

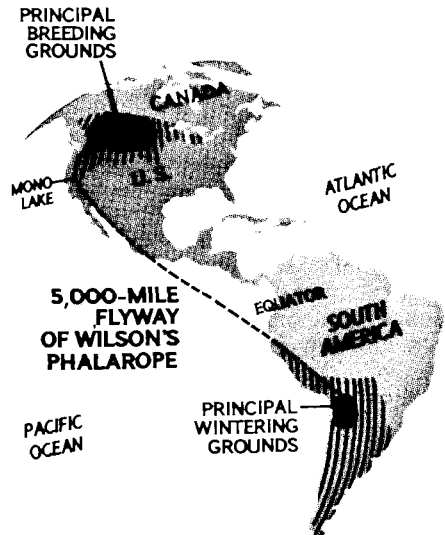
et al. (1958) observed over 3000 at Lake Lenore, in eastern Washington, as late as 22 November.

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

WILSON'S PHALAROPE

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

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



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

(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 non-breeding season is based largely on long-term

TABLE 6
MORPHOMETRICS OF WILSON'S PHALAROPES FROM MONO LAKE, CALIFORNIA

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

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

METHODS

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

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

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

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

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

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

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

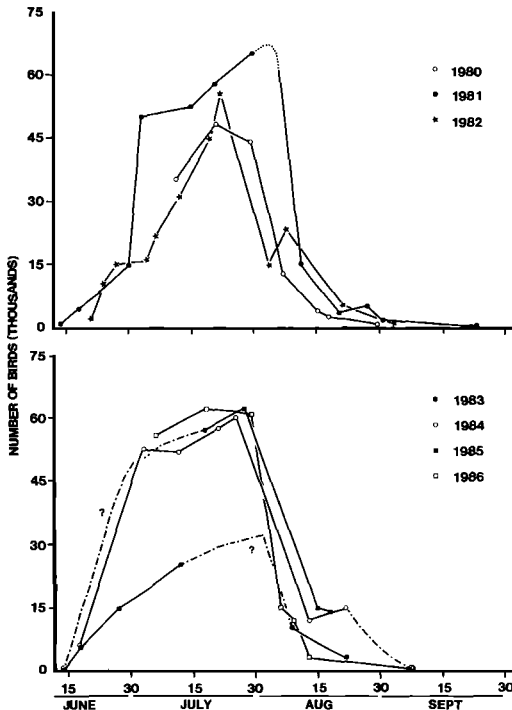


FIGURE 26. Numbers of Wilson's Phalaropes at Mono Lake, California, 1980-1986. Details in Appendix III.

THE ANNUAL CYCLE AT MONO LAKE CHRONOLOGY

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

During this study postbreeders began to arrive at Mono Lake in mid-June (earliest 12 June); nearly all were females, whose major influx occurred in the last week of June and first days of July. By 8 July, 50,000 migrants were often present (Fig. 26). Numbers increased through July with the appearance of adult males, most of which

arrived between 7 and 25 July. Their numbers were supplemented by very small numbers of juveniles, which typically appeared about 20 July (earliest 12 July). Peak numbers for the year of 50,000-65,000 were realized in the last week of July, then dropped almost overnight to 15,000-20,000 when females departed, mostly between 31 July and 4 August. Usually numbers then declined slowly until the middle of the month, as adult males migrated. In some years (1982 and perhaps 1984) there seemed to be a second influx of males in early August, but data for that phase of the migration are too imprecise to confirm whether this was a regular event. By 1 September only a few hundred stragglers remained; nearly all were juveniles. Late dates were: adult female—14 August, adult male—4 September, juvenile—27 September.

