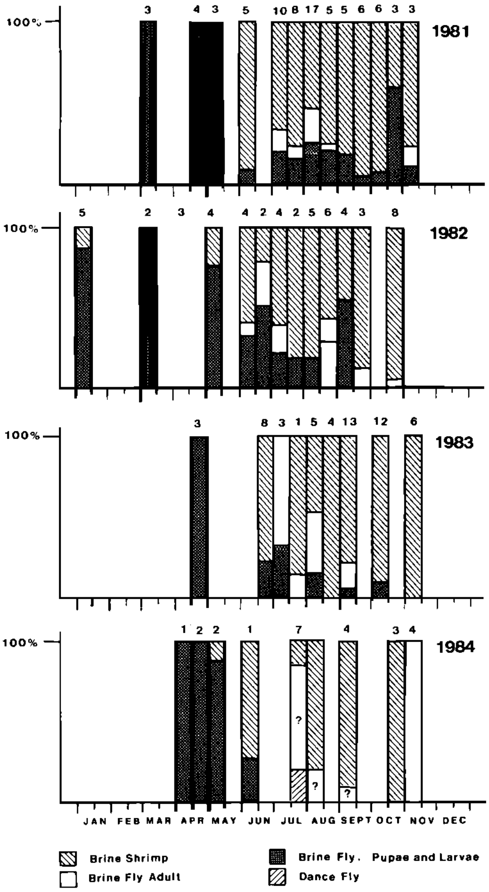

FIGURE 11. Food taken by Eared Grebes at Mono Lake, 1981–1984. Stages of brine flies were not separated in samples from July–September 1984; this is indicated by a question mark.

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.

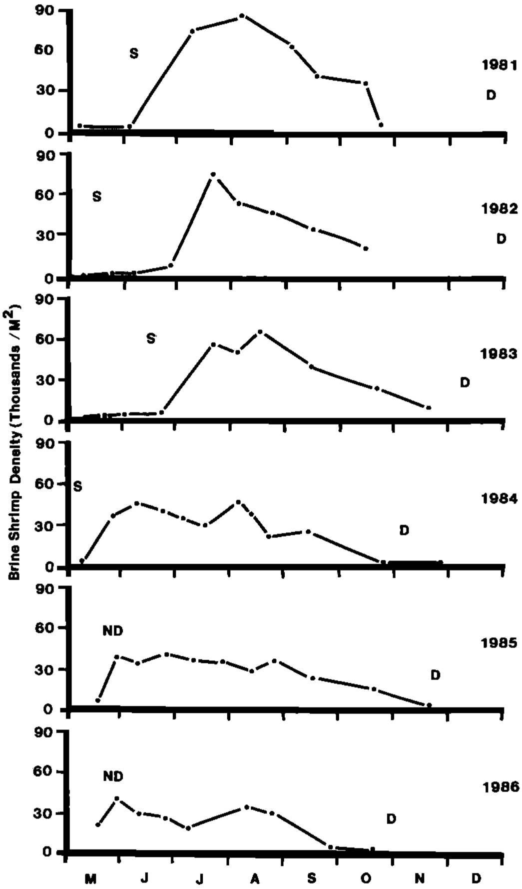

FIGURE 12. Densities of adult plus juvenile (stages 8–11) brine shrimp at Mono Lake. Data for 1981–1984 provided by C. Foley and B. White, Los Angeles Department of Water and Power, and for 1985–1986 by J. Melack and G. Dana. "S" indicates when shrimp were first found in gizzards, "D" periods of major 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

