THE BREEDING BIOLOGY OF THE FORK-TAILED STORM-PETREL (OCEANODROMA FURCATA)

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ABSTRACT.—The reproductive biology of Fork-tailed Storm-Petrels (*Oceanodroma furcata*) breeding in the Gulf of Alaska reflects adaptations in response to severe climatic conditions, distant and unpredictable food resources, and predation. Adults build meager nests in natural or excavated cavities and arrive and depart only at night. During incubation, parents frequently neglect eggs for several days at a time, and embryos can survive up to 28 days of neglect during incubation periods that may extend more than 60 days. Even when adults attend eggs, incubation temperatures (29.7°C) are well below those of other birds. Fork-tailed Storm-Petrels switch mates more frequently after nests fail than when chicks successfully fledge. They do not recognize their own eggs or chicks. Egg laying, egg size, chick growth rates, and chick mortality vary between and within seasons, possibly because of seasonal and annual differences in food availability. The variability in the onset of breeding and the variability in growth between years suggest that Fork-tailed Storm-Petrels are responsive to oceanographic conditions and may be good indicators of regional productivity. *Received 31 May 1979, accepted 30 October 1979.*

FORK-TAILED Storm-Petrels (*Oceanodroma furcata*), one of the most common marine birds breeding in Alaska, nest on islands along the coast from northern California through the Alaska Peninsula and Aleutian Islands. Despite their abundance and wide distribution, however, few continuous breeding studies on Fork-tailed Storm-Petrels have been conducted, and published information on their biology consists predominantly of reports of brief colony visits or isolated observations (Mailliard 1923, Willett 1923, Richardson 1960, Iverson and Krog 1972, Harris 1974). This paper summarizes the result of two summers spent studying Fork-tailed Storm-Petrels breeding on the Barren Islands in the Gulf of Alaska.

Storm-petrels (Hydrobatidae) lay a clutch of one egg and raise no more than a single chick per year. Incubation and nesting periods are protracted, chick-growth rates are slow, reproductive maturity is delayed, and adult survival rates are high (Lack 1967, 1968). The reproductive adaptations of Fork-tailed Storm-Petrels breeding at the northern limit of the distribution of storm-petrels represent extremes among the family and reflect the ecological factors confronting them. Most important, the constraints of predation, spatial and temporal availability of food, and climate are evident in features of their reproductive biology.

STUDY AREA AND METHODS

The Fork-tailed Storm-Petrel is the only storm-petrel known to breed in the Barren Islands, Alaska (58°55′N, 152°10′W) (Bailey 1976). All of the islands in the archipelago have large colonies of seabirds with the exception of Ushagat Island, where Arctic foxes (*Alopex lagopus*) have been introduced. In spite of their name, the Barren Islands are covered in summer by relatively lush, subarctic maritime tundra vegetation, comprised principally of grasses (*Elymus, Festuca*), sedges (*Carex*), and Umbelliferae (*Heracleum, Angelica*). The glaciated terrain is characterized by steep, vegetation-covered talus slopes separated by relatively gentle valleys with sandy soil.

From 14 May to 6 September 1976 (DB, MN) and from 20 May to 24 August 1977 (NW, ESW), we studied the East Amatuli Island population, one of the largest known. An estimated 300,000 individuals breed on the 435-ha island (Sowls et al. 1978). We also visited colonies on Sugarloaf, Sud, and West Amatuli islands. In 1976 and 1977 we monitored nests and performed manipulations at six subcolonies,

each containing 43–180 nests, to determine egg-laying and incubation patterns, hatching dates, chick development, and reproductive success. By visiting different sample plots at different intervals (from as seldom as four times during the summer to as frequently as every day), we attempted to assess the impact of our observations on breeding success. Eggs and chicks were weighed with 50-g and 100-g Pesola scales (to 0.1 and 0.5 g, respectively) and measured with Vernier calipers (to 0.1 mm). We captured adults by hand in burrows or with mist nets and collected, measured, and sexed 30 individuals in 1976. Average precipitation and wind conditions during the breeding season were calculated from NOAA weather data (1974–1978) from Kodiak Island, which lies about 100 km southwest of the Barren Islands. We recorded rainfall on the island with a rain gauge and temperature extremes with a Taylor maximum-minimum thermometer. We measured the thermal environment of the nest and body temperatures of chicks and adults (see Wheelwright and Boersma 1979 and Boersma and Wheelwright 1979 for further details) using a Yellow Springs telethermometer. In May 1979 one of us (DB) returned and measured egg temperatures with a TH-65 Digital T.C. thermometer. In this paper standard deviations are given following the mean.

RESULTS

Body size and brood patch.—Like most procellariiform birds, Fork-tailed Storm-Petrels are sexually monomorphic in plumage, although vocalizations differ (Simons pers. comm., pers. obs.). Measurements of bill, wing, and tarsus of males and females from the Barren Islands were not significantly different (*t*-test: $P > 0.1$; $n = 14$ males and 14 females).

