STATUS, CHRONOLOGY, AND ECOLOGY OF NESTING STORM PETRELS IN NORTHWESTERN CALIFORNIA

STANLEY W. HARRIS
Humboldt State University
Arcata, California

Information on storm petrels of the Pacific Coast of North America includes reports by early egg and specimen collectors of pelagic observations, beach-wrecked specimens, cursory visits to nesting islands, and taxonomic discussions. Aside from accounts of nest sites and nesting islands, little basic biological information is available. Osborne and Reynolds (1971) surveyed nesting populations of sea birds along the California coast and Osborne (1972) intensively studied nesting rocks from the Oregon border to Cape Mendocino, Humboldt County, California. The present study was conducted to document the status, chronology, and ecology of nesting storm petrels in northern California.

STUDY AREA

Most work was on Little River Rock, 2 miles S of Trinidad, Humboldt County, California, 41°02′ N, 124°09′ W, with occasional visits to other nesting islands in northwestern California. With the possible exception of Castle Island, Del Norte County, Little River Rock supports the largest population of nesting Leach's Storm Petrels (*Oceanodroma leucorhoa*) and Fork-tailed Storm Petrels (*O. furcata*) in California. Little River Rock is a basalt sea stack, about one-quarter mile offshore, with a surface area at sea level of about 2 acres. Mostly bare rock, it has two nearly vertical peaks interconnected by a saddle of ancient marine deposits of sand and shells. The east peak is a conical dome about 75 ft in diameter and 75 ft high. The west peak is 126 ft high, has a flat triangular top about 50 ft wide, and the west side drops precipitously 40 ft to a rock and soil-covered slope about 30 × 75 ft in size. Intensive studies were confined to accessible areas of the west peak.

The rock has four general vegetation types. Coastal brushfields of *Baccharis pilularis* 2 ft high cover about half the west peak and a mixture of *Baccharis, Gaultheria shallon, Garrya elliptica,* and *Rhus diversiloba* to 4 ft high covers most of the east peak. The shrubs have an understory of grasses. The soil is 6–8 inches deep with a loose texture, allowing easy excavation by burrowing petrels. Portions of the east peak and half the top and the entire scree slope of the west peak are vegetated predominantly by stands of *Festuca californica, Elymus mollis, Fragaria chiloensis,* and *Scrophularia californica.* These areas have a thick sod and rocky soils to 9 inches deep. Steep rocky slopes with poor soil and moisture retention support growths dominated by *Dudleya farinosa, Sedum spathulifolium, Mesembryanthemum chilense,* and *Plantago lanceolata.* The soil in these areas ranges from a few plant fragments to mixtures of organic and rock particles 3 inches deep. Some sheltered pockets hold clumps of *Elymus mollis* and succulents. *Polypodium scouleri* clings to the top of the vertical east and northeast sides of both peaks. With the exception of Castle Island which lacks coastal brushfields, these vegetation types are found on all islands used by petrels in northwestern California.

Besides petrels, Little River Rock was a nesting site for 25–30 pairs of Western Gulls (*Larus occidentalis*), 15–20 pairs of Pigeon Guillemots (*Cepphus columba*), 5–10 pairs of Pelagic Cormorants (*Phalacrocorax pelagicus*), 1 pair of Black Oystercatchers (*Haematopus bachmani*), 2–4 pairs of feral Rock Doves (*Columba livia*), and 2 pairs of Song Sparrows (*Melospiza melodia*). Tufted Puffins (*Lunda cirrhata*) and Rhinoceros Auklets (*Cerorhinca monocerata*) were flushed from the rock or the immediate waters in two summers and these species may have attempted to nest on the rock.

Gulls were especially common in their nesting season when they were the major predator on petrels. Other potential predators on petrels were a Great Horned Owl (*Bubo virginianus*), seen to fly over the island once in summer, and a Peregrine Falcon (*Falco peregrinus*), flushed from the rock once in January. One Western Garter Snake (*Thamnophis elegans*) was removed from the island in 1965. Besides petrel eggs, other potential prey for the snake included a large population of Banana Slugs (*Ariolimax columbianus*) and various insects. One Slender Salamander (*Batrachoceps attenuotus*) was found in a petrel burrow in May 1965. Access to Little River Rock by mammals could be gained by running across about one-quarter mile of exposed beach and rocks during very low tides or by swimming. Remains of dead petrels were found once, indicating a mammal may have visited the island. That mammals do visit some local islands occasionally was substantiated by Osborne (1972) who found 60 dead petrels apparently killed by a Mink (*Mustela vison*) on an island that could be reached only by swimming at least 200 yards.

METHODS

Between 23 October 1964 and 3 May 1969, 36 visits were made to Little River Rock. Twenty-nine were overnight visits and one to four mist nets were operated on 27 nights in every month except November. Occasional visits were made to other islands.

Most data are based on the times of capture or recapture in mist nets of 5569 Leach's Storm Petrels and 122 Fork-tailed Storm Petrels, the examination of these birds and their burrows, and the literature, particularly the unpublished field notes of C. I. Clay.

Three locations were available where nets could be set close to nesting areas to avoid trampling burrows, soil, or vegetation, and also to avoid exposing assistants to the danger of falling from cliffs. One very full 3-shelf net (42 ft long) and one 4-shelf net (36 ft long) were placed along two sides of the triangular top of the west peak on 19 visits. The second location, operated on 19 visits, held one

4-shelf net along a bare rock ridge which was 4–5 ft wide, 30 ft long, and on a 30-degree slope about 30 ft down the nearly vertical south side of the island. The uphill end of this net was only 45 ft from the closest of the two nets on top of the island. The third location, operated seven times, held a 4-shelf net (30 ft long) set along a relatively level bare rock ridge at approximately the same elevation and about 100 ft away from the south ridge location.

Black nets with 2⅜-inch stretched meshes were used. Because birds tended to bounce off nets stretched taut by wind, moisture, or the weight of caught birds, three nets were modified for maximum fullness. Two 7 × 45-ft nets were sewed together vertically, even-numbered horizontal support strings removed, and the combined net collapsed to 7–8 vertical ft and shortened to 30–36 ft.

Nets were set before sunset and removed after sunrise. The number of net-hours was based on the time between local sunset and local sunrise. Published sunrise and moonrise times were delayed by 30 min to adjust for the height of the coastal mountains.