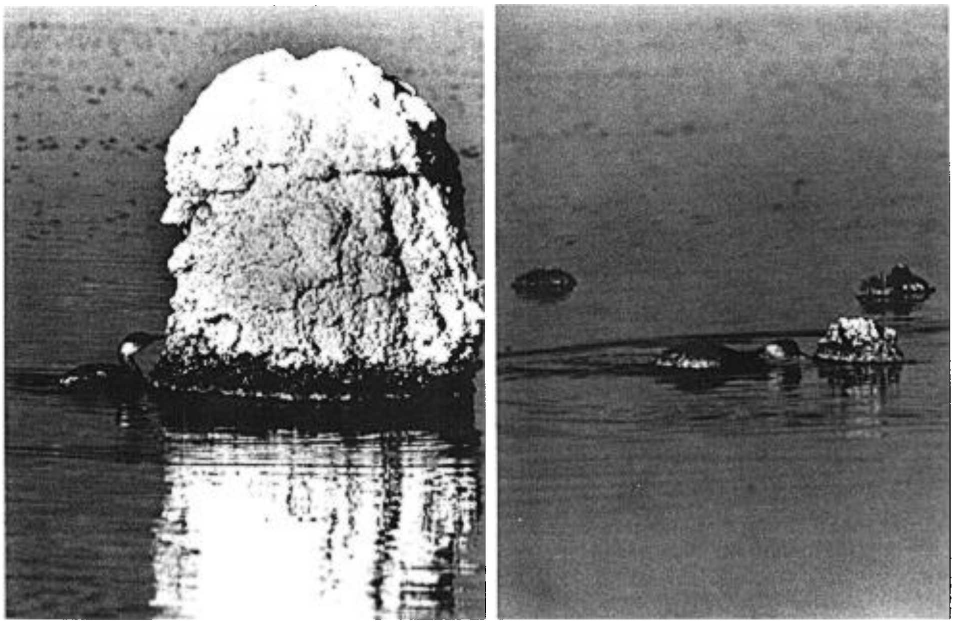

FIGURE 13. Two surface foraging techniques employed by a single grebe. Left, gleaning adult brine flies from emergent tufa; right, lunging at adult flies as they emerge from beneath the surface of the lake.