Before the initiation of incubation, both male and female Fork-tailed Storm-Petrels lost the feathers of the brood patch. In their congener, the Madeiran Storm-Petrel (*O. castro*), this may occur as early as 6 weeks before egg laying (Harris 1969); most Madeiran Storm-Petrels molt the brood patch 3 weeks before laying (Allan 1962). The brood patches of Fork-tailed Storm-Petrels were poorly vascularized in May 1976. By June most incubating adults had well vascularized brood patches (Fig. 1), and by August, several weeks after most chicks had hatched, brood patches had begun to refeather. Fork-tailed Storm-Petrels therefore maintained unfeathered brood patches for 2–3 months. In contrast, the brood patch of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) may refeather within a few days after chicks hatch (Ainley et al. 1974). Fork-tailed Storm-Petrels that periodically spent days alone or with a prospective mate in a burrow in which eggs were not laid that season (these were assumed to be nonbreeders) also developed vascularized and defeathered brood patches. Harris (1969) noted that nonbreeding Madeiran Storm-Petrels develop brood patches as well.

Activity patterns.—Except during the breeding season, storm-petrels rarely visit land. They typically arrive at and leave colonies only under cover of darkness (Ainslie and Atkinson 1937, Davis 1957, Allan 1962, Waters 1964). Like other species, Fork-tailed Storm-Petrels began to arrive at the island shortly after sunset and usually departed well before sunrise. As nights became progressively shorter during the summer, birds appeared later (Manuwal and Boersma 1977). On clear moonlit nights, birds arrived 1–2 h later than on evenings with heavy cloud cover. Late in the summer, the capture rate of birds netted in a 2.3- × 13.5-m mist net declined (late June–early July: $\bar{x} = 0.95 \pm 0.19$ individuals netted/min; late July–early August: $\bar{x} = 0.33 \pm 0.09$/min; *t*-test: $P < 0.001$), presumably because non-breeders and failed breeders visited the island less regularly and because birds no longer displayed aerially.

Nesting sites.—Storm-petrels generally nest in excavated or naturally occurring burrows up to several meters deep (Lockley 1932, Harris 1969, Beck and Brown 1972, Ainley and Lewis 1974). Fork-tailed Storm-Petrels on East Amatuli were
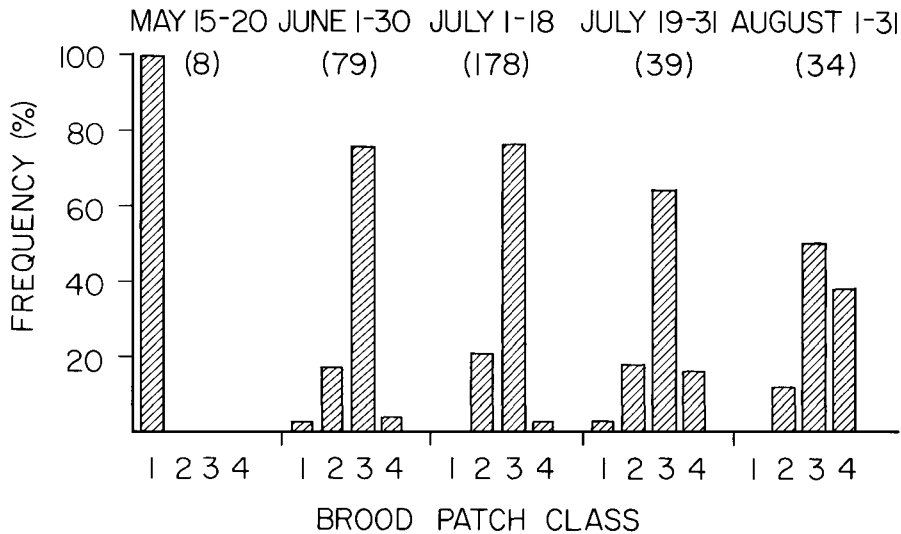
Fig. 1.   Development and refeathering of brood patches of Fork-tailed Storm-Petrels in 1976. Sample sizes are in parentheses. Brood patch class 1: completely feathered; 2: defeathered but unvascularized; 3: vascularized; 4: unvascularized and beginning to refeather.

opportunistic in their choice of nesting sites, digging burrows in soil, occupying natural rock cavities under boulders, in rock rubble, or in cliff crevices, or utilizing cavities excavated by other species such as the Tufted Puffin (*Lunda cirrhata*). In 59 easily accessible nests, the mean length of burrows from entrance to nest chamber was 33.3 ± 11.6 cm, with an average entrance height of 9.8 cm and a width of 9.4 cm. In 39% of the nests, incubating birds were visible from outside the burrow. Within the same subcolony, the mean nearest-neighbor distance between burrows was 2.6 m. Only 5% of the burrows had more than one entrance, although often a single entrance led to 2–4 different nests. Nest chambers commonly had little or no nest material, and many eggs were laid directly upon soil or rock. In some burrows we observed incubating birds arrange grass around the egg. All nests were rudimentary, perhaps because round fungus beetles (*Leiodidae*) may debilitate or kill torpid chicks; beetle density was positively correlated with dry weight of nest material (Wheelwright and Boersma 1979).

Egg laying.—Fork-tailed Storm-Petrels lay a single egg. Like eggs of many burrow nesters (Lack 1968), the egg is white, often encircled at the blunt end by a ring of light brown spots. The egg is large relative to body size, as in other Procellariiformes (Heinroth 1922, Rahn et al. 1975). In 1977, eggs weighed on the day that they were laid averaged 12.6 ± 1.0 g (n = 93), approximately 21% of adult body weight. Egg dimensions in 1976 were: length 3.45 ± 0.11 cm, width 2.62 ± 0.08 cm (n = 33); in 1977 they were: length 3.46 ± 0.13 cm, width 2.63 ± 0.08 cm (n = 183); and in 1979 they were: length 3.46 ± 0.12 cm, width 2.61 ± 0.07 cm (n = 62). Eggs laid in June 1976, 1977, and 1979 were similar in length and width. Eggs laid early (before 4 June) were significantly greater in length and width than eggs laid later in the same breeding season (Mann-Whitney U: P < 0.02 and 0.001 for 1976 and 1977, respectively).