COMPOSITION OF THE POPULATION

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

SIZE OF THE MONO LAKE FLOCK

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

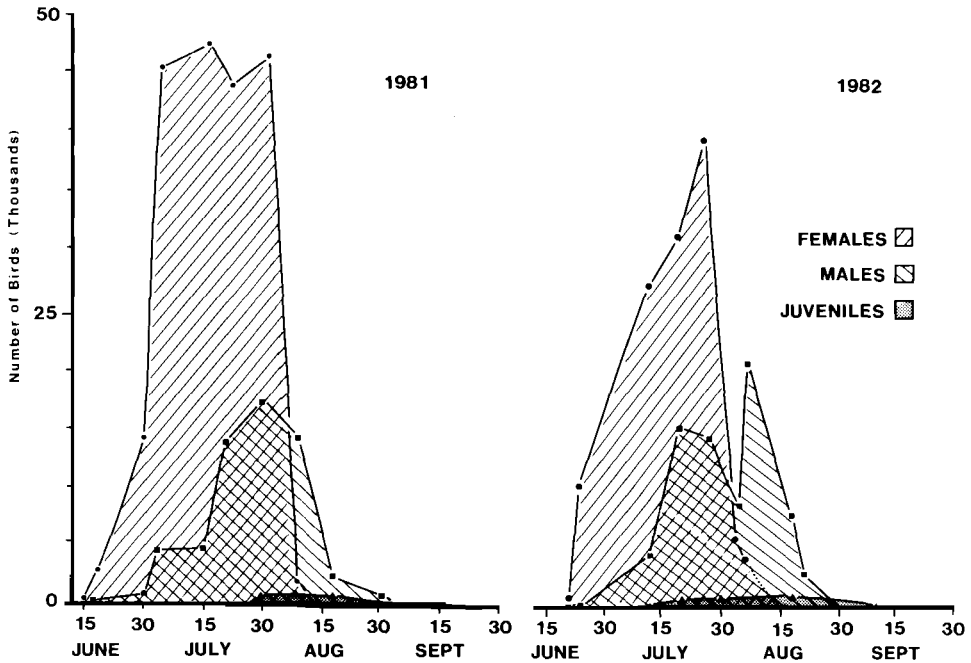


FIGURE 27. Composition of Wilson's Phalarope population at Mono Lake, California, 1981-1982. Details in Appendix III.

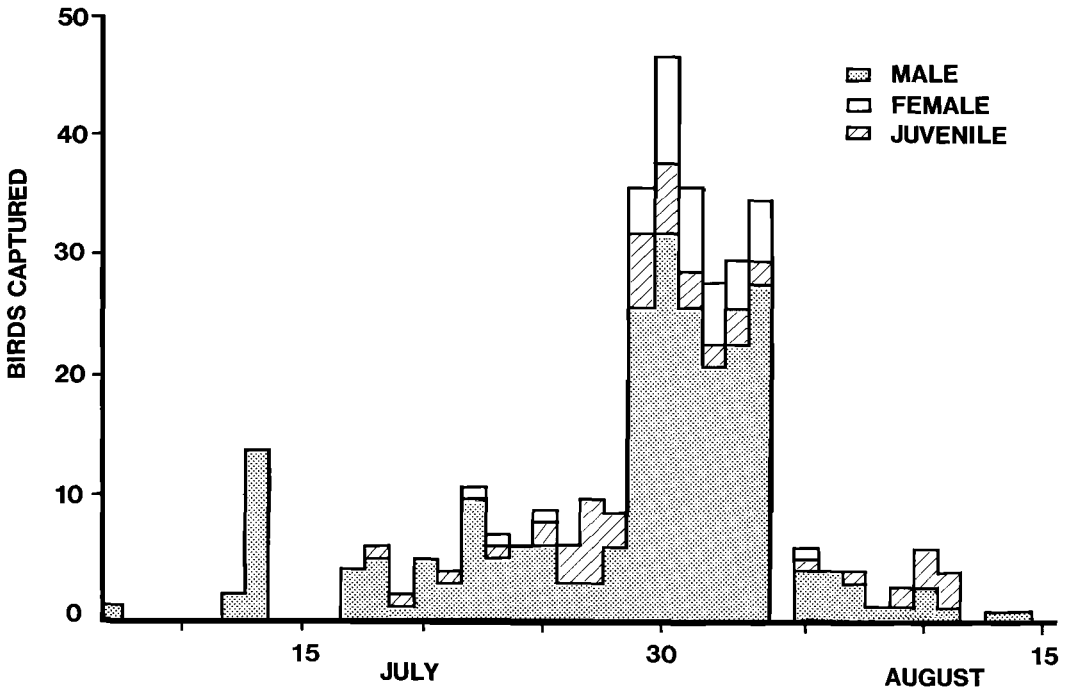


FIGURE 28. Composition of Wilson's Phalarope population at Mono Lake, California, in 1980-1981 as indicated by banding studies.

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

ANNUAL VARIATION

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

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

BEHAVIOR

DISTRIBUTION AND DAILY MOVEMENTS

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

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

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

By mid-July, when much body molt had been completed, the females' behavior changed. They began to disperse widely over the lake and spent much of the day offshore, and when they did come ashore it was in early morning and late

afternoon to visit fresh water (p. 40). Roosting at night took place in large but diffuse flocks well offshore, from which the birds dispersed by 07:00 each morning.