Each banding location was worked by a crew of two to four people. One person removed birds from one net, placed them in cloth bags, and delivered the bags to banders. Each bag was tagged with time of delivery and net of capture. Battery-operated headlights provided illumination.

Most nights had partly to overcast skys, no precipitation except dew, and temperatures between 40° and 50°F. Often there was an onshore breeze after sunset and an offshore breeze before dawn. Wind was sufficient to reduce net efficiency part of the time on about half the visits. There was one night of intermittent drizzle which developed into steady rain at 04:00 and 3 nights were very cold with frosty mornings.

Nets tended by experienced crew members caught 20–80% more birds than those tended by beginners because experienced workers were more efficient in removing birds from nets.

STORM PETRELS IN NORTHWESTERN CALIFORNIA

Status. Storm petrels have been recorded nesting or possibly nesting at 11 sites between the Oregon border and Cape Mendocino, but presently are found on only 5 sites and possibly on 3 others (table 1). Leach's Storm Petrel nests commonly south to Little River Rock and the rock is the southernmost breeding station for the Fork-tailed Storm Petrel (Clay 1916; A.O.U. 1957; present study). The Ashy Storm Petrel (*O. homochroa*) rarely straggles north to the waters off northwest California in fall. Osborne (1972) believed that petrel colonies on Green Rock, Off-Trinidad Rock, and Blank Rock, Humboldt County, were reduced or eliminated because of soil erosion caused by the activities of early collectors and the removal of vegetation by nesting Common Murres (*Uria aalge*) and Brandt's Cormorants (*Phalacrocorax penicillatus*). The major colony on Whaler Island, Del Norte County, was destroyed in the 1930s and 1940s when the island was quarried and incorporated into the Crescent City harbor breakwater, providing access to mammalian predators. Clay (unpubl. data) found a few petrels nesting there in 1939 after the original breakwater had been in place a short time, but Osborne (1972) found none in 1969–72.

Although the many rocks along the Mendocino County coast are poorly studied, Osborne and Reynolds (1971) did not report nesting petrels between Little River Rock, Humboldt County, and Bird Rock, Marin County. Emerson's (1906) reference to Leach's Storm Petrel nesting in Mendocino County is probably an error and should refer to either Humboldt or Del Norte County. To the south, Leach's Storm Petrel nests on the Farallon Islands (Grinnell and Miller 1944, race *beali*) and off the Baja California coast (Grinnell and Miller 1944; A.O.U. 1957, races *willetti*, *chapmani*, and *socorroensis*). The Ashy Storm Petrel nests on the Farallon Islands west of San Francisco, on San Miguel and Santa Cruz Islands near Santa Barbara (Grinnell and Miller 1944) and on Bird Rock, Marin County (Osborne, pers. comm.).

Population estimates and selection of nesting cover. On Little River Rock, Leach's Storm Petrels nested everywhere burrows could be dug, but rarely in rock depressions behind screens of succulent vegetation. A few nested in artificial burrows of old automobile tires. I estimated 2500–3000 burrow openings were present on the west half of the island in April 1965. Extrapolating Yull's (unpubl. data) sampling of soil depths and burrow densities to estimates of the vegetation for the entire island yields an estimate of 6590 burrow openings in 1966 (2640 in brushfields, 2800 in grass and forbs, and 1150 in succulents and ferns). These crude estimates indicate a population level which apparently had reached near saturation for burrows. All available soil was riddled with burrows by early summer each year.

Occupancy rates are unknown, but some burrows were short, blocked by rock, and did not have nest chambers. Other burrow systems had multiple entrances and/or nest chambers. I judge the island supported possibly 5000 pairs of Leach's Storm Petrels (table 1), or one pair for every 2 ft^2 of vegetation, equalling Dawson's (1908) estimate of 40,000 birds in one acre on an island in Washington.

Based on burrow densities, petrels preferred to nest in short coastal brushfields (1.2 burrows/ft^2) with loose, easily dug soils. Burrows in grass sod (0.8/ft^2), while less vulnerable to collapse, were more difficult for petrels to excavate. The low density in succulents and

TABLE 1. Status of nesting storm petrels in northwestern California.[a]

Site	Historical status		1965–72 status	
	Leach's	Fork-tailed	Leach's	Fork-tailed
Del Norte County				
Castle Island	Many	Few	2500	Few
Whaler Island	Many	Few	None	None
Humboldt County				
Green Rock	Present	Present	1 dead bird	3
Pewetole Island	No data	No data	Odor of petrel present, 1968, no birds seen.	
Off-Trinidad Rock	12	Present	None	None
Blank Rock	Few	Few	None	None
Prisoner Rock	Few	None	75	6 dead birds
Split Rock	No data	No data	Odor of petrel present, 1965, 1968, no birds seen.	
Button Rock	No data	No data	1 in 1965	None
Tepona Rock	No data	No data	300	1
Little River Rock	Present	No data	5000	100

[a] Numbers are estimated or observed number of nesting pairs. Data from Clay (unpubl. data, 1916), Dawson (1923), Osborne (1972), and Present Study.

ferns (0.3/ft^2) reflects poor soil development under such cover.

Only about two Fork-tails were netted for every 100 Leach's caught. At this rate, and based on an estimated population of 5000 pairs of Leach's Storm Petrels, the nesting population of Fork-tailed Storm Petrels on Little River Rock did not exceed 100 pairs (table 1).

Fork-tails nested in natural rock crevices or similar cavities. No Fork-tails were found during the examination of several hundred burrows in soil. Osborne (1972) recorded a Fork-tail nesting in a rock depression behind a growth of succulents on Tepona Rock and he found three nests in old Tufted Puffin burrows on Green Rock. Clay (unpubl. data, 1916, 1925) collected Fork-tails and their eggs on Whaler Island mostly by "turning over boulders" in rock piles. Dawson (1923) found this species in a rock crevice on Blank Rock in 1916, and Clay (1916) stated that others also were collected there in similar locations. Howell (1920) found a Fork-tail on Whaler Island in a separate pocket of the same burrow with a Leach's Storm Petrel, but stated that the Fork-tailed Storm Petrel preferred to nest at the edges of banks where small stones were present or between piles of rocks, while Leach's Storm Petrel preferred the "softest dirt."