Early chick survival is correlated with egg size. Chicks that died within 10 days
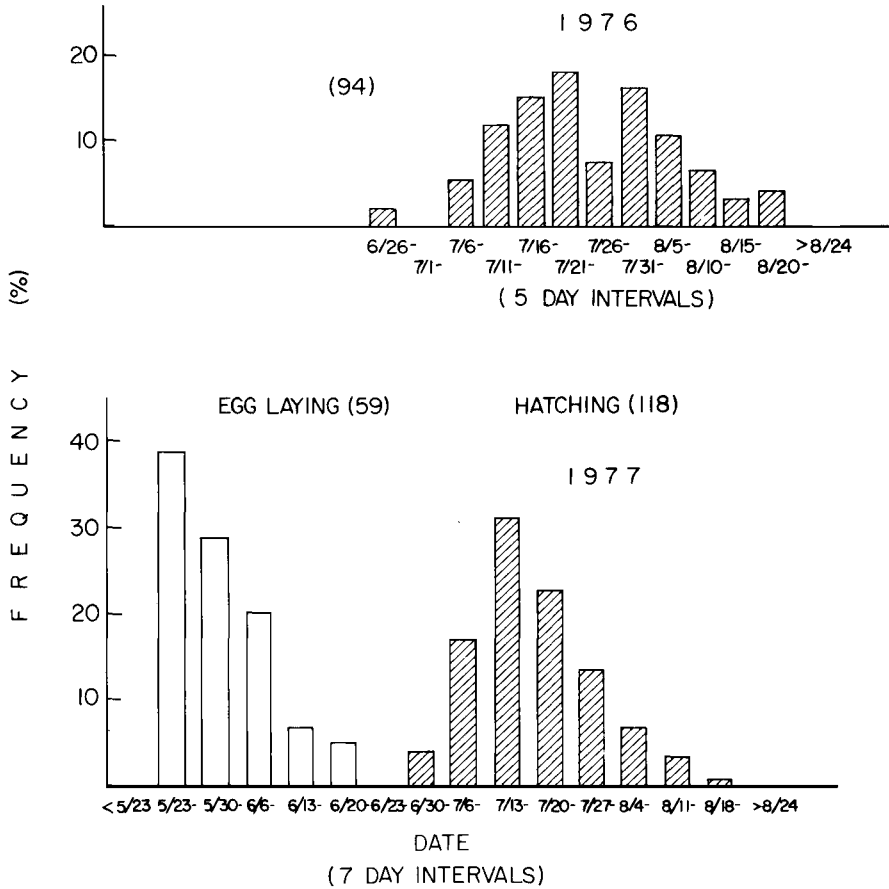
Fig. 2.   Relative frequencies of egg laying and hatching of Fork-tailed Storm-Petrels in 1976 and 1977. Sample sizes are in parentheses. In 1976 a severe storm occurred 26–29 July. Note that hatching frequency is calculated for 5-day intervals in 1976 and 7-day intervals in 1977.

of hatching came from smaller eggs than chicks that survived, regardless of when the eggs were laid (t-test: $P < 0.005$, $n = 34$). In other species of seabirds, chicks hatching from large eggs have a higher probability of surviving to fledging than those hatching from small eggs (Parsons 1970, 1975; Schifferli 1973; Davis 1975; Nisbet 1978).

We discovered the first eggs of the breeding season on 21 May 1976 and on 23 May 1977. In 1978, Simons (pers. comm.) found eggs by mid-April. Although egg laying was not highly synchronous in 1977, it began with a peak in late May and tailed off until late June (Fig. 2). The period of egg laying may be lengthy in many other storm-petrels as well (Lockley 1932, Allan 1962, Harris 1969, Wilbur 1969). Between years, the onset of egg laying for Fork-tailed Storm-Petrels may vary by as much as 53 days (Clay 1925).

Egg-removal experiments provided information on the ability of birds to replace eggs. Of 36 eggs removed on the day they were laid, 29 (81%) were replaced. To minimize disturbance, we usually banded only one parent, and therefore we could be certain only in a single case that both members of the original pair remained

together and replaced the removed egg. Nonetheless, 11 replacement clutches involved at least one of the original mates; only 2 pairs had a documented change in one of the mates. Replacement eggs appeared an average of 20.9 ± 1.6 days after removal of the first egg ($n = 11$). Three weeks, however, is probably an overestimate of the time between copulation and egg laying, at least of the first egg. In our experiment several days may have elapsed before the pair reunited in the burrow and copulated. After we removed the replacement egg from one nest, a third egg was laid by the same female 20 days later. Replacement eggs ($n = 30$) were significantly smaller in length (3.45 ± 0.15 cm) and width (2.59 ± 0.08 cm) than original eggs (Mann-Whitney U: $P < 0.02$ and 0.001, respectively) but not different from other eggs laid late in the season in undisturbed nests (Mann-Whitney U: $P > 0.3$).