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

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

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

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

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

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

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

Juveniles mostly frequented mudflat or near-shore habitats throughout their stay. Although



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

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

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

HYPERPHAGIA

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

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

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

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

ROOSTS

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

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

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

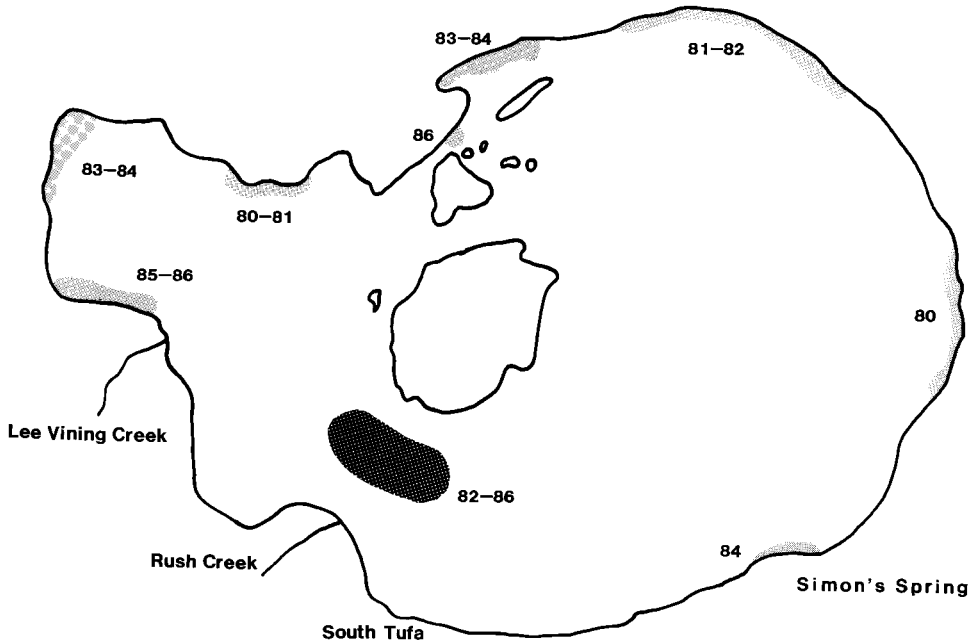


FIGURE 30. Location of diurnal roosts of Wilson's Phalaropes on the periphery of Mono Lake, California, 1980-1986, and of the nocturnal roost (cross-hatched) in mid-lake.

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

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

USE OF FRESH WATER

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

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

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

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

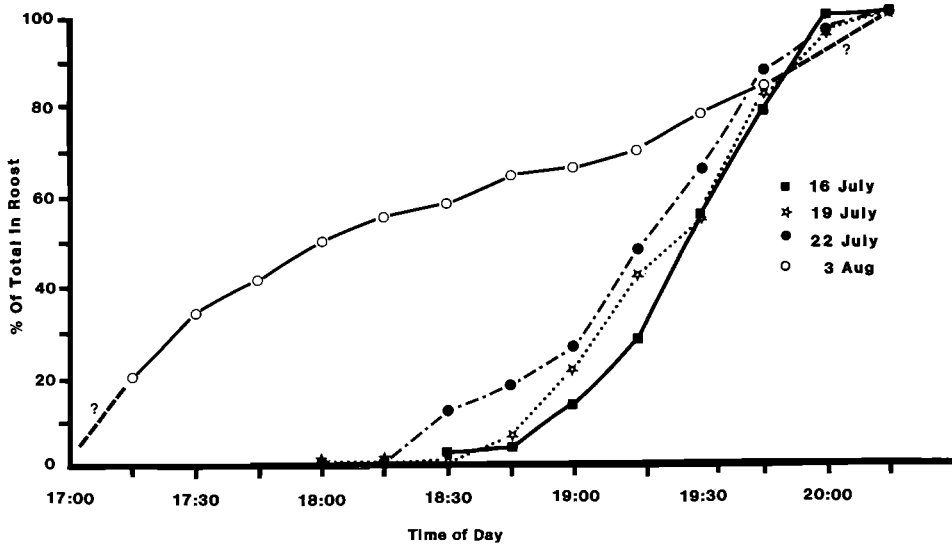


FIGURE 31. Schedule of Wilson's Phalaropes arriving at a nocturnal roost in 1982. Total counts were: 16 July, 33,755; 19 July, 31,985; 22 July, 42,320; 3 August, 10,847.

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

INTERACTIONS

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

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

cause the great bulk of fattening adults impaired their agility.