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,

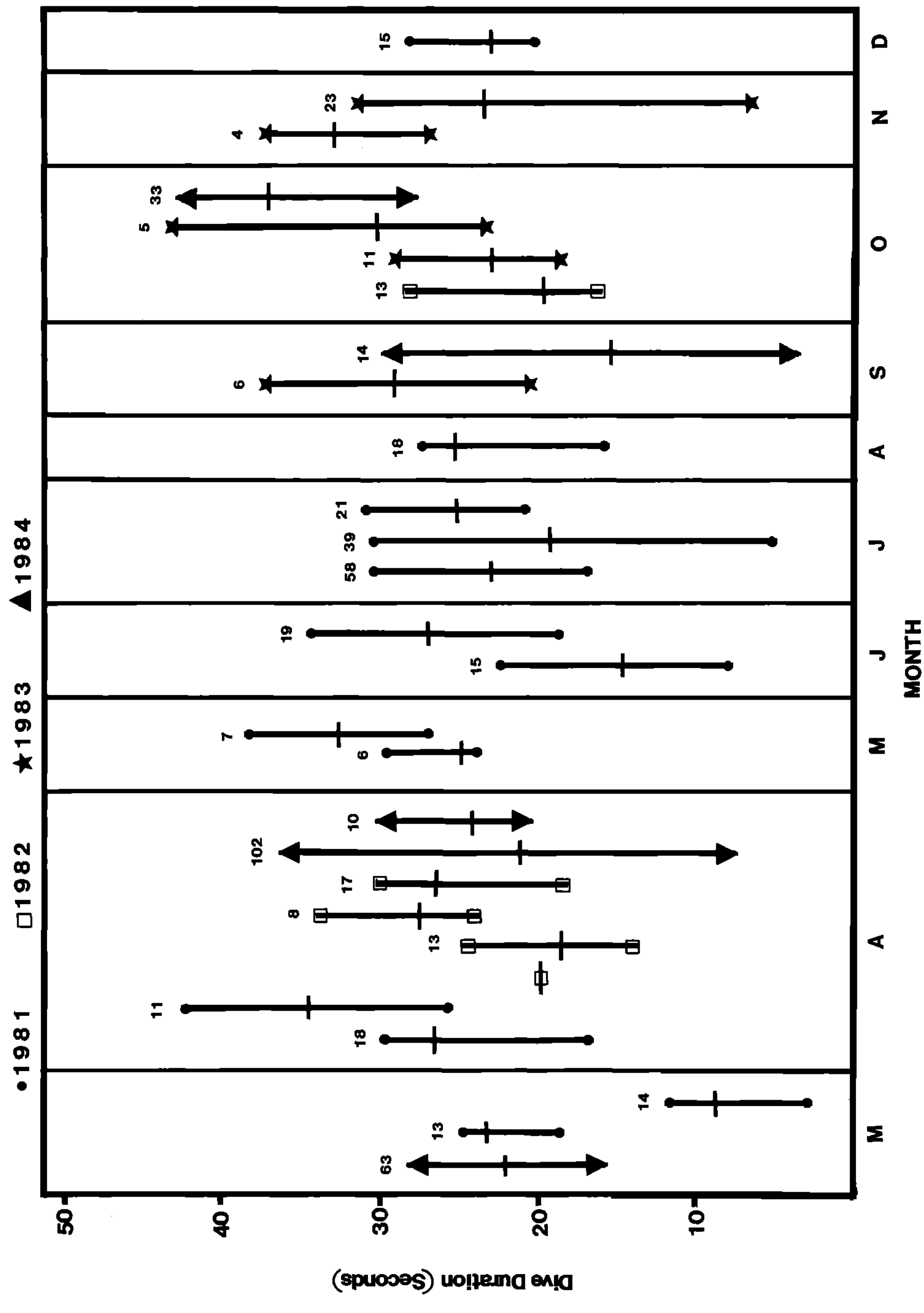

FIGURE 14. Seasonal differences in dive durations (range and mean) of Eared Grebes at Mono Lake, California, 1981–1984. Numbers above columns are sample sizes.

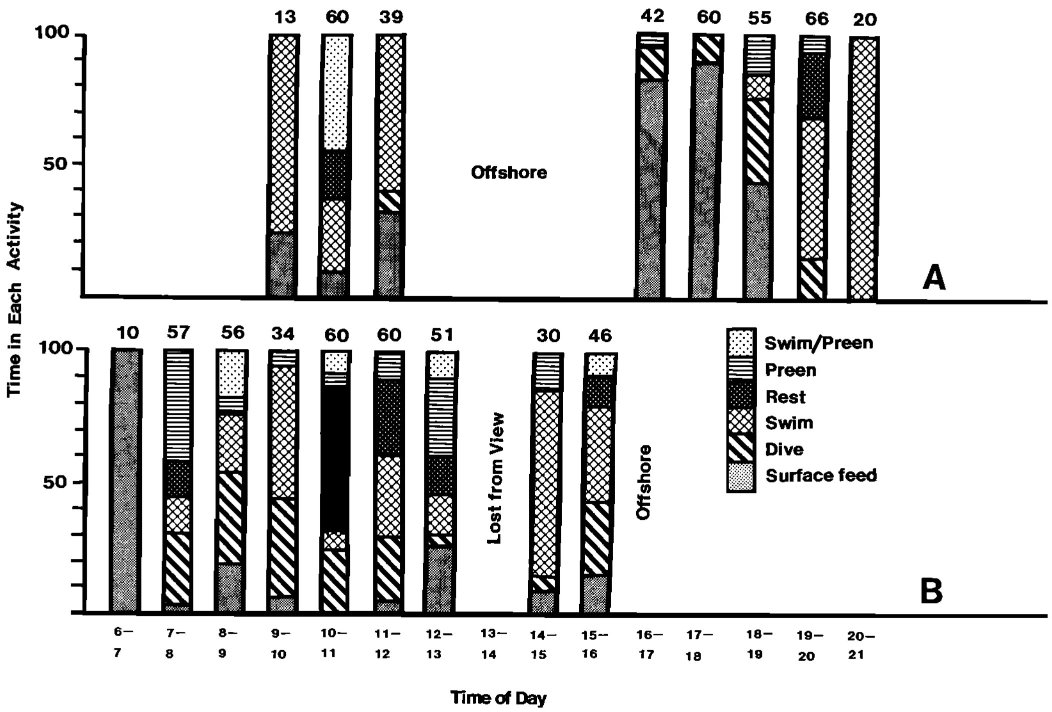

FIGURE 15. Activity patterns of two individual grebes (A, B) on 22 July 1981. Numbers above bars are minutes of observation. Also see Figure 16.

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*).