Incubation and egg neglect.—Incubation periods in 1977 ranged from 37 to 68 days, with a mean of 49.8 ± 6.7 days ($n = 33$). The wide variance resulted from frequent and extended periods when eggs went unattended, during which embryos apparently developed little. The embryos survived extreme periods of egg neglect, lasting up to 7 days continuously or totaling as much as 28 days during the incubation period. Neglected eggs, however, had lower hatching success, and nestlings had higher mortality than those from nonneglected eggs (Boersma and Wheelwright 1979). There were no differences in length and width between eggs neglected more than 11 days and eggs neglected 11 or fewer days (Mann-Whitney U: $P > 0.1$ and $P > 0.3$, respectively; $n = 33$). Daytime burrow air temperatures and internal temperatures of unattended eggs averaged 10°C. Internal egg temperatures, taken within the air sac of one egg that subsequently hatched, did not exceed 27.5°C (Wheelwright and Boersma 1979). The mean temperature at the center of 22 incubated eggs that were removed from the burrow and immediately inserted with a thermocouple probe was 29.7° ± 3.1°C (Boersma unpubl. data 1979). Drent (1975) reported the mean incubation temperature of birds from 10 orders as 35.7°C. Fork-tailed Storm-Petrels, in comparison, had incubation temperatures far lower than those known for other birds.

Both sexes incubated the egg, usually exchanging nest duties every 2–3 days, although we documented incubation shifts of up to 5 days. One such bird lost 14.5 g (19% of its initial body weight) during a 5-day incubation shift. Adults lost on the average 3.7 ± 1.1 g, or about 5.7 ± 1.8% of their initial body weight, over a 20-h period on the first day of incubation ($n = 17$).

Daily handling of adults caused desertion of 43 nests. One adult returned after 23 days to resume incubation and two others after 18 days, which suggested a strong attachment to the nest and egg. Individuals varied in their tolerance to handling. Slight disturbance, while not necessarily causing desertion, did depress hatching success. In 1977 nests checked daily (but in which adults were not handled until eggs hatched) had a hatching success of 58% ($n = 59$), compared to 70% (1976: $n = 89$) and 84% (1977: $n = 100$) for nests visited only four times late in the incubation period. (The latter, however, probably overestimates hatching success, because eggs may have been removed before our initial observation and thus not included in the sample; if corrected by a prehatching egg-loss rate of 7% derived from the 59 nests checked daily, a revised estimate would be 78%.) Table 1 compares hatching and fledging success of nests disturbed at different frequencies in 1976 and 1977.

Reproductive success and mate fidelity in successive seasons.—Sixty-five birds banded in 1977 were recaptured on nests the following year. Of these, 54 retained the same mate both years, while 11 birds had new mates. Thus, 27 of the 38 pairs

TABLE 1. Nesting success of Fork-tailed Storm-Petrels on the Barren Islands in 1976 and 1977. Nests were visited only four times late in incubation, and adults were never handled.

	1976		1977	
	Number	Per-centage	Number	Per-centage
Sample size	89	100	100	100
Eggs that hatched	62	70	84	84
Chicks survived (reproductive success)	35	39	58	58
Chicks died	27	30	26	26
Eggs that failed to hatch	27	30	16	16
Infertile	3	3	1	1
Abandoned, infertile	9	10	8	8
Ejected from nests	5	6	7	7
Unknown	10	11	0	0
Chick mortality		44		31

(71%) remained together during two successive breeding seasons. At least 82% of the 11 individuals that had new mates in 1978 had suffered breeding failure in 1977, and none was known to have fledged young. In contrast, of the birds that retained the same mates both years, only 19% definitely failed to raise fledglings. Previous breeding success was unknown for 18% of the birds that changed mates and for 48% of the birds that remained with the same mate. Morse and Buchheister (1979) showed that site fidelity far exceeded mate fidelity in Leach's Storm-Petrel and may be responsible for remating. Although possibly important in Fork-tailed Storm-Petrels as well, mate fidelity appears to be more strongly correlated with previous reproductive success.

Egg and chick recognition; twinning experiments.—Fork-tailed Storm-Petrels did not recognize their own eggs or young. We exchanged eggs in six nests, either when adults were present or when eggs were unattended, and in all cases the replacement was accepted and incubated. We replaced chicks that had recently died (3 of them at 3–5 days and the fourth at 20 days) with other chicks. Three of the replacements were over 25 days old and weighed up to eight times as much as the original chick, yet all of them were accepted and fed for the rest of the summer. For a chick that died at age 2 days, we substituted an egg; one adult incubated it for 1 day before deserting the nest.

To test whether Fork-tailed Storm-Petrels are capable of raising two chicks, we experimentally doubled broods by adding chicks of similar size and age to five nests that had young less than 6 days old. The introduced chicks were fed in all of the four nests that fledged a chick. In one nest both chicks died, one 3 and the other 8 days after the "twin" was added. In the other nests adults did not discriminate between the two chicks and brooded both until one of them died. In the four successful nests, 2 original chicks and 2 introduced chicks were reared to fledging. Fork-tailed Storm-Petrels are apparently physically or behaviorally unable to rear more than one chick to fledging, as has been shown in Leach's Storm-Petrel (Huntington 1963, Lack 1966).