Northward, Fork-tails have been recorded in burrows in soil. Finley (1902, 1905) found them among, and sometimes in, the same burrows as Leach's Storm Petrel. In Washington and Alaska, Grinnell (1897), McGregor (1906), Willett (1914), Heath (1915), Bent (1922), and Richardson (1960) found both species in burrows. Gabrielson and Lincoln (1959) stated that Fork-tails nest in burrows in soft soil, but at Amukta they nest in crevices in "clinker-type" lava. Stejneger (1885) found them in deep holes in basaltic rocks.

Although the two species overlap in their use of nest sites, one way the Fork-tailed Storm Petrel appears to avoid direct competition with Leach's Storm Petrel in California is by selecting rock crevices as nest sites. Both species sometimes gather roots or other plant debris into a form of nest. There was great individual variation in this respect, and most Fork-tailed Storm Petrel eggs found in this study were on bare rock in the nest cavity. One Fork-tail nest found by Osborne on Green Rock in an old puffin burrow consisted mostly of coarse grass stems.

THE NESTING SEASON OF LEACH'S STORM PETREL

Landfall, burrow renovation, and courtship. Using capture rates on moonless nights as an index of activity, it is clear that Leach's Storm Petrel was virtually absent from Little River Rock between late October and early February (table 2). No petrels were seen or heard during the night of 23–24 October 1964 when no nets were operated (Osborne, pers. comm.). Only one burrow in the earliest stages of excavation was seen 19 December 1965 and no Leach's Storm Petrels were caught in two nets that night.

Renovation and construction of burrows began on a minor, intermittent scale in January.

TABLE 2. Number of Leach's Storm Petrels netted per net-hour, Little River Rock, Humboldt County, California, 1965–69.

Moonless nights		Moonlit nights	
Date	Birds per net-hour	Date	Birds per net-hour
19 Jan 1966	0	—	—
27 Feb 1965	13.6	5 Mar 1966	0.8
—	—	18 Mar 1968	5.8
3 Apr 1965	12.2	1 Apr 1966	7.5
23 Apr 1966	13.0	13 Apr 1968	1.0
27 Apr 1968	23.8[a]	—	—
1 May 1965	13.2	3 May 1969	4.7
13 May 1967	17.2[a]	—	—
5 Jun 1965	13.7	13 Jun 1968	30.0[a]
23 Jun 1966	14.4	20 Jun 1967	27.5[a]
19 Jul 1966	7.8	6 Jul 1966	25.0[a]
23 Jul 1968	11.4[a]	22 Jul 1967	10.0
18 Aug 1966	5.7	—	—
3 Sep 1967	3.3	9 Sep 1965	3.5
25 Sep 1965	2.4	—	—
14 Oct 1966	0.2	—	—
23 Oct 1965	0.2	—	—
19 Dec 1965	0	—	—

[a] Averages for these dates not entirely comparable with other dates because only net operated was run by an experienced crew member.

Approximately 30 "early burrow scratchings" were seen 8 January 1967, and "a few early digging signs" were seen 19 January 1966, 27 January 1968, and 5 February 1966. No Leach's Storm Petrels were caught in three nets during the night of 19–20 January 1966. It is possible that some of the early diggings were the work of Fork-tailed Storm Petrels since two Fork-tails were netted in December and one in January.

By mid-February, Leach's Storm Petrels began to visit the island regularly on warm dark nights, and by early March, some burrows were nearly completed. On the night of 12–13 February 1965, a heavy flight of petrels arrived only after moonset at 04:00. A few incomplete burrows were present and three birds were flushed during daylight of 13 February. On 18 February 1966, a "considerable" number of incomplete, moderately deep burrows was present and on 24 February 1967 the brushfields had been "heavily" dug but almost no recent digging was noted in grassy areas. The grassy top of nearby Tepona Rock was "heavily dug-riddled" with some completed burrows on 25 February 1968.

This is much earlier than first landfall dates reported for North Atlantic petrels (Gross 1935; Gross 1947; Palmer 1962; Waters 1964) and is earlier than the late April-early May landfalls suggested for the Aleutian Islands (Palmer 1962) and Japan (Fennell 1953). Clay (1925) found some pairs of Leach's Storm Petrels in burrows on 22 March, and Thoreson (1960) suggested the Ashy Storm Petrel may be active on the Farallon Islands all year.

March to May was a time of courtship and intensive burrow construction. Courtship of Leach's Storm Petrel included conspicuous and vocal aerial displays; many birds were netted during the courtship period. The breeding status of these "flighting" birds was uncertain and it is possible that many nonbreeders were present. Certainly many birds come to land only irregularly at this time as all burrows were not visited every night and band return rates were low. Thus, during the night of 18–19 March 1968 birds entered only 7 of 37 marked burrows and they entered only 36 of 125 burrows on the night of 3–4 April 1965.

Recapture rates of netted birds rarely exceeded 6% from month to month. Only 15.2% of the Leach's Storm Petrels banded were later recovered or recaptured (684 birds with recoveries or returns of 4483 banded prior to 3 May 1969). This low return rate prevailed despite the setting of nets on top of nesting areas. A possible reason for a low return of netted birds could be that the spring flights contain many nonbreeders that visit several islands in courtship. No nets were operated on other islands, but one dead Leach's Storm Petrel, originally banded on Little River Rock on 13 June 1968, was found on Prisoner Rock, 2 miles to the north in the summer of 1972. If petrels did commonly visit other nesting colonies in large numbers during spring flights, I would have expected them to visit various portions of Little River Rock on subsequent nights. To test this postulate, I analyzed the returns obtained between locations on Little River Rock and found little interchange between locations at any season. More than 90% (range 90–99) of the recaptures were of birds originally banded in the same nets, even though the distance between the top nets and the south ridge net was only 45–50 ft in a straight line and 30 ft vertically. I conclude that the birds visited very specific portions of the rock and did not wander about the island as might be expected of birds traveling from colony to colony. I cannot explain what became of the large segment of banded birds not recaptured except that my once-a-month banding was not intensive enough or that many nonbreeders made only rare visits to the island. I do not believe that large numbers visited other colonies regularly.

Huntington (1963) suggested that colonies were interdependent concerning recruitment of breeders but such recruitment was mainly from birds banded as nestlings.