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

FOOD AND FORAGING

FOOD

As noted above, brine shrimp are found throughout the lake and during the phalaropes' migration period occur in densities of 30,000 to 90,000/m² lakewide (Fig. 12). Brine flies are commonest near shore. Although both are consumed by phalaropes, differences in the distribution and behavior of male, female, and juvenile phalaropes resulted in important differences in the birds' diets. Throughout their stay adult females fed mainly on brine shrimp (Fig. 33), which occurred in 75% of the stomachs, whereas brine flies were found in 58%. In adult males the situation was reversed; brine flies occurred in 76% of samples, shrimp in 57%. Other food items occurred in trivial quantities. In a small sample juveniles fed only on brine flies. Gravel was present in most samples (Table 7).

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



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

tion; for females the division point was 20 July, for males 31 July. In each sex the percentage of shrimp by volume increased in the latter part of the season, females from 60.3% to 78.6%, males from 35.4% to 43.1%. Although these shifts were not statistically significant (χ^2 test) because of the great variability among samples, they paralleled behavioral data showing the phalaropes' increasing use of offshore habitats, and I have no doubt of their biological reality. In each half of the sea-

son shrimp comprised a greater percentage of the diet of females than of males. Overall, shrimp comprised 66% by volume of prey taken by females vs 38% by males ($\chi^2 = 7.59$, $P < .01$).

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

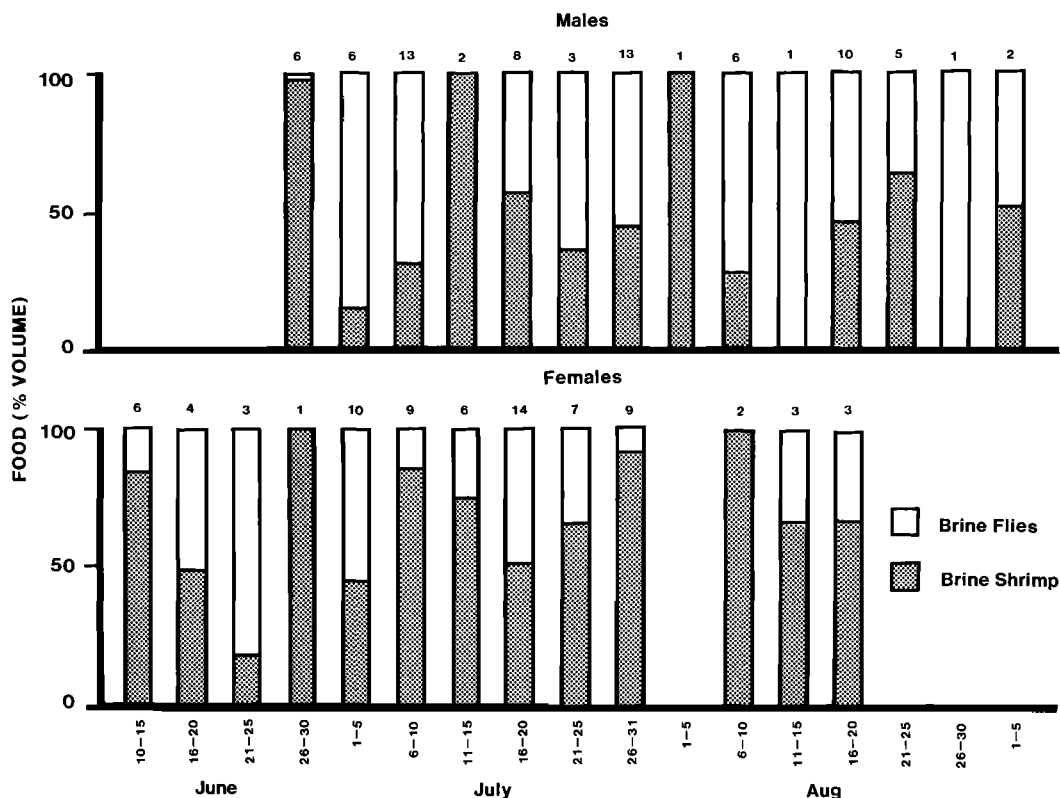


FIGURE 33. Seasonal changes in food (% volume) of Wilson's Phalaropes at Mono Lake, California.

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

FORAGING BEHAVIOR

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

employed at Mono Lake, evidently because the abundance of food at the surface made it unnecessary.

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

MASS

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

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

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

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

* Based on 1980-1981 data only.

more than doubling their bulk. Most of the increase occurred in the last half of the season (2.0 g/day on a population basis), when birds were hyperphagic, rather than in the first several weeks when they were molting and spending much time

in roosts (~0.4 g/day) (Fig. 36). By early August, females weighing 100 g were common (maximum 123, 14 August), and by mid-August many males exceeded 90 g (maximum 103 g, 28 August).