Hatching and development.—Hatching extended from 26 June to 24 August in 1976 and from 3 July to 19 August in 1977 (Fig. 2). The bimodality in hatching frequency in 1976 may have been caused by severe storms between 26–29 July, which may have prevented adults from returning to the island. Adults apparently
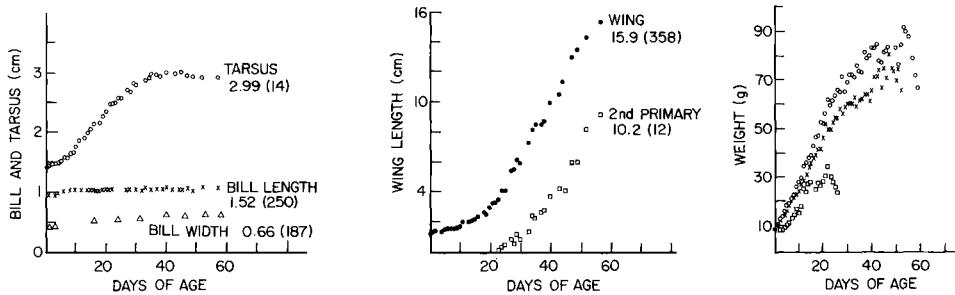
Fig. 3. The growth rate of tarsus, bill, and wing of known-aged Fork-tailed Storm-Petrel chicks in 1976 are given in panels 1 and 2. Adult measurements and sample size are given for each body part. Panel 3 shows daily mean weight of known-aged Fork-tailed Storm-Petrels in 1976 ($n = 20$) and 1977 ($n = 34$). The correlation coefficient $r = 0.99$ from 0–21 days in 1976 and 1977, and $r = 0.81$ in 1976 and $r = 0.94$ in 1977 from 22–51 days of age. The standard error of the mean (SE) was less than 1 g until 34 days of age in 1976 and 40 days of age in 1977. O = 1976 data; × = 1977, and □ = chicks that died.

assisted chicks in emerging from eggs by removing pieces of the shell (Simons per. comm., pers. obs.). An adult was always present on the day of hatching and usually remained with the chick for the first several days, irregularly brooding it until an average of 5.3 days following hatching ($n = 34$). Chicks that were not brooded on days 2 and 3 invariably died ($n = 12$). Of those brooded only one of those days, 60% survived ($n = 15$). All nine hatchlings brooded on both days survived. After the first 5 days, an adult seldom spent the day in the burrow, although occasionally a chick was brooded sporadically up to 15 days of age.

We chronicled the development of 20 known-age chicks in 1976, but only three of them had fledged by the time we left the island. Within 6 h of hatching the chick was a ball of gray down with white wing tips. The eyes were closed and the tarsi were white. As the nestling aged, the tarsi darkened, and within 10 days all chicks had light gray tarsi.

As early as day 2, but no later than day 10, the eyes opened and were dark, as in the adult. As with other birds, egg tooth loss was highly variable: 18% of the 20 chicks lost the egg tooth at 6–10 days, 53% at 11–15 days, 23% at 16–20 days, and 6% at 21–25 days. One chick of uncertain age retained the egg tooth for over 44 days.

Secondary feathers emerged by 14 days of age, and primaries emerged by 20 days of age. Most chicks began growing tail feathers after 22 days. Between 22 and 30 days, secondary, primary, tail, and contour feathers split their sheaths. Wing feathers erupted sequentially, starting with the secondaries closest to the body and continuing outward through the primaries. Because of the variability in feeding frequencies and the resulting irregular growth patterns, chicks cannot be aged precisely by feather development or morphological measurements.

The bill grew to adult proportions quickly. In contrast, tarsi grew almost imperceptibly during the first week but more rapidly thereafter. Wing and tail feathers grew quickly between 23 and 33 days of age (Fig. 3). Body parts more critical to feeding grew first, followed by the less immediately important structures such as tail feathers.

Shortly after hatching, chicks were fed and began gaining weight. Initially, the

TABLE 2. Food samples from Fork-tailed Storm-Petrels captured on East Amatuli Island.

Capture date	Sample size	Percent regurgitating orange oil	Percent regurgitating digested fish
June 25–July 7	187	100	0
July 10	32	93	7
13	42	100	0
19	13	85	15
23	17	100	0
31	9	100	0
August 10	23	71	29
21	12	67	33

mean weight of chicks increased almost linearly, although individuals showed wide daily variations. Within a 24-h period chicks could lose 10 g or gain 30 g. Chicks, which often weighed over 100 g at their peak weight, lost weight for 4–5 days prior to fledging (Fig. 3). As the adults continued to return to the burrow, chicks evidently refused food (as in Common Puffins, *Fratercula arctica,* Harris 1976) or were fed less. Two chicks fledged at 61 days of age and one at 66 days. This compares to a mean of 61 days for the Storm-Petrel (*Hydrobates pelagicus*), 60 days for Wilson's Petrel (*Oceanites oceanicus*), and 65–71 days for the Black-bellied Storm-Petrel (*Fregetta tropica*) (Davis 1957, Beck and Brown 1971). Fledglings were approximately 10% heavier than mean adult body weight in August 1976.

Chicks that died grew more slowly and lost weight before they died, suggesting starvation. The growth curve for weight in Fig. 3 was divided into two parts for the purpose of comparative analysis, because the rate of growth started to decrease at 21 days of age. Chicks reared in 1976 grew more quickly during both phases than chicks reared in 1977 (analysis of covariance: $P < 0.001$ and $P < 0.001$, respectively). We compared the mean weights of chicks in both years once they had exceeded the average adult weight of 58 g. Chicks were heavier in 1976 than in 1977 (t-test: $P < 0.001$) (Fig. 3). The frequency of adult visitation of early (before 26 July) and late hatchlings was not significantly different between 1976 and 1977 (Mann-Whitney U: $P > 0.1$).