The main call of Leach's Storm Petrel is a "cackle," usually given during "flighting," but also heard in this study from burrows in both daylight and at night, from birds hanging in nets, being removed from nets, and in holding bags. A second call, a "purring or churring," is given in the burrow and is said to be uttered by a mated or mating pair (Gross 1935). Both types of calls were heard as early as mid-February and as late as mid-July, and the "cackle" was heard occasionally until late September. Some digging continued well into July, long after breeders had eggs, and it is possible that some nonbreeders frequented the island intermittently in one or more years for pair formation and territory establishment.

Adults frequently were found in burrows in daytime in February–June and pairs occurred in burrows regularly from 22 March (Clay 1925) to 5 June. These pairs were never found in burrows containing eggs or young.

Egg-laying and incubation. The first eggs of Leach's Storm Petrel usually appeared on Little River Rock in mid-May. On 13 May 1967, I examined 10 burrows and found two fresh eggs under incubation. That night, 7 of 146 Leach's Storm Petrels netted had eggs present in their cloacas. Of eight dates in May when some burrows were examined by Clay (unpubl. data) or me, eggs were found only twice.

A comparison of weight and plumage data with growth curves for Leach's Storm Petrel (Gross 1935; Palmer 1962) and *O. castro* (Allen 1962; Harris 1969) revealed a crude picture of hatching and egg-laying dates for 62 young (table 3). The peak of egg-laying was in late May and early June, and by mid- to late June, most eggs were laid (table 3). This agrees generally with the scattered reports of fresh eggs on other California-Oregon colonies (Finley 1902, 1905; Dawson 1911; Howell 1920) and is 2–3 weeks earlier than colonies in Alaska (Grinnell 1897; Willett 1914; Heath 1915) and the North Atlantic (Gross 1947). Eggs were found on all nine dates in June when burrows were checked by Clay (unpubl. data) or me. Birds carrying eggs in their cloacas were netted on the nights of 5–6 June 1965 and 13–14 June 1967. The latest "fresh" eggs were three found by Clay (unpubl. data) on Prisoner Rock on 24 June 1912. Back-dating young in burrows indicated that the latest eggs were laid in early July (table 3).

TABLE 3. Estimated egg-laying and hatching dates for 62 immature Leach's Storm Petrels in burrows, Little River Rock, Humboldt County, California.

Estimated week of egg-laying[a]	Estimated week of hatching[b]	No. of birds examined[c]
May 6–12	June 16–22	1
13–20	23–30	3
21–27	July 1– 7	26
28– 3	8–14	11
June 4–10	15–21	7
11–17	22–28	5
18–24	29– 4	6
25– 1	Aug 5–11	2
July 2– 8	12–18	1

[a] Egg-laying dates calculated by adjusting for a 41–42 day incubation period (Palmer 1962) from estimated hatching dates.
[b] Hatching dates estimated by comparing weights and notes on feather growth to data in Gross (1935), Allen (1962), Palmer (1962), and Harris (1969).
[c] Birds were examined as follows: 6 July 1966 (3 birds); 22 July 1967 (4 birds); 23 July 1968 (29 birds); 3 September 1967 (25 birds); 9 September 1965 (1 bird).

Large numbers of birds were netted at night throughout the egg-laying and incubation period (table 2).

Hatching, growth of young, and fledging. The first young hatched in late June (table 3). Clay (unpubl. data) and Jewett (1921) recorded "just hatched" young on 2–4 July. The peak of hatching occurred in early to mid-July. On 23 July 1968, 6 of 38 occupied burrows on Little River Rock held incubating adults and 32 held young petrels, two being brooded by adults.

Immature petrels gain weight until they exceed the average adult weight of 40–42 g (Huntington 1963; Harris 1969). The heaviest young weighed 70 g and their weights steadily declined to about adult weight at fledging. Harris (1966, 1969) suggested that the accumulation of fat by the young allows adults to leave colonies earlier than if they had to supply food regularly and that chicks have a better chance of survival if adults are forced to leave early because of food shortages. Petrels apparently continue to feed nestlings (Harris 1969) and do not desert them before fledging as do some shearwaters (Lockley 1930; Serventy 1958). In such an event, it does not seem likely that the main reason for fattening of chicks is to allow adults to leave early as Harris (1969) suggested. The peak weight seemed to be attained just as massive irruption of body feathers began and the decline in weight roughly coincided with the rapid development of body plumage and the completion of the growth of flight feathers. It is conceivable that fattening provides the necessary food reserves for the completion of immature feather growth at a time when

adults may need additional energy for their own molts (see later).

Young weighed about 6 g at hatching, and their eyes opened at 7–12 days (20 g). Pinfeathers appeared first on the wings and tail. These began to unsheath at 18–22 days (35–45 g). Some body feathers appeared about the same time but, except for those on the face, were hidden by persistent down for several weeks. The apparent order of feather irruption was rectrices and remiges, wing and tail coverts, breast and upper abdomen, head (beginning on face), hind neck, back, sides, mid-neck, rump, lower abdomen. The last down to wear off was on the lower abdomen. One fledgling netted on 9 September 1965 still had some down on its abdomen as did a fledgling found alive on a lawn in Arcata, California, on 15 September 1972. Several young had ticks present on the webs of their feet and on their faces when burrows were examined on 23 July 1968.

Assuming a fledging age of 65–75 days (Gross 1935; Harris 1969), the peak of fledging occurred in late August and during September. The latest young fledged in mid- to late October. A few adults in molt were netted in late October (table 2), suggesting that the latest young were still being fed.

Patterns of daily use—dark nights. From February through August on dark nights, the first Leach's Storm Petrels were netted 60–90 min after local sunset and about 30–60 min after "complete" darkness. Although occasional birds were observed 10–20 min before the first capture, I feel the records of netted birds accurately represent arrival times, the intensity of flight activity, and departure times. These arrival times generally agree with data reported by Ainslie and Atkinson (1937) for a British colony and by Harris (1969) for *O. castro*. They are substantially earlier relative to sunset than those reported by Waters (1964), who worked at a high latitude with a long period of post-sunset twilight.

Typically, flight activity at the island increased steadily to moderate levels in the first 2 hr, reaching a major peak between 01:30 and 03:00. There was little seasonal variation in these daily patterns, except that in September there was a slight tendency for the birds to come to land later at night. In contrast, Palmer (1962) stated that Leach's Storm Petrel comes to shore earlier as the season advances. All eight birds caught in October (two visits) were captured between 02:30 and 04:30.