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

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

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



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



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

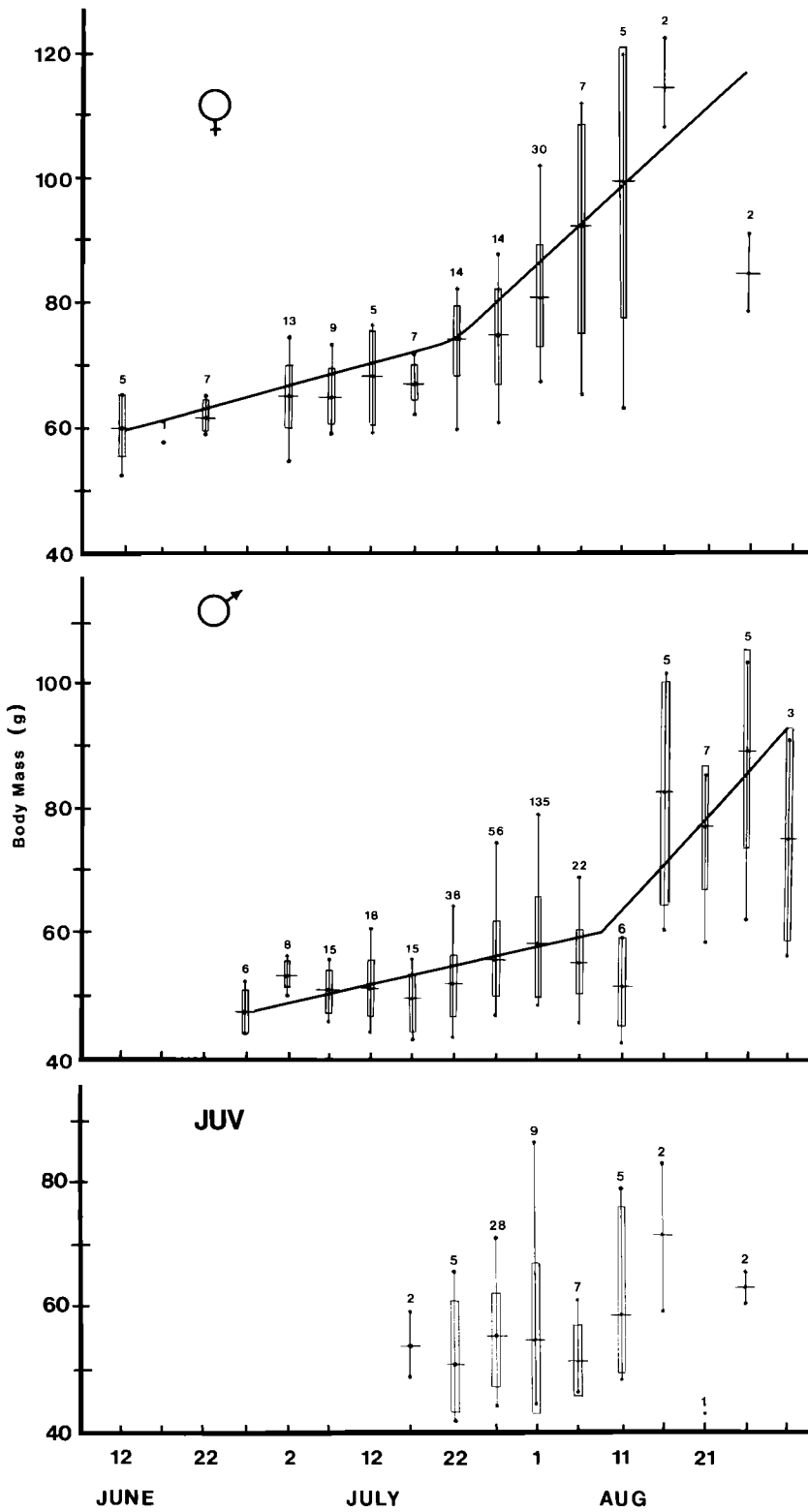


FIGURE 36. Body mass (range, mean \pm 1 SD) of adult females, adult males, and juvenile Wilson's Phalaropes. Lines are fitted by eye.

SAMPLING

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

MOLT

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

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

MORTALITY

Mortality at Mono Lake was barely detectable. Only two phalaropes were found in six seasons (1981–1986), despite intensive beached bird censuses (53, covering 516 km) from early June

through early September 1981–1984. Losses to predators were trivial. Coyotes cannot capture healthy phalaropes, and avian predators (p. 29) were too rare to pose a threat, although Prairie Falcons, which are resident, and Northern Harriers (*Circus cyaneus*), which appear in the first week of August, probably captured a few each year. The only attack I witnessed, by a harrier on a swimming phalarope, was unsuccessful.