In 1976 chicks that hatched late in the season were significantly heavier during the first 3 weeks following hatching than chicks that hatched early in the season (Spearman rank: $P < 0.01$). By 6 weeks of age the rankings were reversed: chicks that hatched before 11 July were significantly heavier than chicks that hatched after 11 July (t-test: $P < 0.05$; $n = 25$). The wing-growth rates of chicks that hatched before 26 July 1976 and chicks that hatched thereafter were not significantly different (t-test: $P > 0.4$, $n = 33$). These trends suggest that, although chicks that hatch late may initially gain weight faster and grow as rapidly (possibly because of increased food availability late in the breeding season), they never attain the peak weights of chicks hatched earlier.

Weight loss in chicks.—Unfed chicks lost 7.6 ± 1.5% of their body weight over an 18-h period and 12.1 ± 3.2% within 24 h ($n = 12$). Chicks that were fed, on the other hand, lost 13.4 ± 5.1% of postfeeding weight within 18 h ($n = 14$). Food loads averaged 12.8 ± 6.6 g or 29.1 ± 12.7% of initial body weight ($n = 14$). Relative weight loss proved to be correlated less with age or size of chicks than with the amount they had been fed the previous night.
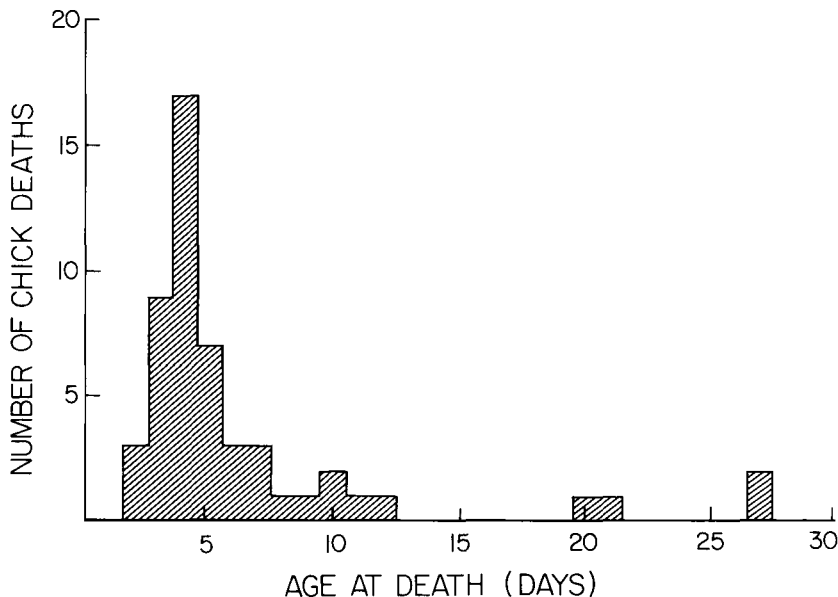
Fig. 4. Mortality of Fork-tailed Storm-Petrel chicks in 1976 and 1977 (n = 51).

Feeding habits.—According to Palmer (1962), Fork-tailed Storm-Petrels feed primarily upon nektonic crustaceans and fish, although they have been seen feeding on beached whales (Gill 1977).

When handled, Fork-tailed Storm-Petrels normally regurgitate a concentrated orange oil that is comprised of digested substances rather than secretions (Imber 1976). Although the oil may act as a defense against predators (Clarke 1977), oil is fed to chicks, and its primary function is nutritive. Later in the nesting season (July and August) when most adults were feeding large chicks, the diet apparently changed to include more fish (Table 2). They then disgorged a white paste or occasionally a whole fish or squid.

Predators and mortality.—The chief predators on Fork-tailed Storm-Petrels on East Amatuli Island are probably river otters (*Lutra canadensis*). River otters apparently are recent arrivals, as Bailey (pers. comm.) did not find any evidence of their presence in 1975. Predation by river otters (characteristically evidenced by a single or pair of dismembered wings) was most common in May and declined in frequency throughout the breeding season. At the entrance of one river otter den containing two pups, we found several hundred Fork-tailed Storm-Petrel wings. On the Wooded Islands, Alaska, where there is a small Fork-tailed Storm-Petrel colony, river otters took 23% of the breeding population of the Fork-tailed Storm-Petrels breeding in sod burrows in 1977 (Hatch et al. 1978).