The flight activity ended abruptly, often in a 15-min period, with only occasional stragglers caught later. The last bird was caught 130–150 min before local sunrise in February and March and 50–90 min before sunrise the rest of the season. Gross (1947) reported that calling stopped about 1 hr before dawn and Martin (1938) stated that petrels called from 22:00 to "near dawn." In every case but one, flight activity at the island ceased before we could detect any light in the eastern sky. These departure times agree reasonably well with those reported by Waters (1964).

The duration of flight activity varied seasonally, averaging about 8 hr in early spring and in fall, and about 6.5 hr in mid-June. This suggests that birds normally are active at colonies during the entire period of deep darkness when they are most secure from diurnal predators such as gulls and falcons. Petrels in high latitudes must compress their aerial displays and burrow excavations into a shorter time than birds in northern California, or adjust their activity schedules closer to sunset and sunrise. At the highest latitudes, where there are no dark nights in summer, nesting petrels probably cannot exist except under special conditions such as in the absence of diurnal predators. The colony on St. Lazaria Island at Sitka, Alaska (ca. 57° N) apparently is the most northerly breeding station in the Pacific for either Leach's Storm or Fork-tailed Storm Petrels. Gabrielson and Lincoln (1959) point out that there are no known colonies of petrels from the Shumagin Islands (55–56° N) eastward to St. Lazaria, even though the Gulf of Alaska coastline contains hundreds of apparently suitable islands and birds of both species are observed regularly at sea there. This coastline lies between 57° N and 60° N. In the North Atlantic, a few colonies of Leach's Storm Petrel occur as far north as southern Greenland, Iceland, and the Faeroe Islands (Bent 1922; Ainslie and Atkinson 1937; Fisher and Lockley 1954), considerably farther north than any of the Pacific colonies. Detailed studies of these colonies should reveal some interesting predator-prey relationships.

Patterns of daily use—moonlit nights. Palmer (1962) reported that moonlight delayed the arrival of petrels at nesting colonies. Ainslie and Atkinson (1937) said the birds came later and left earlier on moonlit nights but the amount of calling was "up to par." Gross (1935) suggested that on moonlit nights petrels were particularly vulnerable to predation by gulls and the petrels flew in to the

TABLE 4. Percent of netted Leach's Storm Petrels showing brood patch defeathering and refeathering, Little River Rock, Humboldt County, California.

Date	Sample size	Percent of birds caught					
		No patch	Being defeathered	Fully defeathered	0–½ refeathered	½-fully refeathered	Fully refeathered
18 Mar 68	225	56	39	5	0	0	0
13 Apr 68	15	47	40	13	0	0	0
23 Apr 66	547	56	20	24	0	0	0
27 Apr 68	337	15	63	22	0	0	0
3 May 69	89	35	58	7	0	0	0
13 May 67	146	3	18	79	0	0	0
13 Jun 68	287	4	3	66	18	6	2
20 Jun 67	274	0	0	58	31	12	0
6 Jul 66	236	0	0	51	–48–		1
19 Jul 66	248	0	0	18	57	25	0
23 Jul 68	116	0	0	9	77	12	2
18 Aug 66	98	0	0	2	64	34	0
3 Sep 67	29	0	0	0	31	52	17
14 Oct 66	3	0	0	0	0	67	33

nest as quickly and quietly as possible. While Lockley (1932) stated that *Hydrobates pelagicus* shunned the land "to some extent," Waters (1964) said that *H. pelagicus* was "particularly numerous" on moonlit nights. Harris (1969) reported that moonlight delayed the peak of activity of *O. castro* until just before dawn.

I found the major effect of moonlight was to reduce the number of birds netted in spring. Capture rates on moonlit nights ranged from less than one bird to eight per net hour compared to 12–17 on dark nights (table 2). Between February and May, the number of Leach's Storm Petrels netted on warm, clear, moonlit nights averaged 49% (range 19–68, 12 comparisons) of the number caught on warm, dark nights at the same locations in the same season. I believe the lower capture rates on moonlit nights accurately reflect less flight activity rather than greater success by birds in avoiding nets. I observed many fewer birds flying and calling on moonlit nights. Capture rates on moonlit nights in June and early July equalled or exceeded those on dark nights and it does not seem likely that birds would be more apt to avoid nets in spring than later.

On some bright nights early in the season, or on bright cold or bright stormy nights anytime in spring, Leach's Storm Petrels failed to come to land almost entirely. Thus, on the night of 12–13 February 1965, petrels came to land only after a 04:00 moonset. Intermittent rain plus bright moonlight appeared responsible for a poor flight on the night of 5–6 March 1966 when birds were netted at only 5% the rate experienced on 27 February 1965, a warm, dark night. Similarly, on 13–14 April 1968, a moonlit, clear, frosty night, only 15 Leach's Storm Petrels were netted in two nets, or 4–7% of the rate on dark nights in mid- to late April.

Moonlight also delayed the arrival of the birds nightly. Thus, on 1 April 1966 and 3 May 1969, 66–81% of the birds were netted in the last half of the night compared to 50–65% on dark nights in the same season and 42–66% were caught after 02:00 on moonlit nights compared to 23–38% on dark nights.

After eggs and young appeared, moonlight had little or no effect on the time of first arrival, the time of departure, the hourly distribution of captures, the intensity of calling, or the total number of birds netted. In June and July capture rates on moonlit nights equalled or exceeded those on dark nights (table 2). When eggs or young were present, adults came to the island to exchange incubation duties or feed young regardless of moon phase, but during the courtship-burrow renovation period, they stayed away more often on bright nights. Most gull pellets containing petrel remains were found in April and May, indicating a greater vulnerability of petrels during the pre-egg stage.

Brood patches. The pattern of brood patch molt supports the general chronology of nesting already developed (tables 3 and 4). The general sequence was one of brood patch defeathering through April, reaching a peak in late May and early June, and progressive refeathering of brood patches beginning in late June. By late July only 10–20% of the birds netted had not begun to refeather their brood patches (table 4), suggesting that 10–20% of the eggs still were being incubated. This agrees with data from 23 July 1968 when only

TABLE 5. Number of Fork-tailed Storm Petrels netted per net-night, Little River Rock, Humboldt County, California, 1965–69.