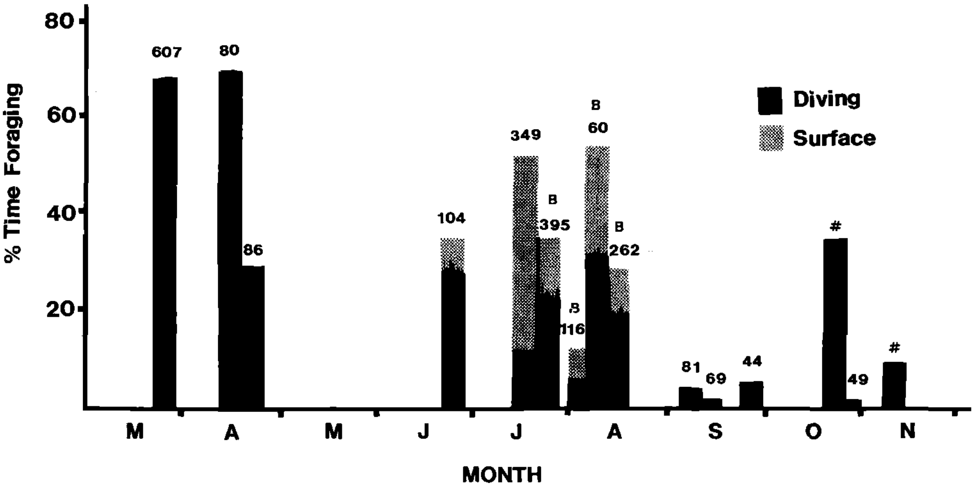

FIGURE 16. Seasonal variation in the percentage of time spent foraging. Numbers above columns are minutes of observation; # indicates estimate based on a minimum of 60 minutes of observation of flocks; B designates a leucistic grebe whose movements were studied on several days. Data from 1981–1984.

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.