Fork-tailed Storm Petrel bones appeared in castings or lay scattered in Glaucous-winged Gull (*Larus glaucescens*) colonies. We released 31 adult Fork-tailed Storm-Petrels singly during the day in one colony to observe the reaction of these potential predators; the storm-petrels were ignored. Bailey (pers. comm.), however, released an adult petrel that was immediately taken by a Glaucous-winged Gull. Common Ravens (*Corvus corax*), Bald Eagles (*Haliaeetus leucocephalus*), and Peregrine Falcons (*Falco peregrinus*), all of which occur in the Barren Islands, are also known
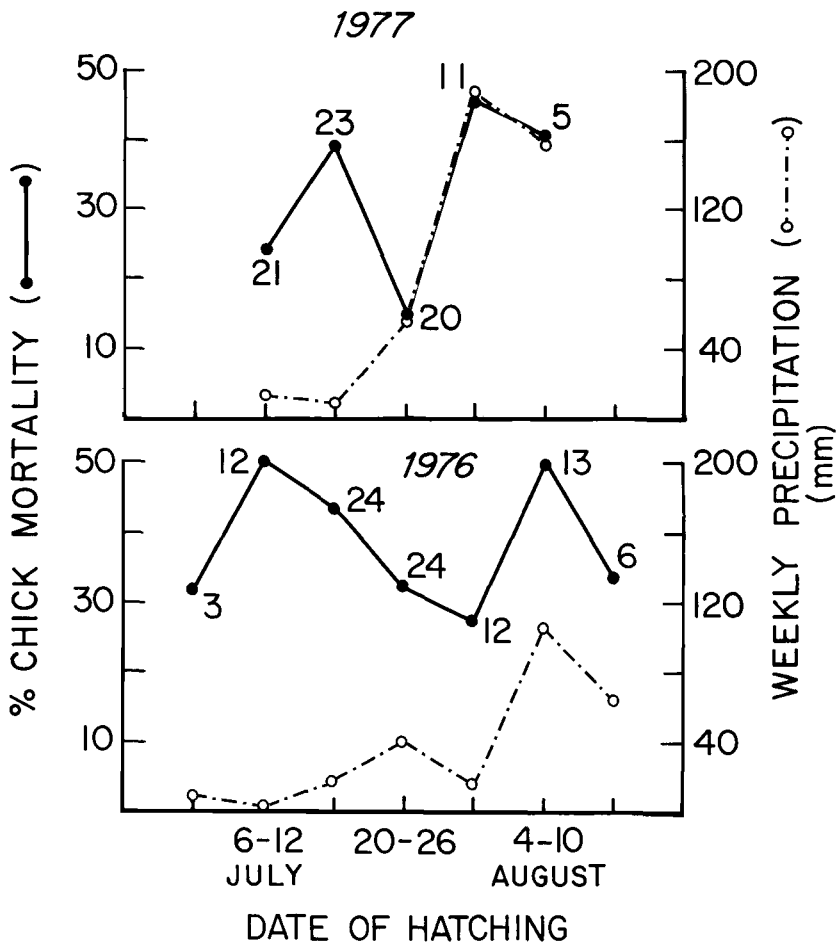
Fig. 5. Weekly precipitation and Fork-tailed Storm-Petrel chick mortality for 7-day intervals during 1976 and 1977. The dotted line represents precipitation and the solid line relative frequency of chick mortality. Numbers next to the dots indicate sample size.

to feed on storm-petrels (Gross 1935, Parslow 1965, Threlfall 1974, Campbell et al. 1977).

Chicks that died usually did so within 12 days of hatching (Fig. 4). None of the chicks regularly observed ($n = 97$, 1976; $n = 118$, 1977) was lost to a predator. No eggs disappeared from our sample plots during the breeding seasons of 1976 and 1977, demonstrating the infrequency of egg predation. Eggs remained in burrows until they hatched or were ejected, buried, or pushed to the side of the nest cavity, presumably by parents rejecting infertile eggs or by other adults attempting to establish themselves in the burrow for the following nesting season.

Effects of storms.—Wind and rain may hamper foraging, make it energetically more difficult to return to the colony, or delay returning birds so that they are unable to arrive under cover of darkness. If so, storm-petrels should be less likely to visit their nests during storms. We compared chick weight loss (an indirect measure of adult visits) following days with at least 10 mm of rain and 30 km/h winds (1976: 10 days; 1977: 13 days) versus days with 0 mm of rain and winds less than 30 km/

h (1976: 7 days, 48 chicks; 1977: 16 days, 34 chicks). If a chick lost less than 3 g/day, we assumed that one or both of its parents had returned and fed it the previous night. In 1976 (though not in 1977) birds returned to the islands less frequently on stormy nights (Mann-Whitney U: $P < 0.007$). Adult foraging ability (as measured by average food loads to chicks, 7.5 ± 2.4 g and 7.3 ± 1.9 g on stormy and calm days, respectively) did not seem to be influenced substantially by weather, as recorded on Kodiak Island. While sea conditions may cause significant variation in feeding rates for other seabirds (Dunn 1973, 1975; Birkhead 1976), it may be that storm-petrels feed far enough away from the island that only large storms affect the foraging ability of adults. Chick mortality in minimally disturbed control plots (checked weekly) fluctuated but was only weakly correlated with precipitation late in the summer (Fig. 5). Chicks that went unfed for several days often went into torpor, with body temperature falling below 13°C (Wheelwright and Boersma 1979). We noticed older chicks, unable to go into torpor, shivering on cold days.

Weather, coupled with food supplies, may be important in determining the timing of reproduction. Using Kodiak weather data, we calculated mean precipitation and wind speeds from 1974–1978. The climate of the Barren Islands is probably similar to that of Kodiak, although winds are more severe on the Barrens. Normally, snow blocks burrows until at least April. Winds are lowest in June, July, and August, and rainfall increases throughout the summer. The period between copulation and chick fledging (the end of parental responsibilities) lasts from 3.5 to 5 months, depending upon the extent of egg neglect. Relatively benign (by coastal Alaskan standards) weather occurs from late May until late September, the period corresponding to the actual breeding season of our Fork-tailed Storm-Petrels.