Season	Moonless nights			Moonlit nights		
	No. nights	No. net-nights	Birds per net-night	No. nights	No. net-nights	Birds per net-night
Feb–early April	3	8	3.7	2	8	0.6
Late April	2	6	5.5	1	2	5.5
May	2	5	2.6	1	2	1.5
June–August	6	14	0.3	2	2	1.0
September	2	5	3.2	1	2	0
October	2	4	0.5	No Data		
December–January	2	5	0.6	No Data		

6 of 38 (16%) occupied burrows still had eggs being incubated and 22 July 1967 when 1 of 5 (20%) occupied burrows had an egg. On 18 August 1966, the brood patches of nearly all birds were being refeathered (table 4), indicating that incubation was nearly complete and agreeing with estimated hatching dates developed from back-dating young birds in burrows (table 3).

THE NESTING SEASON OF THE FORK-TAILED STORM PETREL

Chronology of nesting. Because of the small number of Fork-tailed Storm Petrels netted, capture rates were expressed as birds per net-night and the data for several years were lumped seasonally (table 5). A few Fork-tails were present throughout the winter, reflecting the more northerly winter distribution of this species at sea compared to Leach's Storm Petrel (Bent 1922). By mid-February, Fork-tails visited the island in moderate numbers, and capture rates peaked in late April, declined in May, and reached the lowest annual levels in summer (table 5).

Fork-tailed Storm Petrels apparently nest 4–8 weeks earlier than Leach's Storm Petrels. Fork-tails had eggs far advanced in incubation or young in burrows on dates when Leach's Storm Petrels had only fresh eggs in Alaska (Grinnell 1898; Mailliard 1898; McGregor 1906; Willett 1914) and Washington (Richardson 1960). Bent's (1922) egg dates of 7 June–15 July for Oregon, Washington, and Alaska were simply repeated by Palmer (1962). Neither author mentioned earlier dates reported by Clay (1916, 1925) for northwestern California. Indeed, although an occasional egg may be laid later, the usual time of egg-laying in California for the Fork-tailed Storm Petrel is in April, coinciding with the peak of capture rates in mist nets on both dark and moonlit nights (table 5). "Fresh" or slightly incubated eggs were found locally on 18 March (present study), 22 March (Clay 1925), 1, 13, 27, and 29 April (present study), and 16 July (Howell 1920). Eggs "far advanced" were found on 13 May (present study) and 14 May (10 eggs, Clay unpubl. data, 1916; Dawson 1923). An egg found by Dawson (1923) on 18 June was "addled."

Brood patch development and capture rates in relation to moonlight both indicate an April peak of egg-laying. On 18 March 1968, 7 of 12 Fork-tails had fully defeathered brood patches. On 13 April 1968, a bright moonlit night, capture rates of Fork-tails equalled those on dark nights in the same season, suggesting that the Fork-tails had a great "need" to visit the island, perhaps to lay eggs or to exchange incubation duties. A similar pattern was exhibited by Leach's Storm Petrels during the peak of their egg-laying and incubation period in June and July (table 2). Nine of 11 Fork-tails examined on the night of 13–14 April 1968 had fully defeathered brood patches and one bird had an egg in its cloaca. That some non- or prebreeders visit the island on dark nights during these relatively heavy April flights is indicated by data for 23 April 1966 and 27 April 1968 when about half the birds did not show any brood patch development. The rapid decline in capture rates during May and the very low rates in summer indicate that most such nonbreeders abandon the island after a short spring period of "flighting."

We never detected flight calling attributable to Fork-tailed Storm Petrels, but such calls could have been overwhelmed by the many calls of Leach's Storm Petrels on most nights. The only calls we heard Fork-tails utter were harsh distress calls given when they were handled.

Assuming 40–42 day incubation and 70–75 day nestling periods (based on similar data for Leach's Storm Petrel), the earliest Fork-tails would hatch in early May and fledge in mid-July. With a mid-April peak of egg-laying, the peak of hatching would occur in late May and the peak of fledging in early August.

TABLE 6. Temporal distribution of netted Fork-tailed Storm Petrels, Little River Rock, Humboldt County, California, 1965–69.

Time caught	Moonless nights (n = 17)			Moonlit nights (n = 9)		
	Total birds caught	No. per net-night	Percent of total	Total birds caught	No. per net-night	Percent of total
Before 20:00	3	0.2	3	0	0	0
20:00–22:00	38	2.2	38	1	0.1	5
22:00–24:00	42	2.5	41	8	0.9	38
00:00–02:00	15	0.9	15	10	1.1	47
02:00–04:00	3	0.2	3	2	0.2	10
After 04:00	0	0	0	0	0	0
Total	101	6.0		21	2.3	

Clay (unpubl. data) collected a young Fork-tail on 19 May 1935 that he recorded as being more than 8 inches long. Other young of various ages were found in June and July by Clay (unpubl. data, 1916), Howell (1920), and F. J. Smith (unpubl. specimen). Howell (1920) found three young "one-half to full grown" on Whaler Island on 16 July 1919. Clay (unpubl. data), collecting on Castle Island from 14 to 24 July 1917, found only two Fork-tailed Storm Petrel nests, both containing young on 19 July. A newly fledged Fork-tailed Storm Petrel was found dead on shore at Trinidad on 6 August 1972.

Daily patterns of use. Fork-tailed Storm Petrels visited the island early at night. Combining all dark nights, 41% of the Fork-tails were caught before 22:00, 82% before midnight, and only 3% after 02:00. Comparable figures for Leach's Storm were 11% before 22:00, 37% before 24:00, and 30% after 02:00. Moonlight delayed the arrival of Fork-tails and reduced the numbers caught (tables 5 and 6). The earlier arrival of Fork-tailed Storm Petrels at the island nightly compared to Leach's Storm Petrel probably reflects a differential distribution between the two species at sea and suggests that the Fork-tail may forage closer to shore. If so, Fork-tails would not have to fly as far after sunset and might arrive at nesting islands earlier than Leach's Storm Petrel. My experience in offshore bird-watching confirms a more nearshore distribution of Fork-tails. Commercial fishermen reported they do not regularly encounter Leach's Storm Petrels closer than about 100 miles from shore.