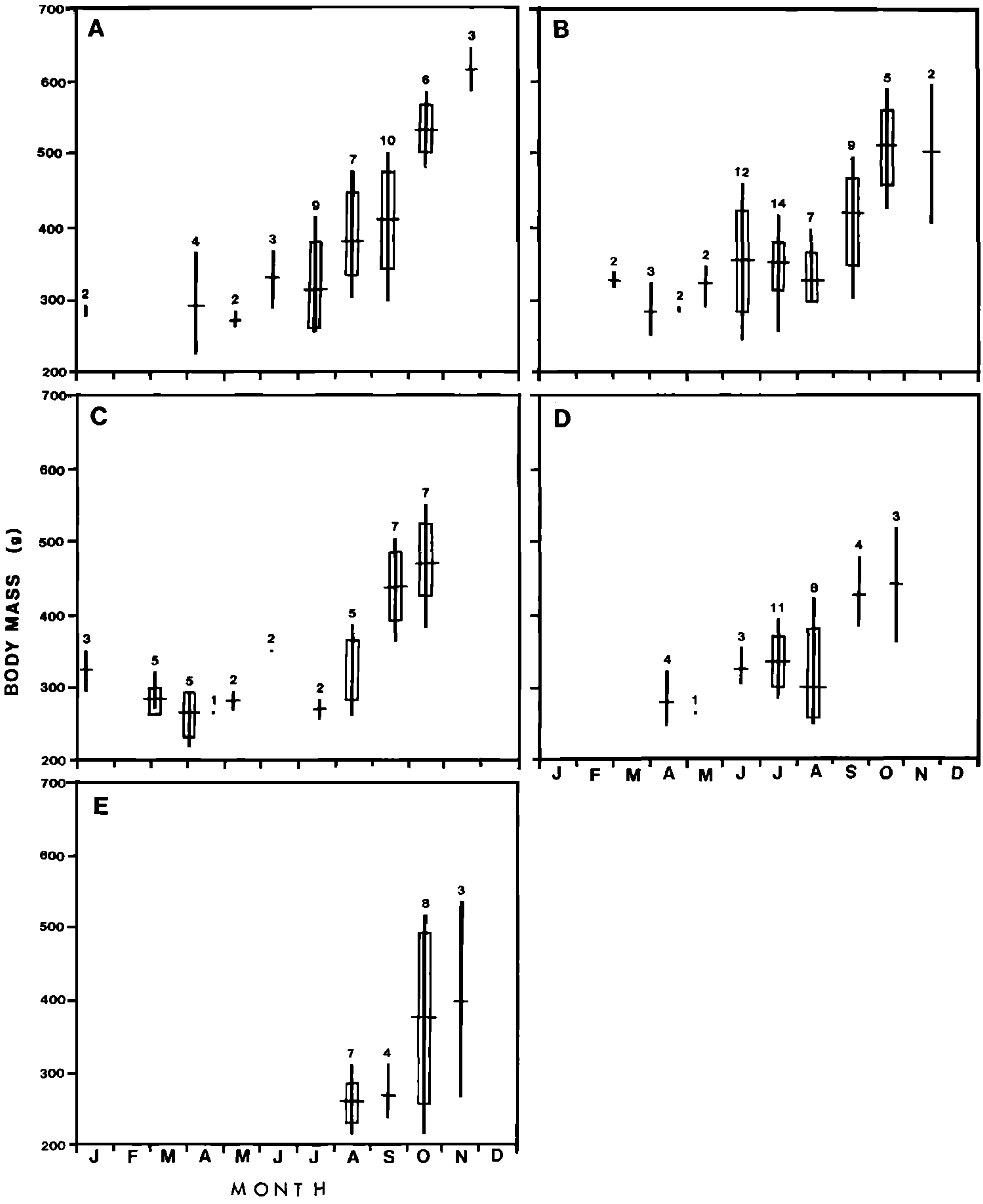

FIGURE 17. Body mass (range, mean ± 1 SD) of Eared Grebes at Mono Lake, 1981–1983. A, adult males; B, subadult males; C, adult females; D, subadult females; E, juveniles (sexes combined).

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.

## 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.

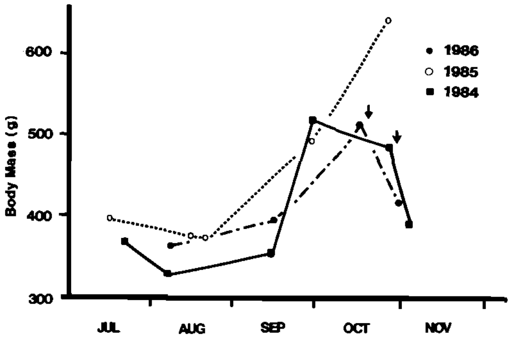

FIGURE 18. Mean body mass of adult and subadult Eared Grebes in the autumns of 1984–1986. Arrows indicate when brine shrimp were no longer detectable from the surface.