DISCUSSION

The reproductive adaptations of the Fork-tailed Storm-Petrel reflect the constraints of the marine environment. The quality, location, and undependability of their food, the severity and unpredictability of the high latitude climate, the brevity of the breeding season, and susceptibility to island predators—all impose selective pressures on different aspects of their breeding biology.

Probably the most important ecological constraint—and the one about which we know the least—is the availability of food in time and space. Secondary productivity can vary annually both in the onset of "blooms" as well as in total biomass produced (Sverdrup et al. 1942). Upwelling off the continental shelf in Kodiak Island waters, which is responsible for the productivity of these waters, is weak and fluctuates unpredictably (Ingraham et al. 1976, Favorite et al. 1976, Hickey 1979). Changes in upwelling patterns have been known to cause massive seabird mortality (Hutchinson 1950) or total reproductive failures (Boersma 1978). The lack of synchrony of egg laying in Fork-tailed Storm-Petrels and the between-season variability in timing of breeding may be the consequence of annual variation in the onset of maximum food abundance.

Spatial fluctuations of food sources also may affect breeding. Crustaceans and schooling fish are patchy, widely dispersed, and mobile. Adult storm-petrels are often absent from the colony for several days and may have to fly long distances to find these resources.

The single-egg clutch, the inability to raise two chicks, the lengthy time required to lay or replace eggs, and the rarity with which most storm-petrels replace eggs

(Gross 1935, Roberts 1940, Harris 1969) suggest that the rate at which storm-petrels can capture and process food is limited. Eggs are able to tolerate the intervening cold spells when adults are gone, but development slows and incubation time increases. Temporary abandonment of eggs and chicks is only loosely correlated with weather conditions. The small size of late-laid eggs and replacement eggs and high chick mortality even during periods of relatively mild weather in mid-summer suggest that food availability declines during the summer.

Fork-tailed Storm-Petrels generally forage on the continental shelf (Harris 1974, Crossin 1974). Recent pelagic observations in Kodiak waters indicate that Fork-tailed Storm-Petrels are most abundant over the shelf from September to June and that they move into nearshore areas in July and August (Lensink et al. 1978, Wiens et al. 1978). The movement to nearshore areas may be related to increased foraging demands on breeding adults, which are feeding chicks during July and August. Although Fork-tailed Storm-Petrels are capable of carrying more than one-fifth of their body weight, the energetic costs of traveling with increasing loads make it less profitable to exploit resources far offshore. Alternately, because nestlings probably grow more rapidly on a high protein diet, adults may shift diets from predominately crustaceans to fish. As a consequence, if fish are more abundant near shore, the dietary switch may require changing foraging areas as well.

The more regular and frequent colony visits by adults with chicks that we see during July and August are consistent with change to nearshore foraging. Nonetheless, although adults forage nearer to shore, chicks frequently go unfed for several nights. At about 2 weeks of age chicks can consume whatever the adult brings, their extensible stomachs accommodating the infrequent large food load that may double their weight. When chicks are not fed, metabolic rates and weight losses are reduced; young chicks eventually go into torpor. Irregular feedings and variable food loads result in slow growth and slow chick development.

At high latitudes, climate dictates the general timing of breeding. Heavy rainfall, high winds, and low temperatures typically preceded a sudden increase in mortality of young chicks. However, Fork-tailed Storm-Petrels seemed capable of foraging and returning to the colony in all but the worst storms. The most noticeable effect of bad weather was reflected in chick (and possibly egg) mortality in the wet burrows.

Predation, as well as food and climate, influences the distribution and reproductive ecology of Fork-tailed Storm-Petrels. Nesting on islands and in burrows reduces chick and egg mortality, particularly for Fork-tailed Storm-Petrels, which often leave eggs and chicks unattended and have few defenses besides regurgitation (which they do with apparent enthusiasm and stunning accuracy). Burrow nesting, in turn, relaxes selection for egg and chick recognition. Nocturnal visits to the breeding colony by storm-petrels are thought to be an adaptation to avoid diurnal predators (Lack 1966, 1968). The fact that Fork-tailed Storm-Petrels delay or fail to return on clear nights is consistent with this interpretation. The brevity of darkness at high latitudes, coupled with diurnal predators and the length of the season of ice-free, productive ocean waters, may be responsible for setting the northern limit of breeding for Fork-tailed Storm-Petrels.

In conclusion, the reproductive strategies of the Fork-tailed Storm-Petrel reflect oceanographic variability in the onset and length of the breeding period, in the frequency and duration of egg neglect, and in differences in chick growth between years. The extended nestling period, slow growth, and death of chicks from star-

vation all suggest that food is limited. Fork-tailed Storm-Petrels may thus be ideal species to use as indicators of changes in regional oceanic productivity.

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REVIEWERS FOR *THE AUK*, 1978–79

The scientific and scholarly quality of a journal results largely from the efforts of the many individuals who serve as reviewers of manuscripts. During the past year as editor, I have continued to welcome their counsel and to enjoy many fruitful interactions with them. Listing these individuals below only hints at the extent of my gratitude to them; many authors, even some whose manuscripts have not been accepted for publication, have also indicated how much they appreciate the perceptive and fair reviews their efforts have received.

Individuals who have contributed reviews of two or more manuscripts are indicated by an asterisk.

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