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

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

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

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

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

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

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

Flight Range

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

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

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

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

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

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

THE USE OF SALINE LAKES

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

1. Both feed mainly on invertebrates and can capture tiny swimming prey, such as brine shrimp, that are unsuitable for or inaccessible to most other waterbirds.

2. Grebes can obtain all and phalaropes nearly all of their water requirements from their prey; both also avoid ingesting lake water when feeding. Thus, they finesse osmoregulatory challenges that preclude most species from occupying hypersaline environments.

3. In both species the body molt is intense and completed with great rapidity, evidently owing to their ability to exploit superabundant prey (Storer and Jehl 1985, Jehl 1987b).

4. While staging, both lay on enormous fat reserves in a very short time. For adult phalaropes, which can double their weight in several weeks, the fat is used to fuel a nonstop flight to South America. The fat deposits of grebes, however, are puzzling. Not only are they far greater than those needed for migration or insulation, they also impair the birds' ability to fly and even to dive, because they impart buoyancy. Why, then, do grebes get so fat? One possibility is that large reserves function to insure against unpredictable conditions, providing the birds with sufficient time to finish molting and rebuild breast muscles in years when food fails early. But that cannot be the whole answer because maximum weights are achieved and maintained long after the wing molt has been completed. Another possibility is that grebes do not regulate their body temperatures easily (p. 23) and may require large fat deposits for thermogenesis in cold periods (H. Ellis pers. comm.). The situation deserves further investigation.

5. Grebes do not become flightless immediately upon arriving at molting stations but postpone wing molt until they have begun to fatten. Weight gain may be the proximate factor that triggers this molt (A. S. Gaunt pers. comm.), signalling that environmental conditions are acceptable for risking 35–40 days of flightlessness. A delay in the start of wing molt relative to body molt also occurs, though less conspicuously, in the phalarope (Jehl 1987b).

6. The pattern of wing molt in Wilson's Phalarope is unusual in that the two inner primaries are typically lost simultaneously and regrown before other primaries are dropped; subsequent primaries (at least to no. 6) are lost and replaced singly. This pattern, which contrasts with that of most other waders, ensures that the wing surface will be essentially intact whenever the birds begin their nonstop migration to South America (Jehl 1987b).

7. The grebe's uropygial gland secretes large quantities of alkanes, which make up 35 to 40% of its total lipid production. Alkanes are rare or absent in other birds (including Wilson's Phalarope, Cheesbrough and Kolattukudy 1988) but are common in the leaves of desert plants, where they retard water loss. Such compounds would seem useful to Eared Grebes, to lessen cutaneous water loss in hypersaline habitats or to protect contour feathers against degradation in highly alkaline waters (Storer and Jehl 1985).

8. Both species are opportunistic. The grebe will shift nesting localities from year to year, forming colonies of up to several thousand pairs, and then breed for several months to take advantage of locally favorable conditions (Palmer 1962; Cramp and Simmons 1977, pers. obs.). Polyandry in the phalarope (Colwell 1986) is also a form of opportunism.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

TABLE 9
CONTINUED

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

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

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

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

EPILOGUE

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

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

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