## 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-

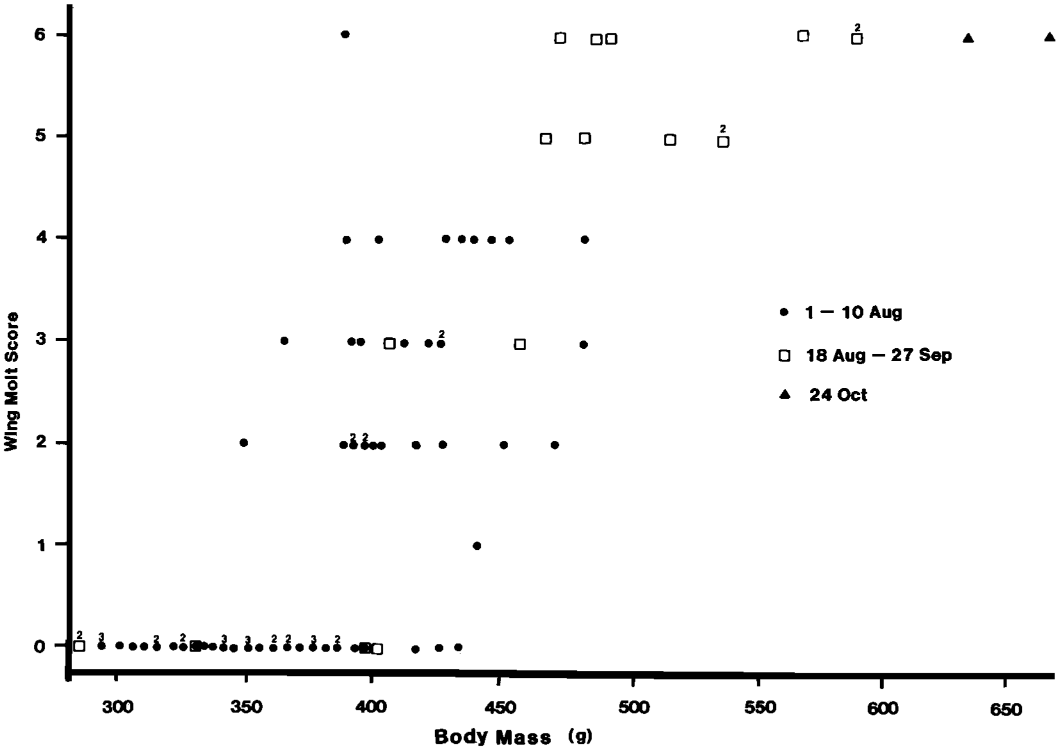

FIGURE 19. Relationship of wing molt to body mass in adult and subadult Eared Grebes. Molt scores range from 0 (no molt) to 6 (primaries fully replaced).

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 nonbreeders 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

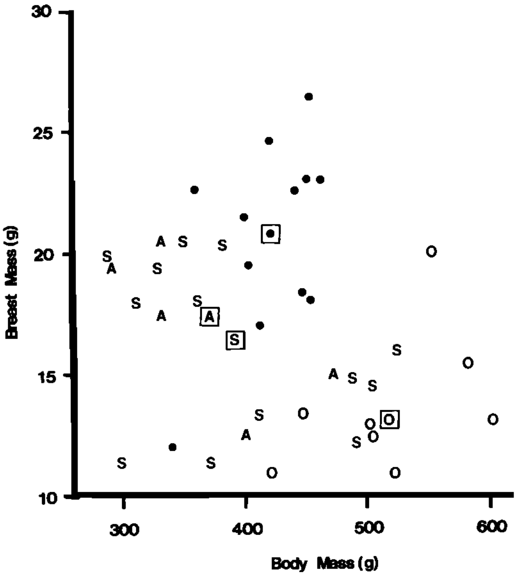

FIGURE 20. Seasonal changes in breast mass (from one side of pectoral girdle) and body mass in adult and subadult Eared Grebes at Mono Lake in autumn 1986. A = 3 August, S = 13 September, O = 14 October, and ● = 28 October. Squares indicate the means for each sampling period.

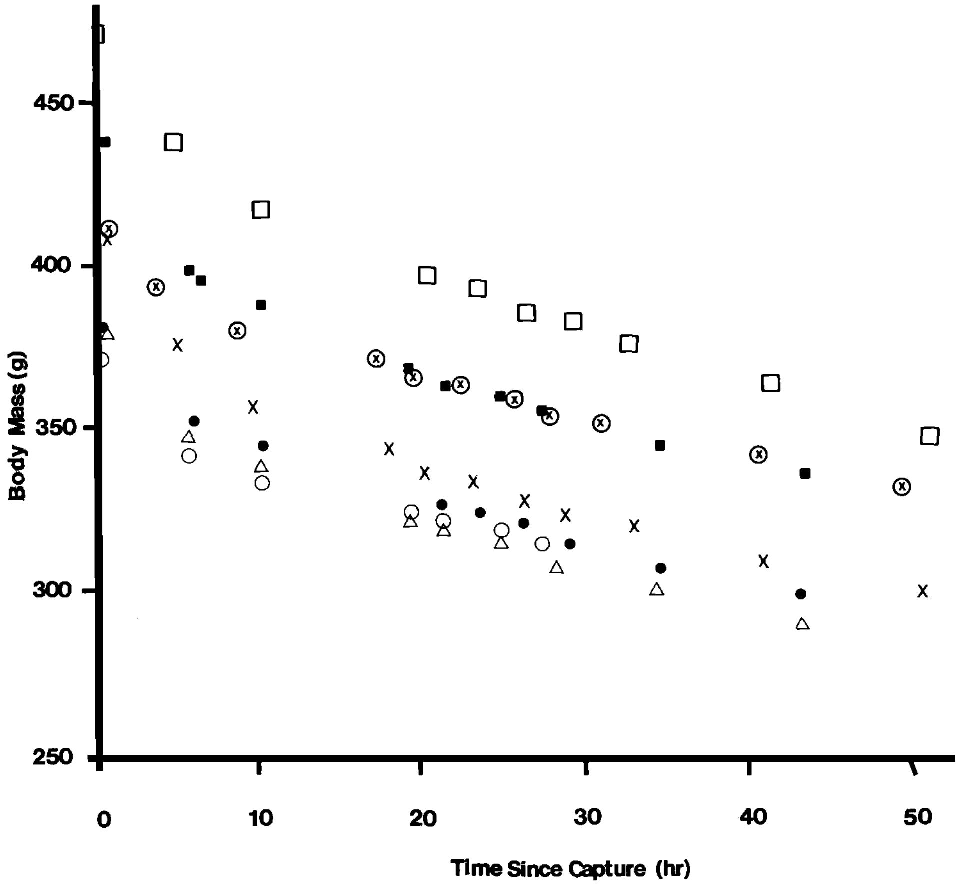

FIGURE 21. Weight loss in fasting, inactive Eared Grebes, in captivity.