I suggest that Fork-tailed Storm Petrels avoid direct competition with the more abundant Leach's Storm Petrel in northwestern California by: (1) selection of slightly different nest sites, i.e., rock crevices; (2) nesting earlier in the year; (3) visiting islands earlier at night; and (4) foraging closer to shore.

MOLTS OF LEACH'S STORM PETREL

Tail and body molt. No molt was observed in May and June. By early July, some birds began to molt body feathers and rectrices. On 23 July 1968, 65% were in obvious body molt, and though 76% had shed some rectrices, only 13% had molted more than half their rectrices. Two of three adults in burrows on 23 July 1968 had shed some rectrices even though both still were incubating eggs. By mid-August, 97% were replacing rectrices and in early September, 81% had molted half or more of the rectrices.

The molt sequence of the 12 rectrices was extremely variable and only roughly symmetrical. Most birds shed one or more of the six innermost rectrices first. The outermost rectrix often was molted early. About half the birds molted four to six rectrices in a pattern best described as "approximately alternate." Most birds molted four to six rectrices more or less simultaneously, delaying the molt of the remaining feathers until regrowth of the early feathers was one-half to three-quarters complete. This maintained a reasonably balanced tail and, though six or more rectrices may have been missing or regrowing, more than half the total surface of the tail usually was present. Many birds molted rectrix number 5 (numbered from the inside out) on each side last. The retention of this long rectrix until the nearly complete regrowth of the adjacent outermost rectrix, and a molt pattern assuring the presence of at least half the surface area of the tail provided adequate flight control throughout the molt period.

Primary molt. Primaries were numbered from the inside out and I ignored the 11th, minute primary. Primary molt began late in the brood period in mid-August when the tail molt was far advanced. On 3 September 1967, 55% of the birds still visiting the island had begun a primary molt. Usually, primaries 1 and 2, the smallest, innermost, were molted

almost simultaneously. Thus, on 3 September 1967, of 53 molting birds, 5 had molted only primary 1, 47 had molted primaries 1 and 2 simultaneously, and 1 bird had molted primaries 1, 2, and 3. The primary molt was symmetrical, and occurred mostly at sea in winter, lasting about 6 months. On 5 March 1966, 77% of the birds caught still were completing primary 10. A few birds did not complete primary 10 until late April. Palmer (1962) suggested that yearlings undergo a primary molt in summer at sea. If so, certainly no such birds show up at Little River Rock. While the absolute relationship between primary molt and breeding status of netted birds is unknown, the patterns of molt observed in this study are precisely those expected of breeders.

MOLTS OF THE FORK-TAILED STORM PETREL

Fork-tailed Storm Petrels exhibited two schedules of primary molt. Eight of 73 birds examined between 5 March and 3 May lacked a few millimeters of growth to complete primary 10. Such birds must have undergone most of the primary molt in fall and winter at sea in a pattern similar to Leach's Storm Petrel. These birds possibly were late successful breeders from the previous year. Some Fork-tails molted primaries in summer. The only bird caught on 23 July 1968 had primaries 1 and 2 newly replaced, primary 3 three-quarters grown, primary 4 in pinfeathers, and primaries 5 through 10 not yet molted. A bird picked up dead at sea on 17 July 1973 had a similar pattern of primary molt. The dead bird had no brood patch, but the netted bird had a defeathered brood patch and the outer rectrix on each side was in pin and the rest not yet molted. On 3 September 1967, all eight birds examined were molting rectrices and the refeathering of their brood patches was nearly complete. One of these birds had replaced all its primaries and the primary molt of the other seven was far advanced. Assuming the primary molt of Fork-tailed Storm Petrels requires 5–6 months (based on similar data for Leach's Storm Petrel), these birds would have started molting primaries in March. For successful breeders, this would be about the time eggs were laid and thus at least some of the birds netted in spring should have already been in molt. Since none of the birds netted between February and May had begun to molt primaries, one must conclude that these September birds either required a maximum of only 3 months for a primary molt, or they represented nonbreeders (or unsuccessful breeders) who had molted at sea during spring and summer in a pattern similar to that suggested by Palmer (1962) for yearling Leach's Storm Petrel. It is possible that such nonbreeders might frequent nesting islands intermittently in late summer and fall for courtship and territory establishment, thus explaining the sudden increase in capture rates exhibited on dark nights in September as compared to summer (table 5).

TABLE 7. Weights in grams of netted Leach's Storm Petrels, Little River Rock, Humboldt County, California.

Date	No. birds weighed	Average weight	SD	Range
18 Mar 68	123	41.0	2.7	34.8–49.6
3 Apr 65	231	41.8	1.9	37.5–48.0
13 and 27 Apr 68	26	42.5	2.5	38.5–48.5
1 May 65	172	41.5	2.2	32.5–50.5
13 May 67	19	41.5	2.4	38.0–45.5
13 Jun 68	287	39.3	3.0	33.3–49.4
23 Jul 68	115	39.3	3.4	31.3–48.0
3 Sep 67	70	40.2	2.7	32.5–45.5

WEIGHTS

Weights were taken to the nearest 0.1 g using a triple-beam balance. One important source of variability in petrel weights is the amount of food present in the stomach. On a night-to-night basis, 15–56% of the birds handled obviously regurgitated semi-solid food, mostly fragments of fish or shrimp-like organisms, and/or stomach oil at sometime during the netting or handling procedure. Since weights were taken immediately before release, nearly all birds that regurgitated had done so before they were weighed. Thus, the weights are of birds with partially emptied stomachs and birds that did not regurgitate.

Netted Leach's Storm Petrels were heaviest in spring and somewhat lighter during the incubation and brood periods (table 7). Fourteen Leach's Storm Petrels taken from burrows without eggs on 3 April 1965 (five pairs and four single birds) averaged 42.0 g (range 37.5–46.5), no essential difference from birds netted the same night (table 7). Huntington (in Palmer 1962) reported that incubating adults were heavier than pairs in burrows without eggs earlier in the season. Harris (1969) reported that adult *O. castro* taken from burrows became heavier through the incubation period and lighter after the eggs hatched. Seven adults (five incubating eggs and two with very small young) taken from burrows on 23 July 1968 averaged 36.7 g (range 32.0–42.4). Two incubating adults

taken from burrows on 13 May 1967 weighed 32.6 and 41.5 g. These few data plus the data from netted birds on 13 June 1967 (table 7), when most birds should have been incubating, suggest that the weights of the Little River Rock Leach's Storm Petrels declined at the beginning, not the end, of incubation.