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

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

MIGRATION

DEPARTURE FROM MONO LAKE

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

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

CONCENTRATION POINTS

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

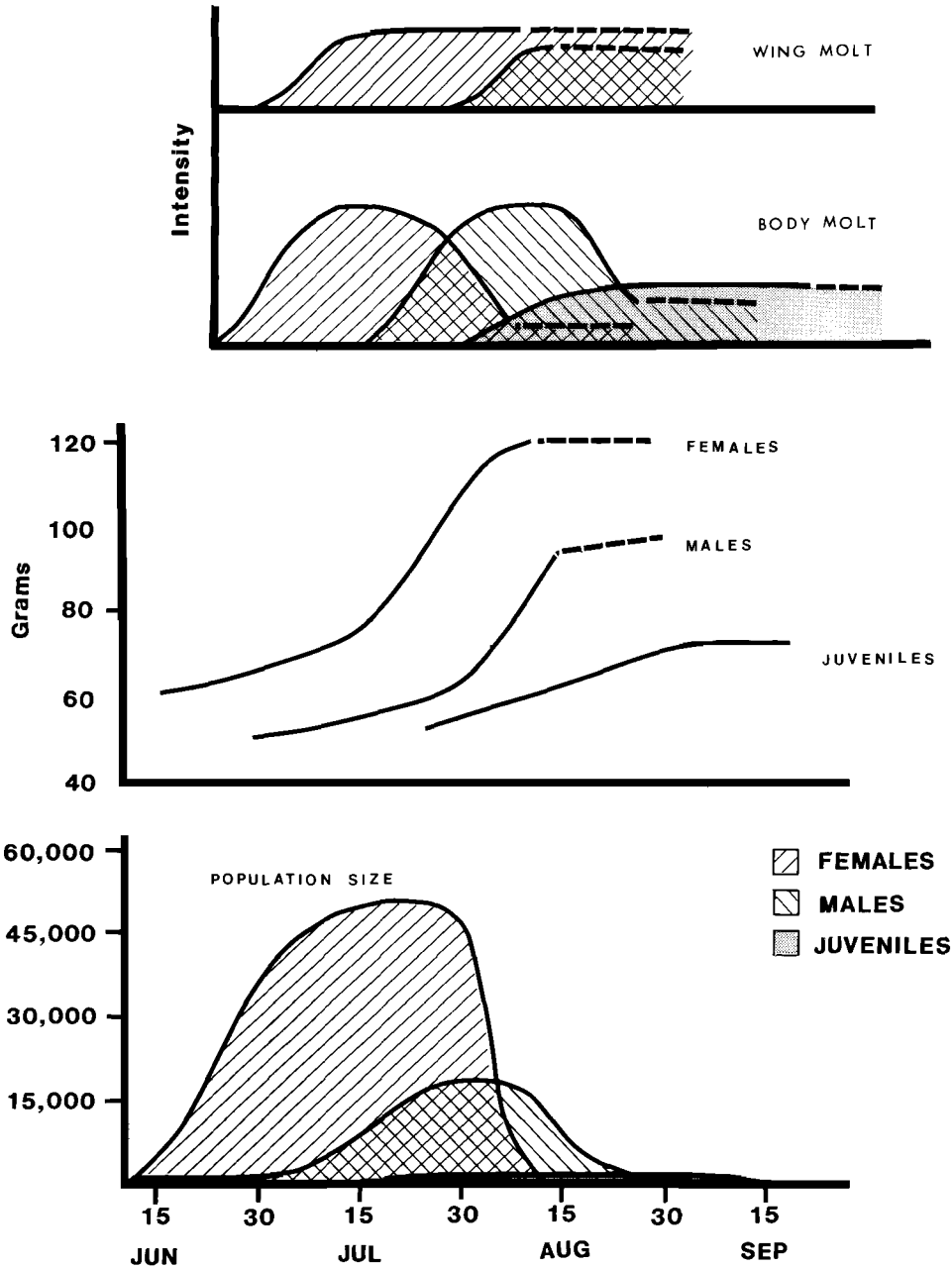


FIGURE 37. A synopsis of the major events in the annual cycle of Wilson's Phalaropes at Mono Lake, California.

early July 1987, and mid-July-early August 1987, my colleagues and I (Jehl et al. 1987, Jehl and Chase, unpubl.) sought other concentration points in the western United States and southern Canada. These surveys were done in as brief a period as possible to minimize the possibility of duplicate counts arising from movements between

staging areas. Localities holding more than 1000 individuals (Table 8, Figs. 38, 39), along with information on areas that have sometimes held significant concentrations are discussed below. With one exception (American Falls Reservoir, Idaho), these were at saline or alkaline lakes that lacked fish.