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

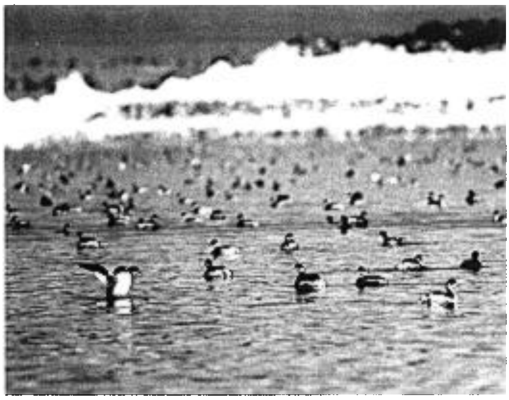

FIGURE 22. Exercise flapping, which aids in rebuilding pectoral muscles, becomes prominent shortly before the major departure period in late fall.

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

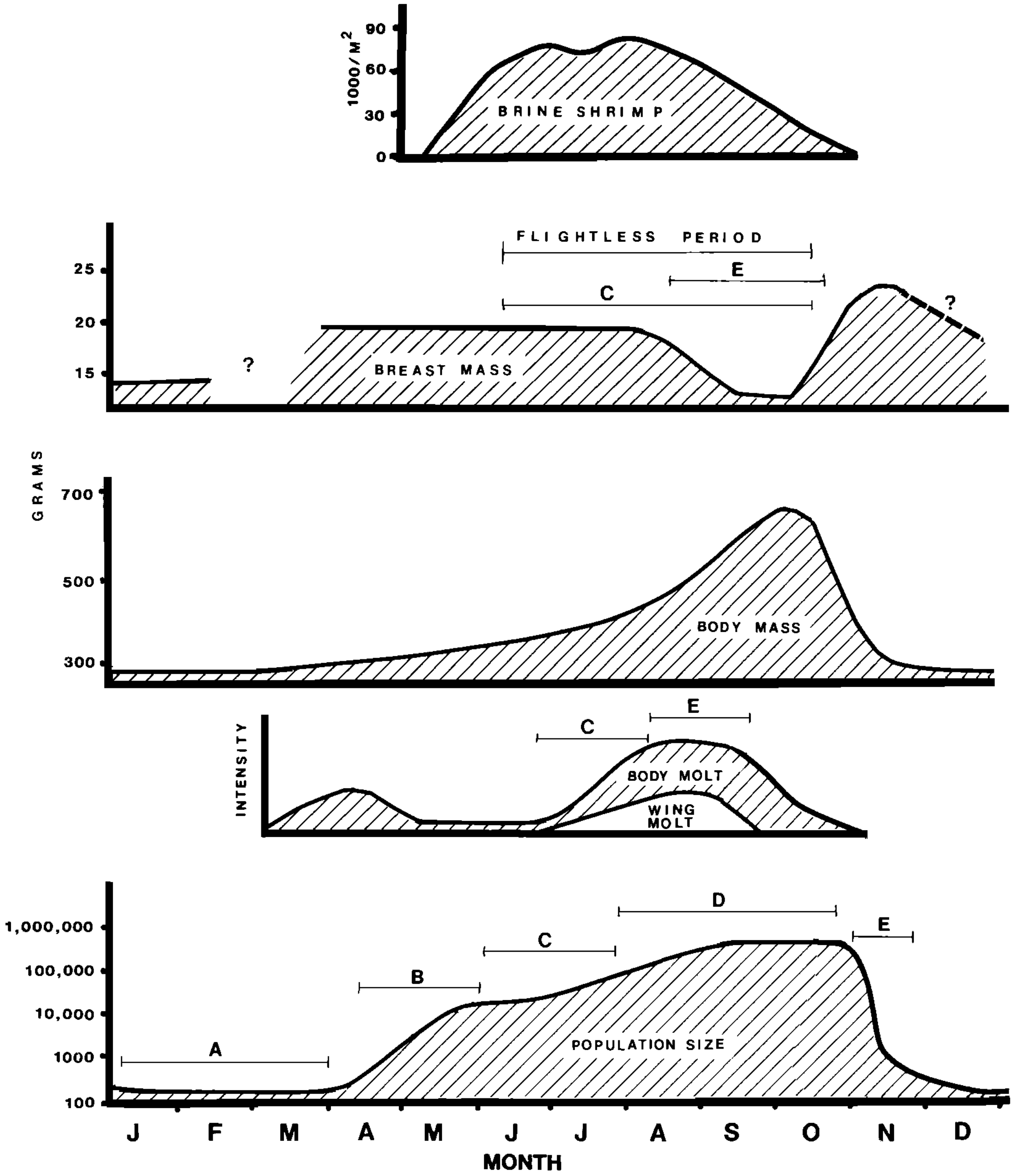

FIGURE 23. A synopsis of the major events in the annual cycle of Eared Grebes at Mono Lake, California. A, winter residents, B, spring migration, C, summering flock, D, staging period, E, departure.

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.

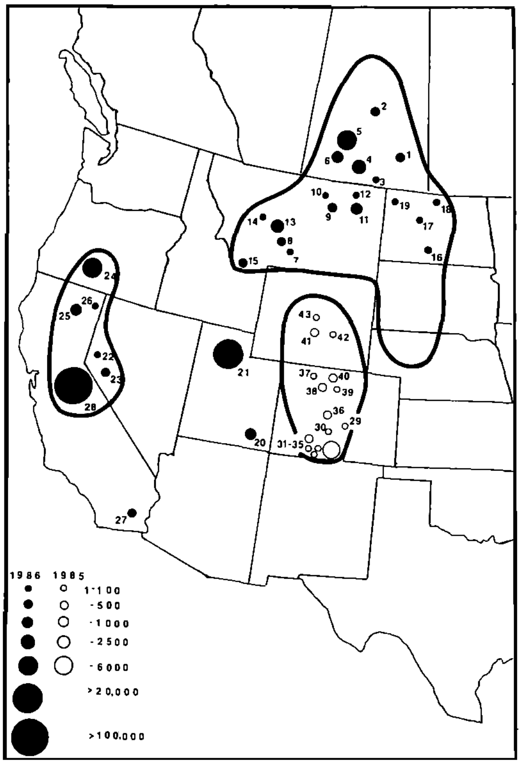

FIGURE 24. Localities at which Eared Grebes were encountered on surveys in August–October 1985 and 1986. Outlines show approximate limits of survey. Localities holding more than 1000 grebes are italicized. SASKATCHEWAN: (1) Southeastern Saskatchewan, (2) Southcentral Saskatchewan, (3) Coteau Lakes, (4) *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.

### *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.

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]

| Area | 1981–1982 |  |  | 1982–1983 |  |  | 1983–1984 |  |  | 1984–1985 |  |  | 1985–1986 |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 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?

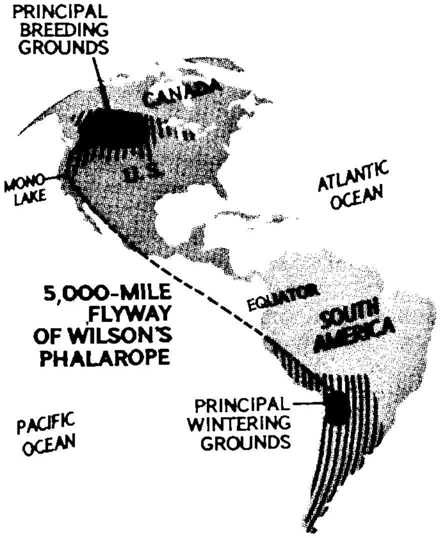

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FIGURE 25. Breeding (North America) and wintering (South America) ranges of Wilson's Phalaropes. Centers of abundance are solid-colored. Based on AOU (1957, 1983), Godfrey (1966), Blake (1977), Hurlbert et al. (1984), and Appendix IV.

## 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).

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