The average weight of 55 netted Fork-tailed Storm Petrels was 55.3 g (range 47.5–62.8; SD 3.7) and there were no significant seasonal variations.

BODY TEMPERATURES

Body temperatures were taken using a 0/50/C 1/5 Schultheis rapid-reading thermometer, calibrated in 0.2°C divisions with a 10-mm immersion. Temperatures were taken either rectally or by inserting the thermometer through the oral cavity and at least 15 mm into the esophagus. The thermometer was held in place until the mercury stabilized, usually within 15 to 20 sec. Both rectal and esophageal temperatures were taken on 4 nestlings and 28 adult Leach's Storm Petrels. Differences between rectal and esophageal temperatures of the 32 birds were statistically insignificant (esophageal temperatures averaged 0.14°C higher than the rectal temperatures—range −1.2 to +1.8; SD 0.7). Warham (1971) found no significant differences in temperatures taken rectally and in the proventriculus in several species of Procellariiformes.

The mean esophageal temperature of 780 netted Leach's Storm Petrels was 38.5°C (range 35.5–41.6; SD 1.1). Folk (1949, 1951) reported a "standard" temperature of 39.1°C of Leach's Storm Petrels in the laboratory, 39.4°C of "exercised" birds, 37.2°C for 14 incubating birds, and 39.0°C for six paired birds in burrows without eggs. I found an average temperature of 37.8°C (range 36.2–40.2; SD 1.1) for 15 adults in burrows (11 with eggs, 2 with very small young, 1 without eggs or young, and 1 whose breeding status was unknown), only slightly lower than active, netted birds. Warham (1971) commented on the small difference in body temperature between very active and inactive petrels.

Folk (1951) and Warham (1971) discussed the relationship between the relatively low body temperatures and the long incubation periods in the Procellariiformes. I crudely measured the surface temperature of the brood patch skin of one incubating adult Leach's Storm Petrel by placing the bulb of the thermometer directly against the skin. Temperatures from this one bird were: rectal temperature 36.2°C; esophageal temperature 36.8°C; brood patch skin temperature 30.2°C. If incubating petrels maintained brood patch skin temperatures of 30 + °C, and if the egg is held snugly in the brood patch during incubation, the low egg temperatures reported by Folk (1951) (14.7°C in daytime and 22.5°C at night) do not seem plausible. Warham (1971) also questioned the low egg temperatures reported by Folk.

Esophageal temperatures of 31 nestling Leach's Storm Petrels ranging in body weight from 13.8 to 53.5 g averaged 38.0°C (range 36.1–39.4; SD 0.7). These chicks presumably all had attained ages at which homeothermy had developed. The smallest chicks weighed 13.8 and 15.9 g, were probably 4–6 days old, and had temperatures of 37.8 and 39.4°C, respectively. The larger chick was accompanied in the burrow by an adult, but all the remaining chicks were alone in their burrows. These data indicate that chicks in burrows are able to maintain adult temperatures from at least as early as the first week of life.

Esophageal temperatures of 35 netted Fork-tailed Storm Petrels averaged 38.5°C (range 35.2–42.0; SD 1.3).

SUMMARY

Leach's and Fork-tailed Storm Petrels are known to breed at five and possibly eight sites in northwestern California. An estimated 5000 pairs of Leach's and 100 pairs of Fork-tailed Storm Petrels nested at Little River Rock, Humboldt County, in 1965–69. Little River Rock is the southernmost known breeding site for the Fork-tailed Storm Petrel. Leach's Storm Petrel preferred to nest in soil under short brushfields, while Fork-tailed Storm Petrels apparently preferred natural rock crevices. Leach's Storm Petrels were absent from nesting areas in northwestern California between late October and mid- to late January. Between late January and mid-May, they visited islands in large numbers on warm, moonless nights for courtship and burrow excavation. Leach's Storm Petrel eggs were laid from mid-May to early July and the peak of hatching was in early to mid-July. Young were fledged from late August to late October. Leach's Storm Petrels arrived at nesting islands 60–90 min after local sunset and departed 50–90 min before local sunrise. Peak numbers were netted between 01:00 and 03:00. The need to escape diurnal predators probably limits breeding petrel colonies to latitudes which provide sufficient darkness in summer. Moonlight reduced the number and delayed the arrival of Leach's Storm

Petrels during the courtship-burrow excavation period, but made no difference in capture rates, hourly distribution of captures, arrival and departure times, or amount of calling during the incubation-brood period. These birds had progressive defeathering of brood patches until late May and early June and progressive refeathering of brood patches beginning in early July, ending in September. A few Fork-tailed Storm Petrels visited the island all year. Highest numbers of Fork-tails were netted in April and fewest, in midsummer. They visited the island earlier in the year, earlier in the night, and nested 4–8 weeks earlier than Leach's Storm Petrels. Fork-tailed Storm Petrels avoided direct competition with the abundant Leach's Storm Petrels in northern California by selecting slightly different nest sites, by nesting earlier, by visiting the islands earlier at night, and perhaps by foraging closer to shore. Leach's Storm Petrel began its body and tail molt late in the incubation period or early in the brood period and the tail molt was complete by late September. While their molt of the rectrices was variable, there was a tendency for the center feathers to be molted first, for some feathers to be molted in an alternate pattern, and for the feather adjacent to the outermost rectrix to be molted last. The primary molt of Leach's Storm Petrel began late in the brood period, was symmetrical, and primaries 1 and 2 were dropped simultaneously. Primary molt occurred mostly at sea in fall and winter and was completed by late April. While a few Fork-tailed Storm Petrels were still completing the growth of the 10th primary in March, some birds replaced all their primaries in summer. Weights of Leach's Storm Petrels averaged 39–42 g, highest in spring and slightly lower during incubation and brood periods. Fork-tailed Storm Petrels weighed 48–63 g, but the few data did not reveal any seasonal variations. Esophageal temperatures of netted birds of both species averaged 38.5°C. Young Leach's Storm Petrels maintained adult temperatures from at least the first week of life.

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