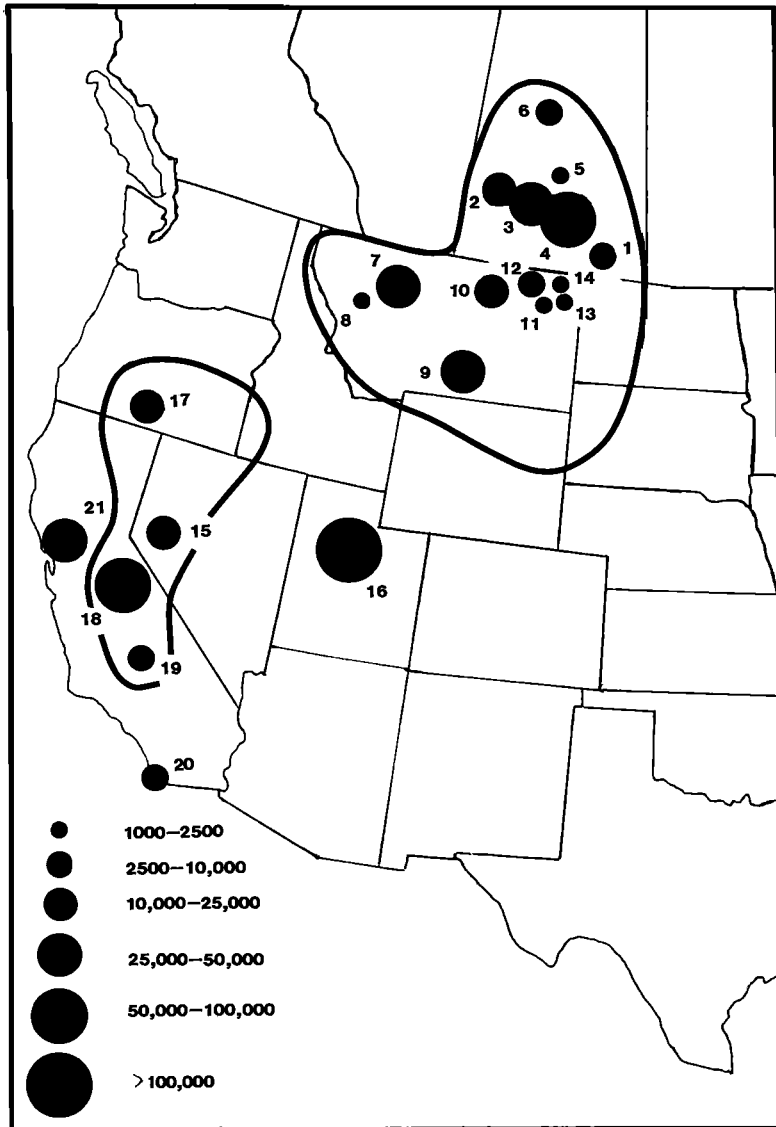


FIGURE 38. Localities at which >1000 Wilson's Phalaropes were encountered on surveys in July 1986. Outlines show approximate limits of major surveys. SASKATCHEWAN: (1) E. Coteau Lake, (2) Reed Lake, (3) Chaplin Lake, (4) Old Wives Lake, (5) Last Mountain Lake, (6) Big Quill Lake. MONTANA: (7) Benton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

California

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

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

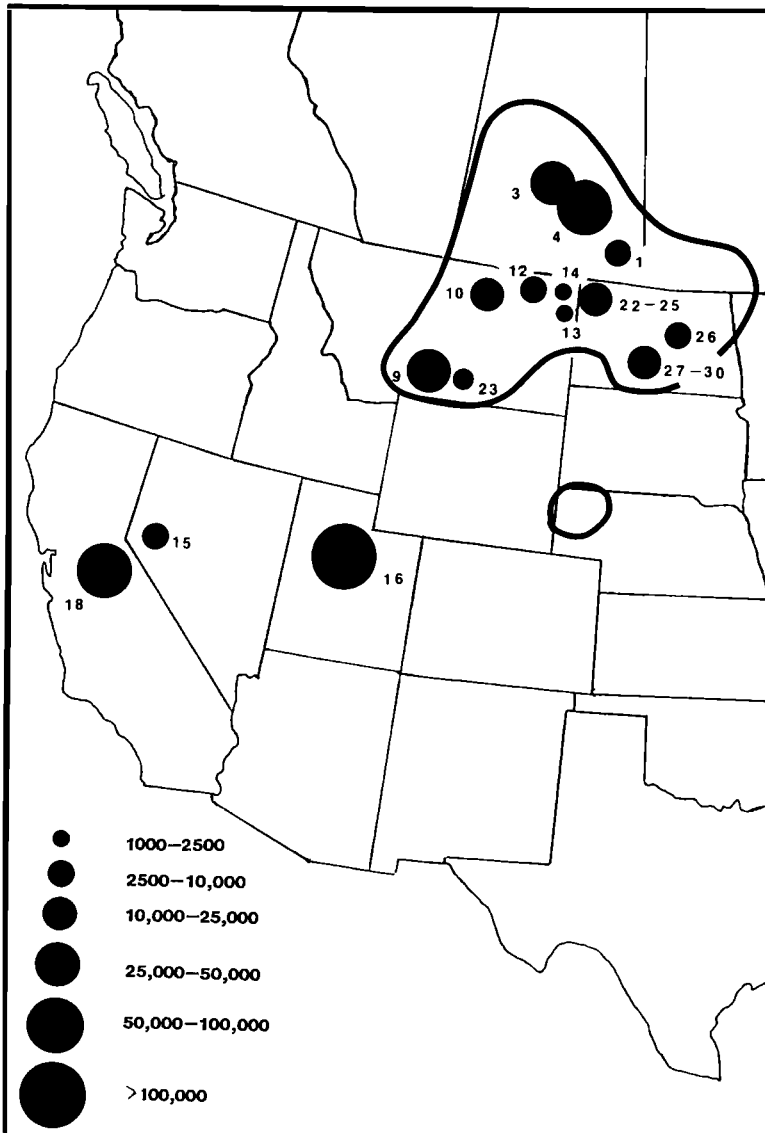


FIGURE 39. Localities at which >1000 Wilson's Phalaropes were encountered on surveys in July 1987. Outlines show approximate limits of major surveys. SASKATCHEWAN: (1) E. Coteau Lake, (3) Chaplin Lake, (4) Old Wives Lake. MONTANA: (9) Big Lake, (10) Bowdoin NWR/Medicine Lake NWR, (12) Round Lake, (13)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

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

Oregon

Lake Abert, in south-central Oregon, is a major concentration point. On 15 July 1982, I saw

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

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

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

TABLE 8
CONTINUED

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

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

^b Numbered lakes are shown in Figures 38 and 39.

^c Average annual peak (P. Kelly pers. comm.).

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

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

Nevada

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

Utah

Great Salt Lake is the largest staging area for Wilson's Phalaropes in the world. Although some early estimates "have placed their numbers in the millions" (N. Nelson pers. comm. to D. Paul), aerial surveys in late July 1982, which were the first attempt to quantify numbers, indicated peak counts of 400,000–500,000. Ecological changes associated with the lake's subsequent rise in the 1980s resulted in major

distributional changes. As with the grebes (p. 32), in 1982 virtually all phalaropes were on the south arm; the north arm was too salty to sustain invertebrates. By 1986 the south arm had freshened too greatly to be attractive, but the north arm was rejuvenated and held nearly all of the flock of 387,000. The same was true in 1987, when peak numbers in late July reached 194,000.

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

Idaho

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

Montana

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

Saskatchewan

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

Kansas

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

North Dakota

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

THE NUMBER OF WILSON'S PHALAROPES

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

In mid-July 1987, ~417,000 phalaropes were located, of which 51,400 (12.3%) were at Mono Lake. Allowing for the facts that (1) the area surveyed was much smaller than in 1986, (2) some major staging areas (e.g., San Francisco Bay, Lake Abert) were not checked, and (3) de-

parture from the Prairie Provinces and Great Plains was relatively early owing to poor breeding conditions (Chase pers. comm.), the adult population and the proportion staging at Mono Lake probably did not differ much from that found in 1986.

MIGRATION ROUTES: A SYNTHESIS

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

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

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

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

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

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

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

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

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

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

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

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

FLIGHT RANGE

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

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

where F is the weight of fat in grams, and S is

the flight speed in miles/hour. FM, flight metabolism in kcal/h, is determined from:

$$\log FM = \log 37.152 + 0.744 \log W + 0.074$$

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

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

THE USE OF SALINE LAKES

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